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9 **Cerebellar tDCS Dissociates the Timing of Perceptual**  
10 **Decisions from Perceptual Change in Speech**

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28 **Abstract**

29 Neuroimaging studies suggest that the cerebellum might play a role in both speech perception and  
30 speech perceptual learning. However, it remains unclear what this role is: does the cerebellum help  
31 shape the perceptual decision? Or does it contribute to the timing of perceptual decisions? To test  
32 this, we used transcranial direct current stimulation (tDCS) in combination with a speech perception  
33 task. Participants experienced a series of speech perceptual tests designed to measure and then  
34 manipulate (via training) their perception of a phonetic contrast. One group received cerebellar  
35 tDCS during speech perceptual learning and a different group received sham tDCS during the same  
36 task. Both groups showed similar learning-related changes in speech perception that transferred to a  
37 different phonetic contrast. For both trained and untrained speech perceptual decisions, cerebellar  
38 tDCS significantly increased the time it took participants to indicate their decisions with a keyboard  
39 press. By analysing perceptual responses made by both hands, we present evidence that cerebellar  
40 tDCS disrupted the timing of perceptual decisions, while leaving the eventual decision unaltered. In  
41 support of this conclusion, we use the drift diffusion model to decompose the data into processes  
42 that determine the outcome of perceptual decision-making and those that do not. The modelling  
43 suggests that cerebellar tDCS disrupted processes unrelated to decision-making. Taken together, the  
44 empirical data and modelling demonstrate that right cerebellar tDCS dissociates the timing of  
45 perceptual decisions from perceptual change. The results provide initial evidence in healthy humans  
46 that the cerebellum critically contributes to speech timing in the perceptual domain.

47

48 **New and Noteworthy**

49 The role of the cerebellum in behaviour has classically been confined to the control of movement.  
50 However, the cerebellum projects to non-motor areas and neuroimaging studies show neural  
51 changes in the cerebellum during perception and language tasks. This paper provides initial  
52 evidence in healthy humans that alterations of the cerebellum impair the timing of perceptual  
53 decisions in speech without impacting the outcome of perceptual decisions.

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55

## 56 **Introduction**

57 The role of the cerebellum in behavior has classically been confined to the control of movement.  
58 The cerebellum is known, for instance, to be involved in motor control through the detection and  
59 correction of movement errors (Wolpert et al. 1998; Smith & Shadmehr 2005; Rabe et al. 2009;  
60 Izawa et al. 2012; Panouillères et al. 2015). However, the cerebellum projects to non-motor areas  
61 (Strick et al. 2009) and several studies suggest a cerebellar contribution to behaviours such as  
62 perception, language, and memory (Desmond & Fiez 1998; Mathiak et al. 2002; Durisko & Fiez  
63 2010; Lesage et al. 2012). A host of neuroimaging studies have noted activity changes in the  
64 cerebellum during speech-sound classification, word recognition and language tasks (Xiang et al.  
65 2003; Ackermann et al. 2007; Stoodley & Schmahmann 2009). Furthermore, recent evidence has  
66 linked neural changes in the cerebellum to perceptual learning during both speech and nonspeech  
67 behaviours (Guediche et al. 2015; Vahdat et al. 2014). To date, direct interventional studies of the  
68 cerebellum's role in speech perception and perceptual learning are lacking. Here we use transcranial  
69 direct current stimulation (tDCS) to provide an initial test of the role of the cerebellum in speech  
70 perception.

71 Neuroimaging meta-analysis suggests that areas in the right cerebellum are active during speech  
72 perception (Stoodley & Schmahmann 2009), but the nature of this activity remains unclear. One  
73 possibility is that the cerebellum contributes to perceptual decision-making. This contribution might  
74 be most meaningful during times of perceptual change. Indeed, at least three neuroimaging studies  
75 suggest that the right cerebellum is involved in perceptual learning. Callan et al. (2003) examined  
76 neural changes in native Japanese speakers following feedback-driven perceptual learning on a  
77 difficult English phonetic contrast. Increases in neural activity were observed in Crus I and lobule  
78 VI of the right cerebellum, areas active during motor and language tasks (Stoodley & Schmahmann  
79 2009). More recent neuroimaging studies provide further evidence that the cerebellum is involved in  
80 perceptual learning. In the first case, Guediche et al. (2015) linked increased activation in the  
81 cerebellum to a task involving adaptation to distorted speech; and in the second, Vahdat et al. (2014)  
82 examined changes in neural connectivity following perceptual learning related to the position of the  
83 right arm during reaching movements. In this case, learning was driven via explicit feedback (as in  
84 Callan et al. 2003) and perceptual-learning-related changes in functional connectivity were observed

85 between supplementary motor area and right Crus I and lobule VI in the cerebellum. This work  
86 presents the intriguing possibility that the cerebellum’s known role in motor learning might be  
87 mirrored in the perceptual domain.

88 There are, of course, other explanations for neural changes in the cerebellum associated with speech  
89 perception. A long line of research suggests that the cerebellum plays a role in the timing of sub-  
90 second behaviors (Spencer & Ivry 2013). For instance, patients with cerebellar ataxia show deficits  
91 in movement timing, such as tapping in sync with a metronome (Spencer et al. 2003; Franz et al.  
92 1996)—deficits not observed in basal ganglia disorders such as Parkinson’s patients (Ivry & Keele  
93 1989). Noninvasive brain stimulation studies support a role for the cerebellum in movement timing.  
94 To give one example, repetitive transcranial magnetic stimulation (rTMS) applied to the cerebellum  
95 can cause increased variability in the pacing of movements (Koch et al. 2007; Théoret et al. 2001).  
96 A smaller amount of research has examined the role of the cerebellum in the timing of non-motor  
97 behaviors. Repetitive TMS of the right cerebellum drove participants to perceive sub-second time  
98 intervals as longer (Koch et al. 2007). Patients with cerebellar degeneration have trouble  
99 discriminating between speech sounds distinguished by their voice onset time (Ackermann et al.  
100 2007). And cerebellar tDCS delivered to the right cerebellum has been shown to alter response times  
101 and, in some cases, measures of accuracy, associated with working memory tasks, difficult serial  
102 subtraction, and linguistic prediction (Ferrucci et al. 2008; Pope & Miall 2012; Miall et al. 2016).  
103 Intriguingly, besides deficits in the timing of behaviors, cerebellar damage seems to leave other  
104 aspects of behaviors, such as movement trajectory and accuracy, relatively unscathed (Spencer &  
105 Ivry 2013).

106 To test the role of the right cerebellum in speech perception we used transcranial direct current  
107 stimulation (tDCS) to alter the cerebellum during a speech perceptual learning task. TDCS was used  
108 (as opposed to TMS) because it can be applied throughout perceptual learning. Anodal stimulation  
109 was used (i.e. the anode was placed over the cerebellum) because it has been shown to alter the  
110 functioning of the cerebellum and influence behaviour in both the motor and cognitive domain  
111 (Galea et al. 2009; Galea et al. 2011; Ferrucci et al. 2008).

112 In the study, participants made perceptual decisions about a series of stimuli that spanned the  
113 phonetic contrast between the words “head” and “had”. Feedback was given to manipulate the point

114 of perceptual uncertainty between the two words, a paradigm recently shown to cause learned  
115 changes in perception that persist for a week (Lametti, Krol, et al. 2014). This perceptual learning  
116 task was ideal for two reasons: 1) Reflecting the cerebellum's role in motor learning, we reasoned  
117 that cerebellar involvement in the outcome of speech perceptual decisions might be greatest during  
118 times of perceptual change. 2) The learning task perturbed the timing of perceptual decisions; this  
119 allowed for the cerebellum's role in perceptual timing to also be assessed. We compared the  
120 acquisition, transfer, and retention of this type of perceptual speech learning between two groups:  
121 one that received tDCS to the right cerebellum throughout learning and another that was given sham  
122 tDCS during the same task. We also compared the timing of perceptual decisions between the  
123 groups by examining gross changes in reaction times throughout the task. Finally, we used the drift  
124 diffusion model to decompose reaction times into processes related to perceptual decision-making  
125 and unrelated processes such as behavioural timing. We hypothesized that, if tDCS effectively  
126 altered the functioning of the cerebellum, changes would be observed in processes unrelated to the  
127 outcome of decision making during speech perceptual learning.

128

## 129 **Methods**

### 130 *Participants and Apparatus*

131 36 neurologically healthy native English speakers participated in the experiments (age range = 18-  
132 35); 21 were female. (One of the 36 participants was excluded from the final analysis because  
133 his/her reaction times differed by more than 2.5 standard deviations from the group mean.)  
134 Participants wore headphones (Bose) and responded to speech stimuli from the headphones by  
135 pressing keys on a keyboard. A direct current stimulator (NeuroConn) was used to apply transcranial  
136 direct current stimulation (tDCS) to the cerebellum. Participants gave their informed consent and the  
137 local ethics committee approved the experiments.

138

## **Figure 1**

139

140

141 *Procedure*

142 Figure 1A shows the procedure. The experiment began with two perceptual tests designed to  
143 measure perception of the words “head” and “had” and the words “head” and “hid” (PT1 and PT2,  
144 respectively). The order of the tests was balanced between participants. Participants then performed  
145 a learning task in which their perception of the phonetic contrast between the words “head” and  
146 “had” was manipulated (PT3 to PT5: see *Perceptual Learning*).

147 During perceptual learning, subjects received either 15 minutes (“real”) or 30 seconds (“sham”) of  
148 transcranial direct current stimulation (tDCS) (see *Transcranial Direct Current Stimulation*).  
149 Perceptual learning was followed by a 5-minute break and two more perceptual tests. The first was a  
150 *head-to-hid* perceptual test that examined whether learning transferred to a different phonetic  
151 contrast (PT6); the second was a *head-to-had* perceptual test that measured aftereffects associated  
152 with learning (PT7). The transfer test always followed learning; it was included to assess whether  
153 the effects of cerebellar tDCS on speech perception were global or limited to trained speech sounds.

154 *Measuring Speech Perception*

155 Speech perception was assessed using two perceptual tests, one that measured the distinction  
156 between “head” and “had” and a second that measured the distinction between “head” and “hid”.  
157 Each perceptual test used nine speech stimuli. Figure 1B depicts the stimuli by their first and second  
158 formant frequency values (F1 and F2). The stimuli were created in Matlab by altering F1 and F2 in  
159 ten steps from formant values associated with the word “head” to those associated with “had” or  
160 “hid” (Lametti, Rochet-Capellan, et al. 2014). An English-speaking male provided the root word  
161 “head” and the continua endpoints, “had” or “hid”. The root word was not included in either  
162 continuum. Stimuli were 0.430 seconds long and started with 0.05 seconds of silence.

163 During each perceptual test the entire set of nine stimuli were played from the headphones in a  
164 random order, one word at a time. After each stimulus participants were prompted by text on a  
165 computer screen to indicate whether they heard “head” or “had” (in the case of the *head-to-had*  
166 perceptual test) or “head” or “hid” (in the case of the *head-to-hid* perceptual test). If participants  
167 thought they heard “head” they pressed “s” on the keyboard with their left hand; if they thought they  
168 heard “had” or “hid” they pressed “l” with their right hand. Participants were instructed to respond

169 accurately and quickly. The entire stimulus set was repeated 20 times in each perceptual test  
170 yielding 180 perceptual decisions per test. Each perceptual test took about 5 minutes.

171 The proportion of “had” or “hid” responses was found for each test. Psychometric functions were fit  
172 to these values using “glmfit” in Matlab. The perceptual boundary—that is, the point on the continua  
173 where “had” or “hid” was reported 50% of the time—was computed from the functions. The  
174 locations on the continua where participants perceived “had”/“hid” 25% and 75% was also  
175 computed from the psychometric functions. The distance between these values was used as a  
176 measure of perceptual acuity as in Vahdat et al. (2014) (e.g. a smaller distance indicates a steeper  
177 psychometric function).

### 178 *Perceptual Learning*

179 The perceptual distinction between the words “head” and “had” was manipulated using feedback  
180 exactly as described in (Lametti, Krol, et al. 2014). Briefly, the perceptual boundary between “head”  
181 and “had” was computed from the baseline phase of the experiment. For the real tDCS group this  
182 boundary averaged 5.39; for the sham group it averaged 5.45. This difference was not significant ( $p$   
183 = 0.8). A new perceptual boundary was then set one stimulus lower than the original, rounded-to-  
184 the-nearest integer, perceptual boundary. Feedback was delivered around this new boundary  
185 immediately following each perceptual decision. Figure 2A shows how the feedback would be  
186 applied based on the average baseline psychometric function (dashed curve) for the *head-to-had*  
187 continuum. If, for instance, a participant’s baseline perceptual boundary was computed as 5.42, a  
188 new perceptual boundary was set at stimulus 4 for training purposes. After this, a response of “head”  
189 for stimuli 1-3 and “had” for stimuli 4-9 resulted in “CORRECT” being displayed on the computer  
190 screen. A “had” response for stimuli 1-3 or a “head” response for stimuli 4-9 resulted in the  
191 appearance of “INCORRECT” on the screen and the addition of 1 point to an error counter at the  
192 bottom of the screen. Perceptual learning consisted of three perceptual tests in a row with this  
193 feedback. Perceptual tests with feedback had 135 perceptual decisions (15 blocks of the 9 stimuli  
194 instead of 20 as in the baseline, transfer and aftereffect tests). There was a 30 second break between  
195 perceptual tests. During the break the error counter was zeroed and participants were instructed to  
196 reduce their errors. Perceptual learning lasted for about 17 minutes (16.81 mean, 1.16 SD).

197 *Transcranial Direct Current Stimulation*

198 Transcranial direct current stimulation was applied to the right cerebellum during learning.  
199 Following the baseline phase of the experiment, the anode was placed in a 25 cm<sup>2</sup> saline-soaked  
200 sponge and positioned 3 cm lateral to the inion on the right side of the scalp. The cathode was  
201 placed in a 25cm<sup>2</sup> saline-soaked sponge and positioned in the center of the right buccinator muscle.  
202 This tDCS electrode configuration has previously been shown to influence behavior attributed to the  
203 right cerebellum and cause neural changes associated with alterations of the right cerebellum (Galea  
204 et al. 2009; Galea et al. 2011; and see Grimaldi et al. 2016 for a review of the impact of tDCS on the  
205 cerebellum).

206 Participants were divided into two groups. A “real” stimulation group (n = 17) received 15 minutes  
207 of stimulation during perceptual learning and a “sham” group (n = 18) received 30 seconds of  
208 stimulation at the start of learning. In each case, the current was ramped up to 2.0 mA over 30  
209 seconds and ramped down to zero over 30 seconds. The electrodes were removed from the scalp  
210 during the break that followed training. Participants were blind to the stimulation condition.

211 *Data Analysis*

212 The proportion of “had” or “hid” responses was computed for each perceptual test on a per subject  
213 basis (Figure 1C, top panel). Training-related changes in this proportion were found by comparing  
214 post-learning perceptual tests to pre-learning perceptual tests. These changes were then averaged  
215 across participants within each group. To visualize perceptual learning (as in Figure 2B), the  
216 proportion of “had” responses was computed for each of the 65 blocks of 9 perceptual decisions that  
217 made up the baseline *head-to-had* perceptual test and the training perceptual tests. These proportions  
218 were then averaged across participants within each group.

219 The time it took participants to come to a perceptual decision by pressing “s” or “l” on the keyboard  
220 was examined. Reaction times were measured from the start of each stimulus. The idea behind  
221 measuring reaction times was that they would peak near the category boundary, or the point where  
222 participants were the most uncertain about whether they heard “had”, “head” or “hid” (Niziolek &  
223 Guenther 2013). In this case, learning-related changes in the perceptual boundary should also be  
224 reflected by reaction time changes.



225 Across stimuli and groups, the mean reaction time was 0.638 seconds (0.161 SD) before training  
226 and 0.602 seconds (0.172 SD) after training. Reaction times greater than 1250 milliseconds were  
227 discarded (~ 5% of the data). The reaction time data was positively skewed. To correct for this,  
228 reaction times were log normalized (using the natural logarithm). Reaction times were also  
229 converted into z-scores on a per perceptual test and subject basis (Figure 1C, bottom panel).  
230 Average z-scores were then computed for each stimulus in each perceptual test. To examine gross  
231 changes in reaction time between the groups, for each perceptual test log normalized reaction times  
232 were averaged across stimuli. This was done first within subjects and then across groups. TDCS-  
233 related changes in reaction time were visualized (as in Figure 5) by averaging log normalized  
234 reaction times across the blocks of 9 stimuli that made up each perceptual test.

### 235 *Diffusion Modelling*

236 The drift diffusion model was fit to participant responses and reaction times using the Diffusion  
237 Model Analysis Toolbox in Matlab (Vandekerckhove & Tuerlinckx 2008). The model assumes that  
238 one decision reflects a correct response and the other reflects an incorrect response. Given that  
239 perceptual boundaries before and after learning were not statistically different from the stimulus in  
240 the middle of the continua (5.24 on average, 1.0 SD), the data were grouped by stimulus quality or  
241 coherence. Stimulus 9 (“had/hid”) was made equivalent to stimulus 1 (“head”), 8 was made  
242 equivalent to 2, 7 was made equivalent to 3, and 6 was made equivalent to 4. A response of “head”  
243 was considered to be correct under this transformation. This left 5 stimuli that differed in stimulus  
244 quality such that the proportion of correct responses decreased as the quality of the stimuli decreased  
245 (see Figure 6A).

246 To further increase the sample size used for modeling, data from PT1 (*head-to-had* continuum) was  
247 combined with PT2 (*head-to-hid* continuum) to create a before-tDCS dataset and data from PT6  
248 (*head-to-had* continuum) was combined with PT7 (*head-to-hid* continuum) to create an after-tDCS  
249 dataset. The model was then fit to the before-tDCS and after-tDCS datasets on a per subject basis  
250 and the model’s parameters were compared between the sham and real tDCS groups. Approximately  
251 5% of the parameters estimated from individual subject data were greater than 2 standard deviations  
252 from the group mean; these values were not included in the final analysis.

253 *Statistical Analysis*

254 Between and within-group comparisons of the measures described above were performed using  
255 split-plot or repeated measures ANOVA. Where appropriate, post-hoc comparisons were performed  
256 using two-tailed t-tests. The significance level for all statistical tests was 0.05; this value was  
257 corrected for multiple comparisons using the Bonferroni method.

258

259 **Results**

260 The aim of the experiment was to test the competing hypotheses that the cerebellum might influence  
261 the outcome of speech perceptual decisions versus playing a role in the timing of decisions. To do  
262 this, a group of participants received tDCS to the cerebellum while they performed a speech  
263 perceptual learning task—a task that altered both speech perception and the timing of speech  
264 perceptual decisions. Their performance during training, on a transfer test, and on an aftereffect test  
265 was compared to participants who received “sham” tDCS (see Figure 1A).

266

**Figure 2**

267 Feedback drove a learned change in response to the stimuli. Figure 2B shows the proportion of  
268 “had” responses during the baseline phase of the experiment (PT1) and during perceptual learning  
269 (PT3, PT4, and PT5). Feedback caused a change in response such that the proportion of “had”  
270 responses increased during learning ( $F(1, 64) = 13.79, p < 0.0001$ : main effect of block). Across the  
271 45 blocks of perceptual decisions that made up the training phase of the study, a block-by-block  
272 comparison revealed no significant differences between the sham and real tDCS groups ( $p > 0.05$  in  
273 every case) and there was no interaction between blocks and the presence or absence of tDCS ( $F(1,$   
274  $44) = 1.03, p > 0.4$ ). This model-free analysis suggests that cerebellar tDCS did not alter the rate and  
275 amount of speech perceptual learning.

276

**Figure 3**

277 Following learning, participants experienced a transfer test (PT6). Figure 3A shows the average  
278 psychometric function (top panel) and log normalized reaction times at each stimulus (bottom panel)

279 for the *head-to-hid* continuum before and after speech perceptual learning on the *head-to-had*  
280 continuum (PT2 vs. PT6). The figure thus depicts the transfer of learning from one phonetic contrast  
281 to another. The left panel shows the sham tDCS group and the right panel shows the real tDCS  
282 group. As compared to baseline, training on the *head-to-had* continuum altered how participants  
283 responded during the *head-to-hid* transfer test. Specifically, the psychometric functions shifted  
284 towards “head” such that participants reported perceiving more “hids”. This change in perception  
285 was reflected by a change in reaction times for some of the stimuli [ $F(8,26) = 5.96, p < 0.001$ :  
286 interaction between stimuli and experimental phase]. Reaction times increased for stimuli 3 and 4 in  
287 the case of the sham group, and stimuli 2 in the case of the real group ( $p < 0.05$ , in each case). This  
288 suggests that participants became less certain about whether these stimuli were “head” or “hid”. On  
289 the other hand, reaction times decreased for stimuli 8 and 9 in the case of the sham group, and  
290 stimuli 7 and 8 in the case of the real tDCS group ( $p < 0.05$ , in each case). That is, participants  
291 became faster to perceive and label these stimuli as “head” or “hid”. These reaction time changes are  
292 consistent with a shift in the perceptual boundary (the point of greatest perceptual uncertainty)  
293 towards “head”. Crucially, the pattern of reaction times following learning did *not* differ between  
294 the sham and real tDCS groups ( $F(8,26) = 0.27, p > 0.95$ : interaction between stimuli and group).  
295 Thus, perceptual learning on the *head-to-had* continuum altered participants’ perception of the *head-*  
296 *to-hid* continuum, and this alternation was not changed by cerebellar tDCS applied during learning.

297 The transfer test was followed by an aftereffect test (PT7). Figure 3B depicts average psychometric  
298 functions for the *head-to-had* continuum and associated reactions times before and after learning  
299 (PT1 vs. PT7) for the sham and real tDCS groups. The figure thus depicts aftereffects associated  
300 with speech perceptual learning. Compared to baseline, perceptual learning altered how subjects  
301 responded during the *head-to-had* perceptual test even after the feedback was removed. Consistent  
302 with the trained perceptual boundary, the psychometric functions moved towards “head” indicating  
303 that subjects reported perceiving more “hads”. This change in perception was, again, reflected by a  
304 change in reaction times to some of the stimuli [ $F(8,26) = 3.40, p < 0.01$ : interaction between  
305 stimuli and experimental phase]. In the case of the sham group, reaction times increased for stimuli  
306 2 and 3 and decreased for stimulus 6 ( $p < 0.01$ , in each case). In the case of the real group, reaction  
307 times increased for stimuli 2 and 3 and decreased for stimuli 6 and 7 ( $p < 0.05$ , in each case). The  
308 reaction time changes agree with a learning-related shift in the perceptual boundary on the *head-to-*

309 *had* continuum towards “head”. Following learning, the pattern of reaction times did not differ  
310 between the sham and real tDCS groups ( $F(8,26) = 0.78, p > 0.62$ : interaction between stimuli and  
311 group). This suggests that the aftereffects of perceptual learning were not altered by cerebellar  
312 tDCS.

313 The learning-related changes in the psychometric functions shown in Figure 3 are quantified in  
314 Figure 4. Specifically, the figure shows changes in the proportion of “had” or “hid” responses from  
315 baseline and the impact of cerebellar tDCS on these changes. During the transfer test, perceptual  
316 learning caused an increase in the proportion of “hid” responses for both the sham and real tDCS  
317 groups ( $p = 0.018, p = 0.011$ , respectively). However, there was no difference in this change  
318 between the two groups ( $p = 0.84$ ). During the aftereffect test, perceptual learning caused an  
319 increase in the proportion of “had” responses for both groups ( $p < 0.0001$ , in both cases). Again,  
320 there was no difference in these changes between the two groups ( $p = 0.94$ ). Finally, we examined  
321 changes in the acuity of the psychometric function (i.e. the steepness of the curves depicted in  
322 Figure 3) across baseline, perceptual training, transfer and aftereffect tests. Cerebellar tDCS did not  
323 have an impact on perceptual acuity [ $F(6,27) = 1.23, p = 0.319$ : interaction between acuity and  
324 group]. In combination with the reaction time measures, this demonstrates that cerebellar tDCS did  
325 not have an impact on both the transfer and retention of speech perceptual learning.

326 **Figure 4**

327 The perceptual data demonstrates that cerebellar tDCS does not have an impact on the outcome of  
328 speech perceptual decision-making for both trained and untrained speech stimuli. We next examined  
329 whether the cerebellum might play a more general role in speech perception related to the timing of  
330 perceptual decisions.

331 The z-scores depicted in Figure 3 give a measure of how perception changed across the stimuli.  
332 However, as the z-scores were computed on a per perceptual test and subject basis, they mask  
333 overall differences in mean reaction time between tests and groups—differences that could provide  
334 evidence for changes in the timing of decisions.

335 **Figure 5**

336 Figure 5A shows average (but still log normalized) reaction times for each perceptual test over the  
337 course of the experiment. The squiggly lines shows how average reaction times evolved during the  
338 training, transfer, and aftereffect tests. Cerebellar tDCS drove significant between-group differences  
339 in average reaction time over the course of the experiment [ $F(6,28) = 2.65, p = 0.037$ : interaction  
340 between perceptual tests and group]. There was no difference in average reaction time between the  
341 groups during the baseline phase of the experiment (PT1 and PT2). The introduction of feedback at  
342 the start of perceptual learning led to an increase in reaction time ( $p < 0.05$ , in each case). The group  
343 that received sham stimulation decreased their response times over the course of perceptual learning  
344 (PT3 vs. PT5:  $p = 0.012$ ) until reaction times did not differ from baseline responses. A similar  
345 decrease was not observed for the group that received real stimulation (PT3 vs. PT5:  $p = 0.73$ ).  
346 Indeed, by the middle of learning and tDCS (PT4), the sham group was responding to the stimuli  
347 faster than the real group ( $p = 0.035$ ). This tDCS-related change in reaction times was also observed  
348 at the end of learning (PT5,  $p = 0.01$ ), and 7 minutes after stimulation during the transfer test  
349 (PT6)—a test that involved responses to *untrained* stimuli ( $p = 0.014$ ). Twelve minutes after tDCS  
350 during the retention test (PT7), there was no longer a difference in average reaction times between  
351 the two groups ( $p = 0.155$ ). The difference in reaction time thus grew with stimulation and wore off  
352 when stimulation was removed. In combination with the lack of a difference in the perceptual  
353 measures (as depicted in Figures 3 and 4), this suggests that independent of the outcome of  
354 perceptual decision-making right cerebellar tDCS impaired the timing of speech perceptual  
355 decisions.

356 To rule out the possibility that the reaction time delay observed in PT4, PT5 and PT6 could be  
357 explained by a perturbation of the motor system, we examined average reaction times from left and  
358 right hand responses separately. Since the right cerebellum projects to frontal lobe motor areas in the  
359 left hemisphere, we reasoned that a perturbation of the motor system caused by right cerebellar  
360 tDCS should have a larger (if not exclusive) impact on right hand responses. To increase the sample  
361 size and the likelihood of seeing an interaction between the response hand and tDCS-related  
362 changes, reaction times from PT4, PT5, and PT6 were pooled into left and right hand responses.  
363 Figure 5B shows that right cerebellar tDCS slowed perceptual responses regardless of the hand used  
364 to indicate perception [ $F(1,33) = 0.59, p = 0.45$ : interaction between the hand used to respond and

365 group]. This result does not fit with a perturbation of the motor system originating in the right  
366 cerebellum.

367 To further explore the impact (or lack thereof) of cerebellar tDCS on perceptual decision-making,  
368 we fit a drift diffusion model to the reaction times and associated perceptual decisions. Diffusion  
369 models have been shown to account for reaction times in a wide range of simple perceptual  
370 decisions such as those in this study (Gold & Shadlen 2007). The model has four key parameters  
371 that break down reaction times and associated perceptual responses into different aspects of  
372 perceptual processing: *Boundary Separation* reflects the decision criteria; *Starting Point* reflects the  
373 bias for one of two perceptual decisions; and *Drift Rate* relates to the rate of evidence accumulation.  
374 In combination, these three parameters define the speed of perceptual decisions, while the fourth  
375 parameter, *Non-Decision Time*, accounts for the time required for processes unrelated to perceptual  
376 decision-making (Ratcliff & McKoon 2008). Cerebellar tDCS could have impaired one or a  
377 combination of these parameters leading to the observed reaction time delay. However, if tDCS  
378 spared processes related to perceptual decision-making, only a difference in the Non-Decision Time  
379 parameter should be observed between the groups.

380

### Figure 6

381 To allow the effect of tDCS on reaction times to be carried by one or more of the parameters we let  
382 all four vary when fitting the data. Figure 6A shows the transformed stimulus categories (see  
383 Methods) and associated perceptual decisions and reactions times to which the model was fit. The  
384 top panel shows the transformed data before tDCS and perceptual learning and the bottom panel  
385 shows the transformed data after tDCS and perceptual learning. Similarly, the top panel of Figure  
386 6B shows the parameters before tDCS and perceptual learning and the bottom panel shows the  
387 parameters after tDCS and perceptual learning.

388 Cerebellar tDCS caused a clear difference in Non-Decision time between the sham and real tDCS  
389 groups [Figure 6B, bottom right: main effect of group:  $F(1,30) = 7.76, p < 0.01$ ]. A difference  
390 between the sham and real stimulation groups was not observed for any of the other parameters (i.e.  
391 there were no other significant main effects or interactions following tDCS). Fitting the model with  
392 fewer free parameters yielded results that were qualitatively and, in most cases, quantitatively

393 similar. This provides additional evidence that, during speech perceptual decisions, disruptions of  
394 the cerebellum spare the perceptual decision making process.

395

## 396 **Discussion**

397 Motivated by fMRI studies showing activity changes in the cerebellum during both speech  
398 perception and perceptual learning, we used tDCS to test whether the cerebellum is involved in  
399 speech perceptual learning versus the timing of perceptual behaviours. The empirical data and  
400 modeling of the perceptual decision-making process support the second hypothesis (with caveats  
401 discussed below). In short, cerebellar tDCS significantly altered the time it took participants to come  
402 to a speech perceptual decision without changing the outcome of their decision.

403 In the experiments, feedback was used to drive a change in the perception of the phonetic contrast  
404 between the words “head” and “had” while tDCS was applied to the right cerebellum. This task  
405 caused an alteration in both perception and the timing of perceptual decisions. For both groups, the  
406 induced change in perception was identical and robust; it was reflected by changes in perceptual  
407 responses and normalized patterns of reaction times across the stimuli, and it transferred to a  
408 different phonetic contrast. Compared to sham stimulation, cerebellar tDCS significantly increased  
409 the time it took participants to respond to the speech stimuli. The alteration in response time grew as  
410 tDCS was applied, it wore off after stimulation came to an end, and it altered the timing of both  
411 trained and untrained speech perceptual decisions. Taken together, the behavioural results show a  
412 tDCS-related dissociation between perceptual change in speech and the timing of perceptual  
413 decisions, implicating the right cerebellum in perceptual timing during speech.

414 Learning, whether for motor or perceptual tasks, typically involves a practice-dependent change in  
415 the timing of behaviors (Spencer & Ivry 2013). As the trial and error process of learning progresses  
416 behaviours become better timed. In the present study, the introduction of feedback at the start of  
417 learning caused an increase in reaction time. The sham group reduced reaction time as learning  
418 progressed, whereas the group receiving cerebellar stimulation did not. Both groups achieved the  
419 same amount of perceptual change, but a disruption of a practice-dependent change in response time  
420 during the task was only observed in the stimulated group. A disruption in response time was also

421 observed during the transfer task, which involved untrained stimuli. Our interpretation of the result  
422 is that the cerebellum does not play a direct role in perceptual decision-making in speech. However,  
423 by perturbing response time, a role for the cerebellum in the timing of when perceptual decisions are  
424 initiated or, possibly, when they are used in behaviour was revealed.

425 If the cerebellum is involved in the timing of speech decisions, as the empirical data suggest, it  
426 leaves open the possibility that the cerebellum might have a greater impact on perceptual change  
427 when perceptual learning places a greater reliance on timing. Speech perceptual learning can be  
428 driven by both externally generated feedback (as in this study) and internally generated error signals.  
429 In the case of the latter, learning is presumably caused by a mismatch between a predicted speech  
430 sound and what was actually perceived (Guediche et al. 2015). There is a large amount of evidence  
431 from the motor control literature that the cerebellum plays a role in motor learning driven by errors  
432 in prediction (Wolpert et al. 1998; Smith & Shadmehr 2005; Rabe et al. 2009; Izawa et al. 2012).  
433 The cerebellum might play a larger role in the outcome of perceptual learning when learning relies  
434 on similar temporal predictions (Spencer & Ivry 2013). Indeed, the cerebellum has a known role in  
435 other forms of learning that depend on temporal predictions. For instance, lesions of the cerebellum  
436 in animal models and humans disrupt classical conditioning (McCormick & Thompson 1984;  
437 Hoffland et al. 2012), which critically depends on the correct timing between unconditioned  
438 responses and conditioned stimuli (Pavlov 1926). It thus remains to be tested whether repeating this  
439 study with a perceptual learning paradigm involving a time-dependent error signal would reveal an  
440 impact of cerebellar tDCS on the outcome of perception. Such an outcome would support our  
441 interpretation of the results presented here.

442 Using the Drift Diffusion Model, we broke down participants' decisions into processes related to the  
443 outcome of speech perception versus unrelated processes. Cerebellar tDCS only impacted the latter  
444 (i.e. "Non-Decision Time"). Importantly, the Non-Decision Time parameter altered by tDCS  
445 includes other processes besides the timing of perceptual decisions, such as the motor act of  
446 indicating perception (but see the next paragraph). Nevertheless, the computational results provide  
447 additional evidence that cerebellar tDCS entirely spared the perceptual decision making process in  
448 speech.



449 One possible explanation for the observed reaction time delay (an explanation that would agree with  
450 the modelling results) is that tDCS simply impaired the motor system. After careful consideration,  
451 we believe this conclusion to be unlikely for at least two reasons. In the study, tDCS was applied to  
452 the right cerebellum. The right cerebellum interacts with speech, language and motor areas in the  
453 left hemisphere. In particular, the right cerebellum projects to left hemisphere motor areas that  
454 control movements of the right hand (Kelly & Strick 2003). One would thus expect impairments in  
455 this motor circuit to only impact right hand responses. On the other hands, word recognition is  
456 largely lateralized to the left hemisphere (DeWitt & Rauschecker 2012). An impairment related to  
457 the timing of word perception should thus be observed in responses from both hands, and this is  
458 precisely what we saw.

459 Does tDCS focally stimulate the cerebellum? This question, which is of paramount importance to  
460 the interpretation of this study, can be addressed by examining the results of studies that pair tDCS  
461 and TMS (Grimaldi et al. 2016). When a conditioning TMS pulse is applied to the cerebellum 5-7  
462 milliseconds before a test TMS pulse is applied to motor cortex a reduction in the ensuing motor  
463 evoked potential is observed. This phenomenon is known as cerebellar inhibition (Pinto & Chen  
464 2001; Daskalakis et al. 2004), and it is thought to be caused by inhibitory output from cerebellar  
465 purkinje cells on cortical motor areas. Importantly, cerebellar inhibition is altered by both anodal  
466 and cathodal cerebellar tDCS (Galea et al. 2009). The direction of the alteration depends on the  
467 polarity of the stimulation. Cerebellar tDCS does not seem to alter the excitability of adjacent areas,  
468 a result supported by behavioural work and studies that model the flow of direct current applied to  
469 the brain (Rampersad et al. 2014; Galea et al. 2011; and see Figure 3 in Grimaldi et al. 2016). Thus,  
470 neurophysiological investigations, behavioural work and computational modelling suggest that  
471 cerebellar tDCS focally alters the functioning of the cerebellum. Nevertheless, as Grimaldi et al.  
472 (2016) point out, more work is needed to determine the precise impact of tDCS on cerebellar  
473 neurons and the locations within the cerebellum that tDCS affects (e.g. cerebellar cortex or purkinje  
474 cells).

475

476 Why did *anodal* tDCS impair behaviour in this study? There are many examples of studies  
477 examining the impact of anodal tDCS on motor behaviour that have observed isolated behavioural  
478 improvements. These results, which have mainly focused on the effects of tDCS when applied to

479 the cerebral cortex, have led to the over-simplified idea that anodal tDCS ought to improve  
480 behaviour, whereas cathodal tDCS should inhibit it. However, we know of no established  
481 mechanistic framework that would support this, and given the complexity and nonlinear dynamics  
482 of cortical and cerebellar processing it is increasingly clear that the heuristic of a sliding scale  
483 rationale is overly simplistic (Bestmann et al. 2015; de Berker et al. 2013; Rahman et al. 2015).  
484 Indeed, anodal tDCS can impair behaviour and cathodal tDCS can improve behaviour, and this  
485 seems especially true when applied to the cerebellum. To give two examples of particular relevance  
486 to the current study, Ferrucci et al. (2008) applied anodal tDCS to the right cerebellum and found  
487 that practice-dependent changes in reaction time associated with a working memory task were  
488 impaired. And in more recent work, Pope and Miall (2012) applied cathodal tDCS to the cerebellum  
489 and observed improvements in performance on a difficult serial subtraction task. In explanation,  
490 Pope and Miall speculate based on the neurophysiology of cerebellar-cortical connections that  
491 cathodal stimulation led to a decrease in inhibitory output from the cerebellum and, by consequence,  
492 a release of cognitive resources. Although there is some evidence that seems to counter this idea  
493 (e.g. Boehringer et al. 2013 report impairments to cognition following cathodal cerebellar tDCS),  
494 the results presented here in combination with neurophysiological investigations of the impact of  
495 tDCS on the cerebellum complement Pope and Miall's hypothesis. In Galea et al (2009), for  
496 instance, anodal cerebellar tDCS was observed to increase inhibitory output from the cerebellum on  
497 motor cortex, while cathodal tDCS was observed to decrease it. Thus, if the present study were  
498 repeated with cathodal cerebellar tDCS one might predict an improvement in the timing of  
499 perceptual behaviour compared to sham stimulation. Of course, the lack of a cathodal group does  
500 not subtract from this paper's main finding: alterations of the cerebellum dissociate the timing of  
501 perceptual decisions from perceptual change in speech.

502 Ambiguous speech sounds are often encountered during conversation (most notably when talking  
503 with a foreign-accented speaker) and we rapidly adapt our perception of speech in these situations  
504 (Bradlow & Bent 2008; Reinisch & Holt 2014). During conversation, external feedback related to  
505 the meaning of ambiguous speech is readily available via body language, contextual information, or  
506 explicit clarification. Here we demonstrate that simple external feedback can drive changes in the  
507 perception of ambiguous speech sounds and these changes are transferable. The timing of this  
508 perceptual behaviour critically depends on the integrity of the right cerebellum. More generally, the

509 work supports a growing body of evidence that the cerebellum plays a role in the timing of  
510 behaviours beyond the motor domain.

511

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531 **Figure Legends**

532 Fig 1: Experimental methods, stimuli and data analysis. (A) The experiment involved seven  
533 perceptual tests. Baseline perceptual tests (PT1 and PT2) were followed by perceptual training (PT3  
534 to PT5), a transfer test (PT6) and an aftereffect test (PT7). The order of the baseline tests was  
535 balanced across participants. (B) The perceptual continua used in the experiment are depicted by  
536 their first formant (F1) and second formant (F2) values. One continua spanned the distinction  
537 between “head” and “had” (black dots) and one spanned the distinction between “head” and “hid”  
538 (grey dots). (C) Perceptual change was assessed by measuring the proportion of “had” and “hid”  
539 responses for each stimulus in each perceptual test (top panel). Perceptual change was also  
540 examined by measuring the time it took participants to respond to the stimuli (bottom panel).  
541 Reaction times were log-normalized and displayed as z-scores.

542 Fig 2: Feedback altered perceptual responses. (A) During perceptual training, feedback was  
543 delivered around a new perceptual boundary (solid vertical line) that was set one stimulus lower  
544 than the perceptual boundary (dashed vertical line) measured during the baseline *head-to-had*  
545 perceptual test. In this example, “CORRECT” was displayed on the screen if the participant  
546 perceived stimuli 1-4 as “head” and “INCORRECT” was displayed if the stimuli were perceived as  
547 “had”. “CORRECT” was displayed on the screen if participant perceived stimuli 5-9 as “had” and  
548 “INCORRECT” was displayed on the screen if they were perceived as “head”. (B) The proportion  
549 of “had” responses (y-axis) was computed for blocks of nine stimuli for the baseline *head-to-had*  
550 perceptual test (PT1) and during perceptual training (PT3-PT5). The introduction of feedback led to  
551 a learned increase in the proportion of “had” responses. The grey lines represent the group that  
552 received tDCS; the black lines represent the group that received sham stimulation.

553 Fig 3: Training altered speech perception. (A) Top panel: Psychometric functions were fit to the  
554 proportion of “hid” responses before (PT2, dashed lines) and after (PT6, solid lines) perceptual  
555 training. Prior training on the *head-to-had* continuum altered the proportion of hid responses on the  
556 *head-to-hid* continuum such that participants were more likely to report hearing “hid”. Bottom  
557 panel: Log-normalized reaction times were computed and displayed as z-scores for each stimulus  
558 before (PT2, dashed lines) and after (PT6, solid lines) perceptual training. Changes in the perceptual  
559 boundary were mirrored by changes in reaction times to some of the stimuli. (B) Top panel:

560 Psychometric functions were fit to the proportion of “had” responses before (PT1, dashed lines) and  
561 after (PT7, solid lines) perceptual training. Following training, participants were more likely to  
562 report hearing “had”. Bottom panel: Log-normalized reaction times were computed and displayed as  
563 z-scores for each stimulus before (PT1, dashed lines) and after (PT7, solid lines) perceptual training.  
564 Changes in the psychometric function were mirrored by changes in reaction times. Error bars  
565 represent +/- a standard error.

566 Fig 4: Training-related changes in the proportion of hid and had responses were computed for the  
567 transfer (PT6 minus PT2) and aftereffect tests (PT7 minus PT1). Training caused an increase (as  
568 indicated by the stars,  $P < 0.05$ ) in the proportion of hid and had responses during these perceptual  
569 tests. Training-related changes in the proportion of hid and had responses did not differ between the  
570 sham (black bars) and real (grey bars) stimulation groups.

571 Fig 5: Cerebellar tDCS slowed reaction times. (A) The mean (log-normalized) reaction time is  
572 displayed for each perceptual test. The grey bars represent the group that received cerebellar tDCS.  
573 The black bars represent the group that received sham tDCS. The approximate timing of the transfer,  
574 aftereffect and retention tests in relation to tDCS and perceptual learning is indicated at the bottom  
575 of the figure. The application of cerebellar tDCS caused a reaction time difference between the  
576 groups (PT3 to PT5). This difference was still present during the transfer test that occurred seven  
577 minutes after tDCS. To visualize how reaction times evolved during training and transfer and the  
578 aftereffect test, log-normalized reaction times associated with blocks of nine perceptual decisions  
579 were averaged and joined via the grey lines (real stimulation) and black lines (sham stimulation) at  
580 the top of the figure. (B) Average reaction times from PT4, PT5 and PT6 were pooled for left and  
581 right hand responses and compared between the groups. A similar tDCS-related difference in  
582 reaction time was observed for left and right hand responses.

583 Fig 6: Drift diffusion modelling. (A) The data were grouped by stimulus coherence. The right side  
584 of the panel shows the proportion of correct responses. The left side of the panel shows reaction  
585 times for each of the transformed stimuli. The top panel shows these measures before tDCS and  
586 learning and the bottom panel shows these same measures after tDCS and learning. (B) A drift  
587 diffusion model was fit to the data shown in (A). The first three boxes in the top and bottom panels  
588 show the parameters that account for the outcome of perceptual decisions. The fourth box shows the

589 parameter that accounts for process unrelated to perceptual decision making. The top panel shows  
590 the parameters before tDCS and the bottom panel shows the parameters after tDCS. Cerebellar tDCS  
591 caused a difference in the parameter that accounts for processes unrelated to perceptual decision  
592 making. The stars indicate parameters that are statistically different at  $p < 0.05$ .

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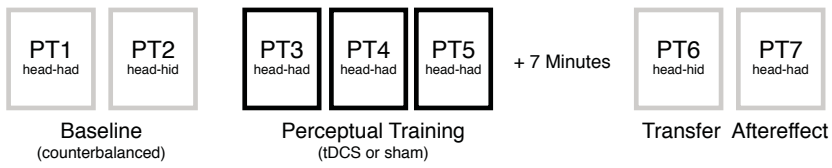
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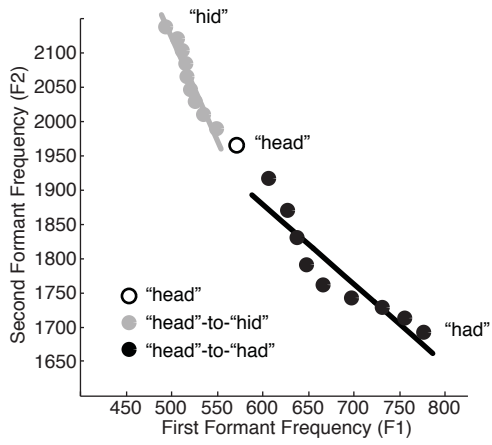
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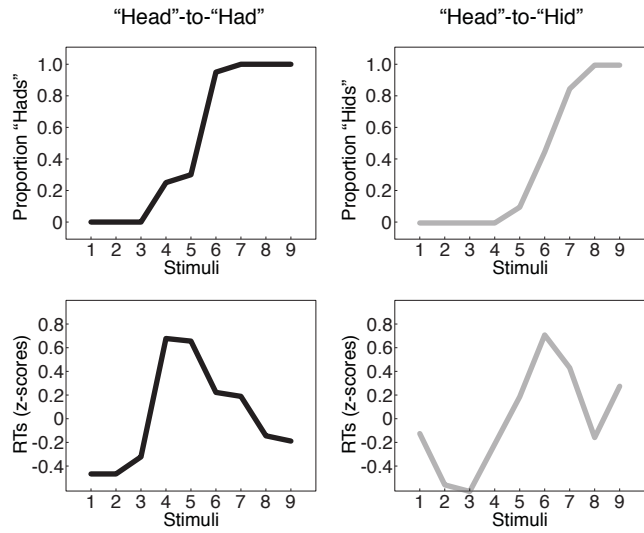
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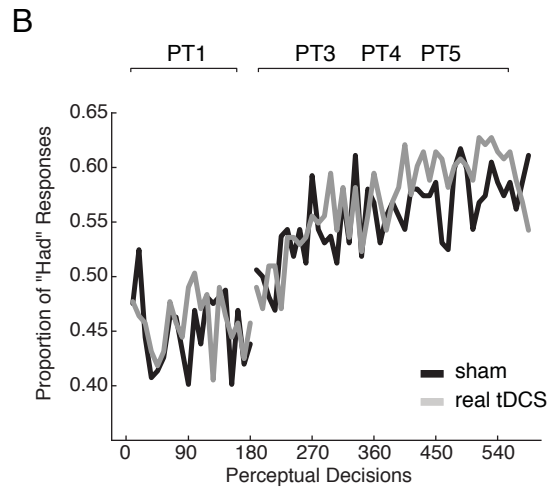
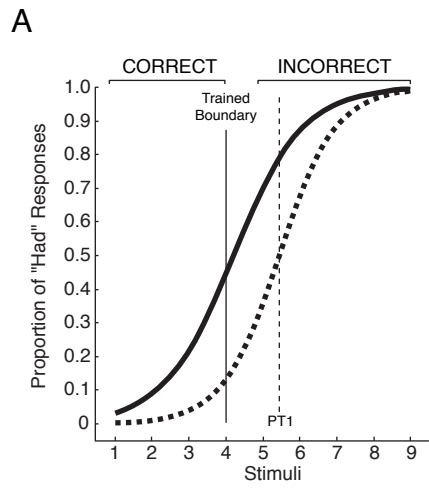


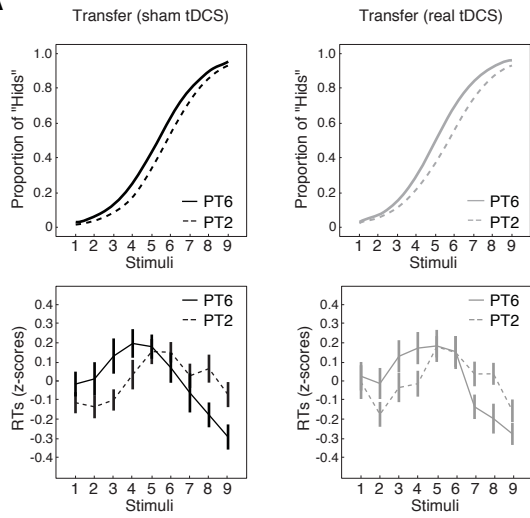
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**A****B**