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

Daniel R. Lametti (1, 3), Leonie Oostwoud Wijdenes (2), James Bonaiuto (3), Sven Bestmann (3), and John C. Rothwell (3)

(1) Department of Experimental Psychology, The University of Oxford

(2) Donders Institute, Radboud University

(3) Sobell Department of Motor Neuroscience and Movement Disorders, Institute of Neurology, University College London

Address correspondence to:

Daniel R. Lametti

Department of Experimental Psychology, The University of Oxford

South Parks Road, Oxford UK, OX1 3UD

Email: daniel.lametti@psy.ox.ac.uk

Phone: + 44 (0) 7577 220 622

Abstract

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

New and Noteworthy

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

Introduction

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

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

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

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

In the study, participants made perceptual decisions about a series of stimuli that spanned the phonetic contrast between the words "head" and "had". Feedback was given to manipulate the point of perceptual uncertainty between the two words, a paradigm recently shown to cause learned changes in perception that persist for a week (Lametti, Krol, et al. 2014). This perceptual learning task was ideal for two reasons: 1) Reflecting the cerebellum's role in motor learning, we reasoned that cerebellar involvement in the outcome of speech perceptual decisions might be greatest during times of perceptual change. 2) The learning task perturbed the timing of perceptual decisions; this allowed for the cerebellum's role in perceptual timing to also be assessed. We compared the acquisition, transfer, and retention of this type of perceptual speech learning between two groups: one that received tDCS to the right cerebellum throughout learning and another that was given sham tDCS during the same task. We also compared the timing of perceptual decisions between the groups by examining gross changes in reaction times throughout the task. Finally, we used the drift diffusion model to decompose reaction times into processes related to perceptual decision-making and unrelated processes such as behavioural timing. We hypothesized that, if tDCS effectively altered the functioning of the cerebellum, changes would be observed in processes unrelated to the outcome of decision making during speech perceptual learning.

Methods

Participants and Apparatus

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

Figure 1

Procedure

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

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

Measuring Speech Perception

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

During each perceptual test the entire set of nine stimuli were played from the headphones in a random order, one word at a time. After each stimulus participants were prompted by text on a computer screen to indicate whether they heard “head” or “had” (in the case of the *head-to-had* perceptual test) or “head” or “hid” (in the case of the *head-to-hid* perceptual test). If participants thought they heard “head” they pressed “s” on the keyboard with their left hand; if they thought they heard “had” or “hid” they pressed “l” with their right hand. Participants were instructed to respond accurately and quickly. The entire stimulus set was repeated 20 times in each perceptual test yielding 180 perceptual decisions per test. Each perceptual test took about 5 minutes.

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

Perceptual Learning

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

Transcranial Direct Current Stimulation

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

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

Data Analysis

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

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

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

Diffusion Modelling

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

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

Statistical Analysis

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

Results

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

Figure 2

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

Figure 3

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

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

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

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

Figure 4

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

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

Figure 5

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

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

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

Figure 6

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

Cerebellar tDCS caused a clear difference in Non-Decision time between the sham and real tDCS groups [Figure 6B, bottom right: main effect of group: $F(1,30) = 7.76$, $p < 0.01$]. A difference between the sham and real stimulation groups was not observed for any of the other parameters (i.e. there were no other significant main effects or interactions following tDCS). Fitting the model with fewer free parameters yielded results that were qualitatively and, in most cases, quantitatively similar. This provides additional evidence that, during speech perceptual decisions, disruptions of the cerebellum spare the perceptual decision making process.

Discussion

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

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

Learning, whether for motor or perceptual tasks, typically involves a practice-dependent change in the timing of behaviors (Spencer & Ivry 2013). As the trial and error process of learning progresses behaviours become better timed. In the present study, the introduction of feedback at the start of learning caused an increase in reaction time. The sham group reduced reaction time as learning progressed, whereas the group receiving cerebellar stimulation did not. Both groups achieved the same amount of perceptual change, but a disruption of a practice-dependent change in response time during the task was only observed in the stimulated group. A disruption in response time was also observed during the transfer task, which involved untrained stimuli. Our interpretation of the result is that the cerebellum does not play a direct role in perceptual decision-making in speech. However, by perturbing response time, a role for the cerebellum in the timing of when perceptual decisions are initiated or, possibly, when they are used in behaviour was revealed.

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

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

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

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

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

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

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Figure Legends

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

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

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

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

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

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

Fig 6: Drift diffusion modelling. (A) The data were grouped by stimulus coherence. The right side of the panel shows the proportion of correct responses. The left side of the panel shows reaction times for each of the transformed stimuli. The top panel shows these measures before tDCS and learning and the bottom panel shows these same measures after tDCS and learning. (B) A drift diffusion model was fit to the data shown in (A). The first three boxes in the top and bottom panels show the parameters that account for the outcome of perceptual decisions. The fourth box shows the parameter that accounts for process unrelated to perceptual decision making. The top panel shows the parameters before tDCS and the bottom panel shows the parameters after tDCS. Cerebellar tDCS caused a difference in the parameter that accounts for processes unrelated to perceptual decision making. The stars indicate parameters that are statistically different at $p < 0.05$.

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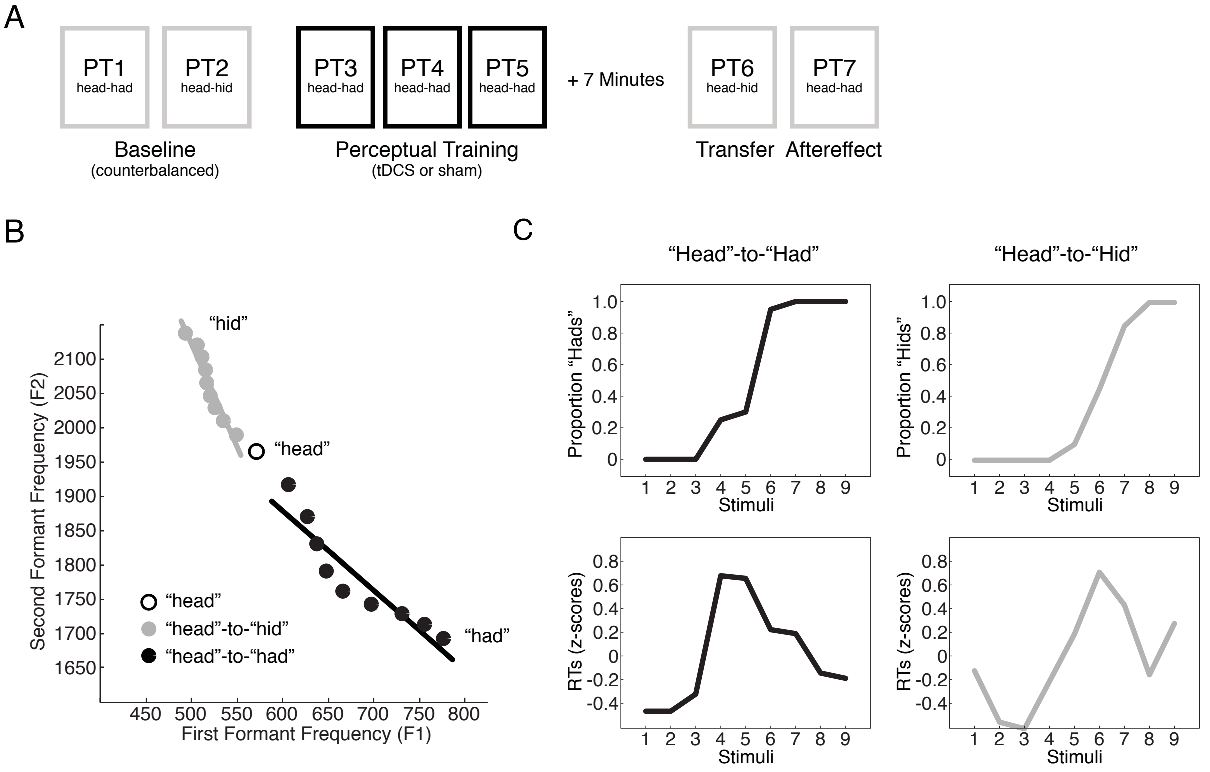
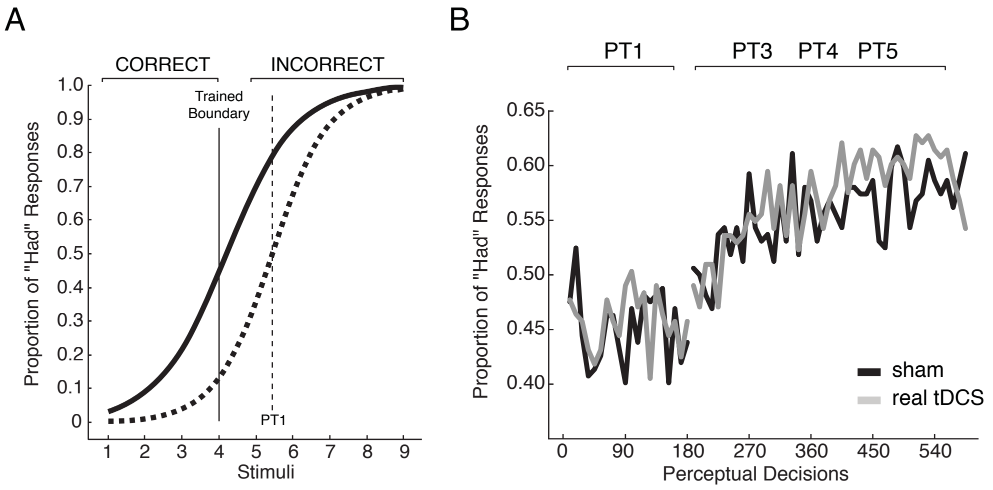
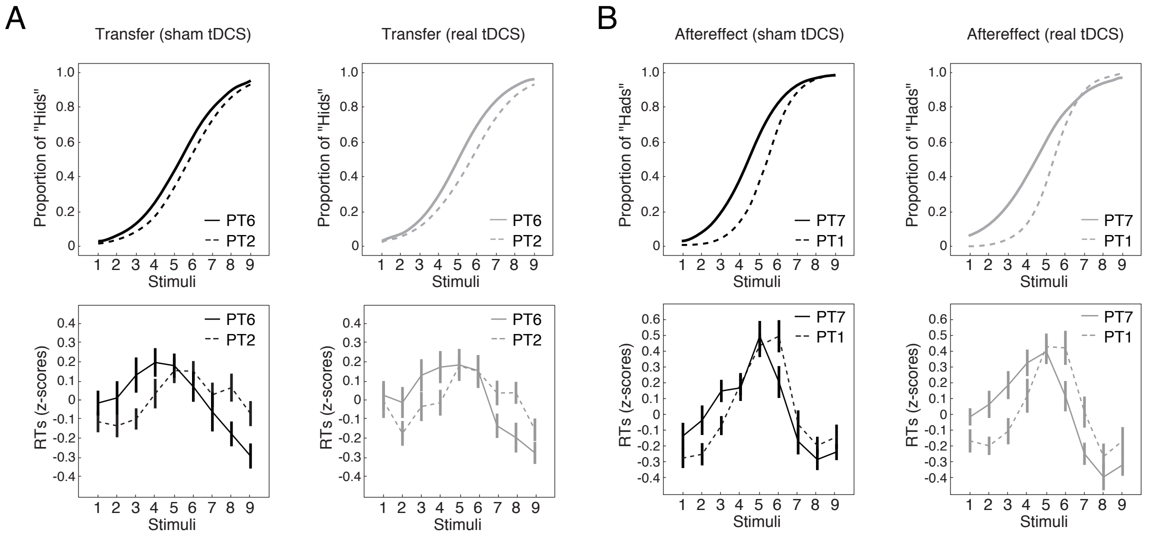
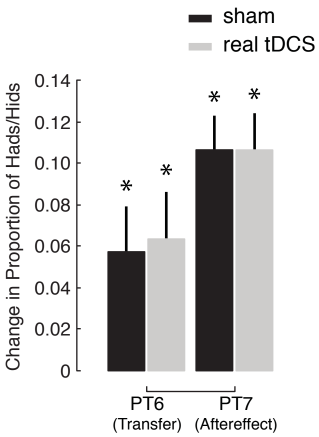
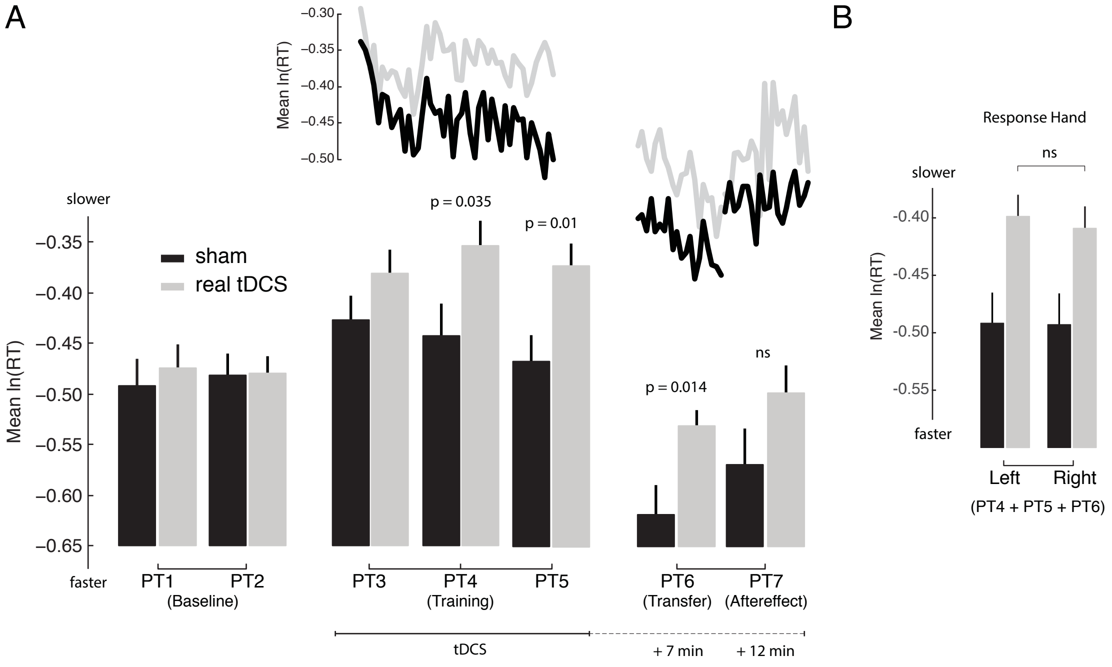
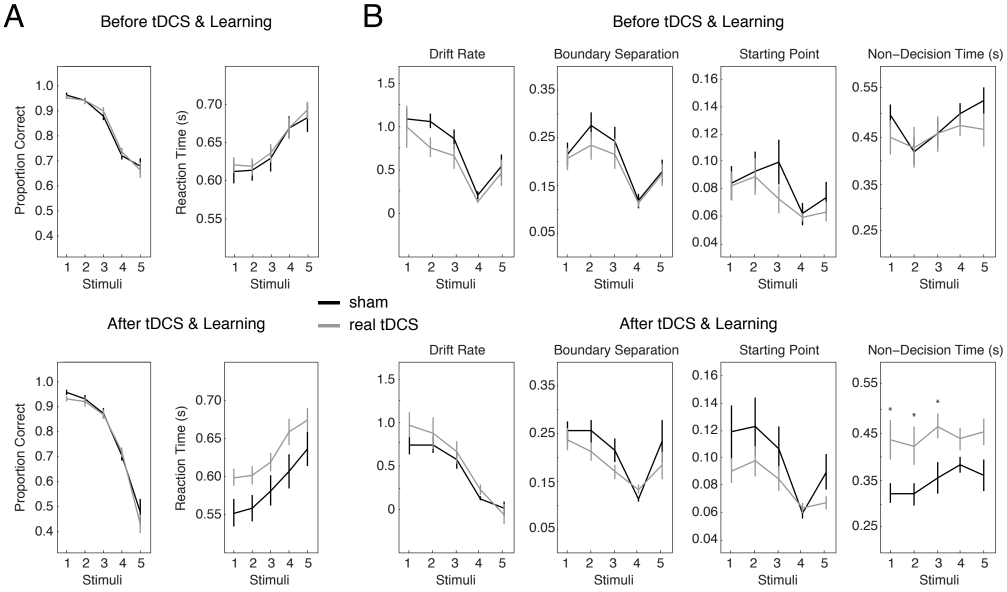

A
PT1
head-had
PT2
head-hid
PT3
head-had
PT4
head-had
PT5
head-had
+ 7 Minutes
PT6
head-hid
PT7
head-had
Baseline
(counterbalanced)
Perceptual Training
(tDCS or sham)
Transfer
Aftereffect
B
"hid"
"head"
"had"
Second Formant Frequency (F2)
2100
2050
2000
1950
1900
1850
1800
1750
1700
1650
450
500
550
600
650
700
750
800
First Formant Frequency (F1)
"head"
"head"-to-"hid"
"head"-to-"had"
C
"Head"-to-"Had"
"Head"-to-"Hid"
Proportion "Hads"
Proportion "Hids"
1.0
0.8
0.6
0.4
0.2
0
1 2 3 4 5 6 7 8 9
Stimuli
RTs (z-scores)
0.8
0.6
0.4
0.2
0
-0.2
-0.4


A
CORRECT
INCORRECT
Trained Boundary
PT1
Proportion of "Had" Responses
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
1
2
3
4
5
6
7
8
9
Stimuli
B
PT1
PT3
PT4
PT5
0.65
0.60
0.55
0.50
0.45
0.40
Proportion of "Had" Responses
0
90
180
270
360
450
540
Perceptual Decisions
sham
real tDCS


A
Transfer (sham tDCS)
Transfer (real tDCS)
B
Aftereffect (sham tDCS)
Aftereffect (real tDCS)
Proportion of "Hids"
Proportion of "Hads"
0
0.2
0.4
0.6
0.8
1.0
PT6
PT2
PT7
PT1
Stimuli
1 2 3 4 5 6 7 8 9
RTs (z-scores)
-0.4
-0.3
-0.2
-0.1
0
0.1
0.2
0.3
0.4
0.5
0.6


sham
real tDCS
Change in Proportion of Hads/Hids
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0
*
*
*
*
PT6
(Transfer)
PT7
(Aftereffect)


A
B
−0.30
−0.35
−0.40
−0.45
−0.50
Mean ln(RT)
slower
faster
−0.35
−0.40
−0.45
−0.50
−0.55
−0.60
−0.65
Mean ln(RT)
sham
real tDCS
p = 0.035
p = 0.01
p = 0.014
ns
PT1
PT2
(Baseline)
PT3
PT4
(Training)
PT5
PT6
(Transfer)
PT7
(Aftereffect)
tDCS
+ 7 min
+ 12 min
Response Hand
slower
faster
ns
-0.40
-0.45
-0.50
-0.55
Mean ln(RT)
Left
Right
(PT4 + PT5 + PT6)


A
Before tDCS & Learning
Proportion Correct
1.0
0.9
0.8
0.7
0.6
0.5
0.4
Reaction Time (s)
0.70
0.65
0.60
0.55
1 2 3 4 5
Stimuli
After tDCS & Learning
sham
real tDCS
B
Before tDCS & Learning
Drift Rate
1.5
1.0
0.5
0
Boundary Separation
0.35
0.25
0.15
0.05
Starting Point
0.16
0.14
0.12
0.10
0.08
0.06
0.04
Non−Decision Time (s)
0.55
0.45
0.35
0.25
After tDCS & Learning
*
*
*