

Improvements in attention and decision-making following combined
behavioural training and brain stimulation

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Running title: Enhanced training outcomes with concurrent tDCS

Keywords: Decision-making; Evidence Accumulation; tDCS; Training;
Transfer

Abstract

In recent years there has been significant commercial interest in 'brain training' – massed or spaced practice on a small set of tasks to boost cognitive performance. Recently, researchers have combined cognitive training regimes with brain stimulation to try and maximise training benefits, leading to task-specific cognitive enhancement. It remains unclear, however, whether the performance gains afforded by such regimes can transfer to untrained tasks, or how training and stimulation affect the brain's latent information processing dynamics. To examine these issues, we applied transcranial direct current stimulation (tDCS) over the prefrontal cortex while participants undertook decision-making training over several days. Anodal, relative to cathodal/sham tDCS, increased performance gains from training. Critically, these gains were reliable for both trained and untrained tasks. The benefit of anodal tDCS occurred for left, but not right, prefrontal stimulation, and was absent for stimulation delivered without concurrent training. Modelling revealed left anodal stimulation combined with training caused an increase in the brain's rate of evidence accumulation for both tasks. Thus tDCS applied during training has the potential to modulate training gains and give rise to transferable performance benefits for distinct cognitive operations through an increase in the rate at which the brain acquires information.

In the last decade the so-called “brain-training” revolution has grown into a multi-billion dollar industry (Hayden, 2012). There are currently thousands of computer-based and online applications encouraging users to exercise their brain through repetition of simple tasks, with the promise of enhancement of cognitive well-being. While there is little doubt that repeated exposure to certain tasks can enhance performance on those same tasks (Dux et al., 2009; Garner, Tombu, & Dux, 2014), the central claims of generalised and enduring cognitive benefits have been difficult to establish (Garner et al., 2014; Jaeggi, Buschkuhl, Jonides, & Shah, 2011; Owen et al., 2010). Similarly, “do-it-yourself” brain stimulation devices have recently been produced with the promise of enhanced, generalisable cognitive benefits, some of which have garnered significant media attention (e.g., *The Guardian* (Chambers, 2013), *The New York Times* (Hurley, 2013), and *The Wall Street Journal* (Sapolsky, 2014)). These battery-operated systems deliver transcranial direct current stimulation (tDCS) via electrodes placed on the wearer’s scalp.

tDCS has previously been applied during training to assess its potential for modulating training-related outcomes. Having participants train on motor tasks during stimulation has been shown to enhance performance benefits for the task that is trained on, but only during application of one polarity of stimulation (anodal tDCS) over the motor cortex (Stagg, Bachtiar, & Johansen-Berg, 2011; Stagg, Jayaram, et al., 2011). Other studies have applied tDCS while participants train on language related processes (Flöel, Rösser, Michka, Knecht, & Breitenstein, 2008; Meinzer et al., 2014) and numeracy tasks (Iuculano & Kadosh, 2013; Kadosh, Soskic, Iuculano, Kanai, & Walsh, 2010). In both of these domains, online tDCS applied during cognitive training enhanced training outcomes in performance measures. What remains unclear from recent work is whether combined training and brain stimulation approaches can yield generalised benefits to untrained cognitive domains. Nor is it known how any such benefits might accrue in terms of modulations of information processing operations. To address these questions, we trained

participants on a decision-making task while they received active or sham brain stimulation. We then applied mathematical modelling to isolate and quantify any performance enhancements.

Participants trained for four consecutive days on a speeded decision-making paradigm, while undergoing active (anodal or cathodal) or sham tDCS, delivered over the left prefrontal cortex, which has previously been implicated in decision-making processes and training (Dux et al., 2009; Filmer, Mattingley, Marois, & Dux, 2013). We then re-tested participants 1-day after cessation of training and again two weeks later, both on the trained task and on an unrelated visual search task, to test for generalisation to a different cognitive domain (in this instance, visual spatial attention). We applied a well validated mathematical model to characterise the latent components of information processing in each task that might potentially be modulated by cognitive training and brain stimulation (Shadlen & Kiani, 2013).

Two prominent models for estimating the latent components of processing in simple decision-making tasks (Mulder, Van Maanen, & Forstmann, 2014) are the linear ballistic accumulator (LBA) model (Brown & Heathcote, 2008; Donkin, Brown, & Heathcote, 2011) and the drift diffusion model (Ratcliff & McKoon, 2008). Both frameworks partition responses into several components, namely: *non-decision time* (i.e., perceptual encoding and motor processes), *drift rate* (the efficiency of information processing), and *response threshold* (the level of decision caution). The LBA treats each possible stimulus-response mapping as a separate accumulator, with all the possible accumulators racing to reach the response threshold. This approach results in a model which can be flexibly adapted to situations in which there are multiple possible response options, such as the decision-making task employed in our study. In contrast, the drift diffusion model is limited to a two-alternative choice design. Also, the drift diffusion framework is less efficient as it models variance in intra-trial drift rate, whereas the LBA includes a noiseless drift rate

with only inter-trial variance in the starting point distribution, thus making it more computationally simple.

To anticipate, we found that anodal stimulation of left prefrontal cortex improved performance for the trained decision-making task, relative to both the sham and cathodal conditions, and this benefit generalised reliably to the visual search task, which had not been trained. Two control experiments revealed that the generalised enhancement with anodal stimulation occurred for left but not right prefrontal tDCS, and was absent for a group where stimulation was delivered without concurrent behavioural training.

Mathematical modelling of response times using the LBA framework revealed that significant improvements in the trained and untrained tasks were due to changes in drift rate, reflecting enhanced efficiency of information processing.

Materials and methods

Participants

Sixty-four right-handed participants (handedness determined via self-report) were recruited. Seven participants were removed from the analysis due to poor performance on the decision-making task during the pre-training phase (accuracy < 70%, defined a priori). The decision to include or exclude participants based on their accuracy was made exclusively on the basis of their pre-training performance, and without knowledge of the outcomes of the training and brain stimulation interventions. Data from a further three participants were not analysed because they missed one or more training sessions. The sample for these groups therefore consisted of 54 participants. Most were randomly assigned to one of the left prefrontal cortex stimulation and training groups (anode, cathode, or sham), with the exception of the last few participants who were deliberately allocated to a specific group to replace missing data, as outlined above. This strategy ensured a sample of 18 participants per group. We determined participant numbers using a power analysis (Faul, Erdfelder, Lang, & Buchner, 2007) based on a prior study by

our group, in which there were 18 participants. In that study we used tDCS to induce changes in decision-making performance in a single-session design (Filmer, Mattingley, Marois & Dux. *J. Neurosci* 2013; $n_p^2 = 0.175$, power = 0.999).

The mean age of this sample was 22 years (SD = 3 years; 39 females). All participants gave informed consent to participate in a study approved by The University of Queensland Human Research Ethics Committee, passed a tDCS safety-screening questionnaire, and were paid for their time. Vision and hearing were normal or corrected to normal for all participants.

Tasks

The experiment consisted of a decision-making task and a visual search task. In the decision-making task, participants discriminated between six different complex tones, with each tone requiring a different keypress on a standard computer keyboard. Each trial begin with a fixation square (0.2 – 0.6 seconds, randomly determined), followed by the complex tone (0.2 seconds), and a response window that lasted for 1.8 seconds (Figure 1b). The particular tone played on each trial was pseudo-randomised, with all tones occurring equally often across each block of the task. Participants were told to respond as quickly and accurately as possible. In the visual search task, participants had to find a target letter ('T'), in arrays of multiple, rotated, distractor letters ('L'), and indicate whether the target was rotated 90 degrees to the left or right. Each trial began with a fixation square (0.4 – 0.8 seconds) followed by the search display (until response; see Figure 1c). Participants were instructed to respond as quickly and accurately as possible. Set size was varied randomly across trials, and consisted of 8, 12, or 16 items. All items were presented at randomly generated coordinates on the screen (without overlapping). Each set size occurred equally often across each block of the task.

tDCS

The study was configured as a between-group design, with each group receiving either anodal, cathodal, or sham tDCS over left prefrontal cortex. Anodal tDCS has been associated with an increase in cortical excitability, and with a decrease in the inhibitory neurotransmitter GABA (Nitsche et al., 2004). In contrast, cathodal tDCS has been associated with a decrease in cortical excitability, and a decrease in the excitatory neurotransmitter glutamate (Liebetanz, Nitsche, Tergau, & Paulus, 2002). Following previous studies (Filmer, Mattingley, & Dux, 2013; Filmer, Mattingley, Marois, et al., 2013), we localised the stimulation site by finding the location on the scalp 1 cm posterior to F3, using the EEG 10-20 system (Jasper, 1958). The reference electrode was placed over the contralateral orbitofrontal region. For the anodal and cathodal conditions, stimulation ramped up for 30 seconds, remained constant for 570 seconds at an intensity of 0.7mA, and then ramped down for 30 seconds. Sham stimulation was identical, but only remained constant for 15 seconds. The target and reference electrodes consisted of rubber pads placed inside saline soaked sponges, and were 5 x 5 cm in size. Participants were blinded as to the stimulation type they received.

Procedure

The experiment was divided into four phases (see Figure 1a for an overview). In the first phase, participants completed pre-training trials for both tasks. In this session, there was an initial practice phase for each task in order for participants to learn the stimulus-response mappings. They then ran through a full block (240 trials) of each task. In the second phase, four training sessions were undertaken on consecutive days. During these training sessions, participants completed the decision-making task (240 trials a day), with concurrent tDCS (anodal, cathodal or sham). The stimulation began 30 seconds before the task (to allow the current to ramp up), with the task then running for 580 seconds. The third phase took place one day after cessation of training. For this post-training phase, participants ran through both tasks again (240 trials for each). The fourth phase was identical to the pre- and

post-training phases, but took place approximately 2 weeks after cessation of training (range = 12-14 days). Seven of the 54 participants were unavailable for the fourth phase, leaving 17 participants in the anodal group, and 15 each in the cathodal and sham groups. All of the sessions took place at approximately the same time of day for each participant.

Control experiments

Forty additional right-handed participants (handedness determined via self-report) were recruited for the two control experiments. Data from four participants were removed due to low accuracy in the decision-making task prior to training. Thus, the final sample consisted of 36 individuals (26 females, mean age = 21, SD = 2), with 18 participants assigned to each of the two experiments. In the first experiment participants received anodal tDCS over the *right* prefrontal cortex (1cm posterior to F4, with the reference electrode over the left orbitofrontal region) while undertaking the training task as described above. This was done to assess whether any observed effect of *left* prefrontal cortex stimulation might have been specific to that hemisphere. A second group received anodal tDCS over left prefrontal cortex, but did not perform decision-making training during stimulation. Instead, participants were asked to keep their eyes open and maintain fixation on a central point on the computer display. This manipulation allowed us to test whether the effects of anodal tDCS over left prefrontal cortex might have arisen from stimulation alone, without any requirement to undertake concurrent response-selection training.

Data analysis

For the decision-making task, a mixed-model ANOVA was used to assess the effect of training and prefrontal stimulation on response times. For the untrained visual search task, performance was compared before and after decision-making training to evaluate the presence of any training transfer. The pre- and post-training data for both tasks were also modelled within the LBA

framework to isolate the components of processing that were modulated by training and tDCS.

Results

Does tDCS facilitate decision-making training?

Based on previous research, we expected that training on the decision-making task should yield faster responses (Dux et al., 2009; Filmer, Mattingley, Marois, et al., 2013; Garner et al., 2014). As shown in Figure 2, performance on the decision-making task improved across successive training sessions for all three stimulation groups (main effect of phase: $F(3, 153) = 83.88, p < 0.001, \eta^2_p = 0.62$). Application of concurrent tDCS modulated this training-related performance improvement (significant interaction of stimulation group \times phase: $F(6, 153) = 3.208, p = 0.007, \eta^2_p = 0.112$). Specifically, there was a greater decrease in response times from the first to the fourth training session in the anodal tDCS group (mean change = 168 ms, SEM = 18) than in the cathodal group (mean change = 100 ms, SEM = 19) or sham group (mean change = 83 ms, SEM = 24), a pattern that specifically emerged in the third and fourth training sessions (see Figure 2). This anodal tDCS benefit remained for the immediate post-training session, where stimulation was no longer delivered (significant interaction for pre- to post-training changes \times stimulation group: $F(2, 51) = 4.10, p = 0.02, \eta^2_p = 0.14$). Thus, anodal tDCS delivered during decision-making training produced a reliable speeding of response times, and this effect outlasted the application of stimulation. Critically, this training-related benefit with anodal stimulation was not due to baseline differences in response times prior to application of tDCS ($F(2, 51) = 0.34, p = 0.72, \eta^2_p = 0.01$), as is evident from the comparable pre-training performance across conditions (Figure 2).

To further examine whether differences in baseline performance across the groups might have accounted for the training-related benefit of anodal stimulation, we conducted a step-wise regression analysis with post-training

performance as the dependent variable, and pre-training performance and stimulation group as independent variables¹. This analysis revealed that significant unique variance is explained by stimulation group membership above and beyond that explained by pre-training performance ($t = 2.887$, $p < 0.01$), confirming a reliable influence of combined training and anodal tDCS on performance.

Does the anodal tDCS training benefit transfer to an untrained task?

To determine whether decision-making training coupled with anodal tDCS generalises to other cognitive domains, we assessed pre- versus post-training behaviour on the untrained visual search task. As shown in Figure 3a, there was a larger improvement in visual search reaction times after training in the anodal tDCS group (mean = 206ms, SEM = 24) than in either the cathodal group (mean = 126ms, SEM = 24) or the sham group (mean = 115ms, SEM = 15; significant interaction of stimulation group x phase: $F(2, 51) = 5.43$, $p < 0.01$, $n^2_p = 0.18$). Moreover, the magnitude of the training benefit for the anodal tDCS group increased with set size (significant interaction of stimulation group x phase x set size: $F(4, 102) = 2.42$, $p = 0.05$, $n^2_p = 0.09$), implying a proportionally greater generalised effect of training for more demanding search arrays. Thus, anodal tDCS paired with decision-making training increases the efficiency of spatial attention deployment during search. Importantly, this reliable transfer of training with anodal tDCS was not due to baseline differences in performance on the visual search task, as search times were statistically indistinguishable across the three stimulation groups prior to training ($F(2, 51) = 1.77$, $p = 0.18$, $n^2_p = 0.07$).

As above, we also performed a step-wise regression analysis to examine whether group membership contributed a unique source of variance beyond that accounted for by baseline performance differences. With performance on the visual search task as the dependent variable, we found that stimulation group membership accounted for post-training performance effects that were

¹ We thank a reviewer for suggesting this analysis

above and beyond those explained by pre-training performance differences ($t = 2.219$, $p < 0.05$), again confirming a reliable influence of combined training and anodal tDCS on visual search performance.

Taken together, the results for the visual search task provide clear evidence for transfer of training induced benefits from combined anodal tDCS and decision-making training to the distinct cognitive domain of visual attention.

Are the benefits of anodal tDCS specific to stimulation of the left prefrontal cortex with concurrent training?

We next performed two control experiments, with a further 18 participants in each. In the first of these experiments we examined whether the performance benefits observed for the anodal condition were specific to stimulation of the left prefrontal cortex. Specifically, we combined the decision-making training regime with anodal stimulation over the *right* (as opposed to left) prefrontal cortex. As expected, RTs were improved after training with right prefrontal cortex stimulation. Comparing performance change across three groups (left anodal tDCS, right anodal tDCS, and sham) revealed a significant interaction between testing phase (pre- and post-training) and stimulation group ($F(2, 51) = 4.501$, $p < 0.05$, $\eta^2_p = 0.15$). Specifically, the magnitude of the enhancement from tDCS was significantly smaller for the right anodal tDCS group than for the left anodal group ($t(34) = 2.1$, $p < 0.05$; see Figure 4a), and was statistically indistinguishable from that of the sham group ($t(34) = -0.84$, $p = 0.41$). Critically, there were no baseline differences in performance prior to training between any of the groups ($F(2,51) = 0.79$, $p = 0.46$). A stepwise regression analysis confirmed that group membership explained variance in post-training performance beyond that accounted for by pre-training performance ($t = 2.674$, $p < 0.05$). We can thus conclude that the beneficial effects of anodal tDCS combined with training are specific to changes arising from left prefrontal stimulation.

In the second control experiment, we asked whether generalised performance

benefits might arise after repeated stimulation with anodal tDCS alone, without concurrent response-selection training. To this end, we applied anodal tDCS over the left prefrontal cortex in isolation, without concurrent training. We then compared the performance of this no-training control group with that of the group that received combined training and left anodal tDCS, and the sham group. There was a significant interaction between the testing phase (pre- and post-training) and stimulation group ($F(2, 51) = 8.373$, $p < 0.01$, $n^2_p = 0.247$). Specifically, the performance benefit for the group that received stimulation alone (without concurrent training) was significantly smaller than that observed for the training group that received left anodal stimulation ($t(34) = 4.29$, $p < 0.001$; see Figure 4a), and was statistically indistinguishable from that of the training group that received sham stimulation ($t(34) = -0.02$, $p = 0.98$). Again, there were no baseline differences in performance prior to stimulation ($F(2,51) = 0.24$, $p = 0.79$). A stepwise regression analysis confirmed that group membership explained significant variance in post-training performance beyond that accounted for by pre-training performance differences ($t = 3.839$, $p < 0.001$). Thus, the performance benefits accrued through anodal stimulation of the left prefrontal cortex only arise when this is combined with response-selection training.

The transfer of training gains reported above were also specific to left prefrontal cortex stimulation and the pairing of behavioural training and tDCS. Comparing the training group that received anodal tDCS over right prefrontal cortex with the groups that received anodal or sham tDCS over left prefrontal cortex, there was a significant interaction between testing phase (pre- and post-training) and stimulation group ($F(2, 51) = 7.346$, $p < 0.01$, $n^2_p = 0.224$). Specifically, there were smaller generalised performance gains for the right prefrontal stimulation group on the visual search task than for the training group that received left anodal tDCS ($t(34) = 3.14$, $p < 0.01$; see Figure 4b), and performance for this right prefrontal group was statistically indistinguishable from that of the training group that received sham stimulation ($t(34) = 0.46$, $p = 0.65$). In addition, for the control group that received anodal

tDCS over left prefrontal cortex alone (i.e., without training), when compared with the groups that received left anodal or sham tDCS with concurrent training, there was a significant interaction between testing phase (pre- and post-training) and stimulation group ($F(2, 51) = 8.089, p < 0.01, \eta^2_p = 0.241$). Specifically, the left anodal stimulation group who did not undertake concurrent training showed reduced gains in visual search performance relative to the training group that received concurrent left anodal stimulation ($t(34) = 3.14, p < 0.01$). Moreover, performance of the left-stimulation alone group was indistinguishable from that of the the sham stimulation group who undertook training ($t(34) = -0.26, p = 0.8$). Importantly, as above, there were no baseline differences in visual search performance across the three groups ($F(3,68) = 2.52, p = 0.07$). Two stepwise regression analyses confirmed that group membership explained variance in post-training performance beyond that contributed by pre-training performance for the comparison of the right anodal group with the left anodal and sham groups with training ($t = 2.249, p < 0.05$), and for the comparison of the left anodal group with no training and the left anodal and sham groups with training ($t = 3.053, p < 0.01$).

Do the performance benefits of paired tDCS and training persist over time?

Forty-seven of the original 54 participants who received training combined with anodal, cathodal, or sham stimulation returned for a follow-up session two weeks after completing the training regime. Compared with pre-training performance on the decision-making task, the anodal tDCS group still showed a numerical benefit compared with the cathodal and sham groups (Figure 2), although this effect was not statistically significant ($F(2, 44) = 1.26, p = 0.29, \eta^2_p = 0.05$). The generalised performance benefit for the visual search task was reliably maintained at follow-up, however (see Figure 3b: phase x stimulation group interaction: $F(2, 44) = 3.64, p = 0.04, \eta^2_p = 0.13$), and this benefit was greater for larger set sizes (near-significant three-way interaction: $F(4, 88) = 2.47, p = 0.06, \eta^2_p = 0.1$).

Modelling the combined effects of tDCS and training on behaviour

We applied the LBA model to the response time and accuracy data to determine which underlying cognitive operations were modulated by brain stimulation and training for both the decision-making (trained) and visual search (untrained) tasks. The modelling included data from both the pre- and post-training phases for the training group that received left prefrontal cortex stimulation. The different LBA model parameters that were fit to the response time data are described in the supplementary materials. Model fits were evaluated using the deviance information criterion (DIC), a measure that considers both the goodness of fit between a model and the data, as well as the complexity of the model (i.e., the number of parameters allowed to vary). Models with low DICs, i.e., those with lower complexity and small deviations from the response time data, are preferred (Speigelhalter, 2002).

The model that provided the best account of performance in the decision-making task across the two training phases included two unconstrained parameters: *drift rate* and *response threshold* (DIC = 453.77). There was little evidence to suggest tDCS and training benefited the non-decision components, namely, perceptual processing and response execution (DIC around 10 points higher: DIC = 463.64). Critically, the modelling demonstrated a significant increase in the *drift rate* from pre- to post-training for the group that received left anodal tDCS. This was quantified formally as a reliable difference in population-level mean drift rates between pre- and post-training using the 95% highest density interval (HDI (Kruschke, 2011)), a Bayesian analogue of the 95% confidence interval (HDI = 0.03 – 1.37). There was no such difference for the cathodal group (HDI = -0.12 – 1.217) or the sham group (HDI = -0.38 – 0.97). Moreover, there was no differential modulation of response thresholds or non-decision components across the three stimulation groups. Collectively, these results demonstrate that decision-making training paired with anodal tDCS significantly increased the efficiency of information processing, as reflected in the rate of evidence accumulation (Figure 5).

For the visual search task, the best model across stimulation groups included the same two unconstrained parameters as the decision-making task, i.e., drift rate and response threshold (DIC = 276.13). There was comparatively little evidence for pre- versus post-training benefits in non-decision components (a DIC value more than 8 points higher: DIC = 284.59). All three training groups that received left prefrontal cortex stimulation exhibited increased drift rates from pre- to post-training (anode HDI = 0.37 – 0.83; cathode HDI = -0.003 – 0.45; sham HDI = 0.01 – 0.48). This difference was greatest, however, for the anodal group (HDI for the differences between groups: anode and cathode = 0.05 – 0.69; anode and sham = 0.02 – 0.67; cathode and sham = -0.34 – 0.3). Here again, therefore, LBA modelling revealed a reliable increase in the rate of information accumulation for those participants who received decision-making training in combination with anodal tDCS, even for the untrained visual search task.

Discussion

We have shown that performance on a simple decision-making task can be reliably improved following four sessions of training combined with anodal tDCS over the left prefrontal cortex. Critically, performance on an untrained visual search task was also facilitated, suggesting that decision-making training combined with anodal tDCS generalises to the distinct cognitive domain of spatial attention. Two control experiments confirmed that the performance benefits for the trained and untrained tasks were specific to the combination of training and stimulation of the left prefrontal cortex with anodal tDCS. This generalised benefit was still evident two weeks after training and stimulation ceased. Response time modelling using the LBA framework revealed that the latent process altered by anodal tDCS and decision-making training arose from an increased efficiency of information processing, reflected by an increase in the rate of evidence accumulation.

Previous studies have investigated changes across a range of trained tasks arising from concurrent tDCS (Iuculano & Kadosh, 2013; Kadosh et al., 2010; Stagg, Bachtiar, et al., 2011; Stagg, Jayaram, et al., 2011), but none has shown transfer of performance benefits to untrained cognitive operations. We deliberately chose our trained and untrained tasks to be as distinct as possible in terms of their information processing demands. Our decision-making task used a 6-alternative-forced-choice design, thus placing high demands on decision-making processes. By contrast, the untrained visual search task used a 2-alternative-forced-choice design, and therefore placed relatively low demands on decision processes. Similarly, whereas the decision-making task employed distinct auditory stimuli to cue individual keypresses, the search task involved purely visual stimulus arrays. Finally, in the decision-making task complex tones were presented in one predictable location and without distractors, whereas in the visual search task the target could appear in one of several locations and was always accompanied by multiple distractor items. Our use of these two tasks supports the notion that tDCS can lead to transferable performance benefits. However, further research will be needed using a range of tasks pre- and post-training to assess the full extent and scope of such improvements.

Clearly both tasks required a single keypress response on each trial, and thus might be argued to rely upon overlapping motor output processes. Could these be the source of the generalised training effect observed for the anodal stimulation group? We believe not for two reasons. First, for the visual search task the anode-specific benefit after training increased as a function of set size (Figure 3), even though the motor responses required remained constant. Second, our modelling under the LBA framework revealed significant post-training changes in the rate of evidence accumulation for the anodal group, but no reliable change in non-decision parameters, including response execution. If a single process relating to information processing was responsible for the benefits in the two tasks (e.g., sustained attention), it follows that this must have been sufficiently broad to modulate them both.

tDCS is widely assumed to modulate cortical excitability in a polarity-specific manner, such that anodal tDCS exerts an excitatory effect and cathodal tDCS has an inhibitory effect (Nitsche & Paulus, 2000). On this view, and given the reliable training benefits we observed with anodal stimulation, one might have expected to observe training *disruption* in the cathodal group. Indeed, such opposing effects of tDCS have been reported in certain motor learning paradigms (Stagg, Jayaram, et al., 2011). In our study cathodal stimulation did not reliably disrupt training effects relative to sham, suggesting the simple “anode-excitation” vs. “cathode-inhibition” model of tDCS effects does not hold under all task conditions. Indeed, some studies have observed tDCS effects on behaviour for just one polarity of stimulation (Filmer, Dux, & Mattingley, 2015; Filmer, Mattingley, & Dux, 2013), while others have shown similar effects for both anodal and cathodal stimulation (Ferrucci et al., 2008; Filmer, Mattingley, Marois, et al., 2013). Our training and transfer effects suggest that the neural processes associated with generalised performance enhancements with decision-making training are uniquely sensitive to anodal stimulation, perhaps via modulation of GABA levels in the left prefrontal cortex (Filmer, Dux, & Mattingley, 2014; Stagg, Bachtiar, et al., 2011; Stagg, Jayaram, et al., 2011).

In the current study we specifically targeted the left prefrontal cortex, as this region has been implicated in various decision-making and learning processes (Dux et al., 2009; Filmer, Mattingley, & Dux, 2013; Filmer, Mattingley, Marois, et al., 2013; Stokes et al., 2013). For example, neurons in the left prefrontal cortex adapt their neural tuning profile to accommodate changes in behavioural context (Stokes et al., 2013). In addition, activity in the left prefrontal cortex is reduced following decision-making training, as measured with fMRI (Dux et al., 2009). Previous tDCS studies have provided causal evidence for the relationship between the left prefrontal cortex and decision-making training (Filmer, Mattingley, & Dux, 2013; Filmer, Mattingley, Marois, et al., 2013). Here we go beyond these earlier findings by showing

that the left prefrontal cortex is a key cortical mediator of generalised training benefits.

We employed response time modelling to better understand the underlying neural effects of combined training and brain stimulation. Using the well-validated LBA framework (Brown & Heathcote, 2008; Donkin et al., 2011), we found that information processing efficiency was selectively enhanced by anodal tDCS over the left prefrontal cortex. This is in line with previous research which has suggested a role for this region in evidence accumulation (Philiastides, Aukstulewicz, Heekeren, & Blankenburg, 2011). Here we go beyond this earlier work by demonstrating a direct link between evidence accumulation processes in prefrontal cortex and transfer of performance benefits to an untrained task.

Our findings offer an important new direction for research into the neural basis of cognitive training. The possibility of generalised performance enhancements from cognitive training with concurrent tDCS has important implications for understanding how local cortical circuits change with experience. Of particular import, our findings suggest that combined decision-making training and anodal tDCS of the left prefrontal cortex can improve performance beyond the trained cognitive domain. This may be of particular benefit for individuals at risk of cognitive decline, such as in healthy ageing, where training interventions have already shown some promise (Lustig, Shah, Seidler, & Reuter-Lorenz, 2009), or in patients with neurological impairments.

Acknowledgements

This research was supported by the Australian Research Council (ARC) Discovery grants to PED (DP110102925 and DP140100266) and JBM (DP110102925), the ARC-SRI Science of Learning Research Centre (SR120300015, PED & JBM), and the ARC Centre of Excellence for Integrative Brain Function (ARC Centre Grant CE140100007, JBM). PED was supported by an ARC Future Fellowship (FT120100033) and JBM by an ARC Australian Laureate Fellowship (FL110100103).

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Figure Captions

Figure 1: Experiment design overview. (A) Outline of the experiment. Participants first undertook a pre-training phase in which they completed an initial practice run and full experimental block of the decision-making and visual search tasks. Participants then trained on the decision-making task, with concurrent anodal, cathodal, or sham tDCS, over four consecutive days. Two post-training sessions were conducted one day and approximately two weeks after training, in which participants again undertook the decision-making and visual search tasks. (B) Trial outline for the decision-making task. (C) Trial outline for the visual search task.

Figure 2: Reaction times in the decision-making task before, during, and after training, plotted separately for the anodal, cathodal and sham stimulation conditions. Error bars represent the SEM for the within-subjects variance (Loftus & Masson, 1994).

Figure 3: Change in reaction times in the visual search task after decision-making training. (A) Change in reaction times from pre- to post-training. Error bars represent SEM for the change in reaction time pre- to post-training. (B) Change in reaction time from pre-training to the two-week follow-up session. Error bars represent SEM for the change in reaction time from pre-training to the follow-up session.

Figure 4: Change in reaction times in the decision-making task (A) and the visual search task (B) from pre- to post-training, plotted separately for the training groups that received anodal stimulation over left or right prefrontal cortex, the training group that received sham stimulation, and the no-training group that received anodal stimulation over left prefrontal cortex only (i.e., without concurrent behavioural training). Error bars represent one SEM for the change in reaction times from pre- to post-training sessions.

Figure 5: Schematic of the linear ballistic accumulator (LBA) model. For a simple decision-making task, the stimulus initially undergoes perceptual processing (grey shading on right). Evidence for a particular decision is then accumulated toward one of the possible stimulus-response mappings (the *drift rate*) until the threshold for a motor response is reached. In this illustration, yellow and green lines depict hypothetical drift rates for pre- and post-training decisions, respectively. The light grey region on the right of the figure illustrates a hypothetical change in decision time with training.









