Differential Frontal Involvement in Shifts of Internal and Perceptual Attention

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Abstract

Background: Perceptual attention enhances the processing of items in the environment, whereas internal attention enhances processing of items encoded in visual working memory. In perceptual and internal attention cueing paradigms, cues indicate the to-be-probed item before (pre-cueing) or after (retro-cueing) the memory display, respectively. Pre- and retro-cues confer similar behavioral accuracy benefits (pre-: 14–19%, retro-: 11–17%) and neuroimaging data show that they activate overlapping frontoparietal networks. Yet reports of behavioral and neuroimaging differences suggest that pre- and retro-cueing differentially recruit frontal and parietal cortices (Lepsien and Nobre, 2006).

Objective/hypothesis: This study examined whether perceptual and internal attention are equally disrupted by neurostimulation to frontal and parietal cortices. We hypothesized that neurostimulation applied to frontal cortex would disrupt internal attention to a greater extent than perceptual attention.

Methods: Cathodal transcranial direct current stimulation (tDCS) was applied to frontal or parietal cortices. After stimulation, participants completed a change detection task coupled with either pre- or retro-cues.

Results: Cathodal tDCS across site (frontal, parietal) hindered performance. However, frontal tDCS had a greater negative impact on the retro-cued trials demonstrating greater frontal involvement during shifts of internal attention.

Conclusions: These results complement the neuroimaging data and provide further evidence suggesting that perceptual and internal attention are not identical processes. We conclude that although internal and perceptual attention are mediated by similar frontoparietal networks, the weight of contribution of these structures differs, with internal attention relying more heavily on the frontal cortex.

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Introduction

In experimental settings, attentional cueing paradigms use spatial cues to direct perceptual attention toward the location where an item is likely to appear. For example, if you are expecting friends to meet you at the main entrance you will be faster to where an item is likely to appear. For example, if you are expecting spatial cues to direct perceptual attention toward the location

However, frontal tDCS had a greater negative impact on the retro-cued trials demonstrating greater frontal involvement during shifts of internal attention.

Conclusions: These results complement the neuroimaging data and provide further evidence suggesting that perceptual and internal attention are not identical processes. We conclude that although internal and perceptual attention are mediated by similar frontoparietal networks, the weight of contribution of these structures differs, with internal attention relying more heavily on the frontal cortex.

Yet, attention comes in a variety of flavors and not all shifts of attention occur between elements in the environment. Recent reports demonstrate that when spatial cues are presented after encoding and maintenance phases, VWM performance improves even in the absence of new information [6–26]. Simply put, spatial pre-cues shift perceptual attention to possible future objects while spatial retrospective cues, termed retro-cues, shift internal attention toward items currently stored in VWM. The standard retro-cue paradigm shifts internal attention by presenting a central retro-cue ~1000 ms after encoding, and a variable amount of time (100–24,000 ms) before retrieval [6–15,17–26]. The duration of the first delay after encoding means that these effects operate beyond
the extent of iconic memory (<500 ms of stimulus presentation) (e.g. Ref. [27]). This growing literature has found that valid retro-cues provide robust VWM performance benefits (5–17%) using various stimuli, timing and design parameters [6–25]. In several studies both pre- and retro-cues have been directly compared. The results show that there is a slightly greater but comparable cueing benefit for both pre-cued items (~14–19%) when compared to retro- (~11–17%) cued items [11,28].

Due to these similarities, there is growing discussion addressing the extent of neural and behavioral similarity between perceptual and internal forms of attention. It is well understood that perceptual attentional benefits are afforded by enhanced processing of the cued item(s) in sensory and attention processing regions (e.g. Refs. [1–3]). Current hypotheses about the mechanism responsible for internal attentional benefits are not as well defined. Several explanations for the mechanism of internal attention include protection from decay [17], inhibition of distractors [12], increased VWM durability [15] and enhancement of the VWM representation [11,12]. Another recent proposal suggests that the retro-cue accesses fragile VSTM, a higher capacity memory store that is separate from lower capacity, more robust WM robust working memory [20,24], but see Ref. [29]. The most parsimonious hypothesis would be that internal and perceptual attention are mediated by similar, if not identical, neural correlates. In accordance with this idea, recent neuroimaging results indicate that activations in early visual areas (V1–V4) are detectable throughout extended periods of VWM maintenance [30–33]. Specifically, data published by Munneke et al. indicated that shifting attention to spatial locations within perception or in VWM produced similar neural activity [33]. In further support of a single mechanism hypothesis, several findings demonstrate similar event-related potential (ERP) and functional magnetic resonance imaging (fMRI) activations associated with shifting perceptual (pre-cues) and internal (retro-cues) attention. These studies have shown similar patterns of activation in parietal, frontal and occipital regions [6,11,28].

However, in spite of the similarity in activation patterns and performance benefits, there are also reports of differences in activations and in behavioral outcomes between the pre- and retro-cue literature. Makovski and Jiang noted behavioral differences when single or multiple retro-cues directed internal attention to one or more objects held in VWM [19]. Their results indicated that while pre-cues provide performance benefits when cues indicate more than one location (e.g. Refs. [19,34]), multiple retro-cues were unable to provide a benefit. Berryhill and colleagues also reported behavioral dissimilarities between pre- and retro-cueing [7]. Their results showed that no retro-cue benefit was elicited when typical exogenous (spontaneous onset) cues were used even though these cues induce shifts of perceptual attention. In their experiments, only arrow cues were able to elicit a retro-cue benefit. Most recently, Tanoue and Berryhill illustrated that internal and perceptual attention differed in the time course for the onset of cueing benefits [26]. Specifically, unlike perceptual attention, internal attentional benefits did not build over time and were quantal in nature. They also found that the eccentricity of items in the stimulus array only affected shifts of perceptual attention. These behavioral results indicate that internal attention has distinctive characteristics that differ from perceptual attention. Thus, these forms of attention may be mediated by separable or partially overlapping mechanisms [7,19,26]. In the neuroimaging literature some differences in activations have been reported in spite of the similarities previously mentioned. There are some functional magnetic resonance imaging (fMRI) experiments directly comparing shifts of perceptual and internal attention initiated by pre- and retro-cues (for a review see Ref. [6]). Perceptual attention selectively activated the intersection of right parietal, temporal, and occipital areas whereas internal attention selectively activated right frontal areas including the middle frontal gyrus and ventrolateral prefrontal cortex [28].

Previously, these prefrontal areas were observed during working memory tasks investigated using neuroimaging [35–41].

Thus, the question remains open: are perceptual and internal attention subserved by a single or multiple neural mechanisms? The neuroimaging data is not clear because in spite of similarities in the activation patterns observed during perceptual and internal attention there are differences. This makes it difficult to know whether these differences are due to task related or task unrelated processes without data from complementary experimental approaches. One approach that may add to our understanding of attentional mechanisms is transcranial direct current stimulation (tDCS). TDCS is a non-invasive brain stimulation technique where electrodes placed on the scalp deliver low-level direct current to underlying cortical tissue. In general, tDCS currents alter the excitability of cortical neurons with effects lasting up to 1 h [42–49]. TDCS applies direct current, consequently the direction of current flow depolarizes (+ anodal) or hyperpolarizes (– cathodal) underlying neural populations and the resulting effects on behavior may be to subtly enhance or impair performance [50]. Although the mechanism of tDCS remains under investigation, previous research suggests that tDCS may alter the synaptic strength of the pyramidal neurons and interneurons [46,51].

TDCS is beginning to be used to study cognitive tasks such as VWM and attention. One relevant study by Weiss and Lavidor [52] reported that cathodal stimulation to the right posterior parietal cortex (area P4) improved attentional processing and memory for flanker stimuli. They found that cathodal stimulation enhanced cognitive performance although motor tasks typically report cathodal tDCS impairments performance [53]. A second recent study reported that simultaneous stimulation of left (+ anodal) and right (– cathodal) parietal regions resulted in improved verbal episodic memory performance. They concluded that stimulation applied to regions associated with attention facilitated learning [54].

Here, we used tDCS to investigate whether internal and perceptual attention rely on the same or different frontoparietal mechanisms. We selected stimulation sites based on previous fMRI findings showing increased parietal activations during perceptual attention and frontal activations during internal attention (for a review see Ref. [6]). Our predictions are straightforward: If internal and perceptual attention reflect a common mechanism, tDCS to these areas should produce similar effects on benefits provided by both pre- and retro-cues. Alternatively, if there are dissociable mechanisms there should be a stimulation site × task interaction.

**Method**

**Experimental design and trial sequence**

**tDCS stimulation**

Participants were tested in three sessions: cathodal P4, cathodal F4 and sham (control condition). These sessions were separated by a minimum of 24-h wash out period. Condition order was counterbalanced across participants. During stimulation conditions the cathodal electrode was placed over participants’ right inferior parietal cortex at position P4 (International 10–20 EEG system) or right frontal cortex F4 while the reference electrode was placed over the left contralateral cheek [52,55–61]. During sham, electrode placement was randomized across participants between P4 and F4 locations. At the beginning and end of each stimulation session (cathodal and sham), current ramped up over a 20 s period [49]. Cathodal stimulation (1.5 mA) was delivered for 10 min in the tDCS session and for up to 20 s in the sham session. This current ramp is important as it allows for participants to be blind to the type
of stimulation they are receiving [62]. A battery driven continuous current stimulator delivered stimulation: Eldith MagStim, GmbH, Ilmenau, Germany. Current was delivered through two 5 × 7 cm electrodes housed in saline soaked sponges. After the 10 min stimulation/sham duration ended, the electrodes were removed and behavioral testing began.

**Behavioral testing**

Three randomly interleaved cue conditions were tested: neutral (33%), pre-cue (33%) and retro-cue (33%). The neutral condition consisted of the letter ‘X’ (1.4° W × 1.4° H degrees of visual angle) presented at both the pre- and retro-cue intervals. This neutral cue was uninformative and served as a control condition. The arrow pre- and retro-cue (1.4° L × 1.1° W degrees of visual angle) was 80% predictive of the test location.

The instructions were identical across trials and sessions. Participants were instructed to remember the color and location conjunction of each stimulus presented in the memory display; see **Fig. 1**. They were informed that the neutral (X) cues were not informative but that the arrow cues might indicate the to-be-probed location. Each trial began with a fixation cross (1500 ms) and was followed by either a neutral or arrow pre-cue (100 ms). After the first cue was presented, the stimulus array appeared (200 ms). The stimulus array consisted of four equiluminant color patches out of a set of 10 possible colors. The stimuli were 2.4° × 2.4° degrees of visual angle and located at 6° from fixation. Following a 2nd delay (1000 ms), either the neutral or arrow retro-cue (100 ms) appeared at central fixation so that it did not overwrite any of the stimuli or probe positions. Next, a probe screen appeared. The probe screen preserved the spatial arrangement of the memory display by indicating stimulus locations with empty annuli as placeholders, while the probe location was filled with a stimulus from the memory array. The task was to decide whether the probe stimulus matched the object shown at that position during encoding. Participants responded by pressing the ‘Y’ key if the color-location conjunction matched (50%) the original memory display and by pressing the ‘N’ key if it did not match (50%). Responses were unspeeded and participants pressed the ‘space’ bar to begin the next trial. Participants completed 250 trials and were given the opportunity for five rest breaks, which occurred every 50 trials. Prior to the experiment, participants conducted a 10 trial practice block. The task began immediately following stimulation and lasted approximately 20 min. This duration ensures that testing occurred within the hour long window of tDCS effects.

**Articulatory suppression**

During all experiments, participants were instructed to repeat a single syllable three-letter word out loud throughout the experiment to avoid verbal encoding of the colors. A different word was specified at each rest period (i.e., every 50 trials).

**Equipment**

Participants were tested individually in a room with dimmed lighting. They sat approximately 57 cm from a 24° Dell LCD computer monitor. The experiment was programmed in ePrime (Psychology Software Tools, PA, USA).

**Participants**

24 neurologically normal volunteers from the University of Nevada psychology subject pool participated (ages 18–44, M = 23.7, 12 male) in exchange for $15/h of participation. One participant’s data was removed from the analysis as an outlier because their performance under sham stimulation was greater than 2 standard deviations from the mean. All participants were subjected to prescreening to ensure that they had never suffered from any form of head injury, were not on any prohibited medications and were right handed. The Internal Review Board of the University of Nevada approved all experimental protocols and participants signed informed consent documents.

**Results**

The primary dependent measure was the effect of tDCS on pre- and retro-cue performance. Thus the data are presented as difference scores (valid arrow cue accuracy – neutral cue accuracy), which highlight the magnitude of the cueing effect. The difference scores were evaluated using a repeated measures analysis of variance (ANOVA) with the within subjects factors of tDCS condition (sham, cathodal parietal (P4), cathodal frontal (F4)) and cue type (pre-cue, retro-cue). There was a main effect of stimulation...
condition \( (F_{2, 44} = 7.06, P = .002) \); see Fig. 2, Table 1. Subsequent planned contrasts revealed that the pre- and retro-cueing benefits were significantly larger in the sham condition as compared to cathodal tDCS to the parietal \( (P = .03) \) or frontal \( (P = .002) \) sites. These results indicate that cathodal tDCS to either parietal or frontal sites suppressed the benefit of pre- and retro-cues. The main effect of cue type was also significant \( (F_{1, 22} = 38.81, P < .001) \) such that pre-cues provided a greater cueing benefit than retro-cues. Importantly, the interaction between stimulation and cue type reached significance \( (F_{2, 44} = 4.33, P = .02) \). This interaction was driven by a significantly smaller retro-cue benefit after frontal rather than parietal stimulation \( (t_{22} = 2.49, P = .02) \). The pre-cue benefit, in contrast, was equivalent after frontal and parietal tDCS \( (t_{22} = .36, P = .72) \). These results show that although cathodal tDCS to parietal and frontal sites suppressed the cueing benefit for pre- and retro-cue performance, frontal stimulation resulted in significantly more impairment to retro-cue performance (Table 2).

Because there was an unexpected main effect of cue condition such that pre-cue performance was significantly greater than retro-cue performance we conducted several correlation analyses to ensure that tDCS effects were not reflecting differences in task difficulty. In other words, the more difficult retro-cue task might have recruited frontal cortex more heavily in those who performed poorly whereas stronger performance would not be as reliant on frontal contributions and would be less affected by tDCS. If so, there should be a positive correlation between sham session retro-cue performance and the retro-cue benefit observed after frontal tDCS. Instead there was a borderline significant correlation in the opposite direction toward a negative correlation \( (r = -.39, N = 23, P = .06) \). A second way of looking at this concern was to see if those who showed larger differences between the pre-cue and retro-cue benefits at sham were correlated with the retro-cue effect observed after frontal tDCS. If so, a negative correlation should emerge. Instead, baseline cueing differences (pre-retro cue performance at sham) were positively correlated with the cueing benefits observed after frontal tDCS \( (r = .46, P = .03) \) stimulation. In summary, those who performed poorly at sham received those who showed a greater difference between pre- and retro-cue at sham less reduction in the retro-cue benefit after frontal tDCS.

Additional analyses investigated several other relevant measures of performance using the same a repeated measures analysis of variance (ANOVA) with the within subjects factors of tDCS condition (sham, cathodal parietal (P4), cathodal frontal (F4)) and cue type (pre-cue, retro-cue). Difference scores derived from the \( d' \) sensitivity values \( (d' \text{ valid} - d' \text{ neutral}) \), revealed a similar pattern. There was a main effect of the tDCS condition \( (F_{2, 44} = 4.34, P = .02) \); see Table 3) such that cathodal stimulation reduced the cueing benefit. Contrasts revealed a significant difference between F4 cathodal and sham conditions \( (P = .006) \). The comparison of P4 cathodal and sham stimulation approached significance \( (P = .08) \). Secondly, there was a significant main effect of cue type \( (F_{1, 22} = 38.74, P < .001) \) such that the cueing benefit was larger for pre-cue compared to retro-cue trials. Importantly, there was a significant interaction between tDCS and cue type \( (F_{2, 44} = 4.30, P = .04) \). This interaction was driven by a greater reduction in the cueing benefit for retro-cue trials \( (t_{22} = 2.38, P = .03) \) compared to pre-cue trials \( (t_{22} = 4.02, P = .08) \) during cathodal F4 but not P4 stimulation.

A third analysis looked at the difference scores between response criterion \( (C = B - d'/2) \); values. Neither main effects \( (tDCS: F < 1, P = ns; \text{cage} = 1.6, P = .22) \) nor the interaction reached significance \( (F_{2, 44} = 1.49, P = .24) \). As such, the tDCS effects observed in the current experiment primarily influenced detection sensitivity rather than shifts of response criterion.

Finally, difference scores defined by median reaction times were also analyzed. There was no significant main effect of stimulation \( (F < 1, P = ns; \text{cage} = 1.6, P = .22) \) nor the interaction reached significance \( (F_{2, 44} = 1.49, P = .24) \). As such, the tDCS effects observed in the current experiment primarily influenced detection sensitivity rather than shifts of response criterion.

### Table 1

Summary of results. The mean (standard deviation) raw accuracy are shown for each of the cue types and stimulation conditions.

<table>
<thead>
<tr>
<th>Stimulation type</th>
<th>Cue type</th>
<th>Neutral</th>
<th>Valid pre-cue</th>
<th>Valid retro-cue</th>
<th>Invalid pre-cue</th>
<th>Invalid retro-cue</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sham</td>
<td></td>
<td>.73 (.07)</td>
<td>.93 (.04)</td>
<td>.89 (.05)</td>
<td>.64 (.13)</td>
<td>.69 (.14)</td>
</tr>
<tr>
<td>Parietal (P4)</td>
<td></td>
<td>.76 (.07)</td>
<td>.92 (.04)</td>
<td>.89 (.05)</td>
<td>.71 (.13)</td>
<td>.69 (.13)</td>
</tr>
<tr>
<td>Frontal (F4)</td>
<td></td>
<td>.78 (.07)</td>
<td>.93 (.04)</td>
<td>.87 (.04)</td>
<td>.70 (.13)</td>
<td>.68 (.14)</td>
</tr>
</tbody>
</table>

### Table 2

Signal detection values. The mean hit rates (HR) and mean false alarm rates (FAR) and standard deviations are shown for each cue types and stimulation conditions.

<table>
<thead>
<tr>
<th>Stimulation type</th>
<th>Cue type</th>
<th>Neutral</th>
<th>Valid pre-cue</th>
<th>Valid retro-cue</th>
<th>Invalid pre-cue</th>
<th>Invalid retro-cue</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sham</td>
<td></td>
<td>.60 (.16)</td>
<td>.94 (.04)</td>
<td>.89 (.07)</td>
<td>.48 (.25)</td>
<td>.58 (.27)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>.06</td>
<td>.08 (.06)</td>
<td>.12 (.06)</td>
<td>.21 (.18)</td>
<td>.17 (.16)</td>
</tr>
<tr>
<td>Parietal (P4)</td>
<td></td>
<td>.63 (.14)</td>
<td>.93 (.06)</td>
<td>.88 (.09)</td>
<td>.56 (.24)</td>
<td>.56 (.24)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>.13 (.07)</td>
<td>.08 (.05)</td>
<td>.10 (.05)</td>
<td>.13 (.16)</td>
<td>.23 (.22)</td>
</tr>
<tr>
<td>Frontal (F4)</td>
<td></td>
<td>.67 (.14)</td>
<td>.94 (.06)</td>
<td>.86 (.07)</td>
<td>.51 (.24)</td>
<td>.56 (.21)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>.11 (.14)</td>
<td>.08 (.04)</td>
<td>.13 (.06)</td>
<td>.12 (.13)</td>
<td>.20 (.19)</td>
</tr>
</tbody>
</table>
Table 3
Signal detection analyses. Mean sensitivity (d') and mean response criterion (C) as well as standard deviations are shown for each cue types and stimulation condition. Positive C values reflect a conservative response bias and negative C values reflect a liberal response bias [63].

<table>
<thead>
<tr>
<th>Stimulation type</th>
<th>Cue type</th>
<th>d'</th>
<th>Standard deviation</th>
<th>C</th>
<th>Standard deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sham</td>
<td>Neutral</td>
<td>1.46 (.50)</td>
<td>3.23 (.64)</td>
<td>6.50 (1.05)</td>
<td>0.51 (.85)</td>
</tr>
<tr>
<td>Parietal (P4)</td>
<td>Pre-cue</td>
<td>2.59 (.60)</td>
<td>9.50 (1.05)</td>
<td>1.50 (1.01)</td>
<td>1.50 (1.01)</td>
</tr>
<tr>
<td>Parietal (P4)</td>
<td>Retro-cue</td>
<td>6.50 (1.05)</td>
<td>9.50 (1.05)</td>
<td>1.50 (1.01)</td>
<td>1.50 (1.01)</td>
</tr>
<tr>
<td>Frontal (F4)</td>
<td>Pre-cue</td>
<td>7.06 (2.50)</td>
<td>9.05 (2.00)</td>
<td>1.05 (1.05)</td>
<td>1.05 (1.05)</td>
</tr>
<tr>
<td>Frontal (F4)</td>
<td>Retro-cue</td>
<td>9.50 (2.00)</td>
<td>9.05 (2.00)</td>
<td>1.05 (1.05)</td>
<td>1.05 (1.05)</td>
</tr>
</tbody>
</table>

Table 4
Median reaction time. Mean median reaction times (standard deviations) are shown for each cue types and stimulation condition.

<table>
<thead>
<tr>
<th>Stimulation type</th>
<th>Cue type</th>
<th>Neutral</th>
<th>Valid pre-cue</th>
<th>Valid retro-cue</th>
<th>Invalid pre-cue</th>
<th>Invalid retro-cue</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sham</td>
<td>Neutral</td>
<td>935.05 (228.93)</td>
<td>784.22 (196.53)</td>
<td>720.35 (155.44)</td>
<td>1080.39 (262.25)</td>
<td>1236.07 (501.75)</td>
</tr>
<tr>
<td>Parietal (P4)</td>
<td>Pre-cue</td>
<td>917.17 (205.25)</td>
<td>766.91 (175.59)</td>
<td>715.24 (153.02)</td>
<td>1028.09 (297.50)</td>
<td>1239.52 (425.08)</td>
</tr>
<tr>
<td>Parietal (P4)</td>
<td>Retro-cue</td>
<td>939.85 (173.18)</td>
<td>776.54 (144.81)</td>
<td>726.85 (145.27)</td>
<td>1137.35 (319.27)</td>
<td>1228.61 (332.59)</td>
</tr>
</tbody>
</table>

attention relied equally on parietal and frontal contributions. These two regions were stimulated because previous fMRI and ERP findings showed that both parietal and frontal regions showed largely similar activation patterns when participants shifted perceptual or internal attention [6,11,28]. We applied tDCS to parietal or frontal cortex and evaluated performance on pre- and retro-cueing trials. As expected, the data showed that cathodal tDCS to either right parietal or frontal cortices modulated the cueing benefits associated with pre- and retro-cue. The observation that tDCS to these sites impaired performance is consistent with previous observations implicating these regions in attention and VWM processes. Consequently, disruption to either site reduced the cueing benefit. The sensitivity and criterion measures indicated that this disruption was not due to a shift in criterion but to a reduction in sensitivity. Secondly, frontal stimulation selectively produced an additional reduction in the retro-cue benefit when compared to parietal stimulation. This interaction confirms the presence of mechanistic differences between perceptual and internal attention. Therefore, although both types of attention rely on frontoparietal networks [6,11,28], the present findings show that these areas contribute differently to performance and thus internal and perceptual attention are mediated by partially separable mechanisms [7,19,26].

PFC involvement in internal attention

Lepsien and Nobre [6] proposed several explanations for the differences in activations observed when neuroimaging perceptual and internal attention. One proposal was that that increased right frontal activation may facilitate shifts of internal attention within VWM but that this activity is not needed for perceptual attention. The other was that right frontal areas were involved in response selection or distractor inhibition at the memory probe stage. We interpret the present results as confirmation and clarification of these proposals. First, right frontal tDCS influenced performance significantly more for internal attention confirming that increased right frontal activations are the result of internal attentional processes. Second, inhibition of PFC activity may have affected participants' ability to shift internal attention to the desired objects or filter distractor items, leading to decreased VWM performance. Importantly, our use of a within subjects design which required each participant to use both cue types (pre- and retro-) following all stimulation conditions (sham, cathodal parietal (P4), cathodal frontal (F4)) should allay concerns that these effects are limited to between participant variability. Therefore, because PFC stimulation impacted retro-cues significantly more than pre-cues, it seems reasonable to conclude that stimulation to right frontal areas had a significantly larger impact on shifts of internal attention. Thus, these results confirm and strengthen those of Nobre et al. [30], by demonstrating that in general, successful shifts of internal attention rely more heavily on cortical areas within the PFC. It also seems reasonable to conclude that disruption of PFC activations would have a larger impact on internal attention because this area has been previously implicated in WM processes [35–41], and unlike perceptual attention, internal attentional item selection is occurring within this mnemonic context. Thus, reduced ability to filter distractors or select desired objects would have a larger negative impact on shifts of internal attention.

This research also extends previous reports from neuroimaging (reviewed in Ref. [6]) and behavioral approaches [7,19,26] by demonstrating that internal and perceptual attention are not identical. Specifically, cathodal tDCS to right PFC and PFC differentially altered internal and perceptual attentional performance. Similar to previous results that showed differences in frontal and parietal activations [6], these findings highlight a dissociation between perceptual and internal attention. Importantly, our results extend the neuroimaging research by demonstrating that not only is there increased PFC involvement during retro-cue trials, but this involvement is necessary for successful shifts of internal attention. These results also further the notion that the mechanisms responsible for shifts of internal and perceptual attention may be dissociable or partially overlapping.

Alternative interpretations and limitations

We turn our attention to several alternative explanations that might account for greater disruption of internal attention after frontal stimulation. Several task-related differences are noteworthy. One possibility is that baseline performance differences between pre-cue and retro-cue trials drove the effect because the pre-cue trials yielded superior performance. Pre-cueing necessarily provides information prior to the arrival of the stimuli whereas retro-cueing comes in after the fact. Previous researchers found no significant difference in reaction time or accuracy between pre- and retro-cue conditions (e.g. Refs. [11,26]). Previous work has used a range of temporal delays between the pre- or retro-cue and the stimulus array [11] pre retro: 1500–2500 ms, [26], pre: 100 ms, retro: 300 ms) without observing the performance difference we found in the neutral condition. Future work is needed to examine whether these differences in timing and the congruend differences in baseline performance reflect more than a peculiarity of the present data set. A related concern that was raised asked whether the pre-cue condition imposed the same VWM demands as the retro-cue task. One reasonable strategy would be to simply attend to the cued item and ignore the other stimuli. To avoid this strategy
invalid cues were included and performance on these invalidly cued trials remained constant or improved after tDCS.

Another explanation for the pattern of results from the current experiment relates to the disruption of other, related cognitive processes after stimulation. Given that a decision regarding both identity and location were required in our task, tDCS may have disrupted maintenance of the represented items rather than disrupting the shift toward specific items via internal attention. Additionally, because tDCS is imprecise stimulation could have influenced frontal areas other than our targeted stimulation site. This may have disrupted VWM maintenance or the programming of covert eye movements to salient spatial locations by stimulating the frontal eye fields. Apart from the classic electrophysiological, neuropsychological and neuroimaging findings demonstrating frontal contributions to VWM (for recent reviews see Refs. [64–67]), recent research has indicated the importance of other frontal areas, such as the frontal eye fields during the maintenance of visuospatial information (e.g. Refs. [68–70]). However, with regard to the maintenance concern, parietal cortex is also involved during VWM maintenance [71–73], yet the influence of parietal and frontal stimulation was different selectively for the retro-cue condition. The second concern is that tDCS might have disrupted the frontal eye fields’ representation of spatial WM coded as coordinates for covert eye movements rather than through an attentional mechanism. Parsing the oculomotor and attentional roles of the frontal eye fields remains a difficult question. Indeed, the frontal eye fields are activated when people shift attention overtly or covertly [74–78]. However, there is evidence to suggest that the oculomotor and attentional functions can co-occur. For example, neurons in the frontal eye fields respond to target stimuli even when a saccade is directed in the opposite direction [79], for targets rather than distractors [80], or when the monkey is rewarded for not making a saccade to the target [68]. However, recent findings show that neurons in this region maintain spatial information during WM tasks even when it is irrelevant to the task [70], suggesting that the frontal eye fields may inevitably maintain spatial coordinates of stimuli. Finally, there is electrophysiological evidence showing that object feature information, such as shape, in addition to spatial information, is represented in the frontal eye fields [81–83]. If we stimulated the frontal eye fields, the mechanism of VWM disruption may have been to interrupt spatial WM or to disrupt shifts of internal attention and future work will be needed to clarify this distinction.

We acknowledge that we did not record eye movements in this study. This is a concern because others have shown that eye movements redirect gaze to locations in VWM [84]. Stimulation to frontal cortex might interrupt oculomotor control centers in frontal cortex that are involved in VWM [85]. Our previous work tracking eye movements during retro-cue task performance in untrained observers revealed that eye movements could not explain the presence or the magnitude of the retro-cue benefit and furthermore, that participants made very few eye movements during the retro-cue task [26]; see also Ref. [11]. However, we cannot confirm that tDCS did not alter eye movement behavior in the present data.

Additionally, several limitations involving the directionality and specificity of tDCS effects must be noted. First, although tDCS is a rapidly advancing technique, the nature of anodal and cathodal stimulation remains only partially understood. A helpful heuristic has been to assume that anodal and cathodal tDCS respectively produce excitatory and inhibitory effects. Although the primary results from the present study are in accordance with the assumed directions of stimulation, there are a number of reports showing that this may be more true of the motor cortex than of cognitive studies (reviewed in Ref. [43]). The participant who was removed from the present analysis showed dramatic improvements in cueing benefits for both pre- and retro-cueing following cathodal stimulation. Previous research in the cognitive domain also reports conflicting evidence concerning the direction of tDCS, and effects include those involving visual Sternberg task [59], picture naming [86] and risk taking [87]. Some of our recent results [58] showed that group differences such as education level may modulate tDCS effects on WM tasks [52]. Future research in this area will continue to clarify the underlying factors characterizing the effect of tDCS to different cortical regions. For example, we suspect that there may be important strategic differences that are associated with variability in neural recruitment.

Furthermore, although tDCS lacks the ability to target narrowly defined cortical regions it has the benefit of safety and a fully blind sham condition. Due to the brain’s size, shape, and vagaries of current flow it is difficult to precisely determine what areas of cortex are being stimulated. New advances in cortical modeling are improving our understanding of the stimulation spread through the cortex [88–90]. Future research in this area will help clarify the effect of tDCS on cortical populations, which is not entirely intuitive. Due to poor specificity of stimulation, our study focused on broad cortical areas, such as PPC and PFC that were identified as being involved in internal attentional processes by previous fMRI research [6]. Future research combining tDCS, modeling and neuroimaging will clarify how tDCS is affecting the underlying cortical tissue and subsequently modulating attentional processing. Finally, our use of a within subjects design, should allay concerns that the tDCS effects discussed here are the result of between subjects differences.

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References


