

Moving Beyond Attentional Biases: Shifting the Interhemispheric Balance between Left and Right Posterior Parietal Cortex Modulates Attentional Control Processes

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Abstract

■ The concept of interhemispheric competition has been very influential in attention research, and the occurrence of biased attention due to an imbalance in posterior parietal cortex (PPC) is well documented. In this context, the vast majority of studies have assessed attentional performance with tasks that did not include an explicit experimental manipulation of attention, and, as a consequence, it remains largely unknown how these findings relate to core attentional constructs such as endogenous and exogenous control and spatial orienting and reorienting. We here addressed this open question by creating an imbalance between left and right PPC with transcranial direct

current stimulation, resulting in right-hemispheric dominance, and assessed performance on three experimental paradigms that isolate distinct attentional processes. The comparison between active and sham transcranial direct current stimulations revealed a highly informative pattern of results with differential effects across tasks. Our results demonstrate the functional necessity of PPC for endogenous and exogenous attentional control and, importantly, link the concept of interhemispheric competition to core attentional processes, thus moving beyond the notion of biased attention after noninvasive brain stimulation over PPC. ■

INTRODUCTION

Attentional control refers to our ability to focus on those aspects of incoming sensory information that are most relevant to us. Shifts of attention can be initiated endogenously to exert voluntary (top-down) control over sensory processing, thus directly contributing to goal-directed behavior, or they can be triggered exogenously by salient or unexpected events (bottom-up) that require immediate evaluation, thus forcing a more automatic reallocation of attention (Corbetta & Shulman, 2002; Kastner & Ungerleider, 2000; Desimone & Duncan, 1995). These attentional control processes are classically investigated with spatial orienting paradigms (Chica, Martín-Arévalo, Botta, & Lupiáñez, 2014; Posner, 1980; Posner, Snyder, & Davidson, 1980), and neuroimaging studies have linked them to two independent but interacting frontoparietal networks with distinct functional roles (Corbetta & Shulman, 2002). The dorsal attention network (DAN) is directly involved in shifts and maintenance of attention and is thus required for both endogenous and exogenous control of attention, whereas the ventral attention network (VAN) acts as a circuit breaker of the DAN in case of unexpected (re)orienting and

is therefore mainly required for exogenous control of attention.

Next to the identification of brain networks underlying attentional control, hemispheric asymmetries within these networks have been extensively investigated, and current functional-anatomical models of attentional control put great emphasis on the lateralization of particular functions in the DAN and VAN (for a recent review, see Duecker & Sack, 2015). Among the most influential ideas has been the concept of interhemispheric competition by mutual inhibition, dating back to early work by Kinsbourne in patients with spatial hemineglect (Kinsbourne, 1977). After a lesion in one hemisphere, these patients fail to attend, explore, and act upon the contralesional side of space. Interestingly, a second lesion in the opposite hemisphere can reduce these attention deficits, commonly referred to as the Sprague effect (Sprague, 1966). On the basis of these observations, it has been proposed that subregions of the DAN, in particular, bilateral posterior parietal cortex (PPC), bias attention toward the contralateral hemifield and, importantly, inhibit each other and maintain a balance between hemispheres under normal conditions. Within this framework, attentional performance critically depends on the interaction between hemispheres, and the occurrence of an interhemispheric imbalance, for example, after stroke, leads to attention deficits because

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of strongly biased attention toward one hemifield. In line with this reasoning, interventions using noninvasive brain stimulation (NIBS) in patients with stroke are currently being explored that aim at restoring the balance between hemispheres by disrupting the hemisphere that is not directly affected by a lesion (Hesse, Sparing, & Fink, 2011; Cazzoli, Müri, Hess, & Nyffeler, 2010; Fierro, Brighina, & Bisiach, 2006).

The application of NIBS over PPC in healthy volunteers induces subtle attention deficits that resemble those observed in patients with spatial hemineglect (Duecker & Sack, 2015). At present, the most popular NIBS techniques are TMS (Hallett, 2007) and transcranial direct current stimulation (tDCS; Paulus, 2011); both modulate cortical excitability by applying either a strong magnetic field or weak electric currents to the brain, respectively. Differential effects of these methods are currently debated, but TMS has arguably stronger effects as it is capable of evoking action potentials, thus leading to pronounced local and remote effects, whereas tDCS rather modulates the local resting potential. Yet, both techniques have been successfully applied over attention networks and affect performance on attention tasks. For example, Hilgetag, Théoret, and Pascual-Leone (2001) observed in a pioneering study that inhibitory TMS over PPC in one hemisphere led to decreased target detection in the contralateral hemifield but also increased target detection in the ipsilateral hemifield. This pattern of results is highly informative as it is consistent with the idea that TMS can create an interhemispheric imbalance that enhances performance in one hemifield at the expense of impaired performance in the opposite hemifield. Similarly, Dambeck et al. (2006) observed intact target detection when left and right PPC were simultaneously disrupted with TMS, again emphasizing that the balance between hemispheres is essential for intact attentional selection, analogous to the Sprague effect mentioned above. Critically for the present purpose, these and many other studies have employed behavioral paradigms that were designed to reveal biases of attention (e.g., simple detection and line bisection tasks), similar to neuropsychological tests of attention commonly used in patients and in line with the central role of attentional biases in Kinsbourne's model. Although obviously being very informative, these behavioral paradigms, which typically do not include an explicit experimental manipulation of attention, provide a very limited view on attentional control. In fact, they fail to shed light on core attentional constructs such as endogenous and exogenous control and spatial orienting and reorienting and are therefore somewhat disjoint from a large body of mostly neuroimaging work that has focused on spatial orienting paradigms to understand the functional organization of attention networks. Of course, there are a few NIBS studies already that have investigated some of these constructs, generally demonstrating the functional relevance of PPC for attentional control. However, hemifield-specific effects were commonly not addressed, and most implementations of

spatial orienting paradigms did not allow separating orienting from reorienting (Xu et al., 2016; Capotosto, Corbetta, Romani, & Babiloni, 2012; Du, Chen, & Zhou, 2012; Moos, Vossel, Weidner, Sparing, & Fink, 2012; Heinen et al., 2011; Capotosto, Babiloni, Romani, & Corbetta, 2009; Thut, Nietzel, & Pascual-Leone, 2005; Chambers, Payne, Stokes, & Mattingley, 2004). Both limitations are particularly relevant here, because (i) attentional biases are generally hemifield specific and (ii) it is a vital prerequisite for investigating attentional control processes to design behavioral tasks that can isolate them. To conclude, it remains largely unknown how fundamental attentional control processes relate to the concept of interhemispheric competition.

Here, we set out to investigate the effects of a NIBS-induced interhemispheric imbalance on core aspects of attentional control. To this end, we created an imbalance between left and right PPC using tDCS. Specifically, we employed a stimulation protocol that has previously been shown to increase cortical excitability in the right hemisphere and, at the same time, decrease cortical excitability in the left hemisphere, thus leading to right-hemispheric dominance (Paulus, 2011). We hypothesized that this tDCS-induced imbalance would lead to impaired attention shifts toward the right hemifield and enhanced, or at least intact, attention shifts toward the left hemifield. Moreover, we speculated that the modulation of brain activity by tDCS would mostly affect attentional control processes mediated directly by PPC, whereas general perceptual processes that depend more on sensory areas might be unaffected. During active and sham stimulations, we assessed performance in three experimental paradigms that isolate distinct attentional processes: first, an endogenous orienting paradigm that required voluntary attention shifts; second, an exogenous orienting paradigm that triggered automatic attention shifts; and third, a detection task that measured perceptual sensitivity and attentional selection in the context of competition between visual stimuli. Collectively, these tasks provide a more nuanced perspective on the functional role of PPC in attentional control and provide a comprehensive overview of the consequences of an experimentally induced interhemispheric imbalance within PPC, thus moving beyond attentional biases.

METHODS

Participants

Twenty-four volunteers (12 women, mean age = 22.8 years, age range = 19–31 years) from the Maastricht University community participated in this study in return for monetary compensation or course credits. All were right-handed, had normal or corrected-to-normal vision, and had no history of neurological or psychiatric illness. Participants were screened for tDCS experimentation safety at the beginning of each experimental session. Written informed consent was obtained before participation, and the study was

approved by the ethics committee of the Faculty of Psychology and Neuroscience at Maastricht University. The research question and hypotheses remained unknown to the participants until the end of the experiment.

Stimuli and Tasks

To assess the behavioral consequences of creating an interhemispheric imbalance in PPC with tDCS, we used three experimental paradigms that isolate distinct aspects of attentional control. Our test battery was composed of an endogenous orienting task, an exogenous orienting task, and a detection task that did not involve an experimental manipulation of attention. These tasks were designed to be as similar as possible while still tapping into different attentional processes, so that behavioral differences between them could be attributed to the differential involvement of those attentional processes.

In the endogenous orienting paradigm (Figure 1), participants performed an orientation discrimination task with central symbolic cues prompting voluntary covert shifts of attention to the cued location. A fixation dot was continuously presented at the center of the screen, and cues consisted of two arrowheads flanking the fixation dot. They pointed to the left ($< \bullet <$) or right ($> \bullet >$), so-called directional cues, or in opposite directions ($< \bullet >$), so-called neutral cues. Gabor patches served as stimuli (spatial frequency = 1.5 cycles per degree, envelope standard deviation = 0.75° , Michelson contrast = 60%, tilted 45° to the left or right) and were

presented at 7° eccentricity either left or right of the fixation dot. Participants were instructed to indicate the orientation of the stimulus (tilted to the left or right) by pressing the NUM1 or NUM2 key on a standard keyboard as fast as possible with the right index or middle finger, respectively.

In the exogenous orienting paradigm (Figure 1), participants performed the same orientation discrimination task as above but with peripheral cues triggering automatic covert shifts of attention to the cued location. Cues consisted of either four small dots surrounding a potential stimulus location (directional cues) or a luminance change of the background color of the screen (neutral cues). We chose this particular type of neutral cue because it has an alerting effect similar to directional cues but is completely free of any spatial component unlike, for example, bilateral peripheral cues or a central cue.

For both orienting paradigms, the combination of three cues (left, right, neutral) and two stimulus locations (left, right) resulted in six experimental conditions. Directional cues gave rise to valid and invalid trials dependent on whether the cued location coincided with the stimulus location. Neutral trials served as baseline condition matching valid and invalid trials in terms of perceptual processing and behavioral responses but lacking attentional components related to directional cues. On the behavioral level, RTs on valid trials are typically faster compared with those on neutral trials (attentional benefits), and RTs on invalid trials are typically slower compared with those on neutral trials (attentional costs). Conceptually, attentional benefits and attentional costs are commonly interpreted as reflecting two attentional processes, namely, orienting of attention and reorienting of attention, respectively.

Endogenous and exogenous orienting paradigms have much in common, but there are important differences in their implementation (Chica et al., 2014). As described above, different kinds of cues are required to elicit voluntary and automatic shifts of attention. Endogenous cues are typically symbolic and should accurately predict the location of the upcoming stimulus in most trials so that it is behaviorally beneficial to perform a voluntary shift of attention. In contrast, exogenous cues are presented in the periphery and do not need to be predictive as they trigger automatic shifts of attention. Following this rationale, we used endogenous cues with 80% validity and exogenous cues with 50% validity. Moreover, endogenous and exogenous cues operate on different timescales with automatic shifts of attention occurring much faster than voluntary shifts of attention, thus requiring a different timing of stimulus presentation (see Figure 1 for exact timing information).

In the detection task (Figure 1), participants were required to detect low-contrast stimuli presented on the left, right, or both sides of the fixation dot. As above, Gabor patches served as stimuli (spatial frequency = 1.5 cycles per degree, envelope standard deviation = 0.75° ,

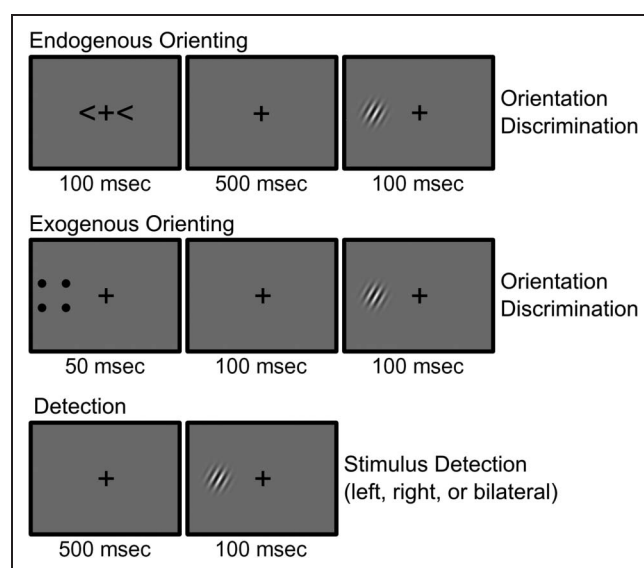


Figure 1. The sequence and timing of events for one possible trial are shown for each experimental task. Central symbolic cues prompted voluntary shifts of attention in the endogenous orienting task. Peripheral cues triggered automatic shifts of attention in the exogenous task. Stimuli are presented without an experimental manipulation of attention in the detection task. A detailed description of all experimental conditions is given in the main text.

random orientation) and were presented at 14° eccentricity. Participants were instructed to indicate the position of the stimulus (left, bilateral, or right) by pressing the NUM1, NUM2, or NUM3 key on a standard keyboard with the right index finger, middle finger, or ring finger, respectively, and to withhold their response in case they did not perceive a stimulus at all. For each of the three conditions independently, the contrast of the stimuli was adaptively changed on a trial-by-trial basis using the QUEST staircase algorithm (Watson & Pelli, 1983), as implemented in the Psychophysics Toolbox extension (Brainard, 1997) for MATLAB (The MathWorks, Inc., Natick, MA). We supplied the following parameters: prior mean was based on a short calibration procedure (see below), prior standard deviation = 1, beta = 3.5, gamma = 0.01, delta = 0.01, and aim performance = 0.5 (50% detection rate). The next contrast value was requested with *QuestQuantile*, and we obtained final detection threshold estimates with *QuestMean*.

For all tasks, stimuli were presented on a gamma-corrected Iiyama ProLite monitor at 57-cm viewing distance. The video mode was 1920 × 1080 at 60 Hz, and background luminance was 100 cd/m². The Presentation software package (NeuroBehavioural Systems, Albany, CA) was used to control stimulus presentation and recording of behavioral responses, interfacing with MATLAB for running QUEST functions.

Procedure and Design

We used a full within-participant design so that all participants received active and sham tDCS while performing all three tasks. Both tDCS sessions were identical except for the stimulation condition (active or sham), and the order of sessions was counterbalanced across participants. At the beginning of each session, participants first practiced the three tasks with corrective feedback to get accustomed to the timing of events and the required responses. We then made all preparations for the application of tDCS, including determining the stimulation sites (P3 and P4), attaching the electrodes, and checking the impedance. Subsequently, participants were comfortably seated in a chair with the head supported by a chin rest and remained in this position until the end of the experiment. After calibration of the eye tracker, the stimulation was started, and participants performed the three tasks, lasting between 35 and 40 min, depending on the duration of the breaks between tasks. Once all tasks were completed, the stimulation was turned off. The order of tasks was counterbalanced across participants but was kept the same for each participant across the two sessions.

In the endogenous orienting paradigm, participants completed four blocks, each consisting of 84 trials presented in randomized order. Including short breaks between blocks, the overall duration of this task never exceeded 20 min. The proportion of valid, invalid, and neutral trials in each experimental block was 4:1:2, result-

ing in 192 valid trials, 48 invalid trials, and 96 neutral trials, thus 336 trials per tDCS session in total. At the beginning of each block, four additional warm-up trials were included that were not considered in the analysis.

In the exogenous orienting paradigm, participants completed two blocks, each consisting of 108 trials presented in randomized order. Including short breaks between blocks, the overall duration of this task never exceeded 10 min. In each experimental block, valid, invalid, and neutral trials occurred equally often, resulting in 72 trials per condition and thus 216 trials in total per tDCS session. At the beginning of each block, four additional warm-up trials were included that were not considered in the analysis.

In the detection task, participants initially performed a short calibration procedure to obtain a first estimate of the individual detection threshold, which was used as a prior for the Bayesian staircase procedure. During this calibration, bilateral stimuli were presented on the screen, matching the positions used during the experimental task, and participants adjusted the contrast level of the stimuli until they could barely see them. At the beginning of the experimental task, two warm-up trials with high-contrast stimuli were included for each condition (left, right, and bilateral) that were very easy to detect and not part of the staircase procedure. Then, participants completed three randomly interleaved staircases (left, right, bilateral) with 40 trials each. The overall duration of this task never exceeded 10 min.

Transcranial Direct Current Stimulation

We applied tDCS over PPC of both hemispheres to induce an interhemispheric imbalance while participants performed the three tasks. Using the international 10–20 electrode placement system, the anode was positioned over P4, presumably increasing cortical excitability in the right hemisphere, whereas the cathode was positioned over P3, presumably decreasing cortical excitability in the left hemisphere. This electrode montage was chosen to maximize the excitability difference between left and right PPC.

A DC stimulator (neuroConn, Ilmenau, Germany) was used with 5 × 5 cm rubber electrodes that were attached to the head with conductive gel (Ten20 conductive paste). Impedance was checked in the beginning of the session and was kept below 20 kΩ. We generally aimed to set the stimulation intensity to 2 mA but reduced it to 1.5 mA in three participants because they reported uncomfortable sensations on the head. In all cases, this intensity adjustment was made in the first session, and the intensity in the second session was changed accordingly. To avoid strong sensations due to the sudden onset or offset of the current, the intensity was ramped over a period of 10 sec at the beginning and end of the stimulation. As a control condition, sham stimulation was applied in one of the two sessions. The overall procedure

was identical to the active tDCS sessions, but the stimulation intensity was first ramped up but then immediately ramped down. This mimicked the skin sensations accompanying active stimulation and ensured that active and sham sessions were perceived as similar as possible.

Eye Movement Control

We performed video-based monocular eye tracking at 1000 Hz with the Eyelink1000 system (SR Research, Mississauga, Ontario, Canada). The standard nine-point calibration and validation procedure was used with the head supported by a chin rest. Saccades and eye blinks were automatically detected by the eye tracker software, and this information was later used for post hoc trial exclusion. For both orienting paradigms, we removed all trials that were contaminated by saccades (exceeding 2° of visual angle) or eye blinks. The critical time window ranged from 100 msec before appearance of the cue until stimulus onset. This ensured that behavioral effects were not confounded by breaks of central fixation during the cue–stimulus interval and that participants indeed performed covert shifts of spatial attention.

Data Analysis

We first inspected individual performance in sessions with sham stimulation to detect extreme outliers in the absence of possible tDCS effects. For each of the three tasks, the data sets of two participants were clearly conspicuous, strongly deviating from the group data, and were therefore excluded from further analyses. Reasons for exclusion were a strong reversal of cueing effects in two participants, accuracies around chance level in the orienting paradigm for two participants, and extremely high detection thresholds for one stimulus location in two participants. Because of partial overlap, these exclusions reduced the sample size to 19 participants for analyses involving all tasks collectively and to 20 participants for analyses involving the orienting tasks.

For the endogenous and exogenous orienting paradigms, all trials contaminated by eye blinks or eye movements were discarded (see above for details). In addition, trials were excluded from analysis in case of incorrect responses, misses, anticipatory responses, or very slow responses. For each condition, trials were identified as outliers if the RT deviated by more than 3 *SDs* from the mean. After application of these exclusion criteria, 84.2% and 89.6% of all trials remained for further analysis for the endogenous and exogenous orienting paradigms, respectively. More specifically, we computed median RTs for each condition, with an average of 19 trials per smallest cell (invalid trials) for the endogenous task and an average of at least 30 trials per smallest cell for the exogenous orienting task.

For the detection task, detection threshold estimates were obtained per condition per participant from the

QUEST staircase algorithm (*QuestMean* MATLAB function). Moreover, we extracted the type of errors that participants made when bilateral stimuli were presented. In such cases, participants failed to perceive both stimuli and thus reported to see nothing at all or, more interestingly, reported seeing only a unilateral stimulus (left or right). These mistakes may reveal a bias when two weak stimuli compete for attentional selection.

We then performed two main analyses to statistically evaluate the effects of tDCS on task performance. In our first analysis, we focused on conditions related to attentional bias (neutral trials of the orienting tasks and the data from the visual detection task). Because of differences in outcome measures, this required standardization of the data (*z* scoring) before submitting the data to a repeated-measures ANOVA with Task (endogenous, exogenous, unilateral detection, bilateral detection), Stimulation (active, sham), and Hemifield (left, right) as within-participant factors. Please note that the factor Hemifield refers to the actual location of the stimulus only for the orienting tasks and unilateral detection thresholds but not the unilateral detection rates on bilateral trials. In the latter case, this factor refers to where a stimulus was perceived in case one of two stimuli was missed. As a consequence, higher values on this outcome measure represent better performance, as opposed to the other ones, and we thus had to invert the sign of the data to make the data compatible with the other tasks.

In our second analysis, we focused on conditions related to attentional orienting and reorienting. All conditions from the orienting tasks were analyzed by submitting median RTs to a repeated-measures ANOVA with Task (endogenous, exogenous), Stimulation (active, sham), Cue (valid, neutral, invalid), and Hemifield (left, right) as within-participant factors. Subsequent analyses focused on difference scores between valid, invalid, and neutral trials to obtain attentional benefits (neutral – valid), attentional costs (invalid – neutral), and the validity effect (invalid – valid). All analyses were performed using IBM SPSS Statistics Version 21 (IBM, Armonk, NY). For all repeated-measures ANOVAs, we report the multivariate test statistics (Pillai's trace), and we used the customary significance level of $p < .05$. Follow-up analyses were conducted with paired *t* tests using Bonferroni correction unless stated otherwise.

RESULTS

We investigated the effects of creating an interhemispheric imbalance in PPC (favoring the right hemisphere) on three spatial attention tasks for which the main analyses are reported below. The structure of the Results section follows from our ambition to move beyond attentional biases and to highlight the importance of separating attentional control processes, including attentional bias, attentional orienting, and attentional reorienting. For didactic reasons, we thus first focus on experimental

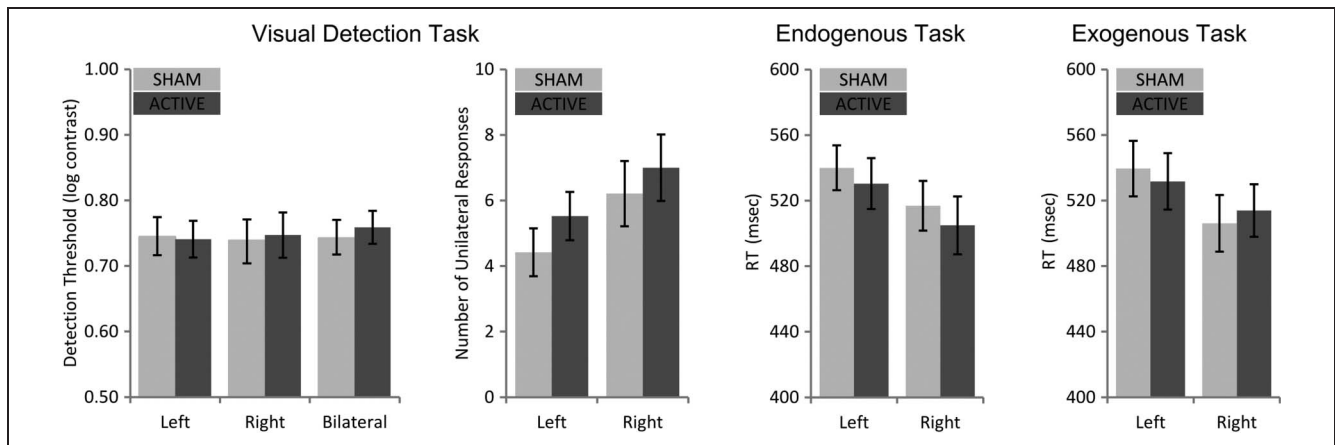


Figure 2. Results for all outcome measures related to the concept of attentional bias. No effect of brain stimulation was found on detection thresholds, error rates in the context of competing visual stimuli, and RTs on neutral trials for both orienting tasks. Please note that the original analysis was performed on z scores, but data have been plotted using the original data. Error bars depict standard errors.

conditions related to the general concept of attentional bias and then present more fine-grained analyses enabled by the use of spatial cues in the orienting tasks. Looking ahead, no brain stimulation effects were observed for all outcome measures pertaining to attentional bias, but a highly informative pattern of results was observed when decomposing orienting tasks assessing attentional orienting processes. Finally, please note that the description of statistical analyses for the orienting tasks is restricted to RT data as no significant effects of stimulation were found on accuracy.

Attentional Bias

We first assessed task performance in all experimental conditions that relate to attentional/perceptual biases in the absence of an experimental manipulation of attention (Figure 2). Specifically, this analysis included all conditions with neutral cues from the orienting tasks and the detection thresholds on unilateral trials as well as the response pattern on bilateral trials from the visual detection task (for details, see Data Analysis section). After the necessary standardization of the data, a repeated-measures ANOVA on z scores with Task (endogenous, exogenous, unilateral detection, bilateral detection), Stimulation (active, sham), and Hemifield (left, right) as within-participant factors was performed. To begin with, there was a significant main effect of Hemifield ($F(1, 18) = 5.021, p < .05$), due to generally better performance in the right hemifield, but also a trend toward a significant interaction between Task and Hemifield ($F(3, 16) = 2.696, p = .08$), presumably reflecting the absence of this right hemifield advantage for unilateral detection thresholds. Critically, however, there was no main effect of Stimulation ($F(1, 18) = 0.543, p > .40$), and all interactions involving this factor failed to reach significance (all $ps > .50$). Taken together, this negative finding suggests that tDCS did not affect perceptual processes or

attentional selection in the absence of an experimental manipulation of attention. Moreover, it also shows that general aspects of task performance remained intact. However, as will be shown below, this does not imply that attentional orienting processes were unaffected as well.

Orienting Tasks: Sham Stimulation

We then further analyzed the data of the orienting tasks, initially focusing only on task performance under baseline conditions (sham stimulation), to establish that central symbolic cues and peripheral cues triggered the expected shifts of spatial attention (Figure 3). A repeated-measures ANOVA on median RTs with Task (endogenous, exogenous), Cue (valid, neutral, invalid), and Hemifield

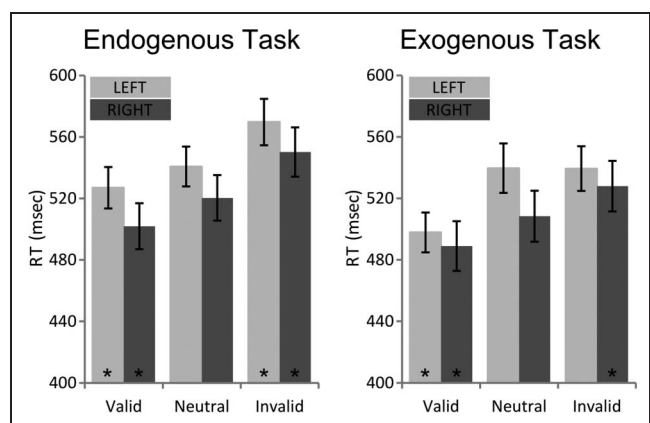


Figure 3. Performance at baseline (sham stimulation) for both orienting tasks. For the endogenous task, the expected pattern of RT differences was found, with significant benefits and costs in both hemifields. For the exogenous task, the pattern of RTs was not fully consistent with our expectations as there was no significant difference between neutral and invalid trials in the left hemifield. Conditions marked with an asterisk (*) are significantly different from the corresponding neutral condition at an alpha level of .05, and error bars depict standard errors.

Table 1. RTs (in Milliseconds) and *SEM* (in Parentheses) for Each Experimental Condition of the Endogenous Orienting Task

<i>tDCS</i>	<i>Left Hemifield</i>		<i>Right Hemifield</i>	
	<i>Sham</i>	<i>Active</i>	<i>Sham</i>	<i>Active</i>
Valid	527 (13.5)	517 (15.7)	502 (14.2)	505 (15.5)
Neutral	541 (13.0)	531 (14.7)	520 (14.8)	507 (16.8)
Invalid	570 (15.1)	560 (15.3)	550 (16.0)	546 (20.5)

(left, right) as within-participant factors revealed significant main effects of Task ($F(1, 19) = 5.065, p < .05$), Cue ($F(2, 18) = 39.778, p < .001$), and Hemifield ($F(1, 19) = 9.710, p < .01$) as well as a significant interaction between Task, Cue, and Hemifield ($F(2, 18) = 4.258, p < .05$). The remaining interactions between Task and Cue ($F(2, 18) = 2.773, p > .05$), Task and Hemifield ($F(1, 19) = 0.501, p > .40$), and Cue and Hemifield ($F(2, 18) = 1.688, p > .20$) all failed to reach significance and were not further explored.

The main effects mentioned above reflect rather general aspects of task performance that hold true even in the presence of the higher-order interaction. First, RTs were faster in the endogenous orienting task than in the exogenous orienting task. Second, RTs were faster in the right hemifield than in the left hemifield (Simon effect; Simon & Rudell, 1967). Third, we observed the typical pattern of RTs across cueing conditions, with valid cues leading to better performance compared with neutral cues (attentional benefits) and invalid cues leading to worse performance compared with neutral cues (attentional costs, but see below for more details).

The three-way interaction between Task, Cue, and Hemifield was slightly surprising as we expected that both orienting tasks elicited similar cueing effects irrespective of hemifield. Yet, follow-up analyses revealed that only the results of the endogenous orienting task fully matched our expectations, whereas the results of the exogenous task showed some deviations.

For the endogenous task, a repeated-measures ANOVA on median RTs with Cue (valid, neutral, invalid) and Hemifield (left, right) as within-participant factors revealed significant main effects of Cue ($F(2, 18) = 20.122, p < .001$) and Hemifield ($F(1, 19) = 7.187, p < .05$) but no interaction between them ($F(2, 18) = 0.282, p > .70$). Critically, there were pronounced attentional benefits (valid vs. neutral, $t(19) = 4.278, p < .001$, planned) and costs (invalid vs. neutral, $t(19) = 4.950, p < .001$, planned). These attentional effects were observed in both hemifields and were similar in magnitude (benefits: $M = 16.1$ msec, $SEM = 3.8$; costs: $M = 29.2$ msec, $SEM = 5.9$) to results from previous studies (e.g., Duecker, Formisano, Sack, 2013).

For the exogenous task, we performed the same analysis as above, again revealing significant main effects of

Cue ($F(2, 18) = 42.776, p < .001$) and Hemifield ($F(1, 19) = 9.065, p < .01$), but also a significant interaction between them ($F(2, 18) = 5.762, p < .05$). Most important for the present issue, attentional benefits were clearly present in the right hemifield ($t(19) = 2.279, p < .05$) and left hemifield ($t(19) = 5.124, p < .001$, planned), but attentional costs were only present in the right hemifield ($t(19) = 4.204, p < .001$, planned), but not the left hemifield ($t(19) = 0.280, p > .90$, planned). The absence of attentional costs in one hemifield was most likely due to problems with the neutral condition, so the decomposition of the exogenous orienting task into benefits and costs may not be fully justified under such conditions (see Discussion). On the upside, the difference in RTs between valid and invalid cues, commonly referred to as the validity effect, was not compromised by this issue, allowing us to investigate this combined measure of attentional orienting and reorienting without problems.

To conclude, we established that both orienting tasks led to shifts of attention under baseline conditions, and we extracted three outcome measures for each of them (validity effect, benefits, and costs). We could thus examine the consequences of creating an interhemispheric imbalance by tDCS on these distinct attentional processes.

Orienting Tasks: Full Model

We first tested a full statistical model including all conditions (also see Tables 1 and 2) by submitting median RTs to a repeated-measures ANOVA with Task (endogenous, exogenous), Stimulation (active, sham), Cue (valid, neutral, invalid), and Hemifield (left, right) as within-participant factors. Critically, this revealed a significant four-way interaction ($F(2, 18) = 3.642, p < .05$), providing a formal basis for assessing tDCS-induced changes for each orienting task separately. Moreover, we immediately reduced the factor Cue to difference scores between the three cueing conditions, so that the validity effect, attentional benefits, and attentional costs became our primary outcome measures.

Orienting Tasks: Validity Effect

The validity effect reflects attentional orienting and reorienting, thus combining multiple processes into one

Table 2. RTs (in Milliseconds) and *SEM* (in Parentheses) for Each Experimental Condition of the Exogenous Orienting Task

<i>tDCS</i>	<i>Left Hemifield</i>		<i>Right Hemifield</i>	
	<i>Sham</i>	<i>Active</i>	<i>Sham</i>	<i>Active</i>
Valid	498 (13.0)	500 (13.7)	489 (16.1)	487 (13.4)
Neutral	540 (16.1)	530 (16.5)	508 (16.6)	513 (15.2)
Invalid	539 (14.5)	525 (14.1)	528 (16.5)	515 (14.5)

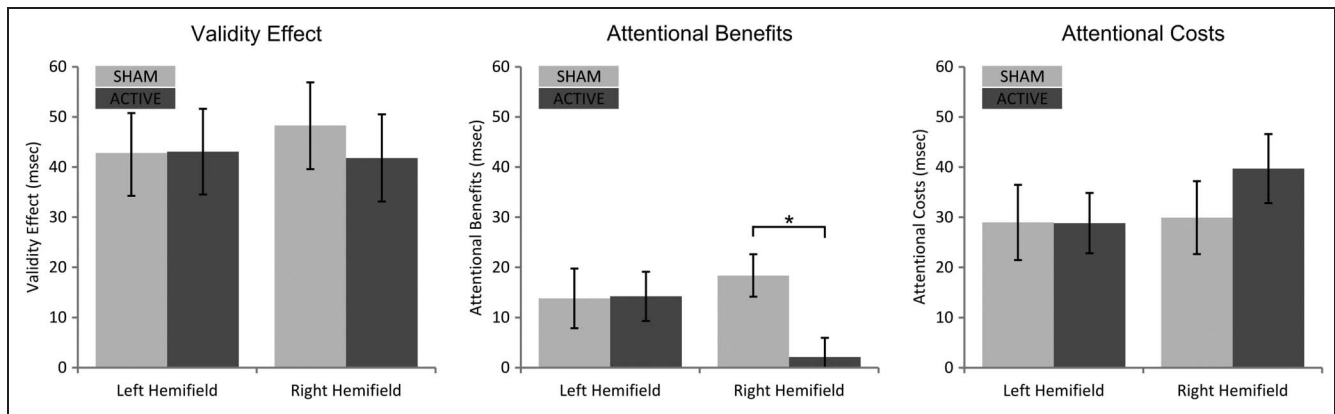


Figure 4. Main results of the endogenous orienting task. No effect of brain stimulation was found on the validity effect (left). Attentional benefits in the right hemifield were affected by active tDCS (center). No effect on attentional costs was observed (right). Differences marked with an asterisk (*) are statistically significant at an alpha level of .05, and error bars depict standard errors.

outcome measure. Although not optimal, this is common practice when a neutral condition is altogether absent or when it failed to produce the expected results, as is the case here for the exogenous orienting task. Beginning with the endogenous orienting task (Figure 4), a repeated-measures ANOVA on the validity effect was performed with Stimulation (active, sham) and Hemifield (left, right) as within-participant factors. No significant main effects of Stimulation ($F(1, 19) = 0.210, p > .60$) and Hemifield ($F(1, 19) = 0.093, p > .70$) were found, and there was no significant interaction between these factors ($F(1, 19) = 0.146, p > .70$). In contrast, the same analysis for the exogenous orienting task (Figure 5) revealed a significant main effect of Stimulation ($F(1, 19) = 4.843, p < .05$) but no significant main effect of Hemifield ($F(1, 19) = 0.005, p > .90$) and no interaction between Stimulation and Hemifield ($F(1, 19) = 0.224, p > .60$). This clearly shows that tDCS reduced the effectiveness of peripheral cues in modulating task performance. Moreover, the absence of an effect on the endogenous orienting task could be taken as an indication that attentional processes contingent on central

symbolic cues remained intact. Yet, the analysis of attentional benefits and costs below will convincingly show that this is not the case.

Orienting Tasks: Benefits and Costs

The segregation of the data into attentional benefits and costs was the final step of our analysis, reflecting orienting and reorienting, respectively. Beginning with the endogenous orienting task again (Figure 4), a repeated-measures ANOVA on attentional benefits was performed with Stimulation (active, sham) and Hemifield (left, right) as within-participant factors. This revealed a significant two-way interaction between Stimulation and Hemifield ($F(1, 19) = 4.997, p < .05$). Because of this interaction, the influence of the factors Stimulation ($F(1, 19) = 8.140, p < .05$) and Hemifield ($F(1, 19) = 0.495, p > .40$) was not further explored. Follow-up paired t tests revealed a strong reduction of attentional benefits in the right hemifield by active tDCS compared with sham stimulation ($t(19) = 3.698, p < .005$). In contrast, no difference

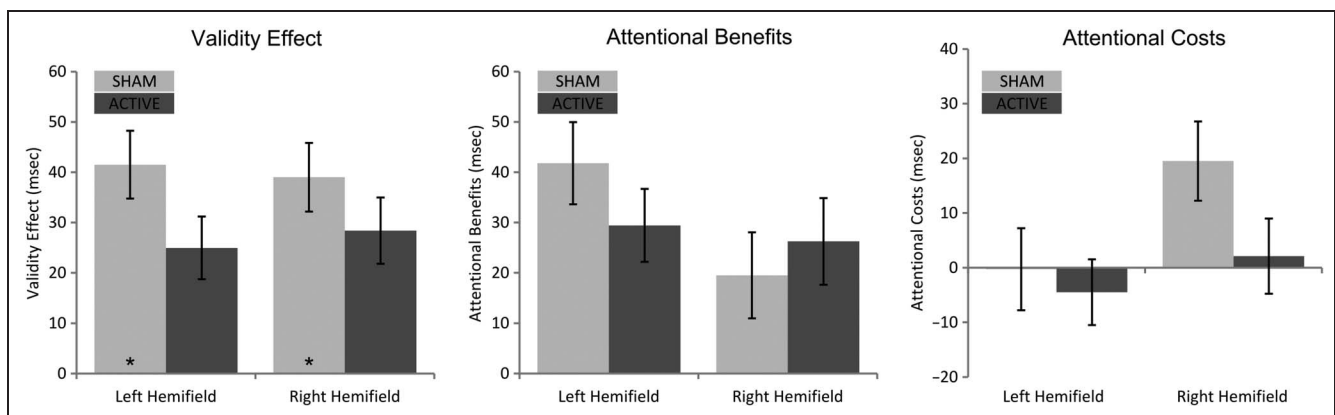


Figure 5. Main results of the exogenous orienting task. There was a main effect of brain stimulation on the validity effect, indicated by the two asterisks (left). No significant effects were found on attentional benefits (center) and attentional costs (right). Differences marked with an asterisk (*) are statistically significant at an alpha level of .05, and error bars depict standard errors.

between active and sham stimulations was found in the left hemifield ($t(19) = 0.082, p > .90$, uncorrected). In other words, tDCS selectively impaired voluntary attention shifts to the right hemifield while leaving voluntary attention shifts to the left hemifield unchanged. We then submitted the attentional costs to a repeated-measures ANOVA with Stimulation (active, sham) and Hemifield (left, right) as within-participant factors. No significant main effects of Stimulation ($F(1, 19) = 0.410, p > .30$) and Hemifield ($F(1, 19) = 0.846, p > .30$) were found, and there was no significant interaction between these factors ($F(1, 19) = 0.500, p > .40$). The effect of tDCS on attentional benefits in the endogenous orienting task mentioned above was thus highly specific and not accompanied by changes of attentional costs.

Finally, we performed the same analysis for the exogenous orienting task (Figure 5), keeping in mind the problems with the neutral condition. A repeated-measures ANOVA on attentional benefits showed a significant main effect of Hemifield ($F(1, 19) = 6.308, p < .05$) due to more pronounced benefits in the left hemifield but failed to show a significant effect of Stimulation ($F(1, 19) = 0.192, p > .60$). The interaction between these factors was close to being significant ($F(1, 19) = 3.821, p = .07$), and for the sake of completeness, we performed a simple effects analysis. However, no significant effects of tDCS (active vs. sham) were observed in the left hemifield ($t(19) = 1.426, p > .10$, uncorrected) and right hemifield ($t(19) = 0.914, p > .30$, uncorrected). We then submitted the attentional costs to a repeated-measures ANOVA, revealing that the main effects of Stimulation ($F(1, 19) = 3.553, p = .08$) and Hemifield ($F(1, 19) = 3.370, p = .09$) were close to reaching significance, whereas the interaction between Stimulation and Hemifield was clearly not significant ($F(1, 19) = 1.303, p > .20$). As indicated above, we would like to remain very cautious with the interpretation of attentional benefits and costs in the exogenous orienting task. For that reason, the data were not further explored at this point.

DISCUSSION

The concept of interhemispheric competition by mutual inhibition has been very influential in attention research (Kinsbourne, 1977). Various studies have investigated the consequences of an imbalance between left and right PPC on attentional biases, typically using line bisection and detection tasks (Duecker & Sack, 2015). Yet, it remains largely unknown how an interhemispheric imbalance affects core attentional processes such as endogenous and exogenous control or spatial orienting and reorienting. We here addressed this open question by creating an imbalance between left and right PPC with tDCS, resulting in right-hemispheric dominance, and assessed performance on three experimental paradigms that isolate distinct attentional processes.

The comparison between active and sham tDCS revealed a highly informative and distinct pattern of results with differential effects across tasks. To begin with, no effects of brain stimulation were found for all conditions related to the concept of attentional bias, indicating that perceptual sensitivity remained unchanged and attentional selection in the context of competing visual stimuli was not biased by tDCS. In contrast, we found differential effects of brain stimulation on both orienting tasks. For the endogenous orienting task, we found a decrease of attentional benefits in the right hemifield, whereas no effect was observed in the left hemifield. For the exogenous orienting task, we found a decrease of the validity effect in both hemifields. These results will be discussed in the following sections. In general, we clearly demonstrate the functional necessity of PPC for endogenous and exogenous attentional control and, importantly, link the concept of interhemispheric competition to core attentional processes, thus moving beyond the notion of biased attention after NIBS over PPC.

Endogenous Orienting

It is widely accepted that PPC is a core node of the DAN that mediates endogenous shifts of spatial attention (Corbetta & Shulman, 2002, 2011). In the framework of interhemispheric competition, it is furthermore theorized that PPC in each hemisphere biases attention toward the contralateral hemifield (Kinsbourne, 1977). We created an imbalance between left and right PPC by decreasing cortical excitability in the left hemisphere and increasing cortical excitability in the right hemisphere. Consequently, we expected that this imbalance leads to impaired attention shifts toward the right hemifield and enhanced, or at least intact, attention shifts toward the left hemifield.

The effects of tDCS on attentional benefits reported here are consistent with this expectation, as we observed decreased benefits in the right hemifield. This clearly demonstrates that a tDCS-induced imbalance in favor of right PPC over left PPC leads to impaired attentional orienting toward the right hemifield. To the best of our knowledge, this is the first time that NIBS over PPC has been found to selectively impair endogenous orienting (when operationalized as attentional benefits). Importantly, our finding critically depended on the presence of a neutral cue condition, allowing separating attentional benefits from attentional costs. Without this neutral condition, only the validity effect could have been considered, leading to a negative result for the endogenous orienting task. As pointed out before, earlier work has often focused on attention biases in the absence of an experimental manipulation of attention. These studies have produced results that appear very similar to the findings reported here, with NIBS over PPC typically impairing detection of visual stimuli in the contralateral hemifield (Dambeck et al., 2006; Hilgetag et al., 2001). However,

it has to be emphasized that there are fundamental conceptual differences between biased attentional selection and a disruption of endogenous orienting. In fact, we did not find an effect of tDCS on neutral trials, which clearly shows that our results are highly specific and cannot be reduced to a general impairment of stimulus detection (in either hemifield).

The decrease of attentional benefits in the right hemifield was not mirrored by an increase of attentional benefits in the left hemifield. This negative result is to some extent inconsistent with the concept of interhemispheric competition by mutual inhibition. Although pioneering work by Hilgetag et al. (2001) indeed reported both a contralateral impairment and an ipsilateral enhancement after TMS over either left or right PPC, later studies have struggled to replicate this finding (Bien, Goebel, & Sack, 2012; Cazzoli, Müri, Hess, & Nyffeler, 2009; Dambeck et al., 2006; Koch, Oliveri, Torriero, & Caltagirone, 2005), although recent tDCS work has reported some enhancing effects of anodal stimulation over right PPC for targets in the left hemifield (Roy, Sparing, Fink, & Hesse, 2015). Although the reasons for this discrepancy are difficult to identify, a possible explanation for the absence of enhanced performance in the present experiment could be that we applied tDCS over both hemispheres simultaneously. As will be discussed in a later section, the effects of our bilateral tDCS montage might not simply be the sum of two unilateral tDCS conditions where excitability is changed in one hemisphere only. Moreover, all participants were recruited from the Maastricht University community, which means that they were highly educated and mostly young adults. These participants presumably performed at a very high level, and further performance increases might be difficult to achieve due to ceiling effects. This notion is supported by evidence from clinical work where similar NIBS protocols have been shown to have beneficial effects on attention in patients with spatial hemineglect (Sparing et al., 2009).

Exogenous Orienting

The DAN also mediates exogenous shifts of spatial attention, but unlike endogenous orienting, this requires interactions with the VAN as well (Corbetta & Shulman, 2002, 2011). Because of this added complexity, it is more difficult to interpret the effects of an imbalance between left and right PPC on exogenous orienting. As stated above, our implementation of neutral trials in the exogenous orienting task did not work as intended. For that reason, we refrain from interpreting the attentional benefits and attentional costs but instead focus on the validity effect, that is, the difference between valid and invalid trials. Nevertheless, we found an effect on this compound outcome measure, with the validity effect being decreased in both hemifields; that is, peripheral cues were less effective in modulating task performance irrespective of stimulus location. This pattern of results is clearly dif-

ferent from the effects on endogenous orienting and, to some extent, surprising because current theories do not propose a differential involvement of the DAN in endogenous and exogenous orienting. For that reason, we believe that an interpretation of this pattern of results must consider current ideas regarding the interactions between the DAN and VAN.

According to current functional-anatomical models of attentional control, exogenous cues activate the right-lateralized VAN, which in turn primarily interacts with the right DAN. It thus stands to reason that increasing cortical excitability in right PPC, as we did in the current experiment, strengthens the right DAN, thus making it more difficult for the ventral network to initiate stimulus-driven reorienting. Although we fully acknowledge the speculative nature of this proposition, it is consistent with decreased effectiveness of peripheral cues in both hemifields assuming that exogenous orienting always relies on ventral and dorsal regions in the right hemisphere, irrespective of hemifield.

Attentional Bias

Many studies have used NIBS over PPC to induce attentional biases using paradigms without an experimental manipulation of attention (Duecker & Sack, 2015). We included a detection task that is conceptually similar to this earlier work, obtaining detection thresholds and error rates in the context of competing visual stimuli. We did not find any effect of tDCS on these outcome measures. These null results perfectly match the absence of effects on neutral trials in both orienting tasks and thus again demonstrate that our findings are very specific to attentional orienting processes. However, this result is in clear contrast to many previous studies that reported attentional biases after PPC stimulation (Benwell, Learmonth, Miniussi, Harvey, & Thut, 2015; Filmer, Dux, & Mattingley, 2015; Bien et al., 2012; Cazzoli et al., 2009; Dambeck et al., 2006; Hilgetag et al., 2001). At present, we cannot offer a conclusive explanation for this discrepancy, but differences between stimulation techniques seem obviously important to consider. Most previous studies applied TMS, whereas here, we used tDCS to create an imbalance between left and right PPC because it allowed us to induce excitability changes in both hemispheres at the same time. Because TMS is arguably more powerful, in particular, with regard to causing remote effects in brain areas connected to the stimulation site, one could argue that perceptual biases after TMS over PPC result from top-down effects on early visual cortex, whereas tDCS seems to act more locally, and the modulation of PPC might thus have weaker effects on sensory areas. Indeed, studies combining TMS and neuroimaging have repeatedly shown that TMS over frontal and parietal nodes of the DAN can cause activity changes in visual areas (Blankenburg et al., 2010; Ruff et al., 2008, 2009). Because of its underlying principles, tDCS might be less effective in causing such effects, although some studies

have reported positive findings with tDCS as well (Benwell et al., 2015; Filmer et al., 2015). At any rate, this issue can only be addressed by a direct comparison of TMS and tDCS and can thus not be solved here.

Further Considerations

Considering the results for all three tasks collectively, we observed an informative pattern of results with clear differences across tasks. Importantly, all three tasks were performed in the same session under the same stimulation conditions in a full within-participant design. These differential effects show that distinct aspects of attentional control can be linked to the proposed mechanism of interhemispheric competition. Yet, the complex interactions within and between the DAN and VAN remain poorly understood, and in particular, the effects on the exogenous orienting task emphasize that current explanatory approaches are overly simplistic. However, we recently integrated existing NIBS work into our so-called hybrid model of attentional control (Duecker & Sack, 2015), and this study is in agreement with this general theoretical framework. Specifically, the model states that parietal nodes (but not frontal nodes) of the DAN interact via interhemispheric competition (see Endogenous Orienting section for a more detailed discussion). Yet, a critical test of this model would require a direct comparison of parietal and frontal brain stimulation.

Finally, the approach of creating an imbalance between left and right PPC by applying tDCS over both hemispheres simultaneously, that is, anodal stimulation over the right PPC and cathodal stimulation over the left PPC, was adequate for our purposes, and our results support our conceptualization of tDCS-induced right-hemispheric dominance with this montage. However, an obvious downside of this approach is that (i) the observed behavioral effects do not necessarily result from stimulation effects on both hemispheres and (ii) stimulation of both hemispheres might not simply be the sum of unilateral stimulation conditions. To disentangle these issues, it would be necessary to also assess the behavioral effects of anodal tDCS over the right PPC and cathodal tDCS over the left PPC in isolation. Although this imposes certain interpretative limits with respect to the exact origin of our effects, the principal rationale of a tDCS-induced interhemispheric imbalance still holds. Yet, discrepancies with earlier work that were pointed out above might still be attributable to such methodological differences.

Conclusions

Our results clearly demonstrate the functional relevance of PPC for endogenous and exogenous (re)orienting and, importantly, stress the relevance of functional asymmetries in attentional control. The present findings suggest that attentional orienting and reorienting rely on complex interactions within the DAN and between the DAN

and VAN, and we encourage follow-up studies to investigate these mechanisms in more detail. Interestingly, our effects on attentional control processes were not accompanied by attentional biases emphasizing the importance of investigating the role of PPC in various attentional states and carefully differentiating between them.

Acknowledgments

This work was supported by the Netherlands Organisation for Scientific Research (NWO), based on a VICI grant awarded to A. T. S. (grant number 453-15-008).

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