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Both Dorsal and Ventral Attention Network Nodes are implicated in Exogenously Driven Visuospatial Anticipation

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Abstract

Neuroimaging and transcranial magnetic stimulation (TMS) studies have implicated a dorsal fronto-parietal network in endogenous attention control and a more ventral set of areas in exogenous attention shifts. However, the extent and circumstances under which these cortical networks overlap and/or interact remain unclear. Crucially, whereas previous studies employed experimental designs that tend to confound exogenous with endogenous attentional engagement, we used a cued target discrimination paradigm that behaviourally dissociates exogenous from endogenous attention processes. Participants engaged with endogenous attention cues, while simultaneous apparent motion cues were driving exogenous attention along the motion path towards or away from the target position. To interfere with dorsal or ventral attention networks, we delivered neuronavigated double-pulse TMS over either right intraparietal sulcus (rIPS) or right temporo-parietal junction (rTPJ) towards the end of the cue target interval, and compared the effects to a sham-TMS condition. For sham-TMS, endogenous and exogenous cueing both benefitted discrimination accuracy. Target discrimination was enhanced at validly versus invalidly cued locations (endogenous cueing benefit) as well as when targets appeared in versus out of the motion path (exogenous cueing benefit), despite motion being uninformative and task-irrelevant, replicating previous findings. Interestingly, both rIPS- and rTPJ-TMS abolished attention benefits from exogenous cueing, while endogenous cueing benefits were unaffected. Our findings provide evidence against independent involvement of the dorsal and ventral attention network nodes in exogenous attention processes.

Keywords: Transcranial Magnetic Stimulation, Spatial Attention, intraparietal sulcus, temporo-parietal junction, anticipation

1. Introduction

While we explore visual scenes based on internal goals, sudden sensory events may occur and concurrently attract our attention. Neuroimaging has revealed a partially segregated large-scale dorsal and ventral fronto-parietal network playing a crucial role in the orchestration of these two processes, i.e., endogenous versus exogenous visuospatial attention deployment (reviewed by Corbetta & Shulman 2002). Dorsal fronto-parietal regions, including the intraparietal sulcus (IPS), have been predominantly associated with endogenous deployment of attention. Conversely, ventral frontal and temporo-parietal regions, including the temporo-parietal junction (TPJ), have been related to (exogenous) (re)-orienting towards task-relevant events that appear at unexpected locations (Corbetta and Shulman, 2002; Kincade et al., 2005; see also Corbetta et al., 2008). Despite substantial, functional magnetic resonance imaging (fMRI) evidence for a dichotomy between dorsal and ventral attention networks from many groups (Asplund, Todd, Snyder, & Marois, 2010; M Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Hahn, Ross, & Stein, 2006; Hu, Bu, Song, Zhen, & Liu, 2009; Natale, Marzi, & Macaluso, 2009; Shulman et al., 2003), other fMRI-studies suggest that the extent of functional dissociation may vary with task-settings, task-demands and task-dynamics (Asplund et al., 2010; Maurizio Corbetta et al., 2008; Maurizio Corbetta & Shulman, 2002; J. M. Kincade, 2005; Mayer, Dorflinger, Rao, & Seidenberg, 2004; Peelen, Heslenfeld, & Theeuwes, 2004). Additionally, transcranial magnetic stimulation (TMS) has revealed mixed results as to a functional dissociation of these networks: Although only few TMS-studies directly compared the implication of dorsal and ventral networks, there is some agreement for a functionally distinct specialisation between dorsal and ventral sub-regions in attentional processes (Chang et al., 2013; Painter, Dux, & Mattingley, 2015; Schenkluhn, Ruff, Heinen, & Chambers, 2008). Chica et al. (2011), on the other hand, found evidence against such a dissociation when directly comparing the involvement of both dorsal and ventral network nodes of the right hemisphere in a classical visuospatial cueing paradigm. They reported that both IPS and TPJ were implicated in exogenous attention, whilst IPS (but not TPJ) was associated with endogenous

control (see also Bourgeois et al., 2013). This finding is supported by fMRI-TMS and TMS-EEG studies, revealing that right IPS may coordinate both endogenous and exogenous attentional shifts (Paolo Capotosto, Babiloni, Romani, & Corbetta, 2012; Paolo Capotosto, Corbetta, Romani, & Babiloni, 2012; Heinen et al., 2011).

In terms of experimental paradigms, predictive symbolic cues are typically employed to engage endogenous attention, whilst transient and non-predictive sensory events, such as brief flashes, are used to test exogenous orienting (Petersen & Posner, 2012; Posner, 1980). Alternatively, visual flicker and apparent motion streams can exogenously drive attention (Ahrens, Veniero, Gross, Harvey, & Thut, 2015; Breska & Deouell, 2014; de Graaf et al., 2013; Rohenkohl, Coull, & Nobre, 2011). However, in the conventional design, tests for exogenous attention are typically employed in isolation, without controlling for endogenous attention (but see Berger et al., 2005; Ahrens et al., 2015). Consequently, participants may endogenously engage with the exogenous cues and adopt strategies to predict forthcoming events, by attempting to extract regularities based on the nature of events, even if this information is random and non-informative (Ahrens et al., 2015; Breska & Deouell, 2014). Indeed, it is difficult to prevent such higher-order cognitive processes from confounding exogenous capture (e.g., Folk et al. 1994; Ansorge & Heumann 2003; for review see, Ruz & Lupiáñez 2002).

Here, we sought to examine the neural substrates of exogenously driven attentional anticipation, when endogenous engagement is controlled for. We investigated to what extent there is a functional segregation (versus overlap) of the dorsal and ventral attention network nodes by combining TMS over TPJ or IPS with a visuospatial attention paradigm previously shown to behaviourally dissociate both types of attention processes (Ahrens et al., 2015). The paradigm prompts endogenous expectations by symbolic spatial cueing that predicts the upcoming target position. Simultaneously, non-predictive and task-irrelevant apparent motion cues exogenously drive anticipatory attention towards or away from the target positions. This design discourages strategic engagement with the exogenous (motion) cues, due to the incentive of engaging with the concurrent symbolic cue instead (carrying

predictive information) and the need to deploy voluntary attention to the symbolic cues by instruction. Our results reveal causal evidence for both dorsal and ventral parietal network nodes to be implicated in exogenous attention.

2. Methods

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

2.2. Participants

A total of twenty-two healthy adult volunteers (average age \pm SD: 23.9 ± 4.5 , 19 female, 3 male) participated in the experiment (based on Ahrens et al. 2015). We only recruited participants who had no previous psychiatric or neurological history, were right handed, had normal or corrected-to normal vision and had no contraindication to TMS (established with a TMS-safety questionnaire (Rossi et al. 2009)). Also prior to the experiment, all participants provided written informed consent. Ethical approval was provided by the College of Science and Engineering Ethics Committee of the University of Glasgow.

Completion of the whole experiment and an average performance level at 80% were inclusion criteria established prior to data collection and analysis (see Ahrens et al. 2015). Based on this, two participants were excluded from further testing after the first session (task-familiarization) as they experienced TMS discomfort. Three further participants had to be excluded from the statistical analysis after completion of the second session (the actual data recording session): one because of an experimenter recording error, one as more than 50% of the responses had been missed and one because of performance at chance level. Hence, a total N of 17 participants was included in the statistical analysis.

2.3. Apparatus

The experiment was presented using E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA) on a LCD monitor (ASUS ROG Swift PG278Q, ©ASUSTeK Computer Inc.) with 100Hz refresh rate and a spatial resolution of 1280 x 1024. A chin rest maintained a constant viewing distance of 35cm to the screen. A CCTV camera was used to monitor eye movements to ensure participants maintained fixation during the task (covert attention shifts). A TMS stimulator (Magstim Rapid²) in combination with a figure of 8-shaped coil (Double 70mm Alpha Coil; The Magstim Company Ltd, UK) was used for double-pulse delivery. TMS Navigation (Brainsight[®] TMS, Rogue Resolutions Ltd) was employed to determine stimulation locations, to guide the placement and orientation of the TMS coil and to allow online tracking for minimizing deviations from the optimal site of stimulation during the experiment.

2.4. Stimuli and Task

A visuospatial attention paradigm using simultaneously presented endogenous symbolic cueing and exogenous apparent motion cueing was implemented (adapted from de Graaf et al. 2013 and Ahrens et al. 2015). A matrix of 5x9 circles (gray placeholders) together with a central fixation cross (white) was presented at all times on a black background (Figure 1, A). The diameter of the placeholders was 1.2cm, with a vertical distance of 3cm and a horizontal distance of 3.4cm. In order to manipulate endogenous attention shifts, central symbolic cues consisting of arrows were presented on top of the fixation cross (Figure 1, B). These arrows were predictive as to the upcoming target location (i.e., 75% cue-validity at the left or right target location). Participants were asked to covertly shift attention towards the indicated target position, while keeping their fixation at the central fixation cross. Simultaneously to endogenous cueing, and in order to manipulate exogenous attention, five placeholders from the row below the fixation cross flashed briefly (for 30ms) in succession, starting with the rightmost circle and ending at the central circle directly underneath the fixation cross, or starting with the leftmost circle

and ending at the same central circle. These motion stimuli flashed rhythmically at 4Hz, giving the impression of apparent motion (i.e., at a stimulus-onset-asynchrony (SOA) of 250ms). This was followed by a target presented for 10ms (1 refresh rate) in the adjacent placeholders, either in or out of the motion path (i.e., to the left or right of the last apparent motion stimuli). Importantly, target appearance in the motion path (congruent) or out of the path (incongruent) was equally probable (i.e., the motion path was uninformative as to the upcoming target locations). The instructions given to the participants explicitly declared these exogenous motion cues as task-irrelevant.

The target consisted of a '+' or 'x' and participants were asked to discriminate the target as accurately and rapidly as possible by button press with their right index and middle finger (keys: 1 for 'x', 2 for '+'; counterbalanced across participants). The engagement of endogenous and exogenous attention was indexed by the advantage of target discrimination at the symbolically cued vs. the un-cued position and at the motion-cued vs. the uncued position respectively. As previously shown, this experimental design results in perceptual benefits from both endogenous and exogenous cueing. These cueing benefits are independent however, hence dissociating endogenous control from exogenous attentional processes and vice versa (Ahrens et al. 2015; also see for similar designs: Berger et al. 2005 employing classic static exogenous cues and Breska and Deouell 2014 employing centrally presented flicker). For the timeline of events within a trial, see Figure 1B.

In order to interfere with ongoing attention deployment, double-pulse TMS (100ms inter-pulse-interval (IPI)) was delivered in a late stage of the cue-target interval between the last motion stimuli and target onset (specifically at -175ms and -75ms prior to target presentation). Double-pulse TMS over visual and parietal cortex disrupts performance in visual and attention tasks (Grasso et al., 2018; Müri et al., 2002; Pitcher, Goldhaber, Duchaine, Walsh, & Kanwisher, 2012) with inhibitory effects at an IPI of 100ms, as previously shown for double-pulse TMS (Müri et al., 2002), triple-pulse TMS (e.g. Sack et al. 2005) or other short TMS trains > 3 pulses (e.g. Romei et al. 2010). TMS was

delivered over either the right intraparietal sulcus (rIPS), right temporo-parietal junction (rTPJ) or as sham (block design, counterbalanced across participants; see paragraph 2.6 on TMS procedure for details).

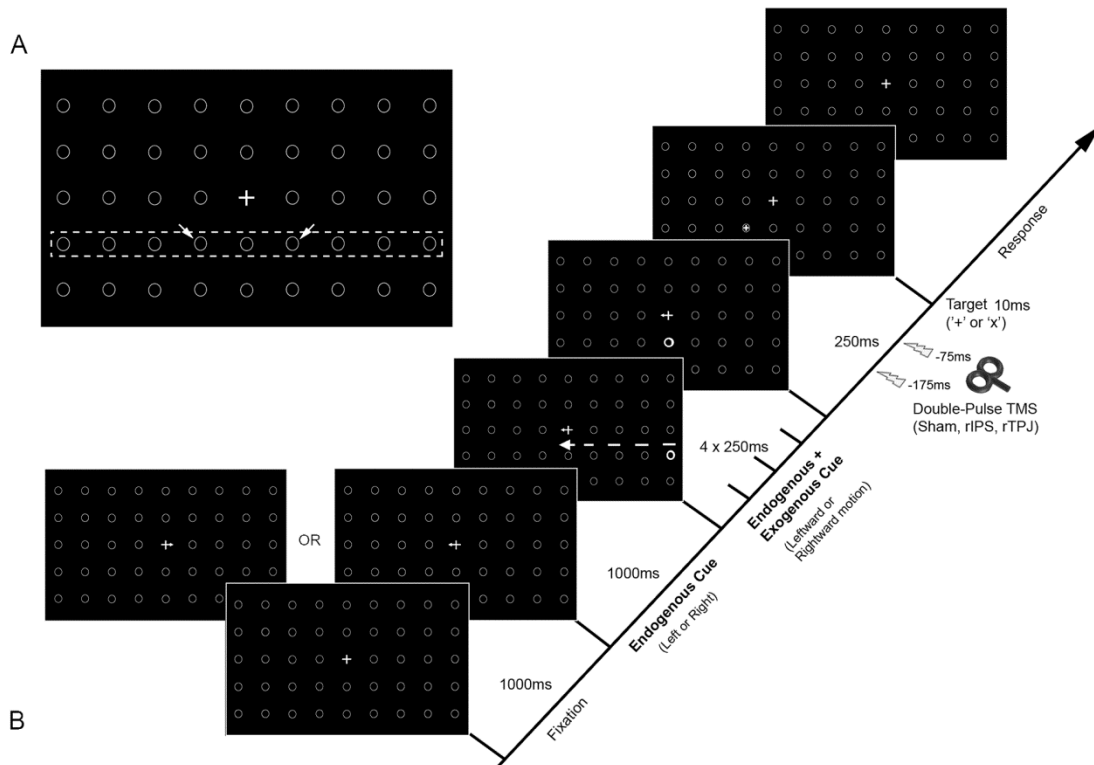


Figure 1: Schematic representation of the experimental design. (A) Fixation cross and placeholders. Dashed rectangle and arrows drawn for illustrative purpose. Arrows indicate the two possible target locations in the left and right visual field. Dashed rectangle indicates the row of placeholders where the apparent motion stimuli were presented. (B) Example trial sequence (note that the timeline is not drawn to proportion). Trials started with a fixation cross (1000ms), followed by an endogenous cue (left or right symbolic arrow; 75% predictive) indicating the probable target location (here left cue). Exogenous cueing consisted of apparent motion stimuli (leftward or rightward). Five adjacent stimuli briefly flashed successively from gray to white at a rate of 4Hz (4 inter-flash intervals of 250ms) giving the impression of apparent motion (50:50 non-predictive as to upcoming target location; here dashed arrow drawn for illustration purpose showing leftward motion). After the last motion stimulus and before target presentation, double-pulse TMS was delivered (100ms inter-pulse interval) over either right intraparietal sulcus (rIPS), right temporo-parietal-junction (TPJ) or sham. The target consisted of a '+' or 'x' and participants were asked to discriminate the target as accurately and rapidly as possible by button press.

2.5. Experimental procedure

Participants visited the laboratory on two separate days for two sessions. Session one served for training of the task and familiarization with the experiment. Participants performed two short training blocks (covert attention shifts with target discrimination). The first training block consisted of endogenous left and right cue trials only, during which participants were instructed to deploy attention covertly and to discriminate targets at both cued and uncued positions (20 trials). In the second block, exogenous motion cues were added but participants were informed that these stimuli were task-irrelevant (32 trials). These training blocks ensured participants understood the concept of the task (covert attention shifts without eye movements). In addition, participants were familiarized with TMS (namely the TMS sensation and click noise). This session lasted for approximately 40 minutes. The second session consisted of the actual TMS experiment. First, visual targets were individually adjusted to near-threshold levels (80% discrimination rate) via modulation of the luminance contrast with the background, to avoid ceiling or flooring. This included testing nine different luminance contrasts that ranged from non-discriminable from the black background (dark grey target) to maximum luminance (white target). A total of 144 trials with 16 trials per contrast were shuffled and presented in randomized order. The display and stimuli used for this titration procedure were identical to the actual experimental display (see paragraph 2.4 on Stimuli and Task) to ensure the same perceptual conditions for both the titration and experimental blocks. The titration was followed by the determination of the individual TMS resting motor thresholds, and co-registration of the participant's head position with the anatomical MRI scan for TMS neuronavigation (see paragraph 2.6 below for details on TMS procedure). The experiment consisted of a total of 480 trials [20 trials x 2 endogenous cues (left and right arrows) x 2 exogenous cues (leftward and rightward motion) x 2 target locations (left and right visual field) x 3 TMS locations (rIPS-TMS, rTPJ-TMS and sham-TMS)]. Active-TMS (i.e., rIPS-TMS and rTPJ-TMS) and sham-TMS trials were distributed across 3 experimental blocks (160 trials per block) with breaks every 80 trials to avoid fatigue (i.e. approximately every 6 minutes). The order of all three stimulation conditions (i.e., the

rIPS-TMS, rTPJ-TMS and sham-TMS blocks) were randomized and counterbalanced across participants. All trials within each block were randomized and presented in an intermixed order. The second session lasted for approximately 1.5 hours. The perceptual measures of interest were discrimination accuracy, reaction time and inverse efficiency (IE) indicating potential trade-offs between the two measures.

2.6. TMS-intensity, -site, and neuronavigation procedure

Resting motor threshold (rMT) was determined over the right motor cortex by visual observation of the resting muscle twitch to individually adjust TMS-intensity during the task. Specifically, and after identifying a reliable muscle twitch, the individual rMT was determined as the minimum single-pulse stimulator intensity that induced a visually detectable resting muscle twitch in five out of ten stimulations. The resulting individual TMS intensity was kept constant across all stimulation sites (set to 100% individual rMT; average rMT \pm SD: 53.3% \pm 7.0 of maximum stimulator output).

Individual anatomical T1 weighted MRI scans were acquired at the Centre for Cognitive Neuroimaging (CCNi) (University of Glasgow) using a 3T MR scanner (Magnetom Trio Siemens, Erlangen, German) and a magnetization-prepared rapid gradient echo sequence (MPRAGE) (Parameters: voxel size = 1 x 1 x 1mm; TR = 1900ms, TE = 2.52ms; inversion time (IT) = 900ms; slice thickness = 1mm; FoV = 256mm; matrix size = 256 x 265; excitation angle = 9°; 192 axial slices). The TMS target sites were based on Talairach coordinates (group averages) obtained from previous fMRI-guided TMS studies that showed an effect on orienting of visuospatial attention: rIPS (x = 16; y = -63; z = 47) and rTPJ (x = -51; y = -51; z = 26) (fMRI study: Kincade et al. 2005; fMRI-guided TMS studies: Chica et al. 2011; Bourgeois et al. 2013) (Figure 2). Brainsight[®] TMS Navigation was used for TMS coil positioning. rIPS and rTPJ coordinates were first projected on each individual reconstructed 3D anatomical MRI scan (i.e., the stimulation target coordinates were de-normalized for rIPS and rTPJ respectively

and projected into native space for each individual anatomical brain scan). The anatomical MRI scans were then co-registered with the respective participant's head to allow for precise positioning and online guiding of the TMS coil. For active-TMS, the coil was held tangentially to the skull and the coil was oriented such that (i) the coil-centre was overlaying the rIPS or rTPJ target site in each individual anatomical MRI scan respectively, and (ii) that the TMS-induced current was running perpendicular to the stimulated gyrus (Raffin, Pellegrino, Di Lazzaro, Thielscher, & Roman, 2015; Thielscher, Opitz, & Windhoff, 2011). For sham-TMS, the coil was turned perpendicular to the surface of the participant's head (between rIPS and rTPJ target locations), such that the current was discharged away from the cortex (Figure 2 shows one example participant).

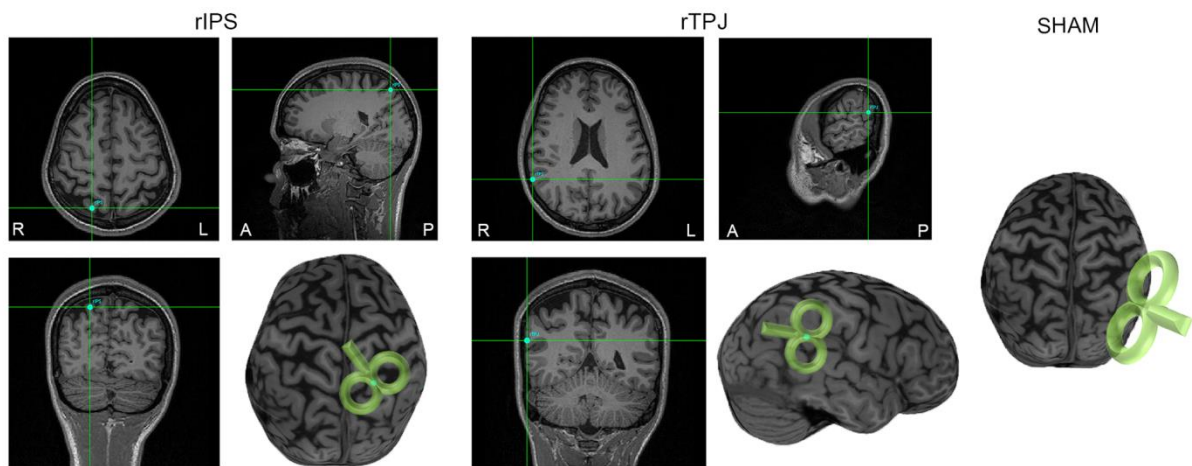


Figure 2: Example of TMS-targeting for one participant illustrating the TMS coil positioning and orientation relative to the right intraparietal cortex (rIPS), right temporo-parietal junction (rTPJ) (see cross-hairs) and for sham stimulation (R=Right; L=Left; A=Anterior; P=Posterior). The TMS coil orientation was determined based on the individual anatomical MRI scan such that the coil handle was always oriented perpendicular to the stimulated gyrus of the respective target sites (rIPS and rTPJ). Slices represent sagittal-, transverse- and coronal- views (T1 structural MRI scans) as well as 3D surface reconstructions of the brain.

Since the aim was to disrupt ongoing attentional anticipatory effects and not low-level motion perception, we assessed the possibility of having stimulated the nearby motion sensitive region hMT+/V5, as opposed to the respective target sites (i.e. rIPS and rTPJ). To this end, we measured the distance between hMT+/V5 and rIPS and rTPJ. The measurements were performed manually on each individual 3D reconstructed anatomical

brain surface using Brainsight®. The average hMT+/V5 talarach coordinates were obtained from previous studies that mapped motion sensitive regions via a functional motion localizer (talarach coordinates: $x = 44$ $y = -68$ $z = -1$; Duecker et al. 2014; in line with Frost and Goebel 2012). On average, the distance from hMT+/V5 to the target sites was 3.49cm (± 0.33 SD) for rTPJ and 6.65cm (± 0.45 SD) for rIPS. Thus, a direct stimulation of hMT+/V5 can be excluded.

2.7. Statistical analysis

2.7.1. Frequentist statistics

First, we established that the expected attentional effects from the endogenous and exogenous cueing were present for accuracy data during sham-TMS and that these effects were independent (no interaction). This directly replicates our previous findings from a study using the same task design but no TMS (Ahrens et al. 2015). To this end, we ran a within-subject (repeated-measure) analysis of variance (ANOVAs) on the sham-TMS data with the factors Endogenous Cueing Direction (Left vs. Right) x Exogenous Cueing Direction (Leftward vs. Rightward) and Target Location (Left vs. Right Visual Field) on discrimination accuracy (performance accuracy). With this ANOVA, the attentional effects from cueing are represented in the 2-way interactions of Cueing Direction (Left vs. Right) x Target Location (Left or Right Visual Field). The presence of these 'baseline' cueing effects (during sham TMS) is the premise for testing any effects of TMS on target processing.

Second, to test for TMS effects, discrimination accuracy was subjected to a full within-subject (repeated-measure) ANOVAs with the factors Stimulation site (sham- vs. rIPS- vs. rTPJ-TMS), Endogenous Cueing Direction (Left vs. Right), Exogenous Cueing Direction (Leftward vs. Rightward motion) and Target Location (Left vs. Right visual field) (Sphericity assumption met, Mauchly's test all $p > 0.2$).

Main effects and interactions of interest were followed up with simple tests (all t-tests). Since our expected cueing effects were derived from the previous behavioural results obtained in Ahrens et al. 2015, we planned one-sided simple tests for comparing effects of validly vs. invalidly cueing on target processing per visual field (left or right).

2.7.2. Bayesian statistics

Additionally, given the prior evidence from our previous study, we ran a Bayesian factor analysis (BF-analysis) (according to Verhagen and Wagenmakers 2014) on accuracy data to provide additional information on how strong the evidence was for the alternative (H_1) or the null hypothesis (H_0). This was tested separately for sham- and active-TMS.

First, in accordance with the Bayesian replication test, we examined whether we could replicate in our sham data the cueing effects observed in our original experiment (Ahrens et al., 2015). To test this, the original experiment was re-analysed by conducting a Bayesian paired-samples T-test (two-sided, default Cauchy prior distribution centred at zero, width=0.36) for each main effect of interest. The resulting posterior distributions served as the informed prior distributions to establish whether sham-TMS resulted in a successful replication (i.e., H_0 : no replication/cueing effects absent; H_1 : replication/cueing effects present).

Second, we used the resulting replication posterior distributions (i.e., the accumulated evidence provided by the data from the original experiment and the sham-TMS data), as an informed prior to test whether the cueing effects were similar or different from these priors during active-TMS. Specifically, if active-TMS has a detrimental effect on performance, we expected evidence for H_0 (cueing effects absent). We report Bayes factors (BF) reflecting the probability of the data given H_r relative to H_0 (i.e., $BF < 1/3$ strongly favour H_0 ; $BF > 3$ strongly favour H_r ; $1/3 < BF < 3$ indicates data insensitivity) (Dienes & Mclatchie, 2017; Verhagen & Wagenmakers, 2014). The ANOVA and Bayes

factor analyses were performed using JASP (JASP Team 2018; Version 0.8.2; open source; <https://jasp-stats.org/>).

2.7.3. *Analysed Variables*

All analyses were run on performance accuracy first. We also ran the above ANOVAs for inverse efficiency (IE) scores (IE = mean RT/proportion correct; Townsend & Ashby, 1983) and reaction times (RT). The IE score and RT results are briefly outlined in the results section (for a detailed description see supplemental material).

3. Results

We sought to firstly replicate our previously published findings (Ahrens et al. 2015) in the absence of TMS-interference, i.e. in the sham-TMS condition. We expected to replicate the influence of both endogenous and exogenous cueing on target processing, and that these effects are independent, resulting in a behavioural dissociation of endogenous from exogenous attentional processes and vice versa. Secondly, we sought to identify shared or dissociated neural substrates by evaluating the effects of active-TMS over rIPS and rTPJ on exogenous versus endogenous cueing benefits respectively. More specifically, we hypothesised that if the two attention systems are distinct, exogenous cueing effects should be abolished during active rTPJ-TMS (as compared to active rIPS-TMS), whereas endogenous cueing effects should be abolished during active rIPS-TMS (as compared to active rTPJ-TMS). Alternatively, exogenous attention may be abolished during both active rTPJ- and rIPS-TMS, supporting common, overlapping substrates.

3.1. *A replication of endogenous and exogenous cueing effects on discrimination accuracy during sham-TMS*

For *Endogenous cueing*, the expected attentional cueing benefit at cued versus uncued positions was revealed by a significant 2-way interaction of Endogenous Cueing Direction (left vs. right cue) x Target Location (left vs. right visual field) for performance

accuracy ($F(1,16)=8.30$, $p=0.01$, $\eta^2=0.34$). Follow up-simple tests showed a higher performance accuracy for validly as compared to invalidly cued target locations for both the left and right visual field (LVF: $t(16) = 2.49$, $p = 0.012$, Cohen's $d = 0.6$, RVF: $t(16) = -2.18$, $p = 0.022$, Cohen's $d = -0.53$). This was supported by the BF-analysis, showing substantial evidence for a replication (H_1 : cueing effects present) of our prior data (Ahrens et al. 2015) during sham-TMS for both visual fields ($B_{10} > 5$; Table 1, Endogenous Cueing).

For *Exogenous cueing*, the expected attentional cueing benefit at cued versus uncued positions was revealed by a significant 2-way interaction of Exogenous Cueing Directing (leftward vs. rightward motion) x Target Location (left vs. right visual field) for performance accuracy ($F(1,16)=5.95$, $p=0.027$, $\eta^2=0.27$). Again, follow up-simple tests showed a higher performance accuracy for validly as compared to invalidly cued target locations for both the left and right visual field (LVF: $t(16)= -1.75$, $p = 0.05$, Cohen's $d = -0.42$, RVF: $t(16) = 1.65$, $p = 0.059$, Cohen's $d = 0.40$). In analogy with the above, the BF-analysis showed substantial evidence for a replication for both visual fields ($BF_{r0} > 3$; Exogenous Cueing; see sham-TMS, Table 1).

Importantly, and also in line with our previous findings (Ahrens et al. 2015) we found that the attention effects of endogenous and exogenous cueing benefits were not interacting. As expected, this was shown in the absent 3-way interaction of Endogenous Cueing Direction x Exogenous Cueing Direction x Target Location for performance accuracy ($F(1,16)=0.23$, $p=0.64$, $\eta^2=0.014$). This indicates that the design effectively isolates endogenous from exogenous shifts of attention, since both cue-types simultaneously (but independently) benefit performance, even when the endogenous and exogenous cue direction is contradictive (i.e. directing attention to opposite visual fields) (see also Berger et al. 2005). Thus, any benefits resulting from exogenous cueing can be interpreted to reflect automatically driven processes, with no contamination of deployment of endogenous processes in response to the exogenous cues (Ahrens et al., 2015; Breska & Deouell, 2014). By extension, this also suggests that participants followed the instructions and engaged with

the task (endogenous shifts of attention), whilst ignoring the exogenous cueing (as by design exogenous cues were task-irrelevant and non-predictive).

3.2. Endogenous cueing effects on target discrimination: no changes with Active-TMS over rIPS or rTPJ.

To test for stimulation effects, performance accuracy was subjected to a full within-subject (repeated-measure) ANOVAs with the factors Stimulation site (sham- vs. rIPS- vs. rTPJ-TMS), Endogenous Cueing Direction (Left vs. Right), Exogenous Cueing Direction (Leftward vs. Rightward motion) and Target Location (Left vs. Right visual field). *Endogenous cueing* led to an overall benefit for discriminating targets at cued versus uncued positions, as revealed by a significant 2-way interaction of Endogenous Cueing Direction (left vs. right cue) x Target Location (left vs. right visual field) ($F(1,16) = 10.90, p = 0.005, \eta p^2 = 0.41$). There was a higher accuracy for discriminating validly as compared to invalidly cued target locations for both the left visual field ($t(16) = 2.66, p = 0.009, \text{Cohen's } d = 0.64$), and the right visual field ($t(16) = -.56, p = 0.011, \text{Cohen's } d = -.62$). Notably, this endogenous cueing benefit was not differentially affected by Sham-, rIPS- or rTPJ-TMS (no 3-way interaction of Stimulation Site x Endogenous Cueing Direction x Target Location: $F(2,32) = 0.16, p = 0.85, \eta p^2 = 0.01$; see Figure 3A).

These findings were supported by the BF-analysis, showing substantial evidence for a replication (H_1 : cueing effects present) for both the left visual field and right visual field effects ($BF_{10} > 9$) across sham- and active-TMS, i.e. averaging across conditions did not annihilate any VF effect (see Endogenous Cueing; Overall average in Table 1). When considering each stimulation condition separately (i.e., sham-, rIPS-, rTPJ-TMS), there was evidence for a replication of the cueing effects (H_1) in both visual fields during sham-TMS ($BF_{10} > 5$). During active-TMS (i.e., rIPS-TMS and rTPJ-TMS respectively), there was evidence for H_1 in the right visual field ($BF_{10} > 3$), while the data were insensitive for

either hypothesis in the left visual field ($BF_{10} < 1$ but $> 1/3$) (Endogenous cueing; see active-TMS in Table 1).

Thus, taken together, the results from the classical ANOVA analysis and evidence revealed by the BF-analysis indicate that the attention effects from endogenous cueing did not show a statistically different pattern across the three stimulation conditions. This speaks in favour of maintained/unaffected endogenous attention across sham- and active-TMS.

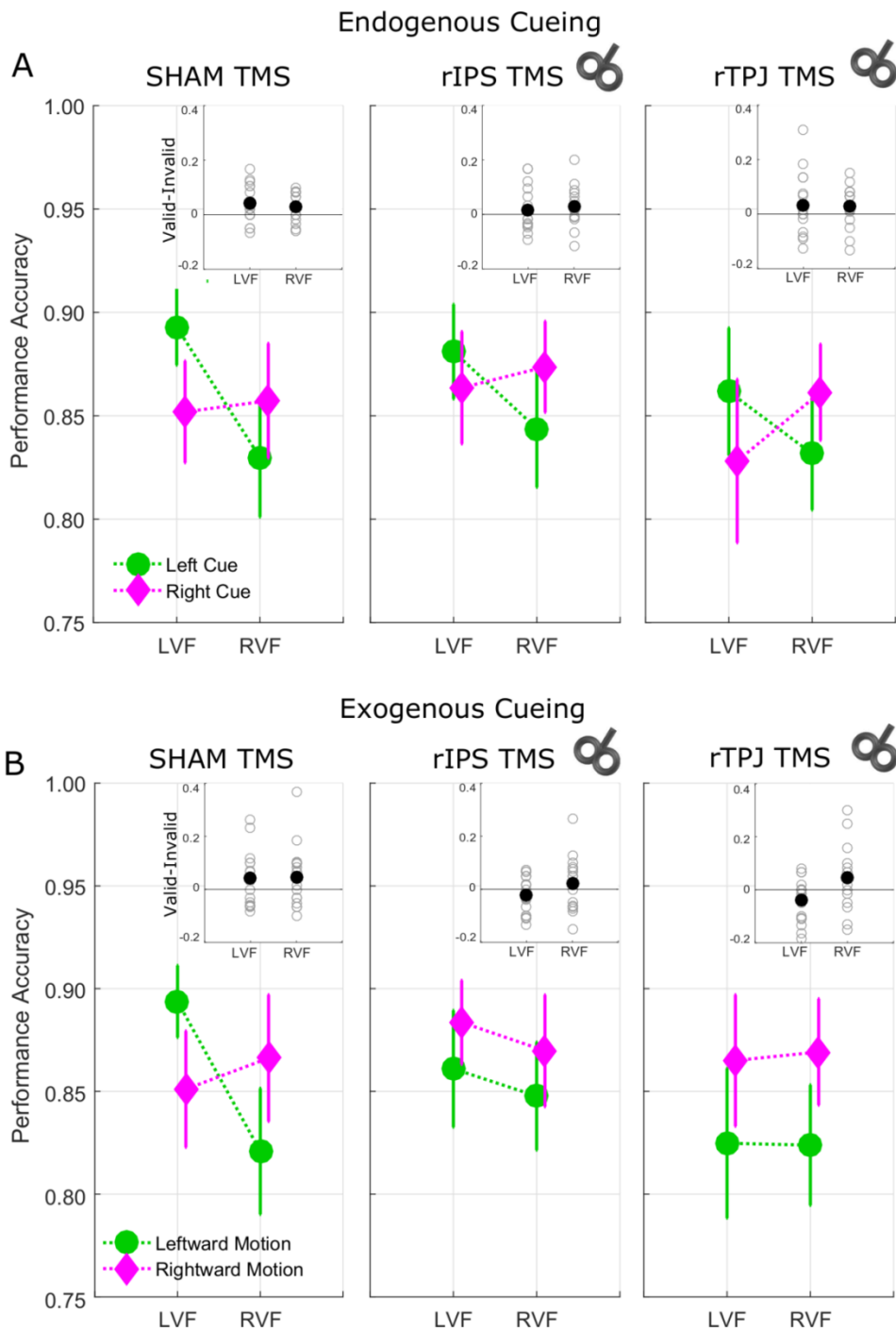


Figure 3: Performance accuracy as a function of cueing type (endogenous vs. exogenous) and TMS conditions (sham vs. rIPS vs. rTPJ). (A) Performance accuracy during the three TMS conditions (sham, rIPS, rTPJ) as a function of endogenous cueing direction (left or right cue) and target location in the left visual field (LVF) and right visual fields (RVF) illustrating endogenous cueing benefits at validly cued versus invalidly cued positions. These benefits were independent of the TMS conditions (sham, rIPS, rTPJ) i.e., there was no 3-way interaction. (B) Identical to (A) but for exogenous cueing. Exogenous cueing benefits depended on the TMS stimulation condition (3-way interaction). The error bars indicate the standard error of the means (\pm SE). Subplots show pairwise differences per individual participants (gray circles) and the grand average (solid black circles) for the contrasts of interest (i.e., valid minus invalidly cued targets in the LVF and RVF respectively). Positive values indicate a cueing benefit (higher accuracy at cued position) and negative values a cost (lower accuracy).

3.3. Exogenous cueing effects on target discrimination are abolished with Active-TMS over rIPS and rTPJ

Unlike for endogenous cueing, we found active-TMS to affect the attention effects from exogenous cueing (Figure 3B). Exogenous attention cueing effects depended on TMS conditions (marginally significant 3-way interaction of Stimulation Site x Exogenous Cueing Direction x Target Location: $F(2,32) = 3.10$, $p = 0.059$, $\eta p^2 = 0.16$) (Figure 3B), while no overall exogenous attention effect was observed (no overall Exogenous Cueing Direction x Target Location interaction: $F(1,16) = 1.33$, $p = 0.27$, $\eta p^2 = 0.077$). Following-up the 3-way interaction, attention effects from exogenous cueing were present during sham-TMS, as already established (significant 2-way interaction of Exogenous Cueing Direction x Target Location for Sham TMS data, see paragraph 3.1 for results). In contrast, during active-TMS, the 2-way interactions of Exogenous Cueing Direction x Target Location were absent for both rIPS-TMS ($F(1,16) < 0.001$, $p = 0.98$, $\eta p^2 < 0.0001$) and rTPJ-TMS ($F(1,16) = 0.016$, $p = 0.90$, $\eta p^2 = 0.001$). This shows that exogenous cueing benefits were only present during sham-TMS, but abolished during both active-TMS conditions. It should be noted, that endogenous and exogenous cueing effects remained independent also during active-TMS (no 4-way interaction of Stimulation x Endogenous Cueing Direction x Exogenous Cueing Direction x Target Location ($F(2,32) = 0.26$, $p = 0.77$, $\eta p^2 = 0.02$)).

Interestingly, the absence of the 2-way interactions during active-TMS appeared to be driven primarily by an impaired modulation of exogenous cueing in/towards the left visual field. As corroborated by follow-up simple tests, this translated in a lack of cueing benefits for LVF-targets appearing in the motion trajectory (i.e., leftward motion) as compared to out of the motion trajectory (i.e. rightward motion) (see Figure 3B, rightmost two panels: relative leftward motion cueing disadvantage for LVF targets), which was observed for both rIPS-TMS (LVF: $t(16) = 1.31$, $p = 0.89$, Cohen's $d = 0.3$) and rTPJ-TMS (LVF: $t(16) = 2.05$, $p = 0.97$, Cohen's $d = 0.4$). Also note that the effect sizes for LVF

discrimination were reversed by active-TMS (Cohen's $d > 0.3$) as compared to sham-TMS (Cohen's $d = -0.42$). In contrast, cueing benefits during active-TMS appeared qualitatively unchanged in the RVF (rTPJ-TMS, RVF: $t(16) = 1.59$, $p = 0.07$, Cohen's $d = 0.36$; rIPS-TMS, RVF: $t(16) = 0.92$, $p = 0.19$, Cohen's $d = 0.22$) as compared to sham-TMS (Cohen's $d = 0.4$).

Importantly, the BF-analysis further supported this finding by revealing evidence for H_0 (i.e., evidence against exogenous cueing effects) during both active-TMS conditions in the LVF ($BF_{10} < 1/3$) but not the RVF ($BF_{10} > 1$ but < 3) (Exogenous Cueing; see active-TMS, Table 1). In fact, this lack of cueing benefit in the LVF was 8.3 times more likely during IPS-TMS and 14.29 more likely during TPJ-TMS under H_0 than under H_1 . While the Bayes factor for the RVF effect showed data insensitivity when broken down by active-TMS conditions, the evidence against cueing effects during active-TMS in the LVF supports our finding that the modulation of exogenous cueing towards/in the left visual field was impaired by rIPS- and rTPJ-TMS.

Hence, taken together, the main conclusion of the classic ANOVA analysis and the evidence revealed by the BF-analysis indicate that active-TMS affected performance by abolishing exogenous attention.

Table 1: Bayes Factor Replication Test for Endogenous and Exogenous cueing

	Endogenous Cueing				Exogenous Cueing			
	δ Value		$BF_{1 0}$		δ Value		$BF_{1 0}$	
	LVF	RVF	LVF	RVF	LVF	RVF	LVF	RVF
Original Exp. (Ahrens et al. 2015)	.65	-.34	-	-	-.30	.38	-	-
Replication*								
Overall average	.65	-.43	16.15	9.25	-.21	.42	.31	4.53
Sham-TMS	.64	-.40	11.88	5.91	-.33	.40	3.44	3.07
Active-TMS**								
rIPS-TMS	.51	-.41	.45	3.65	-.22	.36	.12	1.10
rTPJ-TMS	.55	-.40	.98	3.26	-.20	.40	.07	2.93

Note: Bayes Factor (BF) > 3 indicates strong evidence in favour of the alternative hypothesis (**marked in bold**), BF < 1/3 can be considered as strong evidence in favour of the null hypothesis (**also marked in bold**), whereas 1/3 < BF < 3 indicates data insensitivity in support for neither hypothesis (*marked in italic*) (Verhagen & Wagenmakers 2014; Dienes 2014). Original experiment: Bayesian paired-samples T-Test (two-sided test, default Cauchy prior centred at 0, width=0.36). *Replication of Overall average (behaviour collapsed across stimulation conditions) and Sham-TMS: Bayesian paired-samples T-Test (one-sided test; posterior distributions obtained from the Original Exp. served as informed priors). **Active-TMS: Bayesian paired-samples T-Test (one-sided test; replication posterior distributions obtained from the Original Exp. and Sham-TMS served as informed priors). δ -Value = effect size; BF_{10} = Bayes Factor; LVF = Left Visual Field; RVF = Right Visual Field; rIPS = right inferior-parietal sulcus; rTPJ = right temporo-parietal junction.

3.4. Analysis of Inverse efficiency (IE) and reaction times (RTs)

Additional analyses of the IE scores and RT in the endogenous cueing conditions revealed the same pattern of results as for the accuracy data, i.e. endogenous attentional cueing effects were present during Sham TMS and unaffected by any of the active TMS conditions (see Supplemental Figures 1A and 2A and Supplemental material for statistics).

Analysis of IE scores in the exogenous cueing condition also revealed the same pattern of results as for the accuracy data: Exogenous attentional effects were present during Sham TMS but abolished during active TMS (see Supplemental Figure 1B and Supplemental material for statistics). However; exogenous cueing effects were absent for RT, even during sham (see Supplemental Figure 2B and Supplemental Material for statistics). Therefore, the RT data were excluded from further analysis exploring the active-TMS effects, since any evaluation of TMS effects on attention deployment requires these effects to be present in the first place.

Overall, the results of these additional analyses confirm the findings on accuracy and rule out influences of accuracy/RT trade-offs.

4. Discussion

The present results provide evidence for the implication of a wider network covering dorsal (rIPS) and ventral (rTPJ) regions in exogenously driven attentional anticipation, speaking against independence and suggesting a functional overlap. Additionally, we found no evidence for TMS affecting endogenous attention. Unlike previous TMS studies (Paolo Capotosto, Corbetta, et al., 2012; Chica et al., 2011), we tested both types of attention

simultaneously which allowed us to exclude, by experimental design, the confound of a potential endogenous engagement during exogenous processes. Hence, the implication of the dorsal (rIPS) system in exogenous anticipation was unlikely due to unintentional co-activation of endogenous substrates. Furthermore, our results revealed that active-TMS over rIPS and rTPJ induced left lateralised effects, in line with previous findings showing contralateral impairment after right hemispheric TMS over the posterior parietal cortex (Dambeck et al., 2006; Fierro et al., 2000; Müri et al., 2002; Pascual-Leone et al., 1994; Thut, Nietzel, & Pascual-Leone, 2005). These results are unlikely explained by TMS interferences with low-level motion sensitive regions (see section 2.6 on TMS site) and are discussed below for exogenous and endogenous processes separately.

4.1. Dorsal- and ventral attention network nodes both causally contribute to exogenously driven attentional anticipation

Our findings provide evidence of rTPJ being causally involved in exogenously driven anticipation as exogenous cueing effects were abolished by TMS. This supports the neuroanatomical model that the ventral fronto-parietal network is implicated in exogenous attention (Maurizio Corbetta et al., 2008; Maurizio Corbetta & Shulman, 2002) and is in line with previous findings showing that rTPJ is important for detecting novel and behavioural relevant stimuli (e.g., Asplund et al. 2010).

Most importantly, our results revealed that rIPS was also engaged in exogenous anticipation, as interferences with TMS abolished the respective cueing benefits. At first sight, this appears to contradict the evidence of rIPS being predominantly associated with endogenous (top-down) modulatory influence on visual activity, as revealed across different neuroimaging modalities including fMRI (Bressler, Tang, Sylvester, Shulman, & Corbetta, 2008; S. Vossel, Weidner, Driver, Friston, & Fink, 2012), fMRI-TMS (Ruff et al., 2008), MEG (Siegel, Donner, Oostenveld, Fries, & Engel, 2008) and EEG-TMS (P. Capotosto, Babiloni, Romani, & Corbetta, 2009; Paolo Capotosto, Babiloni, et al., 2012). However, in line with our results, some previous TMS studies have also reported a causal

association of the right IPS with exogenous attention (Bourgeois et al., 2013; Chica et al., 2011). For example, Chica et al. (2011) employed a classical exogenous visuospatial cueing paradigm and showed that after long cue-target intervals (at 800ms), TMS over both rIPS and rTPJ affected exogenous cueing. Yet, in contrast to our experimental design, previous studies have typically tested exogenous attention in isolation, thus participants may have deployed higher-order control mechanisms to endogenously predict information from exogenous cues, even if non-informative. This endogenous engagement may have led to a co-activation of rIPS in addition to rTPJ, resulting in a mixed contribution of endogenous and exogenous processes. Whilst excluding this possibility, we corroborate previous findings by showing that both network nodes are indeed involved during exogenously driven anticipation. This extends the classical view of rIPS being not only the source of top-down influence on visual areas but also responsive to bottom-up driven attention.

Additionally, since rIPS and rTPJ were mutually implicated in exogenous attention, this strongly supports the notion of collaborative roles and interplay between dorsal fronto-parietal and ventral fronto-parietal attention networks (Chica, Bartolomeo, & Lupiáñez, 2013; Parks & Madden, 2013; Simone Vossel, Geng, & Fink, 2014). Casual directional influences between these two networks have been demonstrated before by analysis of functional and effective connectivity in fMRI (S. Vossel et al., 2012; Wen, Yao, Liu, & Ding, 2012) and combined TMS-fMRI (Leitao, Thielscher, Tunnerhoff, & Noppeney, 2015). Furthermore, anatomo-clinical data have revealed that (re-)orienting deficits in spatial neglect, which usually occur after damage of the right ventral network, can be accompanied by lesions in the dorsal system (Halligan, Fink, Marshall, & Vallar, 2003; Marshall, Fink, Halligan, & Vallar, 2002). Interestingly, the same deficits have been reported after focal IPS lesions without ventral damage (Gillebert et al., 2011). Although our results are consistent with these findings, we cannot conclude to what extent TMS over IPS may have affected the ventral regions, or TMS over TPJ influenced the dorsal regions by spread of activity across the network, or both.

It should be noted that compared to classic experimental designs testing exogenous orienting (e.g., by employing brief luminance changes for cueing), the current study emphasised exogenously driven anticipation triggered by apparent motion. Consequently, participants form expectations about the upcoming motion sequence which likely activate different processes than brief attentional cues, such as automatic prediction mechanisms in early visual cortex (Ekman, Kok, & Lange, 2017). Thus, a direct comparison to the neuroanatomical substrates associated with typical attentional (re-)orienting is limited. Nevertheless, rhythmic visual stimulations such as motion and flicker have been shown to drive exogenous attention shifts without the need for high-level cognitive resources (for flicker see: Breska and Deouell 2014; for apparent motion see: Rohenkohl et al. 2011; de Graaf et al. 2013; Ahrens et al. 2015). Thus both classic cueing and the here implemented motion cues trigger exogenous attention processes.

Since active-TMS effects on exogenous cueing were region-unspecific, we need to consider whether these may be explained by non-specific TMS effects, such as the auditory click sound, somatosensory sensation or enhanced levels of arousal/vigilance. Despite these inevitable non-specific confounds of TMS, they appear unlikely to explain the current (specific) pattern of results for several reasons: Firstly, in line with previous findings showing TMS over attention areas to affect the visual field contralateral to the TMS site (Dambeck et al., 2006; Fierro et al., 2000; Müri et al., 2002; Pascual-Leone et al., 1994; Thut et al., 2005), our results show visual field-specific effects (i.e., in the left visual field) after stimulation over the right hemisphere, which is indicative of a primarily neural origin of the TMS effects, as opposed to primarily peripheral effects from sounds or touch. Secondly, non-specific TMS sensations (such as the sound or touch) would be expected to be associated with a right visual field bias after right hemisphere stimulation (Duecker and Sack, 2013), yet no such perceptual biases were observed. Third and most importantly, we found task-specific TMS effects, where exogenous cueing was abolished, but endogenous cueing effects remained unaffected, speaking against global TMS effects. Finally, none of the effects of active TMS were observed with sham TMS.

Therefore, we are confident that our findings reflect specific rather than non-specific TMS effects. Nevertheless, to further exclude any non-specific confounds and probe for region-specificity, future studies should consider an active-TMS control site over a brain region that presumably is not implicated in exogenous attention.

4.2. No effects of TMS over rIPS or rTPJ on endogenous spatial attention shifts: Consideration of temporal window and compensatory mechanisms

There is consistent evidence from both neuroimaging and TMS studies for the implication of rIPS in endogenous control of visuospatial attention (Chica et al., 2011; Maurizio Corbetta & Shulman, 2002; J Michelle Kincade et al., 2005). In contrast and contradictory to previous findings, our data revealed no TMS effects on endogenous attention after rIPS stimulation. Since TMS affected exogenous cueing benefits but endogenous benefits were maintained, this suggests a neural dissociation between both attentional processes, at least for the tested time window. However, alternative considerations and methodological limitations are likely to explain the absence of the TMS effects on endogenous cueing in the current study.

Neuroimaging has shown that as time progresses following endogenous cue presentation, activity steadily increases, spreading from the cuneus over both lateral intraparietal areas, to result in a co-activation of a large-scale bilateral, dorsal frontoparietal network (Maurizio Corbetta & Shulman, 2002; Simpson et al., 2011). This possibly reflects initial extraction of the cue information, followed by shifts of covert attention and finally transitioning into sustained deployment of attention (see also, Grent't-Jong & Woldorff 2007; Green & McDonald 2008; Lauritzen & Silver 2010; Siegel et al. 2008; Simpson et al. 2011). In the current study, we presented the TMS pulses 2075-2175ms after endogenous cue onset (175-75ms before target presentation). Hence, the time of the TMS administration fell into an interval when multiple, bilateral brain regions of the dorsal network had likely been recruited for task execution. This large-scale recruitment possibly compensated for TMS disruption, allowing the maintenance of

endogenous attention cueing effects without significant performance costs. Additionally, the stimulation intensity may have been sub-threshold or the time window of interference too short to affect endogenous orienting. Finally, it is conceivable that the TMS pulses were delivered at a suboptimal time window, when IPS was not critical for task performance. For instance, previous research has shown that the implication of parietal brain regions (right angular gyrus) in spatial orienting can be transient and intermittent, displaying time periods when TMS has no effect on performance (Chambers, Payne, Stokes, & Mattingley, 2004). Other studies have revealed that visuospatial attention is sampling information periodically at theta and alpha frequency (Landau and Fries, 2012; Song et al., 2014), even when attention is sustained (Fiebelkorn, Saalman, & Kastner, 2013). For TMS, this translates into a periodic pattern of visual task disruption at theta frequency (5Hz) during attentional orienting (see Dugué et al., 2016 for a study on endogenous orienting). Therefore, we cannot exclude that our stimulation may have fallen into a low-sensitive sampling phase, although the chosen double-pulse TMS design (with 100ms ITI) should have minimized this scenario. Given that 100ms covers half a 5Hz (theta) cycle, it is likely that either of the two pulses coincided with a high sensitivity sampling phase and hence, that our TMS design should have affected voluntary orienting even if cyclic.

4.3. Behavioural dissociation of endogenous and exogenous attention

While during sham-TMS, endogenous cueing benefitted perception at cued locations (relative to uncued locations) as expected, simultaneously presented exogenous motion cues also enhanced performance at motion cued versus uncued positions despite being task-irrelevant and non-predictive as to the upcoming target location. Importantly, and replicating our previous findings (Ahrens et al., 2015), exogenously driven attention benefits occurred independently of the endogenous benefits, as perception was enhanced even when the direction of both cue-types was

contradictive, i.e. attention shifts were directed into opposite visual fields (see also Berger et al. 2005). Therefore, this result further adds to the evidence that these two processes can be behaviourally dissociated (Ahrens et al., 2015; Berger et al., 2005; Coull, Frith, Büchel, & Nobre, 2000; Funes, Lupiáñez, & Milliken, 2007; Hopfinger & West, 2006; Lupiáñez et al., 2004; Pinto, van der Leij, Sligte, Lamme, & Scholte, 2013). Our findings that active-TMS affected exogenous cueing benefits but that endogenous benefits were maintained also suggests a dissociation between both processes in terms of neural underpinnings, for the tested time window at least, although our data cannot speak to the neural substrates of endogenous orienting (see paragraph above 4.2).

4.4. Conclusion

By ruling out confounding effects of endogenous processes on exogenous attention benefits, we provide conclusive evidence against independent involvement of the dorsal and ventral attention network nodes (i.e. rIPS and rTPJ) in exogenously driven attention. This highlights that the dorsal and ventral attention network can be activated in conjunction by exogenous events, suggesting that the functional roles of the ventral and dorsal attention system overlap.

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No part of the study procedures or analyses were pre-registered prior to research being conducted, however instead were based on, and contained a direct replication of Ahrens et al. 2015. The individual data, experimental material, analysis and plotting codes are available on <https://osf.io/j9erp/>.

References

Ahrens, M.-M., Veniero, D., Gross, J., Harvey, M., & Thut, G. (2015). Visual Benefits in Apparent Motion Displays: Automatically Driven Spatial and Temporal Anticipation Are

- Partially Dissociated. *PLoS One*, 10(12), e0144082. <http://doi.org/10.1371/journal.pone.0144082>
- Ansorge, U., & Heumann, M. (2003). Top-Down Contingencies in Peripheral Cuing: The Roles of Color and Location. *Journal of Experimental Psychology: Human Perception and Performance*, 29(5), 937–948. <http://doi.org/10.1037/0096-1523.29.5.937>
- Asplund, C. L., Todd, J. J., Snyder, A. P., & Marois, R. (2010). A central role for the lateral prefrontal cortex in goal-directed and stimulus-driven attention. *Nature Neuroscience*, 13(4), 507–512. <http://doi.org/10.1038/nn.2509>
- Berger, A., Henik, A., & Rafal, R. (2005). Competition between endogenous and exogenous orienting of visual attention. *Journal of Experimental Psychology. General*, 134(2), 207–221. <http://doi.org/10.1037/0096-3445.134.2.207>
- Bourgeois, A., Chica, A. B., Valero-Cabré, A., & Bartolomeo, P. (2013). Cortical control of inhibition of return: Causal evidence for task-dependent modulations by dorsal and ventral parietal regions. *Cortex*, 49(8), 2229–2238. <http://doi.org/10.1016/j.cortex.2012.10.017>
- Breska, A., & Deouell, L. Y. (2014). Automatic Bias of Temporal Expectations following Temporally Regular Input Independently of High-level Temporal Expectation. *Journal of Cognitive Neuroscience*, 26(7), 1555–1571. <http://doi.org/10.1162/jocn>
- Bressler, S. L., Tang, W., Sylvester, C. M., Shulman, G. L., & Corbetta, M. (2008). Top-Down Control of Human Visual Cortex by Frontal and Parietal Cortex in Anticipatory Visual Spatial Attention. *Journal of Neuroscience*, 28(40), 10056–10061. <http://doi.org/10.1523/JNEUROSCI.1776-08.2008>
- Capotosto, P., Babiloni, C., Romani, G. L., & Corbetta, M. (2009). Frontoparietal Cortex Controls Spatial Attention through Modulation of Anticipatory Alpha Rhythms. *Journal of Neuroscience*, 29(18), 5863–5872. <http://doi.org/10.1523/JNEUROSCI.0539-09.2009>
- Capotosto, P., Babiloni, C., Romani, G. L., & Corbetta, M. (2012). Differential contribution of right and left parietal cortex to the control of spatial attention: A simultaneous EEG-rTMS study. *Cerebral Cortex*, 22(2), 446–454. <http://doi.org/10.1093/cercor/bhr127>
- Capotosto, P., Corbetta, M., Romani, G. L., & Babiloni, C. (2012). Electrophysiological Correlates of Stimulus-driven Reorienting Deficits after Interference with Right Parietal Cortex during a Spatial Attention Task: A TMS-EEG Study. *Journal of Cognitive Neuroscience*, 24(12), 2363–2371. http://doi.org/10.1162/jocn_a_00287
- Chambers, C. D., Payne, J. M., Stokes, M. G., & Mattingley, J. B. (2004). Fast and slow parietal pathways mediate spatial attention. *Nature Neuroscience*, 7(3), 217–218. <http://doi.org/10.1038/nn1203>
- Chang, C. F., Hsu, T. Y., Tseng, P., Liang, W. K., Tzeng, O. J. L., Hung, D. L., & Juan, C. H. (2013). Right temporoparietal junction and attentional reorienting. *Human Brain Mapping*, 34(4), 869–877. <http://doi.org/10.1002/hbm.21476>
- Chica, A. B., Bartolomeo, P., & Lupiáñez, J. (2013). Two cognitive and neural systems for endogenous and exogenous spatial attention. *Behavioural Brain Research*, 237(1), 107–123. <http://doi.org/10.1016/j.bbr.2012.09.027>
- Chica, A. B., Bartolomeo, P., & Valero-Cabré, A. (2011). Dorsal and ventral parietal contributions to spatial orienting in the human brain. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 31(22), 8143–8149. <http://doi.org/10.1523/JNEUROSCI.5463-10.2010>
- Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P., & Shulman, G. L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat Neurosci*, 3(3), 292–297. <http://doi.org/10.1038/73009>

- Corbetta, M., Patel, G., & Shulman, G. L. (2008). The Reorienting System of the Human Brain: From Environment to Theory of Mind. *Neuron*, 58(3), 306–324. <http://doi.org/10.1016/j.neuron.2008.04.017>
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews. Neuroscience*, 3(3), 201–15. <http://doi.org/10.1038/nrn755>
- Coull, J. T., Frith, C. D., Büchel, C., & Nobre, a. C. (2000). Orienting attention in time: Behavioural and neuroanatomical distinction between exogenous and endogenous shifts. *Neuropsychologia*, 38(6), 808–819. [http://doi.org/10.1016/S0028-3932\(99\)00132-3](http://doi.org/10.1016/S0028-3932(99)00132-3)
- Dambeck, N., Sparing, R., Meister, I. G., Wienemann, M., Weidemann, J., Topper, R., & Boroojerdi, B. (2006). Interhemispheric imbalance during visuospatial attention investigated by unilateral and bilateral TMS over human parietal cortices. *Brain Research*, 1072(1), 194–199. <http://doi.org/10.1016/j.brainres.2005.05.075>
- de Graaf, T. a, Gross, J., Paterson, G., Rusch, T., Sack, A. T., & Thut, G. (2013). Alpha-band rhythms in visual task performance: phase-locking by rhythmic sensory stimulation. *PLoS One*, 8(3), e60035. <http://doi.org/10.1371/journal.pone.0060035>
- Dienes, Z., & Mclatchie, N. (2017). Four reasons to prefer Bayesian analyses over significance testing. *Psychonomic Bulletin and Review*, 1–12. <http://doi.org/10.3758/s13423-017-1266-z>
- Duecker, F., Frost, M. A., de Graaf, T. A., Graewe, B., Jacobs, C., Goebel, R., & Sack, A. . (2014). The Cortex-based Alignment Approach to TMS Coil Positioning. *Journal of Cognitive Neuroscience*, 26(10), 2321–2329.
- Duecker, F., & Sack, A. T. (2013). Pre-Stimulus Sham TMS Facilitates Target Detection. *PLoS ONE*, 8(3), 4–9. <http://doi.org/10.1371/journal.pone.0057765>
- Dugué, L., Philippe, M., & VanRullen, R. (2015). Theta Oscillations Modulate Attentional Search Performance Periodically. *Journal of Cognitive Neuroscience*, 27(5), 945–958. <http://doi.org/10.1162/jocn>
- Dugué, L., Roberts, M., & Carrasco, M. (2016). Attention Reorients Periodically. *Current Biology*, 26(12), 1595–1601. <http://doi.org/10.1016/j.cub.2016.04.046>
- Ekman, M., Kok, P., & Lange, F. P. De. (2017). Time-compressed preplay of anticipated events in human primary visual cortex. *Nature Communications*, 8(May), 1–9. <http://doi.org/10.1038/ncomms15276>
- Fiebelkorn, I. C., Saalmann, Y. B., & Kastner, S. (2013). Rhythmic sampling within and between objects despite sustained attention at a cued location. *Current Biology*, 23(24), 2553–2558. <http://doi.org/10.1016/j.cub.2013.10.063>
- Fierro, B., Brighina, F., Oliveri, M., Piazza, A., La Bua, V., Buffa, D., & Bisiach, E. (2000). Contralateral neglect induced by right posterior parietal rTMS in healthy subjects. *NeuroReport*, 11(7), 1519–1521. <http://doi.org/10.1097/00001756-200005150-00031>
- Folk, C. L., Remington, R. W., & Wright, J. H. (1994). The structure of attentional control: contingent attentional capture by apparent motion, abrupt onset, and color. *Journal of Experimental Psychology. Human Perception and Performance*, 20(2), 317–329. <http://doi.org/10.1037/0096-1523.20.2.317>
- Frost, M. A., & Goebel, R. (2012). Measuring structural-functional correspondence: Spatial variability of specialised brain regions after macro-anatomical alignment. *NeuroImage*, 59(2), 1369–1381. <http://doi.org/10.1016/j.neuroimage.2011.08.035>
- Funes, M. J., Lupiáñez, J., & Milliken, B. (2007). Separate mechanisms recruited by exogenous and endogenous spatial cues: evidence from a spatial Stroop paradigm.

- Journal of Experimental Psychology. Human Perception and Performance*, 33(2), 348–362. <http://doi.org/10.1037/0096-1523.33.2.348>
- Gillebert, C. R., Mantini, D., Thijs, V., Sunaert, S., Dupont, P., & Vandenberghe, R. (2011). Lesion evidence for the critical role of the intraparietal sulcus in spatial attention. *Brain*, 134(6), 1694–1709. <http://doi.org/10.1093/brain/awr085>
- Grasso, P. ., Làdavas, E., Bertini, C., Caltabiano, S., Thut, G., & Morand, S. (2018). Decoupling of Early V5 Motion Processing from Visual Awareness: A Matter of Velocity as Revealed by Transcranial Magnetic Stimulation Evidence. *Journal of Cognitive Neuroscience*, 19, 1–15. http://doi.org/https://doi.org/10.1162/jocn_a_01298
- Green, J. J., & McDonald, J. J. (2008). Electrical neuroimaging reveals timing of attentional control activity in human brain. *PLoS Biology*, 6(4), 730–738. <http://doi.org/10.1371/journal.pbio.0060081>
- Grent-'t-Jong, T., & Woldorff, M. G. (2007). Timing and sequence of brain activity in top-down control of visual-spatial attention. *PLoS Biology*, 5(1), 0114–0126. <http://doi.org/10.1371/journal.pbio.0050012>
- Hahn, B., Ross, T. J., & Stein, E. A. (2006). Neuroanatomical dissociation between bottom-up and top-down processes of visuospatial selective attention. *NeuroImage*, 32(2), 842–853. <http://doi.org/10.1016/j.neuroimage.2006.04.177>
- Halligan, P. W., Fink, G. R., Marshall, J. C., & Vallar, G. (2003). Spatial cognition: Evidence from visual neglect. *Trends in Cognitive Sciences*, 7(3), 125–133. [http://doi.org/10.1016/S1364-6613\(03\)00032-9](http://doi.org/10.1016/S1364-6613(03)00032-9)
- Heinen, K., Ruff, C. C., Bjoertomt, O., Schenkluhn, B., Bestmann, S., Blankenburg, F., ... Chambers, C. D. (2011). Concurrent TMS-fMRI reveals dynamic interhemispheric influences of the right parietal cortex during exogenously cued visuospatial attention. *European Journal of Neuroscience*, 33(5), 991–1000. <http://doi.org/10.1111/j.1460-9568.2010.07580.x>
- Hopfinger, J. B., & West, V. M. (2006). Interactions between endogenous and exogenous attention on cortical visual processing. *NeuroImage*, 31(2), 774–789. <http://doi.org/10.1016/j.neuroimage.2005.12.049>
- Hu, S., Bu, Y., Song, Y., Zhen, Z., & Liu, J. (2009). Dissociation of attention and intention in human posterior parietal cortex: An fMRI study. *European Journal of Neuroscience*, 29(10), 2083–2091. <http://doi.org/10.1111/j.1460-9568.2009.06757.x>
- JASP Team. (2018). JASP (Version 0.8.2) [Computer Software].
- Kincade, J. M. (2005). An Event-Related Functional Magnetic Resonance Imaging Study of Voluntary and Stimulus-Driven Orienting of Attention. *Journal of Neuroscience*, 25(18), 4593–4604. <http://doi.org/10.1523/JNEUROSCI.0236-05.2005>
- Kincade, J. M., Abrams, R. A., Astafiev, S. V, Shulman, G. L., & Corbetta, M. (2005). An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, 25(18), 4593–4604. <http://doi.org/10.1523/JNEUROSCI.0236-05.2005>
- Landau, A. N., & Fries, P. (2012). Attention samples stimuli rhythmically. *Current Biology*, 22(11), 1000–1004. <http://doi.org/10.1016/j.cub.2012.03.054>
- Lauritzen, T. Z., & Silver, M. A. (2010). Top-down flow of visual spatial attention signals from parietal to occipital cortex. *Journal of Vision*, 9(13), 1–21. <http://doi.org/10.1167/9.13.18.Top>
- Leitao, J., Thielscher, A., Tunnerhoff, J., & Noppeney, U. (2015). Concurrent TMS-fMRI Reveals Interactions between Dorsal and Ventral Attentional Systems. *Journal of*

- Neuroscience*, 35(32), 11445–11457. <http://doi.org/10.1523/JNEUROSCI.0939-15.2015>
- Lupiáñez, J., Decaix, C., Siéoff, E., Chokron, S., Milliken, B., & Bartolomeo, P. (2004). Independent effects of endogenous and exogenous spatial cueing: Inhibition of return at endogenously attended target locations. *Experimental Brain Research*, 159(4), 447–457. <http://doi.org/10.1007/s00221-004-1963-5>
- Marshall, J. C., Fink, G. R., Halligan, P. W., & Vallar, G. (2002). Spatial awareness: A function of the posterior parietal lobe? *Cortex*, 38(2), 253–257. [http://doi.org/10.1016/S0010-9452\(08\)70654-3](http://doi.org/10.1016/S0010-9452(08)70654-3)
- Mayer, A. R., Dorflinger, J. M., Rao, S. M., & Seidenberg, M. (2004). Neural networks underlying endogenous and exogenous visual-spatial orienting. *NeuroImage*, 23(2), 534–541. <http://doi.org/10.1016/j.neuroimage.2004.06.027>
- Müri, R., Bühler, R., Heinemann, D., Mosimann, U., Felblinger, J., Schlaepfer, T., & Hess, C. (2002). Hemispheric asymmetry in visuospatial attention assessed with transcranial magnetic stimulation. *Experimental Brain Research*, 143(4), 426–430. <http://doi.org/10.1007/s00221-002-1009-9>
- Natale, E., Marzi, C. A., & Macaluso, E. (2009). fMRI correlates of visuo-spatial reorienting investigated with an attention shifting double-cue paradigm. *Human Brain Mapping*, 30(8), 2367–2381. <http://doi.org/10.1002/hbm.20675>
- Painter, D. R., Dux, P. E., & Mattingley, J. B. (2015). Distinct roles of the intraparietal sulcus and temporoparietal junction in attentional capture from distractor features: An individual differences approach. *Neuropsychologia*, 74, 50–62. <http://doi.org/10.1016/j.neuropsychologia.2015.02.029>
- Parks, E. L., & Madden, D. J. (2013). Brain Connectivity and Visual Attention. *Brain Connectivity*, 3(4), 317–338. <http://doi.org/10.1089/brain.2012.0139>
- Pascual-Leone, A., Gomez tortosa, E., Grafman, J., Alway, D., Nichelli, P., & Hallett, M. (1994). Induction of Visual Extinction by Rapid Rate Transcranial Magnetic Stimulation of Parietal Lobe. *Neurology*, 44(April 1993), 494–498.
- Peelen, M. V., Heslenfeld, D. J., & Theeuwes, J. (2004). Endogenous and exogenous attention shifts are mediated by the same large-scale neural network. *NeuroImage*, 22(2), 822–830. <http://doi.org/10.1016/j.neuroimage.2004.01.044>
- Petersen, S. ., & Posner, M. (2012). The attention system of the human brain: 20 years after. *Annual Review of Neuroscience*, 21(35), 73–89. <http://doi.org/10.1146/annurev-neuro-062111-150525>.The
- Pinto, Y., van der Leij, A. R., Sligte, I. G., Lamme, V. A. F., & Scholte, H. S. (2013). Bottom-up and top-down attention are independent. *Journal of Vision*, 13(3), 1–14. <http://doi.org/10.1167/13.3.16>.doi
- Pitcher, D., Goldhaber, T., Duchaine, B., Walsh, V., & Kanwisher, N. (2012). Two Critical and Functionally Distinct Stages of Face and Body Perception. *Journal of Neuroscience*, 32(45), 15877–15885. <http://doi.org/10.1523/JNEUROSCI.2624-12.2012>
- Posner, M. I. (1980). Orienting of attention. *The Quarterly Journal of Experimental Psychology*, 32(1), 3–25. <http://doi.org/10.1080/00335558008248231>
- Raffin, E., Pellegrino, G., Di Lazzaro, V., Thielscher, A., & Roman, H. (2015). Bringing transcranial mapping into shape : Sulcus-aligned mapping captures motor somatotopy in human primary motor hand area. *NeuroImage*, 120, 164–175. <http://doi.org/10.1016/j.neuroimage.2015.07.024>
- Rohenkohl, G., Coull, J. T., & Nobre, A. C. (2011). Behavioural dissociation between exogenous and endogenous temporal orienting of attention. *PLoS ONE*, 6(1), 1–5. <http://doi.org/10.1371/journal.pone.0014620>

- Romei, V., Gross, J., & Thut, G. (2010). On the role of prestimulus alpha rhythms over occipito-parietal areas in visual input regulation: correlation or causation? *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *30*(25), 8692–8697. <http://doi.org/10.1523/JNEUROSCI.0160-10.2010>
- Rossi, S., Hallett, M., Rossini, P. M., Pascual-Leone, A., Avanzini, G., Bestmann, S., ... Ziemann, U. (2009). Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. *Clinical Neurophysiology*, *120*(12), 2008–2039. <http://doi.org/10.1016/j.clinph.2009.08.016>
- Ruff, C. C., Bestmann, S., Blankenburg, F., Bjoertomt, O., Josephs, O., Weiskopf, N., ... Driver, J. (2008). Distinct causal influences of parietal versus frontal areas on human visual cortex: Evidence from concurrent TMS-fMRI. *Cerebral Cortex*, *18*(4), 817–827. <http://doi.org/10.1093/cercor/bhm128>
- Ruz, M., & Lupiáñez, J. (2002). A review of attentional capture : On its automaticity and sensitivity to endogenous control. *Psicológica*, *23*, 283–309.
- Sack, A. T., Camprodon, J. A., Pascual-Leone, A., & Goebel, R. (2005). The Dynamics of Interhemispheric Compensatory Processes in Mental Imagery. *Science*, (April), 702–704.
- Schenkluhn, B., Ruff, C. C., Heinen, K., & Chambers, C. D. (2008). Parietal Stimulation Decouples Spatial and Feature-Based Attention. *Journal of Neuroscience*, *28*(44), 11106–11110. <http://doi.org/10.1523/JNEUROSCI.3591-08.2008>
- Shulman, G. L., McAvoy, M. P., Cowan, M. C., Astafiev, S. V., Tansy, A. P., d'Avossa, G., & Corbetta, M. (2003). Quantitative Analysis of Attention and Detection Signals During Visual Search. *Journal of Neurophysiology*, *90*(5), 3384–3397. <http://doi.org/10.1152/jn.00343.2003>
- Siegel, M., Donner, T. H., Oostenveld, R., Fries, P., & Engel, A. K. (2008). Neuronal synchronization along the dorsal visual pathway reflects the focus of spatial attention. *Neuron*, *60*(4), 709–19. <http://doi.org/10.1016/j.neuron.2008.09.010>
- Simpson, G. V., Weber, D. L., Dale, C. L., Pantazis, D., Bressler, S. L., Leahy, R. M., & Luks, T. L. (2011). Dynamic Activation of Frontal, Parietal, and Sensory Regions Underlying Anticipatory Visual Spatial Attention. *Journal of Neuroscience*, *31*(39), 13880–13889. <http://doi.org/10.1523/JNEUROSCI.1519-10.2011>
- Song, K., Meng, M., Chen, L., Zhou, K., & Luo, H. (2014). Behavioral Oscillations in Attention: Rhythmic Pulses Mediated through Band. *Journal of Neuroscience*, *34*(14), 4837–4844. <http://doi.org/10.1523/JNEUROSCI.4856-13.2014>
- Thielscher, A., Opitz, A., & Windhoff, M. (2011). Geometry on the electric field induced by transcranial magnetic stimulation. *NeuroImage*, *54*(1), 234–243. <http://doi.org/10.1016/j.neuroimage.2010.07.061>
- Thut, G., Nietzel, A., & Pascual-Leone, A. (2005). Dorsal posterior parietal rTMS affects voluntary orienting of visuospatial attention. *Cerebral Cortex*, *15*(5), 628–638. <http://doi.org/10.1093/cercor/bhh164>
- Townsend, J. T., & Ashby, F. G. (1983). *The stochastic modeling of elementary psychological processes*. Cambridge: Cambridge University Press.
- Verhagen, J., & Wagenmakers, E. J. (2014). Bayesian tests to quantify the result of a replication attempt. *Journal of Experimental Psychology: General*, *143*(4), 1457–1475. <http://doi.org/10.1037/a0036731>
- Vossel, S., Geng, J. J., & Fink, G. R. (2014). Dorsal and Ventral Attention Systems: Distinct Neural Circuits but Collaborative Roles. *The Neuroscientist*, *20*(2), 150–159. <http://doi.org/10.1177/1073858413494269>

Vossel, S., Weidner, R., Driver, J., Friston, K. J., & Fink, G. R. (2012). Deconstructing the Architecture of Dorsal and Ventral Attention Systems with Dynamic Causal Modeling. *Journal of Neuroscience*, 32(31), 10637–10648.
<http://doi.org/10.1523/JNEUROSCI.0414-12.2012>

Wen, X., Yao, L., Liu, Y., & Ding, M. (2012). Causal Interactions in Attention Networks Predict Behavioral Performance. *Journal of Neuroscience*, 32(4), 1284–1292.
<http://doi.org/10.1523/JNEUROSCI.2817-11.2012>