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Low-frequency rTMS to the frontal lobe increases eye-movement carryover

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Abstract

The persistence of attentional set from one task to a secondary unrelated task, revealed through carryover of eye movements, has been attributed to increased activation in the parietal lobe and decreased activation to the frontal lobe. To directly test this, we adopted a modified version of the Thompson and Crundall (2011) paradigm using low-frequency repetitive TMS to P3 and F3. In each trial, participants viewed letter-strings that were arranged horizontally, vertically, or randomly across the screen before viewing a road image and providing a hazardousness rating for it. The orientation of the letter search influenced eye movements to the road images and this carryover was greater following stimulation to F3 than to P3 (or sham). Furthermore, hazardous ratings were lower following P3 stimulation. These results confirm the involvement of attentional orienting and switching mechanisms in the carryover of eye movements. It is suggested that this “attentional inertia” effect will increase with greater orienting of attentional resources in an initial task and poor inhibition of previously-relevant settings between tasks.

Keywords

Eye movement carryover; attentional inertia; orienting; low-frequency TMS; frontal lobe; parietal lobe

1. Introduction

In studies of visual search, a phenomenon has been observed where participants maintain a particular search strategy or behaviour – an exogenous, bottom-up strategy (automatic and stimulus driven) or an endogenous, top-down strategy (goal-driven, voluntary and suppressible; Posner, 1980; Itti & Koch, 2000) – across tasks, sometimes to the detriment of the second task. Attentional settings relevant for one task have been shown to persist to a second task (e.g., Leber & Egeth, 2006; Leber et al, 2009). This was initially argued to be due to shared stimuli between the tasks, and prolonged practice with the initial task. However, Thompson and Crundall (2011) found evidence of short-term carryover of attentional settings between two very different tasks that required different attentional ‘sets’ or strategies. In their studies, participants viewed letter-strings that were orientated across the screen horizontally, vertically, or randomly and were asked to count the number of vowels present. Subsequently, participants viewed static images or video clips and eye movements were measured. Thompson and Crundall's results were clear: carryover of eye movements was observed from the letter-search task to the second task. Specifically, vertical eye movements were more prevalent after participants had viewed a vertical letter-string, even briefly and reduced following the horizontal letter-string. These results were replicated by Hills, Thompson, and Pake (2018) who found that the carryover effect influenced judgements made to the second task, and by Thompson, Howting, and Hills (2015) who demonstrated that the effect was stronger with increased time spent completing the letter search task.

The influence of top-down settings on the subsequent allocation of attention and eye movements has also been studied by Longman, Lavric, and Monsell (2013). Using a task switching paradigm that manipulated spatial shifts of attention between trials, they found that participants were more likely to fixate previously-relevant locations and they suggested a component of “attentional inertia” whereby attentional settings are allocated to the initial task and these will persist to a second task until they can be inhibited.

Such as to best adapt the environment to human tendencies in attention and visual search, it is crucial to elucidate the cognitive and neural mechanisms behind these. While models of attention include the involvement of both bottom-up and top-down processing (Itti & Koch, 2000), they do not explicitly describe the mechanism of this the carryover effect. In an attempt to deconstruct and explore its origin, Hills, Thompson, Jones, Piech, Painter, and Pake (2016) ran a series of correlations between the magnitude of the carryover effect and various tests of inhibition. Based on a pattern of significant correlations with orienting in the attentional network task (Fan, McCandliss, Sommer, Raz, & Posner, 2002) and task switching (Monsell, 2003), Hills et al. suggested that the carryover effect was due to both an over-orienting of attention to the letter-string task and a failure of task switching, an aspect of executive function. This explains the increased carryover when the first is more prevalent than the second (Thompson et al., 2015) as this will result in greater orienting to this initial task (relative to the second), making the attentional settings more difficult to inhibit.

In terms of the neural substrates underpinning these processes, a wealth of neuroscientific and neuropsychological studies have localised cognitive control and attention to a frontoparietal network (Duncan, 2010; Scolarì, Seidl-Rathkopf & Kastner, 2015), but particular roles have been attributed to the right hemisphere and within it the temporo-parietal junction and the inferior frontal gyrus in the orienting and reorienting of attention (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Konrad, Neufang, Thiel, Specht, Hanisch, Fan,... & Fink, 2005; Fox, McCourt & Javitt, 2003; Spagna, Kim, Wu & Fan, 2018), and to the dorsolateral prefrontal cortex (DLPFC) in task switching (Dove, Pollmann, Schubert, Wiggins, & Von Cramon, 2000; Dedoncker, Brunoni, Baeken, & Vanderhasselt, 2016; Kim, Cilles, Johnson, & Gold, 2012; Leite, Carvalho, Fregni, Boggio & Gonçalves, 2013; Hyafil, Summerfield & Koehlin, 2009; Tsuchida & Fellows, 2012).

In light of the above and in order to test the substrates of the carryover effect proposed by Hills et al., it is reasonable to hypothesise that, if the carryover effect is indeed related to a failure of task-switching, low-frequency repetitive transcranial magnetic stimulation (rTMS) over the frontal lobe would *increase* the carryover effect through impairing task-switching ability. TMS of 1Hz has been routinely used in this way to disrupt information processing and thus create temporary lesions in the cortex (Hallett, 2000; Jahanshahi & Rothwell, 2000; Pascual-Leone et al., 2000; Walsh & Rushworth, 1999); repetitive application of TMS affects brain plasticity such that brain excitability may be modified even after stimulation has ceased (Priori, Hallett, & Rothwell, 2009). As such, application of rTMS to the DLPFC specifically has been previously demonstrated to affect task-switching ability (Vanderhasselt, de Raedt, Baeken, Leyman & D'haenen, 2006; Vanderhasselt, de Raedt, Baeken, Leyman, Clerinx & D'haenen, 2007). Task-switching plays a central role in executive functioning (Banich, 2009) and lower activation in this region has been associated with poorer performance in decision making, inhibition, switching, and cognitive control. Indeed, Chambers, Bellgrove, Stokes, Henderson, Garavan, Robertson, ... & Mattingley (2006) have shown that TMS to the frontal lobe caused a detriment in response inhibition as measured by the go/no-go task. The localisation of task-switching to DLPFC is further supported by facilitatory effects of another method, transcranial direct current stimulation, which increases DLPFC activity along as task-switching performance (Leite et al, 2013; Dedoncker et al, 2016). By decreasing the activity in the frontal region, we anticipate that the ability to switch tasks would be reduced, therefore increasing any attentional inertia.

With respect to the relationship between attention orienting and parietal cortex, Giesbrecht, Woldorff, Song, and Mangun (2003) have shown that the parietal lobe is responsible for exogenous, bottom-up attentional orienting. The slower, voluntary, top-down endogenous orienting involves a more extensive frontoparietal network, including the frontal eye field and dorsal posterior parietal cortex (Bressler, Tang, Sylvester, Shulman, Corbetta, 2008; Hannula, Neuvonen, Savolainen, Hiltunen, Ma, Antila, ... & Pertovaara, 2010; Hopfinger, Buonocore, Mangun, 2000). It seems probable that the carryover effect is more akin to exogenous orienting since it is driven by the response to stimuli, rather than an emotional need to orient toward something. Higher activation in the parietal lobe has been associated with increased abilities to orient to stimuli (Fan, McCandliss, Fossella, Flombaum, & Posner, 2005) and perform visual search tasks. Indeed, low-frequency TMS directed to this region has led to decreased performance in tasks such as the Posner cueing paradigm (Du, Chen, & Zhou, 2012). Temporary lesions to the parietal lobe disrupt the disengagement of orienting attention (Rushworth, Krams, & Passingham, 2001), and using tDCS to alter the balance of excitability in this region also affects attentional orienting (Duecker, Schuhmann, Bien, Jacobs, & Sack, 2017). Furthermore, the parietal lobe is implicated as a core brain region in visual search and visual search is the crucial

cognitive mechanism in hazard perception. Based on this, low-frequency stimulation to this region would be expected to *decrease* the carryover effect because participants will be unable to orient their attention to the letter-strings successfully, thus reducing the likelihood of the over-orienting that might result in attentional sets being carried over between tasks.

As such, in order to test the attribution of the carryover effect to over-orienting of attention and failure of task-switching (Hills et al., 2016), two clear hypotheses may be made regarding the effect of low-frequency TMS to the frontal and parietal lobes. Firstly, rTMS to the frontal lobe should increase the carryover effect if we assume that the carryover is due in part to exogenous orienting; secondly, rTMS to the parietal lobe should decrease the carryover effect. We tested these hypotheses in a modified version of the paradigm of Thompson and Crundall (2011), measuring eye movement carryover from a letter-string task to a hazard rating task following low-frequency rTMS to either frontal (electrode F3) or parietal (electrode P3) cortex. In addition to eye movement carryover, we also recorded hazard ratings as these have been shown to be influenced by the carryover effect (Hills et al., 2018).

2. Method

2.1. Participants

A voluntary sample of 30 Bournemouth University students (25 females, aged 18-30) took part in this study as part of a course requirement or for £15. Sample size was determined through an *a priori* power analysis, calculated with G-Power and based on the difference between the magnitude of the carryover effect following F3 and P3 tDCS (from Experiment 3 in Hills et al., 2016). The former effect size being $f = .53$, this indicated that to find a significant result with .80 Power, 30 participants would be required. Participants were divided equally among the three TMS conditions. All participants had normal or corrected-to-normal vision and passed the safety screening for use of rTMS (Rossi, Hallett, Rossini & Pascual-Leone, 2009). The study's protocol was approved by Bournemouth University Faculty of Science and Technology Research Ethics Committee and adhered to the principles of the Declaration of Helsinki.

2.2. Design

A 3 x 3 mixed design was employed, with the between-subjects variable of rTMS site (sham, F3, or P3), and the within-subjects variable of letter-string orientation (horizontal, vertical, random distribution). Random distribution of letters is not exactly a string, but for continuity of language throughout, we use this term for all conditions. Participants were randomly allocated to be in one of the three rTMS conditions through choosing a piece of paper with a condition number on it. The dependent variables were hazard rating, saccade length in the hazard task (measured in pixels), and magnitude of carryover of eye movements from the letter search to the hazard task for both horizontal and vertical eye movements calculated using the formula

$$\text{Carryover} = (\text{EM}_c - \text{EM}_r) + (\text{EM}_r - \text{EM}_i)$$

where EM_c represents the number of eye movements in the hazard rating task consistent with the letter-string orientation per participant, EM_i is the number of eye movements in the hazard rating task inconsistent with the letter-string orientation, and EM_r is the number of eye movements in the hazard

rating task following the randomly orientated letter-string. This was done separately for horizontal and vertical carryover.

2.3. Apparatus

We used a DuoMAG, type XT TMS to deliver 1Hz rTMS. The device contains a figure 8-shaped coil and an electromyography (EMG) recording headbox (to measure muscle response and find the lowest motor threshold). Materials also included two Deymed Diagnostic disposable electrodes, placed on the participant's right hand, alongside a Velcro wraparound Ground Electrode on the right wrist. The DuoMAG, type XT (MagTower) was used as a specifically designed counterweight balanced coil-holder for TMS, making coil positioning easier for the experimenter.

All stimuli were presented on a 17" (1280 x 1024 pixel) LCD full colour monitor using Experiment Builder. Eye movements were recorded using an EyeLink 1000 Tower Mount, due to its high level of accuracy achieved through a remote, 2000 Hz fibre optic camera (SR Research Ltd., 2010). Participants maintained a constant distance of 75cm from the monitor by resting their head on a standard chin and forehead rest.

2.4. Materials and Procedure

Participants gave full informed consent before taking part in this study. They were verbally advised about the rTMS in addition to being provided with a written information sheet, and the safety screening was issued both verbally and in written form to ensure participants were safe to proceed. Following this, participants were sat comfortably in an air-conditioned laboratory and asked to keep their movement to a minimum. Their eye movements were calibrated to the eye-tracker using the default calibration settings. Subsequently, the scalp sites necessary for stimulation were located prior to testing using the 10-20 system for TMS positioning (Herwig, Satrapi, & Schönfeldt-Lecuona, 2003). In order to utilise the correct stimulation, the lowest resting motor threshold for each participant was established starting from position C3 to find the hotspot. Two electrodes were placed over the right abductor pollicis brevis muscle, connected to an EMG recording headbox, and a Velcro wraparound Ground Electrode was attached to the participant's right wrist. Stimulation was delivered with intensity increased from 10% until the lowest motor threshold was established. The resting motor threshold was decided based on the lowest amount of stimulation eliciting a motor response of at least 50 μ V for at least five out of ten stimulation following single-pulse TMS stimulation (Rothwell et al., 1999; Tranulis et al., 2006).

The rTMS protocol was set at 1Hz at 100% of the resting motor threshold for one train of 1200 pulses, with no inter-train interval, for a stimulation period of 20 minutes. This frequency was chosen within the safety guidelines (Rossi et al. 2009; Wassermann 1998). rTMS was used since it can modify excitability in the cortex that continues even after stimulation has ceased (Priori, Hallett, & Rothwell, 2009), continuing to cortical and sub-cortical levels (Fox, Ingham, George, Mayberg, Ingham, Roby,... & Jerabek, 1997) for approximately 25 minutes. For those in the sham (control condition), the procedure was identical. However, during the apparent rTMS procedure, the coil was placed over the vertex and facing away at a 90° angle to ensure no rTMS stimulation was delivered.

Immediately after the completion of the 20-minute stimulation, participants sat at the eye-tracker and began the experimental protocol. Calibration followed the standard in-built calibration procedure:

Pupil thresholds were kept between 75 and 110; auto-threshold was used to control corneal reflection; a standard nine-point calibration and validation was run. Materials and procedure are described in detail elsewhere (see Hills et al., 2016; 2018) and summarised here. Each trial was preceded by a fixation cross displayed for 500ms that they were required to view for the trial to begin (this acted as an eye position validation procedure). This was followed by a letter-string that was arranged either horizontally, vertically, or randomly across the screen. Letter strings subtended 10° of visual angle. Participants had to report the number of vowels (there were always either 3 or 4 present) using the numerical keypad. Feedback was provided in the form of a red (for incorrect) or green (for correct) screen for 1000ms (see figure 1). The letter-string and feedback screen was repeated two more times for half of the trials (to decrease awareness of the timing of the trials, Thompson et al., 2015). Subsequently, participants were presented with a road image (subtending 17.15° of visual angle) taken from a driver's position and were required to rate the hazardousness of the image by using the numerical keypad. This remained on screen for 2000ms. Drift correction (for eye movement re-calibration) was applied every ten trials.

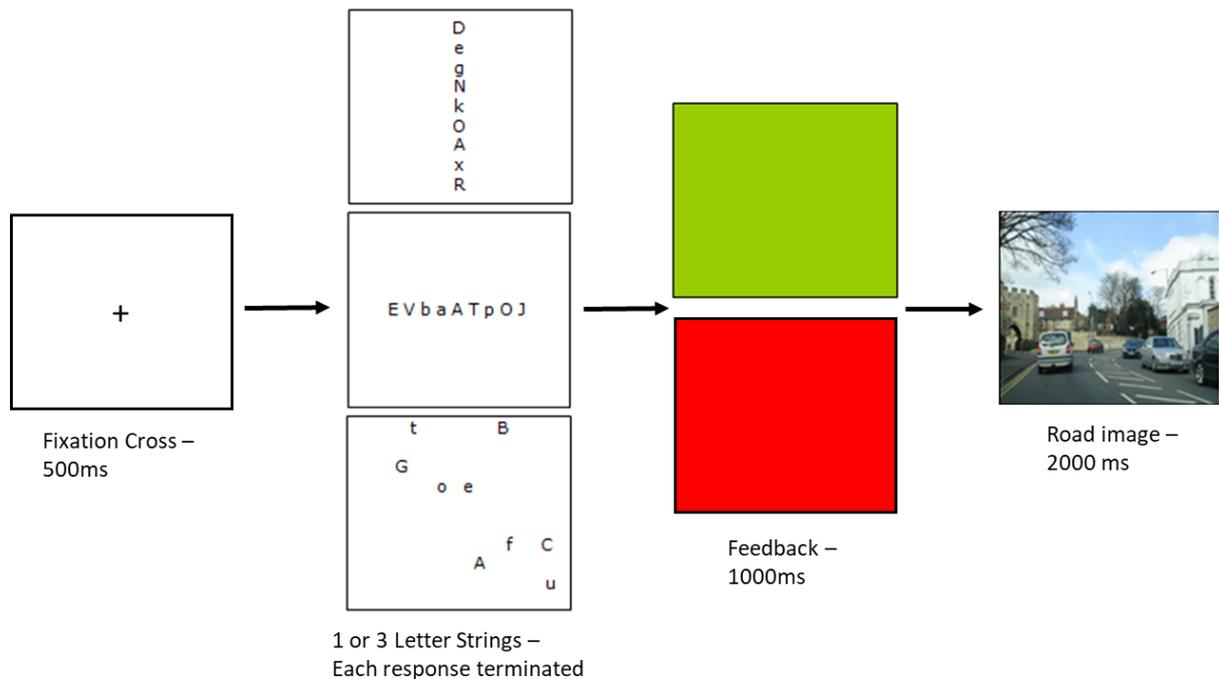


Figure 1. Task procedure. In each trial participants completed one or three letter searches (letters were always in the same orientation for each trial) before viewing a road image and rating this for hazardousness.

There were a total of 108 trials divided equally among letter-string orientation conditions (again, divided equally among one- or three-letter-strings prior to the hazard rating task). There were an equal number of letter-strings with 3 or 4 vowels across different conditions. Trials were presented in a random order and road images were selected at random to appear in each trial and were not repeated within the task. This experimental task typically lasted 22 minutes. On completion of the task, participants were thanked and debriefed.

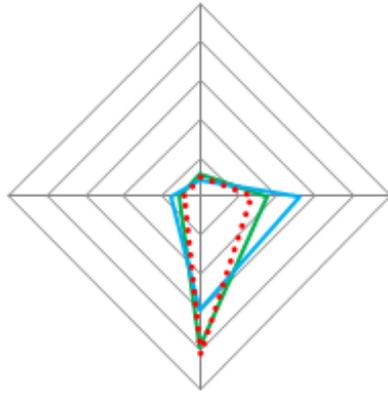
3. Results

Fixations and saccades were operationalised using the EyeLink's default thresholds: Saccadic velocity threshold was kept at 30°/s; Saccadic motion threshold was kept as 0.2°; eye-movement acceleration threshold was kept at 8000°/s²; fixation updates were set to 100ms. A similar analysis structure pipeline as in Hills et al. (2018) was applied here. We excluded any trials in which participants did not count the number of vowels correctly (2% of trials - there was no significant difference in accuracy across the trials). To calculate the carry-over magnitude we coded saccade direction using a similar method to Gilchrist and Harvey (2006). Analyses were conducted after the initial fixation on the road: the direction of each saccade following this fixation until a key was pressed was measured in degrees, and saccades were then coded into one of four 90° bins: upward (316° through 0° to 45°), downward (126° to 225°), leftward (226° to 315°), and rightward (46° to 125°). Figure 2 represents the mean number of saccades made in each direction. To calculate the magnitude of carryover, we collapsed across left and right movements to create a single horizontal eye movement measure, and across up and down to create a single vertical eye movement measure.

In addition to traditional null hypothesis significance testing, we employed Bayesian analysis (Dienes, in press). For this, our priors were determined by the difference between the magnitude of the carryover effect following F3 and P3 tDCS (from Experiment 3 in Hills et al., 2016). Given we had a clear control condition (sham stimulation), we employed the Dunnett post-hoc test throughout (except where we compare across stimulation conditions, in which case the Bonferroni-correction was employed).

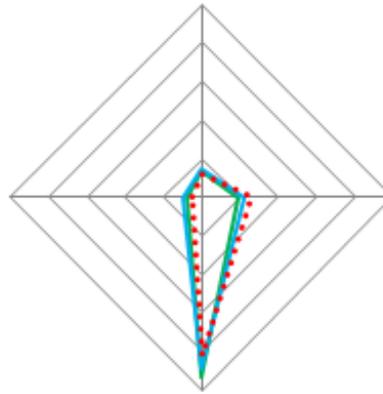
The magnitude of horizontal carryover data (as calculated with the formula described above) was subjected to a 3 x 2 mixed-factorial ANOVA with rTMS site as the between-subjects factor and orientation of the carryover (horizontal or vertical) as the within-subjects factor. Means and standard errors are shown in Figure 3. There was a main effect of rTMS site, $F(2, 27) = 8.52$, $MSE = 38.10$, $p = .001$, $\eta_p^2 = .39$, $BF_{10} = 19.80$. Post hoc tests showed that carryover was significantly larger following F3 stimulation compared to P3 stimulation (mean difference = 8.05, $p < .001$, $BF_{10} = 427$). Carryover was larger following F3 stimulation compared to sham, though not significantly (mean difference = 4.30, $p = .066$, $BF_{10} = 3.87$). Carryover was smaller following P3 stimulation compared to sham, though not significantly (mean difference = 3.75, $p = .116$, $BF_{10} = 2.36$). Observed power for these non-significant effects was .37. Neither the main effect of carryover direction, $F(1, 27) = 0.11$, $MSE = 2.54$, $p = .749$, $\eta_p^2 < .01$, nor the interaction, $F(2, 27) = 1.52$, $MSE = 2.54$, $p = .596$, $\eta_p^2 = .04$, were significant.

Horizontal Letter-Strings



Vertical Letter-Strings

— Control — F3 P3



Random Letter-Strings

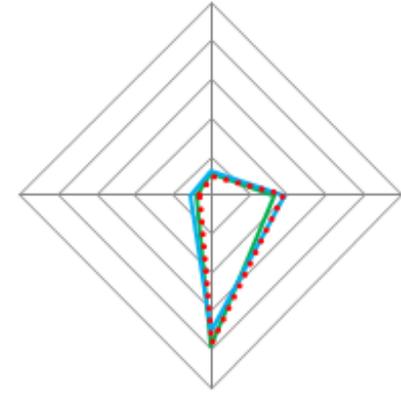


Figure 2. The mean number of saccades made in each cardinal direction split by the preceding letter-string and by rTMS site.

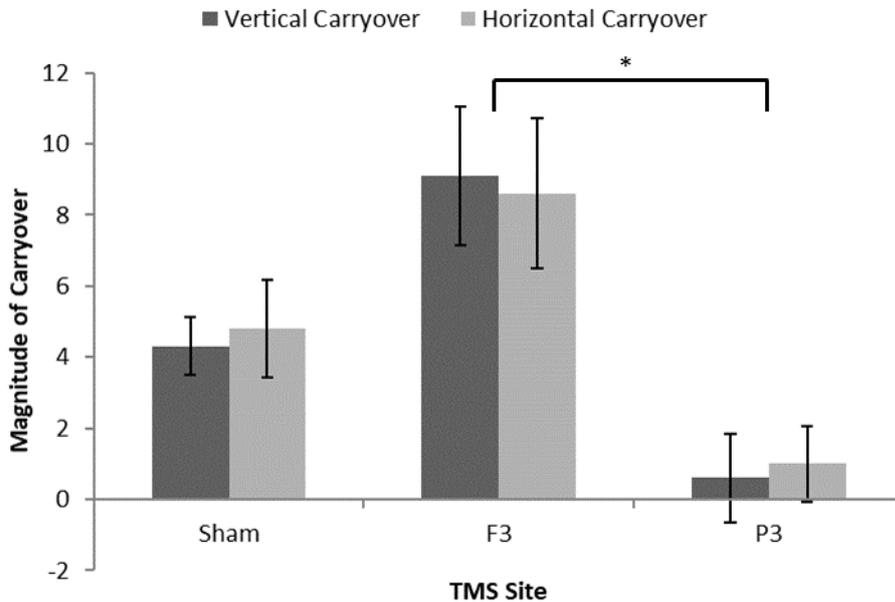


Figure 3. Mean magnitude of horizontal and vertical eye movement carryover from letter-strings to hazard rating task split by rTMS site. Error bars show standard error of the mean. Significant results ($p < .05$) are denoted by *.

A 3 (TMS site) x 3 (letter-string orientation) mixed-subjects ANOVA was carried out on the saccadic length data, shown in Figure 4. This revealed a main effect of letter-string orientation, $F(2, 54) = 15.00$, $MSE = 2.10$, $p < .001$, $\eta_p^2 = .36$, $BF_{10} = 1645.54$, in which pairwise comparisons revealed that saccade length was longer following the random letter-string than both the vertical (mean difference = 1.95, $p < .001$, $BF_{10} = 65814.48$) and horizontal (mean difference = 1.54, $p = .001$, $BF_{10} = 160.42$) letter-strings. There was no difference in saccade length following horizontal and vertical letter-strings (mean difference = 0.41, $p = .725$, $BF_{10} = 0.61$). Neither the main effect of rTMS site nor the interaction were significant, $F(2, 27) = 1.13$, $MSE = 32.65$, $p = .339$, $\eta_p^2 = .08$, $BF_{10} = 0.88$ and $F(4, 54) = 1.78$, $MSE = 2.10$, $p = .146$, $\eta_p^2 = .12$, respectively.

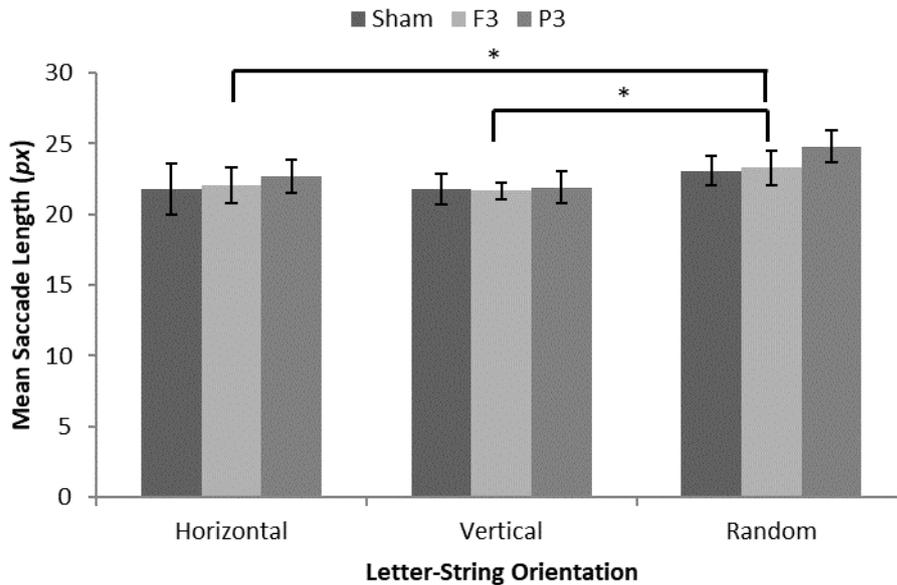


Figure 4. Mean saccade length (px) split by letter-string orientation and rTMS site. Error bars represent standard error of the mean. Significant results ($p < .05$) are denoted by *.

Finally, we carried out a parallel 3 x 3 mixed-subjects ANOVA on the hazard rating data, shown in Figure 5. This revealed a main effect of letter-string orientation, $F(2, 54) = 27.86$, $MSE = 0.08$, $p < .001$, $\eta_p^2 = .51$, $BF_{10} = 906193.81$, in which corrected pairwise comparisons demonstrated that hazard ratings were lower following the vertical letter-strings than both the horizontal (mean difference = 0.45, $p < .001$, $BF_{10} = 850056.08$) and random (mean difference = 0.48, $p < .001$, $BF_{10} = 117108441.35$) letter-strings. There was no difference in hazard ratings following the horizontal and random letter-strings (mean difference = 0.03, $p = 1.00$, $BF_{10} = 0.41$). There was also a main effect of rTMS site, $F(2, 27) = 6.51$, $MSE = 3.52$, $p = .005$, $\eta_p^2 = .33$, $BF_{10} = 906193.81$. Corrected pairwise comparisons revealed that hazard ratings were lower following rTMS to P3 than F3 (mean difference = 1.73, $p = .004$, $BF_{10} = 77.09$) and, to a lesser extent, sham (mean difference = 1.06, $p = .069$, $BF_{10} = 3.00$). There was no difference in hazard ratings following sham and F3 rTMS (mean difference = 0.68, $p = .29$, $BF_{10} = 0.96$). These main effects were qualified by a marginal interaction, $F(4, 54) = 2.36$, $MSE = 0.08$, $p = .064$, $\eta_p^2 = .15$. This interaction was revealed through a larger effect of letter-string for P3, $F(2, 18) = 17.32$, $MSE = 0.09$, $p < .001$, $\eta_p^2 = .66$, $BF_{10} = 329.98$, than F3 TMS, $F(2, 18) = 3.39$, $MSE = 0.06$, $p = .056$, $\eta_p^2 = .27$, $BF_{10} = 0.94$, and for sham, $F(2, 18) = 9.16$, $MSE = 0.09$, $p = .002$, $\eta_p^2 = .50$, $BF_{10} = 17.40$.

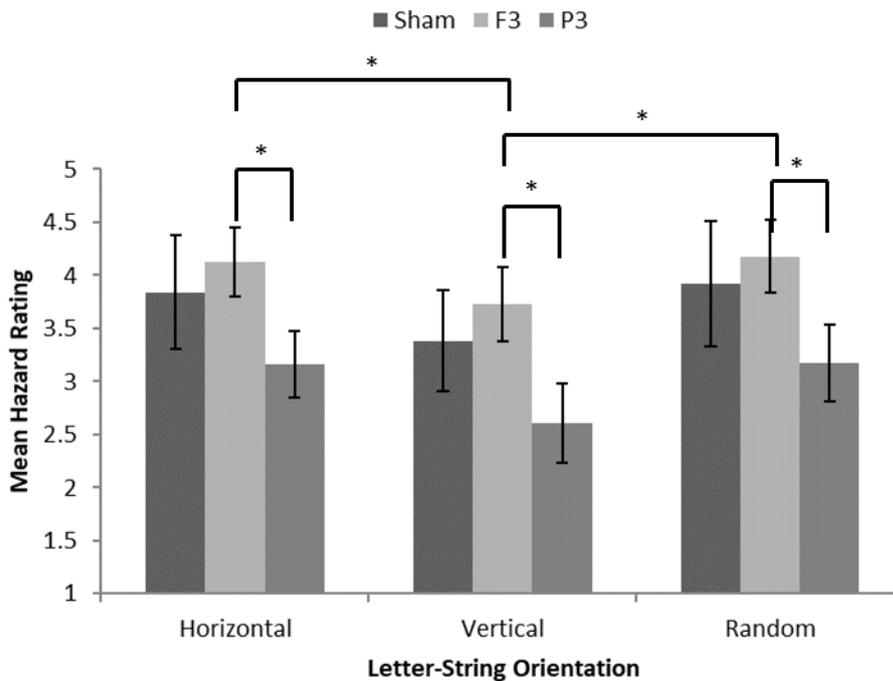


Figure 5. Mean hazard rating split by letter-string orientation and rTMS site. Error bars represent standard error of the mean. Significant results ($p < .05$) are denoted by *.

4. Discussion

In line with the predictions made, we found that the magnitude of eye movement carryover depended on the site of low-frequency rTMS: Carryover was larger following rTMS to the frontal lobe than to the parietal lobe (and the sham condition). Our Bayesian analysis shows that we have evidence in support of our experimental hypotheses, even when the traditional null hypothesis significant testing results did not prove significant. It has been argued that the persistence of attentional settings between two unrelated tasks is associated with increased attentional orienting and reduced set switching (Hills et al., 2016). By creating a temporary lesion to brain areas implicated in orienting and switching (e.g., Chambers et al., 2006; Giesbrecht et al., 2003) we have shown carryover varies according to key attentional mechanisms. By demonstrating that carryover is modulated by rTMS to frontal and parietal lobes, we have shown the importance of the fronto-parietal network in this effect. Parietal regions subsume attentional orienting that allow focused attention to be paid to the letter-strings. If this region is disrupted, then orienting is reduced (albeit, our results only show marginal evidence for this hypothesis, with low power). Thompson et al. (2015) argue that allocation of attention in the letter search task occurs via attentional weighting (see Bundesen, 1990), with weights allocated to relevant areas of space. Attentional inertia is due to persistence of these weights from one task to the next (Longman et al., 2013). Reduced orienting would potentially mean a reduction in the weighting given to the relevant locations in the letter search, making it easier to disengage from them and reducing the carryover. rTMS to P3 marginally decreased carryover because it reduces orienting. It makes sense that hazard ratings would be lower because participants are not orienting their attention effectively and so are not able to identify the hazards appropriately.

Frontal brain regions are associated with task switching. When moving from the letter-search to the hazard rating task participants are switching between two tasks and switching between two attentional sets. This requires inhibition of the initial attentional set and eye movement strategy and adoption of the new goal- and context-appropriate attentional set and eye movement strategy. It is proposed that disruption of the frontal lobe causes an enhanced carryover effect because participants are less able to inhibit the attentional set established for the letter search task and activate the top-down set relevant to the hazard rating task. This explanation neatly explains all of our findings and provides more evidence for the neurological basis of the carryover effect.

The pattern of significance also confirms our assertion that the carryover effect is driven by exogenous mechanisms rather than endogenous ones. If the carryover effect was due to endogenous mechanisms, we would expect the involvement of the frontal eye field (Bressler, et al., 2008; Hannula, et al., 2010; Hopfinger, et al., 2000), which can be affected by rTMS to F3. It follows that, if the carryover effect was driven by endogenous cueing, low-frequency rTMS to F3 should have decreased the carryover effect through disturbing the frontal eye field. Since the reverse was observed, we may be confident that the carryover effect is due to exogenous cueing.

Past studies have focused on saccade direction (e.g. Hills et al., 2018) and the horizontal and vertical spread of search (e.g. Thompson & Crundall, 2011). In the present study, we found that carryover was observed in two other metrics as well: saccade length and hazard ratings. Saccade length was also affected by the layout of the preceding letter-strings. In the vertical and horizontal letter-strings the stimuli are presented close together and they occupy a specific area of the screen. In the random letter search the stimuli can be presented anywhere on the screen and on average they are much more widely spaced. This would necessitate longer saccades between the letters and would also encourage the allocation of attention to the whole screen. Further, the distance from the end of the random letter-string (typically the bottom right of the screen given how most people read in English) is larger than the distance from the end of the horizontal and vertical letter-strings to the centre of the screen, which is where the eyes return to during the feedback screen (Hills et al., 2016). We propose that the increased saccade length in the hazard rating task following a random letter search demonstrates the carryover of this eye movement style or attentional set, with a wider focus and therefore increased spread of search across the images. This new measure provides more evidence for the persistence of top-down attentional settings between two unrelated tasks. There was no interaction with the site of rTMS, suggesting that the mechanism of saccade length carryover is different to that of saccade direction. Indeed, this is unlikely to be related to attentional orienting and thus unlikely to be affected by parietal rTMS. It may be related to the functioning of the frontal eye field given its involvement in saccade planning (Moore & Fallah, 2001), and to the dorsolateral prefrontal cortex given its involvement in task switching (Sohn, Ursu, Anderson, Stenger, & Carter, 2000). Both regions are affected by rTMS to F3, precluding the use of rTMS to establish the mechanisms of this effect.

In addition to showing the effect of attentional inertia on a further eye movement measure, the present study also found that hazard ratings were lower following the vertical letter-strings than the horizontal and random letter-strings (supporting evidence from the Bayesian analysis, whereas the results were marginal in significance). This supports previous work by Hills et al. (2018) and Thompson et al. (2011) and shows that performance in one task may be influenced by stimuli in an initial task. Vertical saccades are far less useful in driving situations and in hazard detection (Crundall, Chapman,

Phelps, & Underwood, 2003; Falkmer, & Gregersen, 2005; Mourant & Rockwell, 1972; Wallis & Horswill, 2007) because most of the potential hazards are located in the horizontal plane. It is therefore not surprising that any carryover from the vertical letters to the picture search would impair hazard ratings more than carryover from the horizontal or random letters. This finding highlights the implications of carryover and indicates that when performance and safety in a task is tightly linked to effective allocation of attention (e.g., the driving task), the way in which secondary information (e.g., in car displays) is presented needs to be carefully considered (Hills et al., 2016, 2018; Thompson & Crundall, 2011).

Whilst the influence of orientation of the letter-strings on hazard ratings did not interact with TMS site, the results did show that hazard ratings were lower following stimulation of P3 than F3 (and sham). The effects of parietal TMS were all the more important on hazard ratings given the significant main effect: Creating a temporary lesion in the parietal lobe generally caused participants to rate the road images as less hazardous. This, potentially, reflects the involvement of the parietal lobe in visual search. If the parietal lobe is less active, then visual search becomes more difficult, and hazards are more difficult to spot.

5. Conclusion

The carryover of eye movements from an initial task to a second, very different task has now been found across a number of studies (e.g., Hills et al., 2016; Thompson et al., 2011). Thompson et al. (2015) proposed that this carry-over reflects a persistence of top-down settings between two tasks and Longman et al. (2013) argue that settings will persist until they have been inhibited. Hills et al. (2016) investigated this by correlating the magnitude of the carryover with different functions of attention and showed that increased carryover was related to increased orienting and reduced switching abilities. The present study aimed to explore this further by applying rTMS to frontal and parietal areas, creating temporary lesions that would impact on the ability to orient and switch attention. We found evidence of attentional inertia, both in previously used measures, and in a new metric of saccade length. Crucially, the experiment showed that stimulation of parietal areas (reducing attentional orienting) marginally reduced the carryover of eye movements between a letter search and a picture search task, and stimulation of frontal areas (reducing switching) increased carryover. We have previously argued that theories of attention should be updated to incorporate the influence of preceding attentional settings. By establishing the role of important mechanisms of attention including orienting, inhibition, and switching we will be better able to predict how attentional inertia may align with established influences of attention.

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