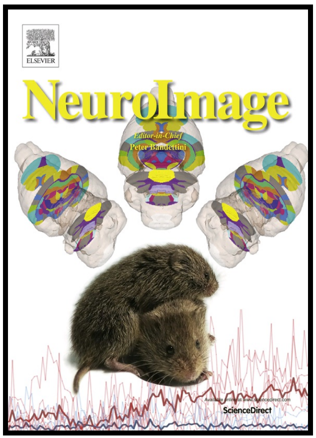

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Predictive position computations mediated by parietal areas: TMS evidence

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Abstract

When objects move or the eyes move, the visual system can predict the consequence and generate a percept of the target at its new position. This predictive localization may depend on eye movement control in the frontal eye fields (FEF) and the intraparietal sulcus (IPS) and on motion analysis in the medial temporal area (MT). Across two experiments we examined whether repetitive transcranial magnetic stimulation (rTMS) over right FEF, right IPS, right MT, and a control site, peripheral V1/V2, diminished participants' perception of two cases of predictive position perception: trans-saccadic fusion, and the flash grab illusion, both presented in the contralateral visual field. In trans-saccadic fusion trials, participants saccade toward a stimulus that is replaced with another stimulus during the saccade. Frequently, predictive position mechanisms lead to a fused percept of pre- and post-saccade stimuli (Paeye, Collins, & Cavanagh, 2017). We found that rTMS to IPS significantly decreased the frequency of perceiving trans-saccadic fusion within the first 10 minutes after stimulation. In the flash grab illusion, a target is flashed on a moving background leading to the percept that the target has shifted in the direction of the motion after the flash (Cavanagh & Anstis, 2013). In the first experiment, the reduction in the flash grab illusion after rTMS to IPS and FEF did not reach significance. In the second experiment, using a stronger version of the flash grab, the illusory shift did decrease significantly after rTMS to IPS although not after rTMS to FEF or to MT. These findings suggest that right IPS contributes to predictive position perception during saccades and motion processing in the contralateral visual field.

Keywords: Predictive position perception; Transcranial magnetic stimulation (TMS); Intraparietal sulcus (IPS); Frontal eye fields (FEF); Flash grab; Trans-saccadic fusion.

1. Introduction

Visual perception allows us to jump out of the path of a speeding car, duck to avoid a low branch, catch a ball, and know when to stop pouring tea in our cup. Each of these examples demonstrates visual prediction of object location across time. Visual prediction is most obvious for an object in motion, where object location is predicted from current trajectory and speed. Prediction is also important when the object relocates in our visual field as a result of our own eye movements. In this paper, we examine both cases of location prediction, one involving eye movement and the other target movement. We attempt to disrupt these position predictions with repetitive transcranial magnetic stimulation (rTMS) to determine which brain areas are involved in these processes, and whether there are common regions underlying both types of predictive position processing.

There is strong evidence that the cortical network that controls eye-movements is a hub for predictive position shifts, seen both in predictive remapping just before the eyes move (Duhamel, Colby, & Goldberg, 1992; Goldberg & Bruce, 1990; Umeno & Goldberg, 1997) and interceptive saccades that compensate for the movement of a target during the delay in saccade execution (Bourrelly, Quinet, Cavanagh, & Goffart, 2016; Fleuriet & Goffart, 2012; Robinson, 1972). We focus on two components of the eye movement network: the frontal eye fields (FEF) and the intraparietal sulcus (IPS), both of which show contralateral, retinotopic representations of saccade targets and attended stimuli when mapped with fMRI (Hagler Jr., Riecke, & Sereno, 2007; Kastner et al., 2007; Sereno, Pitzalis, & Martinez, 2001). FEF and IPS both show remapping: responses to targets at locations where they will be after the saccade lands – their future location in the visual field. Some cells show these predictive responses even before the saccade begins (Duhamel et al., 1992; Goldberg & Bruce, 1990; Umeno & Goldberg, 1997). Behavioral studies also show that attention is remapped just before a saccade (Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011). These physiological and behavioral studies demonstrate a transfer of activation to the predicted next location of a target but do not address whether there is any transfer of the target's properties. A recent study (Paeye et al., 2017) presented evidence that remapping may carry a representation of the saccade target to its predicted post-saccadic location (the fovea) even though the target is removed before the saccade lands (also see Wolf & Schütz, 2015). In the Paeye et al. study, the saccade target was removed and replaced with another stimulus. The two components were fused into a single pattern on 67% of trials. We will use this trans-saccadic perceptual fusion to further study predictive position remapping during saccades.

In addition to predicting the effects of the saccade on our visual field, the saccade system also predicts the effects of moving stimuli across our visual field. Specifically, saccades land quite accurately on moving targets, a feat that requires computation of the future target location based on current position, target speed and trajectory. Physiological recordings show that some units in the superior colliculus (and FEF (Cassanello, Nihalani, & Ferrera, 2008) code for the landing location of a moving target as opposed to its current retinal location. This extrapolation of the moving target's location is mirrored in perceptual tests where several motion-induced position shifts demonstrate a displacement of perceived position of a moving target (flash lag, Eagleman & Sejnowski, 2007; Nijhawan, 1994; flash drag, Whitney & Cavanagh, 2001; flash grab, Cavanagh & Anstis, 2013). Predictive, motion-induced position shifts have been demonstrated at various stages of the visual system, in single-cell animal recordings (Berry, Brivanlou, Jordan, & Meister, 1999; Fu, Shen, Gao, & Dan, 2004; Sundberg, Fallah, & Reynolds, 2006) and human studies (Maus, Fischer, & Whitney, 2013; Vetter, Grosbras, & Muckli, 2015; Whitney et al., 2003). We will use one of the perceptual motion-induced position shifts, the flash grab, as our test of predictive position coding for moving targets. In the flash grab stimulus, a flash presented on a rotating stimulus just as it reverses direction is perceptually shifted (or 'grabbed') in the direction of the subsequent motion (Cavanagh & Anstis, 2013). This shifted location of the flash reflects a prediction of where the flash would have been if it actually moved with the rotating stimulus.

To investigate predictive position mechanisms within FEF and IPS, we examined whether rTMS over right FEF and right IPS diminished predictive position effects for stimuli presented in the left visual field. We used the two cases of predictive position effects mentioned above: trans-saccadic fusion and the flash grab illusion. In the first experiment, we compared fusion reports and motion-induced shifts for 2 sessions without rTMS (first and last), with the effects of rTMS on right FEF, right IPS, and our control site, peripheral early visual cortex (V1/V2). We hypothesized that rTMS to right FEF and right IPS would produce a significant reduction in trans-saccadic fusion and the flash grab illusion in comparison to the levels seen for the no TMS and control sessions (peripheral V1/V2).

Our second experiment focused on a more robust version of the flash grab illusion to further investigate the trend of rTMS effects that we found in the first experiment. We also included right MT as an rTMS target site to examine the extent to which low-level motion centers contribute to the position predictions. Previous evidence has indicated that the flash grab effect depends on attention and attentive tracking of the moving target (Cavanagh & Anstis, 2013; Vito et al., 2015). These functions are likely to involve the frontoparietal network (Culham et al., 1998; Sheremata & Silver, 2015; Szczepanski, Konen, & Kastner, 2010). Consequently we hypothesize that IPS should be involved to a greater extent than right MT, which is more relevant for low-level motion processing (Battelli, Alvarez, Carlson, & Pascual-Leone, 2009; Culham, Cavanagh, & Kanwisher, 2001).

2. Methods & Materials

2.1 Participants.

21 participants including authors GE and RVR (10 female; 23-41 years) with normal or corrected-to-normal vision were recruited for the two experiments. All participants gave written consent, and the study was approved by the local ethics committee "CPP Sud-Ouest et Outre-Mer I" protocol number 2009-A01087-50. Standard TMS exclusion criteria were employed (Rossi, Hallett, Rossini, & Pascual-Leone, 2009). Seventeen participants were recruited for experiment 1; five participants were removed (leaving 12) from the statistical analysis as their perceptual effects fell outside our criterion range (see Analysis section). Ten participants were recruited for experiment 2, six of which had performed the first experiment. There was a six-month time lapse between experiment 1 and experiment 2, alleviating concerns about carry-over effects.

2.2 Apparatus & Visual Stimulation.

Participants viewed the stimulus on a 16-inch Sony Triton Monitor (1280 x 1024; 85 Hz) at a distance of 60 cm. A chin and forehead rest supported participant's head. Throughout the experiment, participants' saccades were recorded using an EyeLink 1000 Plus. Calibration was conducted at the beginning of each run and briefly again during the experiment if the participant moved (Figure 1c). All stimuli were presented using MatLab 2013a and Psychophysics Toolbox extensions (Brainard, 1997; Kleiner, 2010) .

2.2.1 Experiment 1

Participants performed two tasks during three blocks of ten minutes. The tasks alternated every 30 seconds within each ten-minute block (Figure 1c). Each block of 30 seconds was introduced by a title slide that indicated the task the participant was to perform. Importantly, the trans-saccadic fusion and flash grab illusion were presented on the left of the screen. The left side stimulus was paired with right side TMS sites (see TMS Protocol).

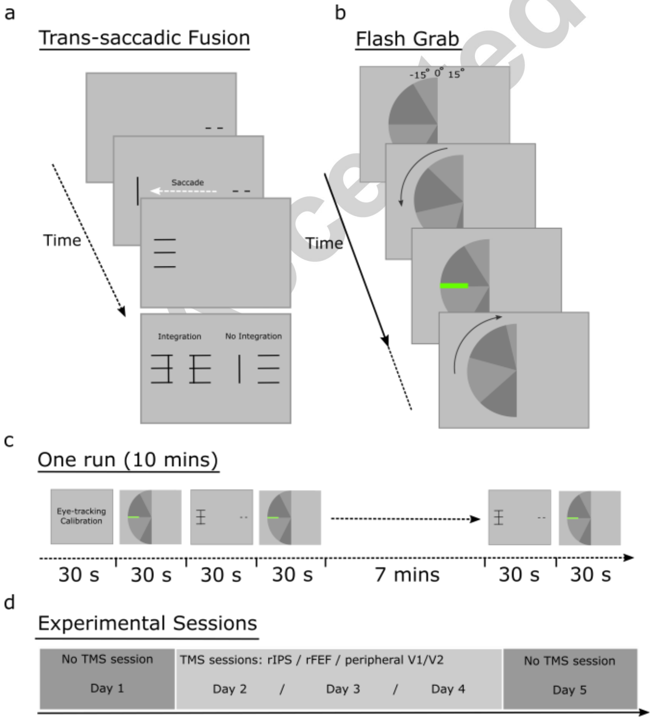

Figure 1: Stimulus and Procedure. 1a) Trans-saccadic fusion stimulus. Participants fixated between two dashes and saccade leftward when vertical bar appeared. During saccade the vertical bar was replaced with three horizontal bars. After saccade, participants judged if the post-saccadic stimulus appeared to be fused with the pre-saccadic stimulus. 1b) Flash Grab illusion stimulus. Participants fixated in the centre of the screen while the semi-circle on display continuously rotated back and forth. A green bar was flashed each time the rotation changed from counter-clockwise to clockwise and participants had to manually alter the disk orientation (and the flashed bar with it) until they perceived the flash to be horizontal. 1c) Participants performed three 10 minute runs, 1c) is a depiction of one of the 10 minute runs. Participants performed initial eye-tracking calibration and then alternated tasks between flash grab and trans-saccadic fusion every thirty seconds. 1d) Illustration of the five experimental sessions across five days. TMS sessions were counterbalanced across participants.

2.2.2 Trans-saccadic Fusion Stimulus.

Participants fixated between two dashes (separated by 2°) located 7° to the right of the center of the screen (Figure 1a). After a random interval of 100-700 ms, the dashes were removed and a black vertical bar (height: 1.4°; width: 0.4°) was presented 14° to the left of the fixation point. Participants were instructed to saccade towards the vertical bar on presentation. During the saccade, the bar disappeared and was replaced by three black horizontal bars (1.24° in width) centered on the same x-coordinate, separated by 0.45° vertically. The three horizontal bars were presented for 45 ms. Participants were instructed to report their percept with one of three responses: no integration, vertical bar integrated with the horizontal bars and appearing to the left of the center of the horizontal bars, or vertical bar integrated with the horizontal bars and appearing to the right of center of the horizontal bars (Figure 1a). The left vs. right integration responses match the responses in the previous study (Paeye et al., 2017) but are not analyzed here.

2.2.3 Flash Grab Illusion (Experiment 1).

Participants fixated at the center of the screen at the center point of a half-disk presented to the left of fixation (Figure 1b). The disk (radius of 13°) was split into six segments of 60° each and continuously rotated counter-clockwise and clockwise from a randomized start-point between -15° and 15° to 120°. Each time the motion changed from counter-clockwise to clockwise, and a green bar (length of 7°) was flashed and the motion of the sectored disk stopped for 47 ms. While observing this reversing motion and the flashes, participants adjusted the range of the rotation of the disk and with it the location of the green bar until they perceived the flash to be horizontal. The bar appeared to be shifted in the direction of the motion after reversal as a result of motion-induced position shift from the rotating disk (Cavanagh & Anstis, 2013). The deviation of the participants' adjustment away from true horizontal was taken as an estimate of the illusory shift they perceived. Participants have up to 30 seconds to adjust the location of the reversal point using the left and right arrow keys. Trial number per block was limited by reaction time to complete each trial within the 30 seconds (average 3.9 trials per block). A spacebar press indicated the participant was finished with the adjustment, which also allowed the participant to move onto the next trial.

2.3 Experiment 2

In experiment 2, participants only performed one task during one run of ten minutes. The task was a different version of the flash grab illusion from experiment 1 presented on the left of the screen, as in experiment 1.

2.3.1 Flash Grab Illusion (Experiment 2).

Participants fixated the center point of a half disk. Only the left side of the disk was visible (Figure 2). The disk (radius 4°) was filled with Gaussian noise summed across different frequencies using fractional Brownian motion and this texture changed on every trial (Adamian & Cavanagh, 2016). Assuming 0° to be at the top of the disk, the disk rotated clockwise and counter-clockwise through 120°, with randomized reversal points between 210° and 330°. A green dot (radius 1.5°) was presented for 47 ms at the second reversal of the trial on the inside of the textured circle. After this final rotation, the participants were instructed to use the mouse to adjust a green dot on the screen to the point at which they had perceived the flash. During the ten minute run participants performed 70 trials.

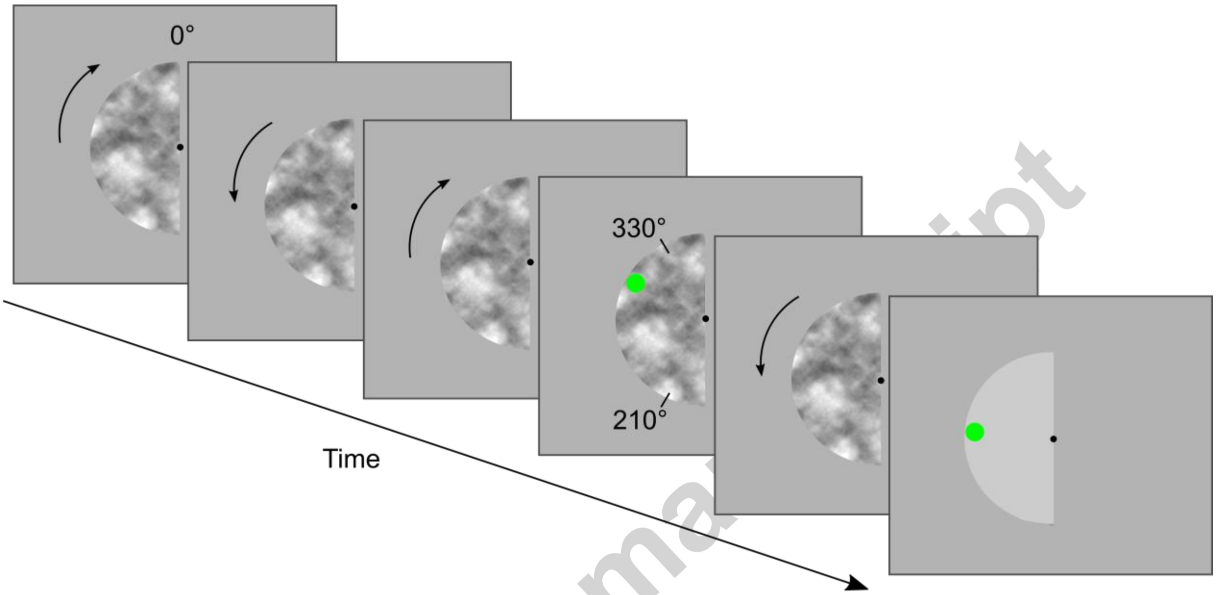

Figure 2: Experiment 2 – Flash Grab Stimulus. Participants fixate on the central fixation point while the texture rotates clockwise 120° followed by counter-clockwise back to the start point. The texture reversed direction of rotation from clockwise to counter-clockwise two times at a randomized point between 210° and 330°. On the second reversal of direction, a green dot is flashed for 47 ms. After the second rotation, participants were presented with a light grey semi-circle at the same position as the rotating texture and a randomly positioned green dot just within the circumference. Participants were required to move the dot to the position where the green dot was perceived within the rotating texture.

2.4 TMS Protocol.

Repetitive TMS was delivered using a MagStim Rapid^2 stimulator and a Double 70 mm alpha coil. Participants received 10 min of repetitive stimulation at a low frequency of 1 Hz over one of three sites, right FEF, right IPS, or peripheral V1/V2 for experiment 1. A fourth site, right MT, was included for experiment 2. Right IPS and FEF were selected (compared to the left hemispheric regions) as these right hemispheric sites have shown clear roles within saccadic remapping and spatial control (Battelli, Pascual-Leone, & Cavanagh, 2007; Plow et al., 2014; Ruff et al., 2009; Silvanto, Muggleton, Lavie, & Walsh, 2009). Right MT was selected above left MT as the stimulus was presented in the left visual field in accordance with the selection of right IPS and FEF. The stimulation intensity was set at 65% (Chanes, Chica, Quentin, & Valero-Cabré, 2012; Muggleton, Juan, Cowey, & Walsh, 2003; O'shea, Muggleton, Cowey, & Walsh, 2004; Silvanto, Lavie, & Walsh, 2006). Once stimulation had been applied, participants immediately performed the two behavioral tasks in alternation during the following 30 minutes (three runs of 10 minutes; Figure 1c) in experiment 1. Only the flash grab illusion was performed by participants for 10 minutes after rTMS to one of the four TMS sites in experiment 2.

2.4.1 Experiment 1 protocol.

The testing was split into five sessions performed over five days (Figure 1d). On day one, participants were familiarized with the paradigm during a training phase. Participants then performed three runs of ten minutes of the behavioral paradigm. After testing, participants peripheral V1/V2 was located for future use. Over days two, three, and four participants underwent 10 minutes of repetitive TMS to one of the three brain sites. These sites were counterbalanced across the 12 participants included in the statistical analysis. The TMS coils were air-cooled in order to reduce coil over-heating, however the coils would overheat after approximately 400 pulses, resulting in a rapid exchange for an identical coil for the final 200 pulses. Immediately after stimulation, participants performed three runs of the paradigm. On the fifth day, participants completed the experiment with a final three runs of the paradigm without prior rTMS stimulation. The final behavioral session on day five was averaged with the first behavioral session to account for any practice effects across the five sessions.

2.4.2 Experiment 2 protocol.

The protocol was split over five days with one TMS condition on each day. Balanced Latin Squares was employed to handle the counterbalancing of five conditions. Peripheral V1/V2 was located for each participant 10 minutes prior to performing rTMS at this site. All other regions were located prior to the testing days. As with experiment 1, the TMS coils were cooled using a ventilation system and were swapped for an identical coil after overheating (at approximately 400 pulses). Participants performed the flash grab task immediately after 10 minutes (600 pulses) of repetitive TMS stimulation.

2.5 Coil Positioning.

Brainsight Frameless Stereotaxy system (Rogue Research, Montreal, Canada) was used to localize the three brain sites for nine of the 12 participants with individual T1-weighted anatomical MR images transformed into Talairach space (along the AC-PC plane) in experiment 1, and to localize the four brain sites for seven of the 10 participants with anatomical MR images in experiment 2. Right FEF was localized using averaged Talairach coordinates (x=26(sd=2), y=0(4), z=47(2) in experiment 1 and x=25(sd=2.4), y=-3(2.1), z=47(1.0) in experiment 2; similar to Paus, 1996: x=31(sd=11), y=-2(5), z=47(5)). These coordinates located the right FEF within the middle frontal gyrus, in front of the junction of the pre-central and superior frontal sulcus (Blanke et al., 2000; Figure 3). The coil was oriented with the current flowing toward the pre-central sulcus (Chanes et al., 2012; Grosbras & Paus, 2002). Localizing right IPS was achieved using individuals' curvilinear overlay of the T1-weighted anatomical. IPS is readily located in the anatomical; specifically we targeted the posterior part of IPS which shows an increased representation of saccades (Grosbras, Laird, & Paus, 2005; Konen & Kastner, 2008; Koyama et al., 2004; Figure 3). The coil was held with the handle pointing backward, in a tangential orientation (Ruff et al., 2008; VanRullen, Pascual-Leone, & Battelli, 2008). The average coordinates for right IPS over the nine participants was x=27(sd=5.2), y=-57(11.9), z=50(7) for experiment 1, and x=28(sd=3.8), y=-51(6.4), z=47(4.8) for the seven participants in experiment 2. Our control site, peripheral V1/V2, was located by initiating peripheral phosphenes and recording the location in Brainsight. At first foveal phosphenes were stimulated with the intention to move the phosphene percept out to the periphery. Foveal phosphenes were found approximately 3 cm above the inion (Romei, Murray, Merabet, & Thut, 2007), and peripheral phosphenes were regularly elicited approximately 1.5 cm to the left or the right (Koivisto & Silvanto, 2012). In all participants we found that the most effective orientation of the coil was with the handle orientated horizontal to the right (Kammer, Puls, Erb, & Grodd, 2005; Salminen-Vaparanta et al., 2013). In experiment 1 and 2, participants peripheral phosphenes were located by sending single pulses at an intensity beginning at 50% and rising as required (within an upper limit of 82%), in each of these participants the peripheral phosphenes were located in left hemisphere V1/V2. For one participant from experiment 1 we employed a train of 7 pulses at 20 Hz to successfully induce phosphenes and located peripheral phosphenes in right V1/V2. There was no significant difference between the task performance of this participant and the other 11 participants in experiment 1 after rTMS to the control peripheral V1/V2 in the two tasks (trans-saccadic fusion: 11 participants mean performance = 70%, 12th participant performance 83%, p=0.052; flash grab: 11 participants mean performance = 5.69°, 12th participant mean performance = 4.032°, p=0.095).

In experiment 2, right MT was localized by initiating moving phosphenes and recording the location in Brainsight. The coil was placed 3cm above and 5cm to the right of the inion (Battelli, Black, & Wray, 2002; Campana, Cowey, & Walsh, 2002; Mather, Battaglini, & Campana, 2016; Théoret, Kobayashi, Ganis, Di Capua, & Pascual-Leone, 2002). The coil was held tangentially to the skull and moved in a grid pattern whilst delivering single-pulse stimulation to locate the strongest subjective impression of phosphenes (Beckers & Zeki, 1995; Mather et al., 2016; Stewart, Battelli, Walsh, & Cowey, 1999; Thompson, Deblieck, Wu, Iacoboni, & Liu, n.d.). Moving phosphenes were elicited between 65% - 80% for seven participants. The remaining three participants who did not perceive phosphenes were stimulated at averaged co-ordinates (x=38(sd=5.0), y=-73(7.0), z=15(4.8)) which are similar to the averaged coordinates of previous studies (Vetter et al., 2015).

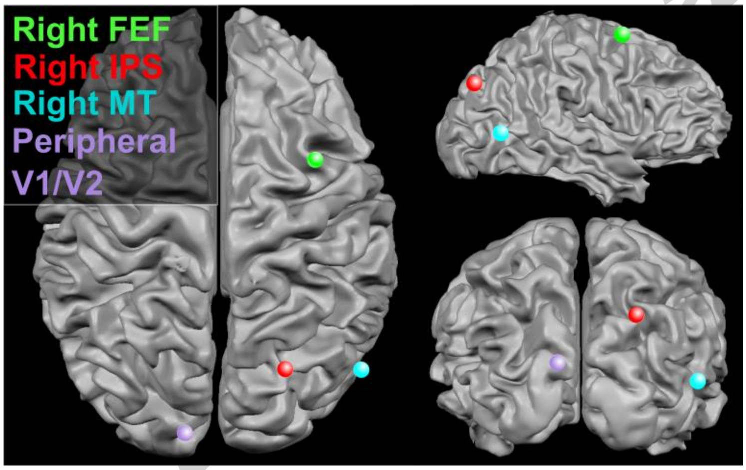

Figure 3: TMS stimulation sites. Averaged coordinates across 12 participants (across both experiments) with individual T1-weighted anatomical MRIs for the right IPS and right FEF TMS sites illustrated on one participant's MRI image. Right MT also depicted on the MRI image from averaged coordinates of seven participants in experiment 2. Peripheral V1/V2 is one example of one participant.

Right IPS, right FEF, and right MT (in experiment 2) localization for the remaining participants without anatomical MR images was determined using averaged co-ordinates from the nine participants along with a 64-channel electroencephalography (EEG) cap (labeled according to the 10/20 extended system). Right FEF was localized as 3.2 cm from FC2 toward C4 and 2.5 cm from FC6 toward C2. Right IPS was localized 3.2 cm from CP2 toward P6 and 2 cm from CP4 toward P2. Right MT and peripheral V1/V2 was located as with the participants with individual T1-weighted anatomical MRIs.

2.6 Analysis.

All analysis was performed in MatLab (2013a). In experiment 1, participants were removed from further analysis if they were at ceiling for perceiving the trans-saccadic fusion (>95%) or did not perceive the flash grab illusion (<2.5°) averaged across the no-TMS sessions. This led to the removal of five participants, leaving 12 for the analyses. All participants perceived a strong flash-grab illusion in experiment 2 and were included in the analysis. Mean detection accuracy for each task, each session and each run was calculated. The no-TMS session data collected on day one was averaged with the no-TMS data collected on day five in experiment 1. Our time-period of interest was the first 10 minutes of data collected in each session when rTMS is most likely to inhibit performance of the targeted regions (VanRullen et al., 2008). Eye-tracking calibration was conducted within the first 30 seconds of each run. In experiment 1, the final 20 minutes of behavioral data were collected to ensure that rTMS effects wore off during the 30-minute time-period. Random effects analysis of variance were performed on the first 10 minutes of data to determine if there was an effect of TMS session in experiment 1 and 2 individually. Post-hoc t-tests revealed which of the TMS sessions drove the result of the random effects ANOVAs. P-values were FDR corrected to account for multiple comparisons. A Mann-Whitney U test was performed between the no-TMS flash grab of experiment 1 versus experiment 2. A non-parametric test was used on this occasion due to the differing number of participants in each experiment (exp 1, n=12; exp 2, n=10).

3. Results

We examined whether the predictive process involved in localization across eye movements and target movements involve the saccade control areas FEF and IPS. After application of rTMS to FEF and IPS we expected a reduction in the predictive positioning of the target when the eyes or the target were in motion. We tested two cases of predictive position perception — trans-saccadic fusion and the flash grab illusion — in two experiments.

3.1 Experiment 1

We collected 30 minutes of data after each rTMS session with the aim of analyzing the first ten minutes for TMS effects and the last 10 minutes to ensure participants performance returned to baseline.

3.1.1 Trans-saccadic Fusion Results

Participants only performed leftward saccades during our trans-saccadic fusion paradigm and participants most often reported that the vertical bar was to the left of the center of the horizontal bars (75.76% leftward responses during no TMS sessions, SEM 0.06%, significantly more frequent than rightward responses, t(11)7.32 p<0.0001).

Over the first 10 minutes, in the absence of rTMS stimulation, participants reported trans-saccadic fusion on 72.05% (SEM 5.29%) of the trials. This frequency is similar to that previously reported for trans-saccadic fusion under similar conditions (67%; Paeye et al., 2017). The frequency of trans-saccadic fusion decreased to 59.69% (SEM 6.01%) over the first 10 minutes after rTMS to right IPS and to 61.64% (SEM 5.68%) after rTMS to right FEF. Fusion did not decrease after rTMS to peripheral V1/V2 relative to no rTMS condition (70.86%, SEM 5.74%). Despite the fluctuations in the frequency of trans-saccadic fusion across the different conditions, participants reported trans-saccadic fusion in all conditions (no TMS: t(11)13.61, p<0.0001; rTMS to IPS: t(11)9.93, p<0.0001; rTMS to FEF: t(11)10.85, p<0.0001; rTMS to V1/V2: t(11)12.34, p<0.0001).

An ANOVA across all these conditions of the first 10 minutes show a main effect of rTMS condition on the frequency of the trans-saccadic fusion reports (F(3,11)=5.21,p=0.0047; Figure 4). Post-hoc comparisons indicated that this effect was being driven by rTMS to IPS. There was a significant difference in fusion after rTMS to IPS in comparison to the no TMS session (t(11)=3.85,p=0.0027) and in comparison to the control TMS site peripheral V1/V2 (t(11)=3.32,p=0.0068). However, we found FEF was not significantly different from the no TMS session (t(11)2.13, p=0.06) or the V1/V2 TMS control site (t(11)1.85, p=0.09), but nor did it differ from the IPS result (t(11)0.51, p=0.62). rTMS to peripheral V1/V2 did not affect trans-saccadic fusion compared to the no TMS condition (t(11)0.45, p=0.66).

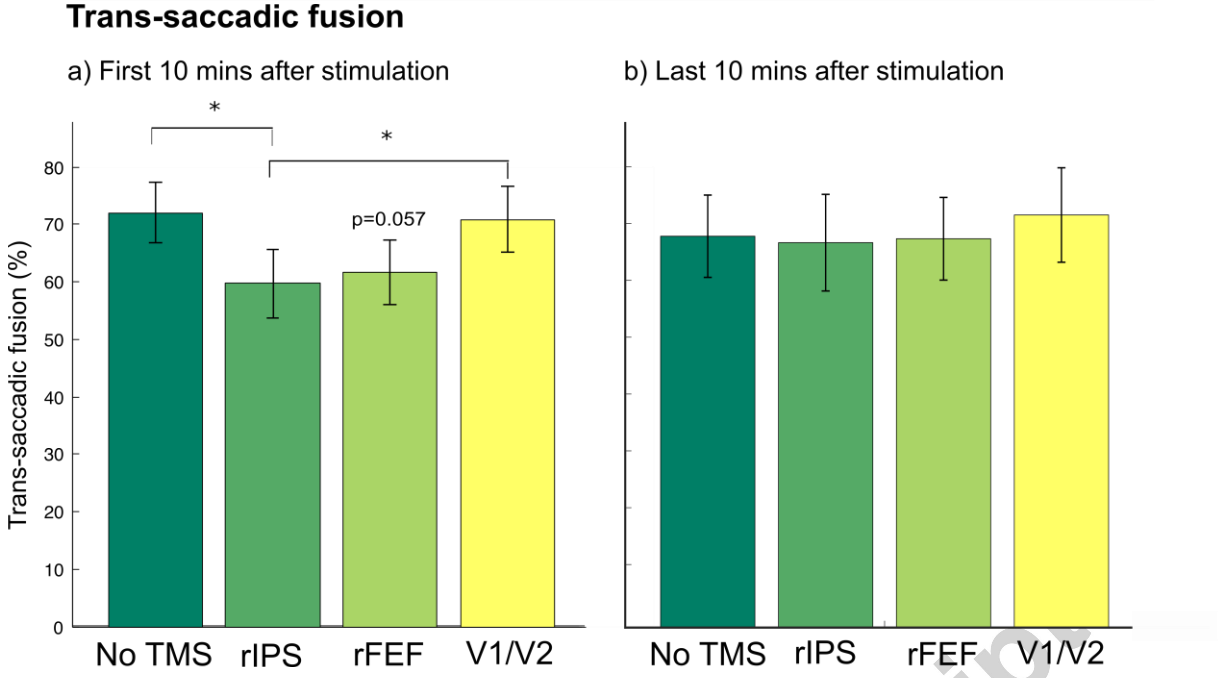

Figure 4: TMS effects on trans-saccadic fusion: 4a) trans-saccadic fusion during first ten minutes after stimulation: Percentage of perceived trans-saccadic fusion across the four TMS conditions (no TMS, TMS to right IPS, TMS to right FEF, TMS to control site peripheral V1/V2). Significant comparisons are signified by *, rTMS to rIPS significantly reduced fusion in comparison to no TMS baseline (t(11)=3.85,p=0.0027) and in comparison to rTMS performed over control region V1/V2 (t(11)=3.32,p=0.0068). 4b) trans-saccadic fusion during last ten minutes after stimulation. Error bars show standard errors of the mean.

There was no significant difference across the conditions (F(3,11)=1.11, p=0.36) during the last 10 minutes after stimulation, demonstrating that rTMS effect on trans-saccadic fusion had subsided by the end of the behavioral experiment.

3.1.2 Flash Grab Illusion Results

When no TMS was performed, participants' adjustments showed an illusory shift of 5.50° for the flash grab effect in the first 10 minutes of the test session. An illusory shift of 5.50° is lower than the 15° shift previously reported with a similar paradigm (Cavanagh & Anstis, 2013). The perceived illusory shift was 4.91° after rTMS to right IPS (Figure 5), 5.27° after rTMS to right FEF, and 5.55° after rTMS to peripheral V1/V2. Across participants, the perceived shift in each condition was significantly above zero (no TMS: t(11)9.03, p<0.0001; rTMS to IPS: t(11)8.93, p<0.0001; rTMS to FEF: t(11)7.34, p<0.0001; rTMS to V1/V2: t(11)6.51, p<0.0001). Although there seems to be a 10% decrease in flash grab after rTMS was applied to right IPS, the repeated measures ANOVA found no significant difference between the four conditions (F(3,11)0.55, p=0.65). Similarly no rTMS effects were found in the final 10 minutes after rTMS stimulation (F(3,11)0.88, p=0.46). Overall, these results showed that rTMS did not significantly decrease the motion-induced position shift for this version of the flash grab illusion.

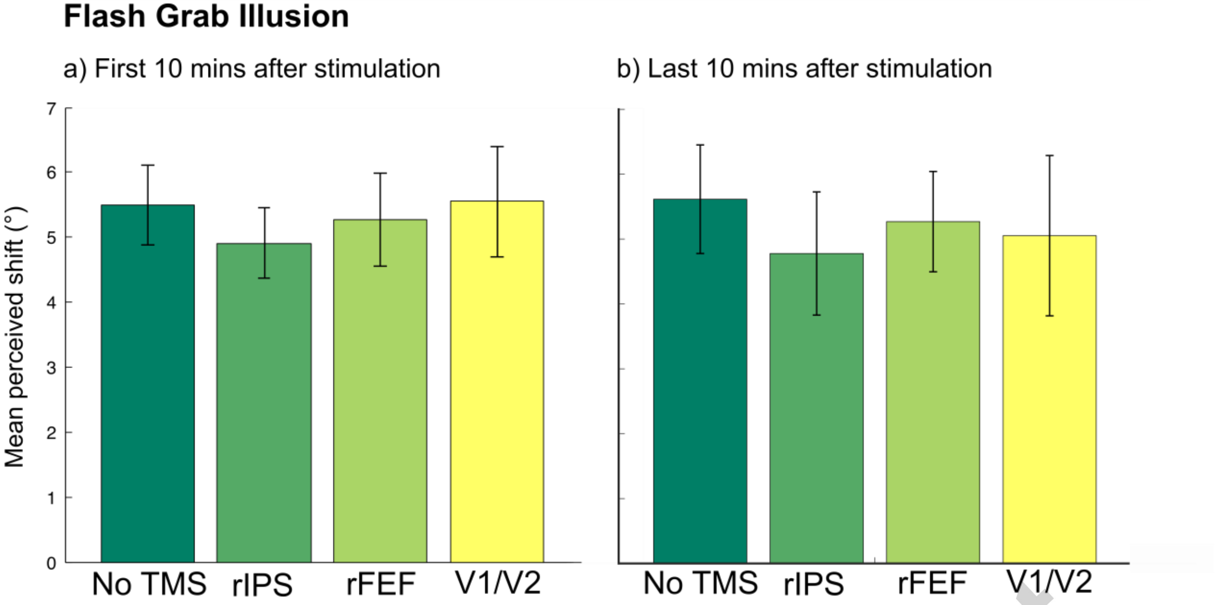

Figure 5: TMS effects on flash grab illusion. 5a) Flash grab during first ten minutes after stimulation: Perceived shift of flash across the four TMS conditions (no TMS, TMS to right IPS, TMS to right FEF, TMS to control site peripheral V1/V2). 5b) Flash grab during last 10 minutes after stimulation. Error bars show standard errors of the mean.

The absence of an rTMS effect on the flash grab illusion here motivated a second experiment using a different version of the flash grab stimulus which reliably causes a larger illusory shift (Adamian & Cavanagh, 2016). With this increased baseline illusory shift, we had the opportunity to verify the trend observed in experiment 1.

3.2 Experiment 2

3.2.1 Flash Grab Illusion Results

In this second experiment, we changed the stimulus and added a new stimulation site, MT. In the two control conditions, without rTMS and with rTMS to peripheral V1/V2, participants perceived the flashed green dot to be shifted by approximately 20.55 and 21.98 degrees of rotation, respectively, away from the veridical position and in the direction of the motion after reversal (Figure 6). This shift magnitude of experiment 2 (n=10) is significantly larger that the 5.50° seen in Experiment 1 (n = 12) (Mann-Whitney U, U = 198, p=0.0008) and is comparable to baseline perceived shift of 25° found previously with this flash grab stimulus (Adamian & Cavanagh, 2016). We believe the differential rTMS effect on the two flash grab experiments is related to the rotation range of the disk and the extended viewing and response time (within the 30 second block) of the first experiment. These design factors may have allowed participants to adapt to the stimulus and produce more veridical behavioral responses in experiment 1.

A random effects ANOVA of the new results found a significant effect of rTMS condition on mean perceived shift (F(4,9)=3.92, p=0.0025). Post-hoc comparisons indicated that rTMS to right IPS resulted in a significant decrease in perceived shift of the green dot in comparison to the no TMS condition (t(9)=2.34, p=0.04) and in comparison to the control condition of rTMS to peripheral V1/V2 (t(9)=3.75, p=0.0046). There was also a significant decrease in perceived shift after rTMS to right FEF in comparison to the control condition of rTMS to peripheral V1/V2 (t(9)=2.34, p=0.045). However there was no significant difference in perceived shift of the flashed dot after rTMS to right FEF (t(9)1.26, p=0.24) or after rTMS to right MT (t(9)1.01, p=0.32) in comparison to the no TMS condition.

There was also a significant difference in perceived shift after rTMS to right IPS in comparison to perceived shift after rTMS to right MT (t(9)2.83, p=0.02). As with the previous experiment, regardless of the alteration in perceived shift caused by rTMS, participants illusory shift was significantly above zero in each condition (no TMS: t(9)25.14, p<0.0001; rTMS to MT: t(9)21.50, p<0.0001; rTMS to IPS: t(9)14.66, p<0.0001; rTMS to FEF: t(9)28.68, p<0.0001; rTMS to V1/V2: t(9)26.35, p<0.0001). .

To ensure participants recovery to baseline, figure 6b illustrates the mean perceived shift per condition within the last two minutes after stimulation. A repeated measures ANOVA demonstrated no significant difference between the 5 conditions during the last two minutes (F(4,9)0.63, p=0.64).

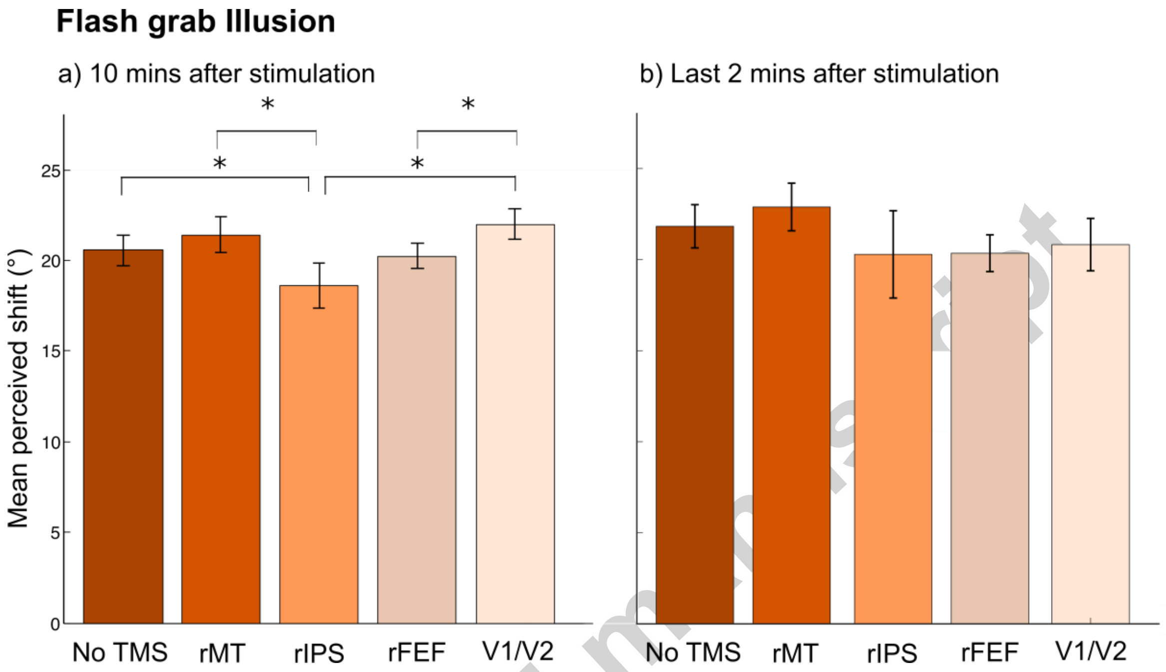

Figure 6: Experiment 2: TMS effects on flash grab illusion 6a: Flash grab during first ten minutes after stimulation: Perceptual shift across the five TMS conditions (no TMS, TMS to right MT, TMS to right IPS, TMS to right FEF, TMS to control site peripheral V1/V2). Difference of TMS conditions to the no TMS baseline. Error bars show standard errors of the mean. Significant comparisons are signified by *, rTMS to rIPS significantly reduced perceived shift in comparison to no TMS baseline (t(9)=2.3402, p=0.044) and in comparison to rTMS performed over control region V1/V2 (t(9)=3.75, p=0.0046). A significant difference was also found between rTMS to FEF and rTMS to control condition rTMS to peripheral V1/V2 (t(9)=2.32, p=0.0455).6b Flash grab during last two minutes after stimulation. Error bars show standard errors of the mean.

4. Discussion

We investigated whether saccade related areas (FEF and IPS) are involved in predictive position perception. In our first experiment we found that repetitive TMS applied over right IPS significantly decreased trans-saccadic fusion for stimuli presented in the left visual field. The decrease in fusion was also mirrored in rTMS over right FEF, however this did not reach significance. In contrast, for the first version of the flash grab effect, rTMS produced only a non-significant trend for reduction of the predictive shifts of position. In our second experiment, we focused only on the flash grab stimulus using a version that produced a much larger shift and we found here that rTMS to right IPS did significantly decrease the perceived shift. Consistent with the fusion results of the first experiment, rTMS to right FEF also caused a moderate decrease in the perceived effect — this position shift was significantly smaller than in the control rTMS condition (V1/V2) but not significantly different from the no TMS condition. Interestingly, repetitive TMS to MT did not significantly modulate the perceived shift in this stronger flash grab effect. Maps of attended regions of the visual field have been located within IPS and FEF (Cassanello et al., 2008; Hagler Jr. et al., 2007), therefore we speculate that rTMS over these regions inhibits the predictive computations accompanying eye and object motion. Our results suggest that there may be one predictive position processing mechanism within IPS which underlies predictions for both eye and target motion.

Clearly rTMS to contralateral IPS did not completely abolish either trans-saccadic fusion or the flash grab effect. In both cases, the results show a loss of 10% to 15%. It may be the case that rTMS silences only a portion of the relevant neuronal population in IPS, or alternatively, that other regions of the saccadic network also contribute to the predictive position calculations. For example, the superior colliculus (SC) is involved in spatial attention and saccadic target selection (Krauzlis, Lovejoy, & Zénon, 2013; Paré & Wurtz, 2001) but its role lies outside the scope of this paper (it is not feasible to stimulate SC with TMS). Previous rTMS experiments in IPS have also resulted in partial suppression leading to a decrease in the "continuous wagon wheel illusion", where a continuously illuminated, rotating wheel is perceived to move in the direction opposite to its physical rotation (VanRullen et al., 2008).

Repetitive TMS to right IPS significantly interrupted predictive position perception, which was not the case after rTMS to right FEF. Importantly, skull thickness over right FEF and IPS is equivalent, and therefore should not affect the difference in behavior after rTMS stimulation to the two sites (Stokes et al., 2005). In a recent article, de Vito and colleagues (Vito et al., 2015) found that neglect patients with damage to attentional networks in the right hemisphere also demonstrate a decreased motion-induced shift in the flash grab illusion presented in the left visual field. In the majority of the patients the brain damage included both right IPS and FEF. Our study supports this finding and indicates that contralateral IPS is involved in the predictive position mechanisms that underlie motion-induced position shifts. Previous research has indicated that IPS and FEF satisfy distinctive but complementary functions in saccades and visual attention (Ruff et al., 2008). Parietal regions perform online coding related to the current visual environment (Culham & Kanwisher, 2001; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Paré & Wurtz, 2001), whereas frontal regions may have a purely top-down role that operates independently of current sensory input (Buschman & Miller, 2007). We propose that IPS acts as a site for integration between top-down attention and bottom-up sensory input resulting in predictive position perception. After rTMS to IPS, information integration is disrupted and predictive position perception is compromised.

Our findings indicate that predictive position perception involves processing in IPS and we suggest that this may be related to the role of the parietal cortex in high-level, attention-based motion processing (Battelli et al., 2001, 2007; P. Cavanagh, 1992; Culham et al., 2001; Williams, Elfar, Eskandar, Toth, & Assad, 2003). In our second experiment, repetitive TMS to right IPS resulted in a decrement of the motion-induced position shift whereas no significant decrease was found after rTMS to right MT; a site specialized for low-level motion computations. In 2001, Battelli and colleagues reported that patients with right parietal lesions had deficits in processing apparent motion stimuli, an example of high-level motion processing. In contrast, these patients were not impaired in low-level motion processing indicating that the parietal cortex contributes to an independent stage of high-level motion processing (Battelli et al., 2001). Williams et al., (2003) also supported dissociable high- and low-level motion processing by reporting more active neurons in monkey LIP than MT or MST during bistable apparent motion. Moreover, our behavioral effect after rTMS on the parietal cortex is supported by de Vito et al., (2015) who found that split-brain patients with parietal lesions did not experience the flash grab illusion in their neglected hemifields. Importantly, there was no overlap between the lesions and V5/MT+ in that study (Vito et al., 2015), which again suggests that the parietal cortex is more directly involved in predictive position perception during motion than MT. It is notable that Vetter and colleagues (2015) found a significant decrease in predictive motion processing with an apparent motion stimulus when online TMS was applied to MT (Vetter et al., 2015). This may have been due to motion noise being injected into the percept by the activation of MT during the presentation of the stimulus; this online noise injection would not be a factor for our offline rTMS.

Due to the use of repetitive TMS we are unable to draw conclusions concerning the timing of predictive position coding in trans-saccadic fusion and the flash grab illusion. We hypothesize that predictive position perception involves the remapping of attention pointers to their expected next location (Cavanagh, Hunt, Afraz, & Rolfs, 2010). Therefore, in the case of trans-saccadic fusion we would expect single pulse TMS to effect trans-saccadic perception beginning at approximately 200 ms before saccade onset (Rolfs, Dambacher, & Cavanagh, 2013). A recent study on trans-saccadic fusion supports this hypothesized timing for the remapping of attention pointers as peripheral information was important for the fusion percept from 200 ms to 50 ms prior to saccade (Wolf & Schütz, 2015). This time-window suggests that peripheral information is being predictively relocated quite early.

5. Conclusion

We first replicate the trans-saccadic fusion percept (Paeye et al., 2017) and the perceived shift of the flash grab illusion (Adamian & Cavanagh, 2016) in our no TMS conditions. Using rTMS we find that the frequency of trans-saccadic fusion is significantly decreased with rTMS over the IPS contralateral to the pre-saccadic stimulus location. There was a lesser disruption following rTMS to contralateral FEF and no effect for rTMS over V1/V2. These effects suggest that saccade-related areas IPS is involved in generating a prediction of where a stimulus will be located following an eye movement. rTMS to contralateral IPS also reduced the perceived shift in the flash grab illusion in our second experiment implying that IPS also plays a role in predicting position for movements of the target as well as movements of the eyes. Our results further support the role of contralateral IPS as a region for computing high-level motion as rTMS in our second experiment disrupted the motion-induced position shift seen in the flash-grab effect whereas rTMS to contralateral MT did not. In summary, contralateral IPS is involved in predicting the next position of a target when either the eyes or the target move.

Competing financial interests

The authors declare no competing financial interests.

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Highlights

- Investigating visual predictive position mechanisms within FEF and IPS
- Predictive object localization across saccades decrease after rTMS to IPS
- Predictive object positioning during motion reduced after rTMS to IPS
- IPS contributes to predictive localization during saccades and motion
- Predictive position perception was not effected after rTMS to FEF