

The Role of the Right Superior Parietal Lobule in Processing Visual Context for the Establishment of the Egocentric Reference Frame

Benjamin D. Lester and Paul Dassonville

Abstract

Visual cues contribute to the creation of an observer's egocentric reference frame, within which the locations and orientations of objects can be judged. However, these cues can also be misleading. In the rod-and-frame illusion, for example, a large tilted frame distorts the observer's sense of vertical, causing an enclosed rod to appear tilted in the opposite direction. To determine the brain region responsible for processing these spatial cues, we used TMS to suppress neural activity in the

superior parietal lobule of healthy observers. Stimulation of the right hemisphere, but not the left, caused a significant reduction in rod-and-frame susceptibility. In contrast, a tilt illusion caused by a mechanism that does not involve a distortion of the observer's egocentric reference frame was unaffected. These results demonstrate that the right superior parietal lobule is actively involved in processing the contextual cues that contribute to our perception of egocentric space. ■

INTRODUCTION

Although an observer can form a perception of an object's spatial attributes (e.g., location, orientation, distance, or size) when viewed in a featureless environment, those judgments typically become more accurate and precise when the object is viewed within the context of a well-lit scene. For instance, the edges of walls, doors, furniture, etc., can provide visual cues that supplement the vestibular, proprioceptive, and somatosensory cues that inform the observer of the body's posture, so that deviations from a normal upright posture can be more precisely taken into account when attempting to determine the orientation of an object in the world (Dyde, Jenkin, & Harris, 2006; Asch & Witkin, 1948). Similarly, visual cues can help the observer understand the direction she is facing in the world (Bridgeman & Graziano, 1989) or her distance from the object (Howard, 2012) to determine the object's spatial location. In this way, visual, vestibular, proprioceptive, and somatosensory cues act in concert to help create an egocentric reference frame in which the object's spatial attributes may be judged.

Although the visual cues that contribute to the creation of an egocentric reference frame are typically beneficial, under certain circumstances they can be misleading. In the classic rod-and-frame illusion, for example, a large tilted frame distorts an observer's perception of vertical, causing an enclosed line to appear to be tilted in a direc-

tion opposite the frame (Figure 1A; Witkin & Asch, 1948). Similarly, a large frame whose center is shifted left or right of the observer's midline causes a distortion in the perceived straight-ahead direction (Dassonville & Bala, 2004; Dassonville, Bridgeman, Bala, Thiem, & Sampanes, 2004), resulting in a misperception of the spatial location of the frame (the Roelofs effect; Roelofs, 1936) and its contents (the induced Roelofs effect; Bridgeman, Peery, & Anand, 1997).

Several imaging studies have provided information on the neural structures involved in making judgments about an object's egocentric location (Schindler & Bartels, 2013; Medina et al., 2009; Zaehle et al., 2007; Committeri et al., 2004; Galati et al., 2000; Vallar et al., 1999) and its orientation (Lopez, Mercier, Halje, & Blanke, 2011; Harris, Benito, Ruzzoli, & Miniussi, 2008). In addition, much is known of the structures involved in processing the vestibular, somatosensory, and proprioceptive cues that contribute to the formation and maintenance of the egocentric reference frame (Kheradmand, Lasker, & Zee, in press; Baier, Suchan, Karnath, & Dieterich, 2012; Bottini et al., 2001; Anastasopoulos, Bronstein, Haslwanter, Fetter, & Dichgans, 1999; Bartolomeo & Chokron, 1999; Brandt, Dieterich, & Danek, 1994). In contrast, much less is known about the structures involved in processing the visual cues that are used to establish the egocentric reference frame. Walter and Dassonville (2008) used fMRI in an attempt to delineate the structures that process the visual cues that contribute to the perception of straight ahead by examining the structures that were activated by the contextual information provided by the large displaced frames that

cause the induced Roelofs effect. A greater activation was observed in a region of the superior parietal lobule (SPL), predominantly in the right hemisphere, when participants made location judgments within the illusion-inducing context, compared with trials in which the same judgment was made with targets presented in isolation, or trials in which a color judgment was made instead. Although this pattern of activation is consistent with the idea that right SPL plays a role in processing the visual cues that are used to establish the egocentric reference frame, this claim would be more conclusive if it could be determined that this activation is more than just incidental.

EXPERIMENT 1

In Experiment 1, we sought to determine whether right SPL plays a causal role in processing the visual cues that contribute to the creation of the observer's egocentric reference frame. To accomplish this, we used low-frequency (1 Hz) offline repetitive TMS (rTMS) to reduce cortical excitability in right SPL (specifically, the region delineated in the study of Walter & Dassonville, 2008) and two control sites (the left SPL and vertex) in separate sessions, effectively deactivating the underlying neural tissue for several minutes (Fitzgerald, Fountain, & Daskalakis, 2006; Chen et al., 1997). Susceptibility to the rod-and-frame illusion was compared before and after the application of rTMS to assess the effects of the associated deactivation. If right SPL is specifically involved in the processing of visual cues for the creation of the egocentric reference frame, rTMS at that site (but not the control sites) should decrease susceptibility to the illusion. On the other hand, if this structure plays a more general attentional role in spatial judgments, a deactivation of this structure with rTMS would be expected to cause a change in the precision of the participants' perceptual reports without necessarily affecting illusion susceptibility.

Methods

Participants

Participants ($n = 12$, three women, ages 18–34) gave their informed, written consent to take part in the study, as per the Institutional Review Board of the University of Oregon.

Experimental Task

Stimuli were created a priori within the graphics program Canvas (ACD Systems, Seattle, WA), with subsequent stimulus presentation and response collection performed by a program created within the Experiment Builder programming environment (SR Research, Kanata, Ontario, Canada). Stimuli were presented on a CRT monitor

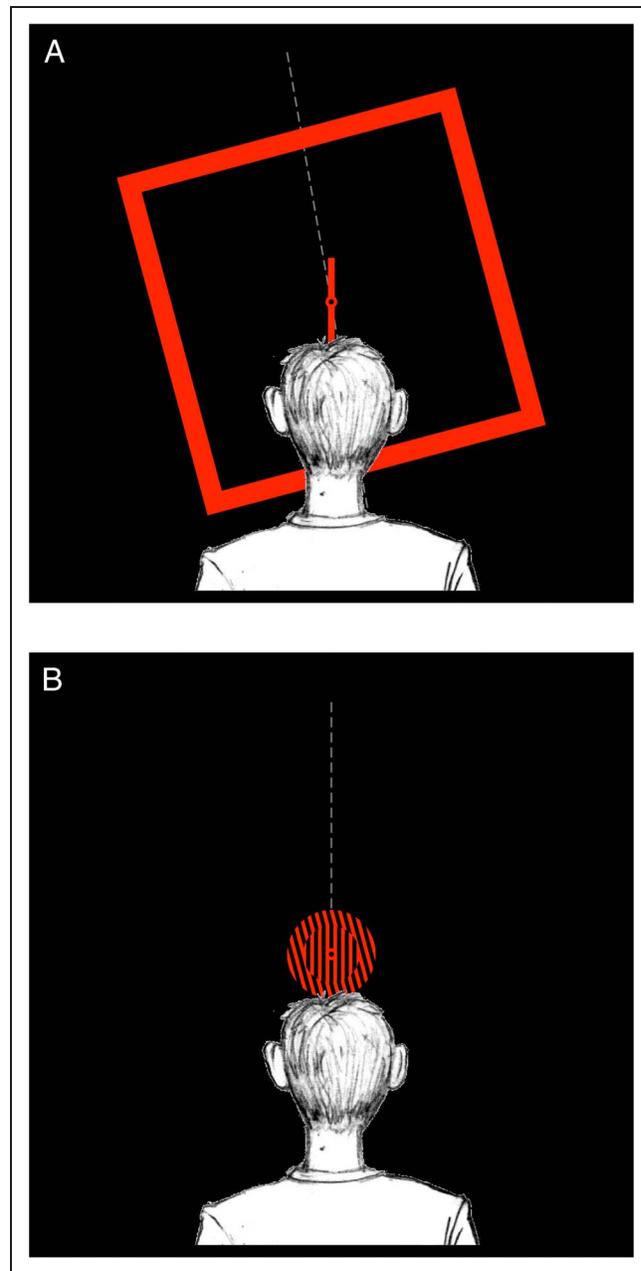


Figure 1. (A) Visual display for evoking the rod-and-frame illusion (Experiment 1), in which a square frame tilted away from gravitational vertical distorts an individual's subjective vertical (dashed line, not seen by observer). When the observer assesses the rod's orientation, the biased perception of vertical causes the rod to appear to tilt in a direction opposite the frame. (B) Visual display for evoking the simultaneous tilt illusion (Experiment 2). The tilt of the grating in the outer annulus causes a repulsion of the perceived orientation of the central array because of local contrast effects in early visual processing, without distorting subjective vertical (dashed line, not seen by participant).

(36.2 cm horizontal \times 27.3 cm vertical, 1024 \times 768 resolution, 60-Hz refresh rate), with the brightness and contrast of the monitor reduced so that the edges of the screen were not visible. In addition, the monitor was placed

within a large box (with a black interior) that covered the top, bottom, sides, and rear of the monitor, with a black-out curtain draped over the open end. Participants viewed the monitor from 24 inches away, with the black-out curtain draped over the head and shoulders to prevent stray light from allowing allocentric cues that might aid the participants in their task.

Each trial of the experimental task began with the presentation of a central fixation point (0.5° in diameter). After acquiring fixation, participants initiated subsequent events by pressing the spacebar on a keyboard. In two thirds of the trials ($n = 180$), a large tilted square frame (subtending 19° of visual angle and rotated 15° clockwise or counterclockwise) was then presented for 400 msec (Figure 1A). After a delay of 300 msec from frame onset, a tilted rod (a line 0.17° wide and 4.8° long, centered on the fixation point, and oriented -6° , -4° , -2° , -1° , 0° , 1° , 2° , 4° , or 6° from vertical, with negative values indicating counterclockwise tilts) was flashed for 100 msec, with the frame and rod extinguished simultaneously. The remaining one third of trials ($n = 90$) were identical, except that the rod was presented in isolation (i.e., no frame was presented). Participants reported whether the rod was tilted counterclockwise or clockwise by pressing one of the two home keys on the keyboard (F or J, respectively). Trials with and without the frame were presented in random order, and no feedback on performance was provided to the participants.

Experiment 1 consisted of three sessions for each participant, with each session separated from the others by a minimum of 1 week. In each session, rTMS was applied to a single cortical site (right SPL, left SPL, or vertex), with site order counterbalanced across participants. Each session began with 16 practice trials with the rod presented in isolation and feedback on the participant's accuracy presented after each trial. Subsequently, a pre-rTMS baseline run of the experimental task was performed (270 trials, 10–15 min), followed by the application of rTMS to the target cortical site for that session (10 min; see below) and then a post-rTMS run of the task (270 trials, 10–15 min).

rTMS

For each participant, MRI was used to collect anatomical scans for use in guiding the TMS stimulator. T_1 -weighted images were acquired using a 3T head-only scanner (Siemens Allegra, Erlangen, Germany), with a phased array head coil and a standard MP-RAGE sequence (repetition time = 2.5 sec, echo time = 4.38 msec, inversion time = 1.1 sec, 176 slices, 1 mm thickness, 0 mm gap, field of view = $256 \times 256 \times 100$ mm), yielding an in-plane anatomical resolution of $1 \times 1 \times 1$ mm. The resulting image was warped to a common MNI (Montreal Neurological Institute) space usingBrainsight neuronavigation software (Rogue Research, Inc., Montreal, Quebec, Canada), and the Talairach coordinates

corresponding to the BOLD activations observed by Walter and Dassonville (2008) were used to delineate target sites in the left and right SPL after first converting to MNI coordinates (MNI: -14 , -68 , 57 and 19 , -66 , 57 , respectively) using the procedure described by Lancaster et al. (2007). The vertex was identified as the midline location on the scalp halfway between the nasion and inion (MNI: 0 , -15 , 90 , on average).

The motor hot spot was identified in individual participants by determining the cortical region at which single TMS pulses (delivered via a 70-mm figure-eight coil connected to a MagStim Rapid stimulator; Magstim, Whitland, UK) could evoke visible movements of the index finger and thumb of the dominant hand. The strength of the magnetic pulse was slowly reduced to the smallest value at which visible movements could still be observed. The strength of the magnetic pulse during the subsequent experimental rTMS session was then set to 110% of this resting motor threshold.

After the baseline magnitude of the rod-and-frame illusion was established in a pre-rTMS run of the experimental task for each participant, the Brainsight frameless stereotaxic system was used to guide the TMS coil to the appropriate cortical ROI, with the participant seated comfortably and a chin rest stabilizing the head. The coil was then locked into place using an adjustable arm, and its position was monitored by the experimenter during the subsequent 10-min stimulation period to ensure that it never deviated more than 2 mm from the ROI. During this period, a low-frequency (1-Hz) rTMS train was administered. After the 10-min stimulation period, participants promptly completed a post-rTMS run of the experimental task.

Data Analysis

For each combination of rod-and-frame tilt, the perceived tilt of the rod was quantified as the proportion of trials in which the participant reported the central stimulus as being tilted clockwise (Figure 2). Psychometric functions were then fit to these data (Microsoft Excel, using a least squares algorithm) to determine the point of subjective equality (PSE; the orientation at which the rod was equally likely to be judged as having a clockwise or counterclockwise tilt), using the equation:

$$\begin{aligned} &\text{proportion "clockwise" responses} \\ &= e^{((\text{rodtilt} - \text{PSE})/\tau)} / \left(1 + e^{((\text{rodtilt} - \text{PSE})/\tau)} \right), \quad (1) \end{aligned}$$

where rodtilt was the orientation of the rod, PSE was the point of subjective equality, and τ was the space constant of the psychometric function. To quantify the magnitude of the illusion, the PSE for the counterclockwise-tilted frames was subtracted from that of the clockwise-tilted frames, with this total effect size statistically compared across conditions.

Results and Discussion

In the pre-rTMS baseline blocks of trials for each cortical ROI, the difference in the PSE between the two frame rotations was significantly greater than 0 (right SPL: mean = $3.05^\circ \pm 0.41^\circ SE$, $t(11) = 7.49$, $p < .001$, Figure 2; left SPL: mean = $2.71^\circ \pm 0.47^\circ$, $t(11) = 5.74$, $p < .001$; vertex: mean = $2.74^\circ \pm 0.51^\circ$, $t(11) = 5.40$, $p < .001$). This pattern of results indicated that participants exhibited the typical effects of the illusion, with the rod appearing to be rotated somewhat clockwise in the presence of the counter-clockwise frame, and vice versa.

A two-way repeated-measures ANOVA, with factors of Session (pre-rTMS and post-rTMS) and Stimulation Site (right SPL, left SPL, and vertex), revealed no main effects of Session, $F(1, 11) = 0.050$, or Site, $F(2, 22) = 0.074$, but a significant interaction of Session and Site, $F(2, 22) = 4.42$, $p = .024$. Simple contrasts revealed a significant reduction of the illusion with stimulation at the right SPL site (mean change = $-0.53^\circ \pm 0.20^\circ$, a decrease of 17.4% from the pre-rTMS baseline; Figures 2 and 3A) compared with the small increases in susceptibility seen with stimulation at either the vertex (mean change = $0.22^\circ \pm 0.24^\circ$; contrast of right SPL vs. vertex: $F(1, 11) = 5.31$, $p = .042$) or left SPL (mean change = $0.23^\circ \pm 0.17^\circ$; contrast of right vs. left SPL: $F(1, 11) = 9.56$, $p = .010$). This decrease in illusion susceptibility after rTMS in right SPL suggests that this structure plays a direct role in processing the egocentric contextual information provided by the tilted frame in the rod-and-frame illusion.

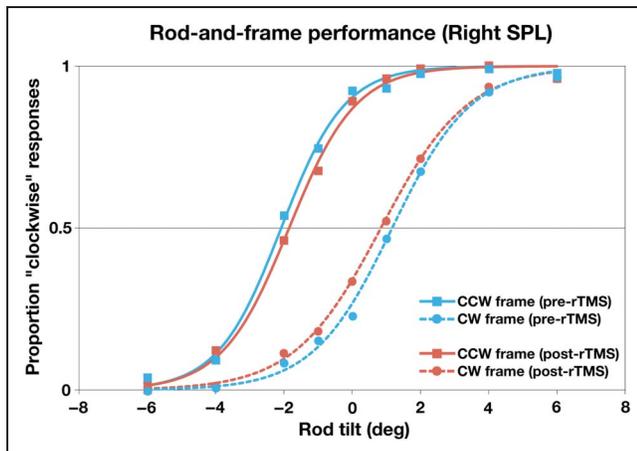


Figure 2. Best fit psychometric functions for the right SPL stimulation site in Experiment 1, showing the proportion of trials (averaged across participants) in which each rod orientation was reported to be rotated clockwise from vertical. Functions are shown for each frame tilt (i.e., CW = clockwise, CCW = counterclockwise) in both pre- and post-rTMS blocks. The point at which each function surpasses a proportion of 0.5 indicates the PSE for that condition, with illusion susceptibility in each block assessed as the difference in PSE for clockwise- and counterclockwise-tilted frames. Whereas the PSEs were biased somewhat in the counterclockwise direction (i.e., shifted toward negative values in this plot), this bias did not reach significance.

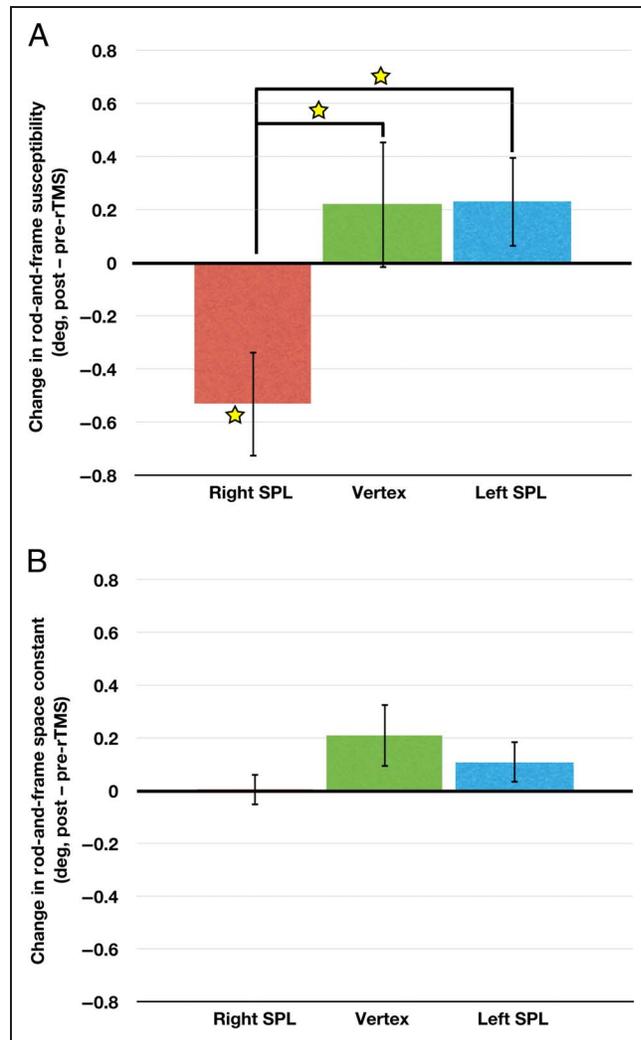


Figure 3. Effect of rTMS on rod-and-frame performance. (A) Total change in susceptibility (post- minus pre-rTMS) for each cortical ROI in Experiment 1. rTMS at only the right SPL site caused a significant change in illusion susceptibility. This change differed significantly from the nonsignificant effects of rTMS at the vertex and left SPL (stars indicate $p < .05$). (B) Total change in the space constant of the psychometric functions (post- minus pre-rTMS) for each cortical ROI. rTMS caused no significant modulation of the space constant for any stimulation site.

Although the general pattern of the results presented so far points to a role for right SPL in processing egocentric contextual information, alternative explanations must also be explored. Given the more general role played by the SPL in attentional modulation (Corbetta, Shulman, Miezin, & Petersen, 1995), it is possible that the decrease in susceptibility is merely an artifact of an rTMS-related modulation of attention similar to that shown with deactivation of other parietal sites (e.g., Chambers, Payne, Stokes, & Mattingley, 2004; Hilgetag, Théoret, & Pascual-Leone, 2001). Indeed, the right SPL stimulation site is located very near the stereotaxic coordinates reported for the superior parietal lobule area 1 (SPL1), which has

been delineated with functional imaging by taking advantage of its topographical representation of the directionality of memory-guided saccades (Konen & Kastner, 2008). Functional activation in a portion of right SPL1 (but not left) has also been shown to be modulated by spatial attention (Szczepanski, Konen, & Kastner, 2010), and single-pulse TMS in SPL1 can cause neglect-like biases in a landmark task (Szczepanski & Kastner, 2013). Without a delineation of the extent of SPL1 in the individual participants of this study, it is unclear whether the right SPL stimulation site falls within that particular cortical region, but it could be conjectured that a more general rTMS-related modulation of attention could be responsible for the decrease in rod-and-frame susceptibility seen here. For example, it may be that after a deactivation of right SPL, the participants are less able to attend to the orientation judgment task altogether. This might be expected to cause a smaller illusory effect of the frame but would also cause a general flattening of the psychometric function (i.e., increasing the value of the space constant, τ , in Equation 1) as inattention to the task caused more variability in the participants' performance. Alternatively, deactivation of right SPL could more specifically decrease the extent to which the tilted frame is able to attract the observer's attention. This would lead to a smaller illusory effect of the frame but would also be expected to cause a sharpening of the psychometric function (i.e., decreasing τ in Equation 1), since an unattended frame would also cause less of a distraction from the task of assessing the tilt of the target line. A two-way repeated-measures ANOVA, with factors of Session (pre-rTMS and post-rTMS) and Stimulation Site (right SPL, left SPL, and vertex), revealed a significant effect of Session, $F(1, 11) = 5.66, p = .037$, on the space constants of the psychometric functions, with shallower psychometric functions in the post-rTMS sessions (mean $\tau = 1.70^\circ$) compared with those of the pre-rTMS sessions (mean $\tau = 1.48^\circ$), possibly an effect of fatigue in the participants. However, there was no main effect of Stimulation Site, $F(2, 22) = 0.19$, nor was there an interaction of Session and Site, $F(2, 22) = 1.35$, indicating that this effect on the slope of the psychometric function could not explain the differential effects of rTMS on illusion susceptibility for the three sites. In addition, there were no significant changes in the space constant of the psychometric functions for any stimulation site during trials in which the rod was presented in isolation (i.e., with no accompanying frame; session: $F(1, 11) = 3.10$; site: $F(2, 22) = 0.43$; interaction: $F(2, 22) = 0.47$).

Importantly, this lack of an rTMS-related change in the space constant of the psychometric function, whether a frame was presented or not, indicates that deactivation of the target site in right SPL does not simply cause a generalized modulation of attention. Instead, the very specific finding of an rTMS-related decrease in rod-and-frame susceptibility suggests that this region in right SPL is actively involved in processing the visual contextual information that leads to the misperception of the rod's orientation

in the illusion. However, to go further and suggest that the right SPL is involved in using the visual context to establish an egocentric reference frame requires a demonstration that deactivation of this structure does not also reduce susceptibility to orientation illusions that are driven by different mechanisms.

EXPERIMENT 2

The large rotated frame within the visual stimulus of Experiment 1 is thought to bring about a misperception of the rod's orientation by causing a distortion of the observer's perception of gravitational vertical (Witkin & Asch, 1948). It is also possible, though, to achieve a contextually-driven illusion of orientation that is subjectively similar, but that is driven by a different neural mechanism. One such illusion is the simultaneous tilt illusion, where the perceived orientation of a central grating is distorted by tilted lines within a surrounding annulus (Gibson, 1937; Figure 1B). However, the simultaneous tilt illusion is thought to be brought about by a perceptual repulsion effect within early visual areas, as neurons encoding the orientations of the lines in the surrounding annulus inhibit those encoding the lines of the central grating (Song, Schwarzkopf, & Rees, 2013; Poom, 2000; Carpenter & Blakemore, 1973; Blakemore, Carpenter, & Georgeson, 1970). Thus, the context of the surrounding annulus in the simultaneous tilt illusion is capable of causing a tilt illusion, but not by distorting the observer's egocentric reference frame.

If right SPL is a selective processor of the visual contextual information that is used to establish the egocentric reference frame, rTMS-related deactivation of the structure should have no impact on susceptibilities to the simultaneous tilt illusion. Experiment 2 provides a test of this hypothesis.

Methods

Participants

Participants ($n = 12$, 10 of whom also participated in Experiment 1) gave their informed, written consent to take part in Experiment 2, as per the Institutional Review Board of the University of Oregon.

Experimental Task

The apparatus was identical to that of Experiment 1. Each trial of the experimental task began with the presentation of a central fixation point (0.5° in diameter). After acquiring fixation, participants initiated subsequent events by pressing the spacebar on a keyboard. In two thirds of the trials ($n = 140$), an outer annulus of oriented bars (5° outer diameter, 3.2° inner diameter, with red and black bars of 0.22° in width alternating in a square wave

pattern, and tilted 15° clockwise or counterclockwise) was then presented for 700 msec, centered around the fixation point (Figure 1B). After a delay of 200 msec from annulus onset, an inner grating (3.2° diameter, with same spatial frequency as the annulus, but tilted -4, -2, -1, 0, 1, 2, or 4° from vertical) was flashed for 500 msec, with the annulus and inner grating extinguished simultaneously. The remaining one third of trials ($n = 70$) were identical, except that the inner grating was presented in isolation (i.e., no outer annulus was presented). Participants reported whether the top of the inner grating was tilted counterclockwise or clockwise by pressing one of the two home keys on the keyboard (F or J, respectively). Trials with and without the outer annulus were presented in random order, and no feedback on performance was provided to the participants.

Experiment 2 consisted of three sessions for each participant, with each session separated from the others by a minimum of 1 week. In each session, rTMS was applied to a single cortical site (right SPL, left SPL, or vertex), with site order counterbalanced across participants. Each session began with 16 practice trials with the inner grating presented in isolation, and feedback on the participant's accuracy presented after each trial. Subsequently, a pre-rTMS baseline run of the experimental task was performed (210 trials, 8–12 min), followed by the application of rTMS to the target cortical site for that session (10 min), and then a post-rTMS run of the task (210 trials, 8–12 min).

The procedures for rTMS application and data analysis were identical to those of Experiment 1.

Results and Discussion

In the pre-rTMS baseline blocks of simultaneous tilt trials, the difference in the PSE between the two annulus rotations was significantly greater than 0 in the stimulation sessions for each cortical target (right SPL: mean = $1.86^\circ \pm 0.22^\circ SE$, $t(11) = 8.41$, $p < .001$; left SPL: mean = $1.89^\circ \pm 0.25^\circ$, $t(11) = 7.67$, $p < .001$; vertex: mean = $1.72^\circ \pm 0.24^\circ$, $t(11) = 7.17$, $p < .001$). This pattern of results indicated that participants exhibited the typical effects of the illusion, with the inner grating appearing to be rotated somewhat clockwise in the presence of the counterclockwise annulus, and vice versa. However, a two-way repeated-measures ANOVA, with factors of Session (pre-rTMS and post-rTMS) and Stimulation Site (right SPL, left SPL, and vertex) revealed no main effects of Session, $F(1, 11) < 0.001$, $p = 1.00$, or Site, $F(2, 22) = 0.040$, $p = .96$, and no significant interaction of the two, $F(2, 22) = 1.28$, $p = .30$, indicating that susceptibility to the simultaneous tilt illusion was unaffected by rTMS at each of the three target sites (Figure 4).

To further assess the specificity of rTMS effects in the right SPL, we specifically tested whether the reduction in rod-and-frame susceptibility observed in Experiment 1 (Figure 3A) was greater than the reduction in simul-

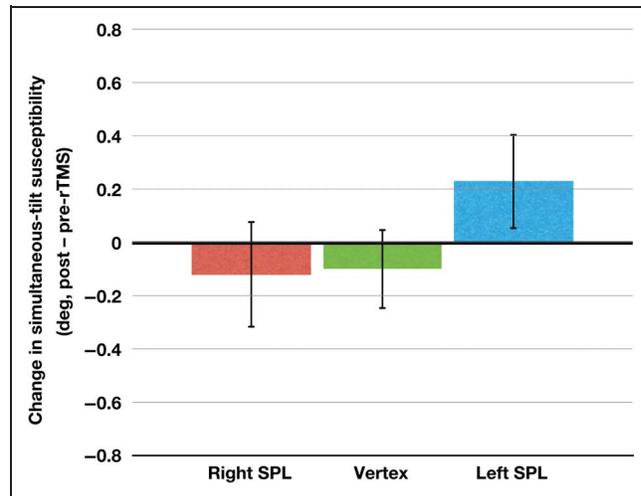


Figure 4. Total change in simultaneous tilt susceptibility (post- minus pre-rTMS) for each cortical ROI in Experiment 2. rTMS caused no significant modulation for any stimulation site.

taneous tilt susceptibility observed in Experiment 2 (Figure 4), using the change in susceptibility with stimulation at vertex as baseline. This comparison confirmed that stimulation of right SPL caused a greater reduction in susceptibility to the rod-and-frame illusion than to the simultaneous tilt illusion (one-way t test, $t(22) = 1.81$, $p = .042$). To test the possibility that a smaller precision in the participants' reports in the simultaneous tilt illusion might have obscured a change in susceptibility in Experiment 2, we compared the space constants of the psychometric functions for the two illusions. However, the space constants did not significantly differ, $t(22) = 0.33$. Another possibility is that the smaller magnitude of the simultaneous tilt illusion made it difficult to detect an actual change in susceptibility that was caused by rTMS in right SPL. However, evidence clearly indicates that a floor effect could not have obscured a change in susceptibility, because there was a significant effect of the simultaneous tilt illusion in both the pre-rTMS (mean = 1.86° , $t(11) = 8.41$, $p < .001$) and post-rTMS sessions (mean = 1.74° , $t(11) = 7.64$, $p < .001$), and there was no significant change in susceptibility when the pre- and post-rTMS sessions were compared directly, $t(11) = 0.60$.

Together, the findings of Experiments 1 and 2 indicate that deactivation of right SPL does not cause a generalized decrease in susceptibility to tilt illusions. Rather, there is a specificity to the effect, with the rod-and-frame illusion (Experiment 1), but not the simultaneous tilt illusion (Experiment 2), significantly diminished by application of rTMS to right SPL. The specificity in the effect can be interpreted to reflect a specificity of the type of processing for which the target site in right SPL is responsible—namely, the processing of the visual contextual information that is used to establish the observer's sense of gravitational vertical.

GENERAL DISCUSSION

The right SPL site that served as an ROI in the current study was previously shown by Walter and Dassonville (2008) to have an activation that was modulated by the presence of visual contextual information (i.e., a large rectangular frame offset from the observer's midline) that led to a distortion of the observer's perception of straight ahead (i.e., the Roelofs effect). This study expands on these findings to demonstrate that the neural activation seen by Walter and Dassonville is not merely incidental but instead plays a causal role in the establishment of the egocentric reference frame for judging the spatial properties of objects within the visual field. Furthermore, it provides a demonstration that the egocentric reference frame to which the right SPL contributes is involved not only in the perception of an object's spatial location but also in its orientation. That the processing involved in determining the location and orientation aspects of the egocentric reference frame would reside in a common neural structure was predicted to be the case (Walter & Dassonville, 2008) based on a prior finding that individual differences in susceptibilities to the Roelofs effect and the rod-and-frame illusion are correlated (Walter, Dassonville, & Bochsler, 2009).

Walter et al. (2009) found that susceptibilities to the Roelofs and rod-and-frame illusions were additionally correlated with susceptibility to the Ponzo illusion, which suggests that the same region of right SPL may also be involved in processing the misleading depth cues that drive that illusion. Indeed, Séverac Cauquil, Trotter, and Taylor (2005) found that right SPL is highly sensitive to perspective depth cues, but their mapping technique (source modeling of visually evoked potentials) was too coarse to allow for a precise comparison to the region tested in the current study. Although imaging work has demonstrated that activity in primary visual cortex reflects the error in size constancy associated with the Ponzo illusion, the authors recognized that this modulation must reflect a feedback signal from a later stage of vision that is capable of processing the depth cues contained in the image (Fang, Boyaci, Kersten, & Murray, 2008; Murray, Boyaci, & Kersten, 2006). Given the findings of the current study that demonstrate right SPL to be involved in processing the visual contextual cues used to establish the egocentric reference frame for the perception of space, this structure should be considered a viable candidate for the origin of this feedback signal.

Given that the right SPL stimulation site of this study falls near or perhaps within SPL1 (Silver & Kastner, 2009), it is useful to consider how our findings might mesh with those of other studies that have examined the role of SPL1 in perception, attention, and sensorimotor control. Although SPL1 is typically defined by its topographical representation of the directionality of memory-guided saccades (Konen & Kastner, 2008), it is by no means exclusively involved in saccadic control.

Parietal regions of reach-related activity also overlap SPL1, indicating that its role in motor control is somewhat independent of effector (Konen, Mruczek, Montoya, & Kastner, 2013). On the other hand, there is some specificity to its motor role, with greater activation associated with memory-guided saccades than for pursuit movements (Konen & Kastner, 2008) and for reaching than for grasping (Konen et al., 2013). SPL1 has also been shown to be influenced by sensory input, with a sensitivity to global coherent motion (Helfrich, Becker, & Haarmeier, 2013; Konen & Kastner, 2008). In addition, the activation of right (but not left) SPL1 is modulated by spatial attention (Szczepanski et al., 2010), and disruption of its processing with single-pulse TMS causes attentional biases that resemble those of visuospatial neglect (Szczepanski & Kastner, 2013). Taken together, these characteristics have led Kastner and colleagues (Silver & Kastner, 2009; Konen & Kastner, 2008) to suggest that SPL1 is the human homologue of macaque area 7a. Indeed, neurophysiological studies have demonstrated that neurons in area 7a are capable of encoding target locations within multiple reference frames, including eye-, head-, body-, and world-centered coordinate systems (Pouget & Snyder, 2000; Snyder, Grieve, Brotchie, & Andersen, 1998; Andersen, Essick, & Siegel, 1985). The findings of the current study and those of Walter and Dassonville (2008) fit well into this framework and further suggest a role for SPL1 in processing visual contextual information for the formation and maintenance of these reference frames, for use in both perceptual judgments and motor guidance (Dassonville & Bala, 2004; Dassonville et al., 2004).

Acknowledgments

The authors thank Bill Troyer for technical assistance. This work was supported by the NIH/Institute of Neuroscience: Systems Physiology Training Program 5 T32 GM007257-33 and was completed as part of the doctoral thesis of B. D. Lester, under the supervision of P. Dassonville.

Reprint requests should be sent to Paul Dassonville, Department of Psychology, 1227 University of Oregon, Eugene, OR 97403, or via e-mail: prd@uoregon.edu.

REFERENCES

- Anastasopoulos, D., Bronstein, A., Haslwanter, T., Fetter, M., & Dichgans, J. (1999). The role of somatosensory input for the perception of verticality. *Annals of the New York Academy of Sciences*, *871*, 379–383.
- Andersen, R. A., Essick, G. K., & Siegel, R. M. (1985). Encoding of spatial location by posterior parietal neurons. *Science*, *230*, 456–458.
- Asch, H. A., & Witkin, S. E. (1948). Studies in space orientation: I. Perception of upright with displaced visual fields. *Journal of Experimental Psychology*, *38*, 325–337.
- Baier, B., Suchan, J., Karnath, H.-O., & Dieterich, M. (2012). Neural correlates of disturbed perception of verticality. *Neurology*, *78*, 728–735.

- Bartolomeo, P., & Chokron, S. (1999). Egocentric frame of reference: Its role in spatial bias after right hemisphere lesions. *Neuropsychologia*, *37*, 881–894.
- Blakemore, C., Carpenter, R. H., & Georgeson, M. A. (1970). Lateral inhibition between orientation detectors in the human visual system. *Nature*, *228*, 37–39.
- Bottini, G., Karnath, H. O., Vallar, G., Sterzi, R., Frith, C. D., Frackowiak, R. S., et al. (2001). Cerebral representations for egocentric space: Functional-anatomical evidence from caloric vestibular stimulation and neck vibration. *Brain*, *124*, 1182–1196.
- Brandt, T., Dieterich, M., & Danek, A. (1994). Vestibular cortex lesions affect the perception of verticality. *Annals of Neurology*, *35*, 403–412.
- Bridgeman, B., & Graziano, J. A. (1989). Effect of context and efferece copy on visual straight ahead. *Vision Research*, *29*, 1729–1736.
- Bridgeman, B., Peery, S., & Anand, S. (1997). Interaction of cognitive and sensorimotor maps of visual space. *Perception & Psychophysics*, *59*, 456–469.
- Carpenter, R. H. S., & Blakemore, C. (1973). Interactions between orientations in human vision. *Experimental Brain Research*, *18*, 287–303.
- Chambers, C. D., Payne, J. M., Stokes, M. G., & Mattingley, J. B. (2004). Fast and slow parietal pathways mediate spatial attention. *Nature Neuroscience*, *7*, 217–218.
- Chen, R., Classen, J., Gerloff, C., Celnik, P., Wassermann, E. M., Hallett, M., et al. (1997). Depression of motor cortex excitability by low-frequency transcranial magnetic stimulation. *Neurology*, *48*, 1398–1403.
- Committeri, G., Galati, G., Paradis, A.-L., Pizzamiglio, L., Berthoz, A., & LeBihan, D. (2004). Reference frames for spatial cognition: Different brain areas are involved in viewer-, object-, and landmark-centered judgments about object location. *Journal of Cognitive Neuroscience*, *16*, 1517–1535.
- Corbetta, M., Shulman, G. L., Miezin, F. M., & Petersen, S. E. (1995). Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science*, *270*, 802–805.
- Dassonville, P., & Bala, J. K. (2004). Action, perception and the Roelofs effect: A mere illusion of dissociation. *PLoS Biology*, *2*, 1936–1945.
- Dassonville, P., Bridgeman, B., Bala, J. K., Thiem, P., & Sampanes, A. (2004). The induced Roelofs effect: Two visual systems or the shift of a single-reference frame? *Vision Research*, *44*, 603–611.
- Dyde, R. T., Jenkin, M. R., & Harris, L. R. (2006). The subjective visual vertical and the perceptual upright. *Experimental Brain Research*, *173*, 612–622.
- Fang, F., Boyaci, H., Kersten, D., & Murray, S. O. (2008). Attention-dependent representation of a size illusion in human V1. *Current Biology*, *18*, 1707–1712.
- Fitzgerald, P. B., Fountain, S., & Daskalakis, Z. J. (2006). A comprehensive review of the effects of rTMS on motor cortical excitability and inhibition. *Clinical Neurophysiology*, *117*, 2584–2596.
- Galati, G., Lobel, E., Vallar, G., Berthoz, A., Pizzamiglio, L., & Le Behan, D. (2000). The neural basis of egocentric and allocentric coding of space in humans: A functional magnetic resonance study. *Experimental Brain Research*, *133*, 156–164.
- Gibson, J. J. (1937). Adaptation, after-effect and contrast in the perception of tilted lines. II. Simultaneous contrast and the areal restriction of the after-effect. *Journal of Experimental Psychology*, *20*, 553–569.
- Harris, I. M., Benito, C. T., Ruzzoli, M., & Miniussi, C. (2008). Effects of right parietal transcranial magnetic stimulation on object identification and orientation judgments. *Journal of Cognitive Neuroscience*, *20*, 916–926.
- Helfrich, R. F., Becker, H. G. T., & Haarmeier, T. (2013). Processing of coherent visual motion in topographically organized visual areas in human cerebral cortex. *Brain Topography*, *26*, 247–263.
- Hilgetag, C. C., Théoret, H., & Pascual-Leone, A. (2001). Enhanced visual spatial attention ipsilateral to rTMS-induced “virtual lesions” of human parietal cortex. *Nature Neuroscience*, *4*, 953–957.
- Howard, I. P. (2012). *Perceiving in depth, volume 3: Other mechanisms of depth perception*. New York: Oxford University Press.
- Kheradmand, A., Lasker, A., & Zee, D. S. (in press). Transcranial magnetic stimulation (TMS) of the supramarginal gyrus: A window to perception of upright. *Cerebral Cortex*. doi:10.1093/cercor/bht267.
- Konen, C. S., & Kastner, S. (2008). Representation of eye movements and stimulus motion in topographically organized areas of human posterior parietal cortex. *Journal of Neuroscience*, *28*, 8361–8375.
- Konen, C. S., Mruczek, R. E. B., Montoya, J. L., & Kastner, S. (2013). Functional organization of human posterior parietal cortex: Grasping- and reaching-related activations relative to topographically organized cortex. *Journal of Neurophysiology*, *109*, 2897–2908.
- Lancaster, J. L., Tordesillas-Gutierrez, D., Martinez, M., Salinas, F., Evans, A., Zilles, K., et al. (2007). Bias between MNI and Talairach coordinates analyzed using the ICBM-152 brain template. *Human Brain Mapping*, *28*, 1194–1205.
- Lopez, C., Mercier, M. R., Halje, P., & Blanke, O. (2011). Spatiotemporal dynamics of visual vertical judgments: Early and late brain mechanisms as revealed by high-density electrical neuroimaging. *Neuroscience*, *181*, 134–149.
- Medina, J., Kannan, V., Pawlak, M. A., Kleinman, J. T., Newhart, M., Davis, C., et al. (2009). Neural substrates of visuospatial processing in distinct reference frames: Evidence from unilateral spatial neglect. *Journal of Cognitive Neuroscience*, *21*, 2073–2084.
- Murray, S. O., Boyaci, H., & Kersten, D. (2006). The representation of perceived angular size in human primary visual cortex. *Nature Neuroscience*, *9*, 429–434.
- Poom, L. (2000). Inter-attribute tilt effects and orientation analysis in the visual brain. *Vision Research*, *40*, 2711–2722.
- Pouget, A., & Snyder, L. H. (2000). Computational approaches to sensorimotor transformations. *Nature Neuroscience*, *3*, 1192–1198.
- Roelofs, C. O. (1936). Die optische Lokalisation. *Archiv für Augenheilkunde*, *109*, 395–415.
- Schindler, A., & Bartels, A. (2013). Parietal cortex codes for egocentric space beyond the field of view. *Current Biology*, *23*, 177–182.
- Séverac Cauquil, A., Trotter, Y., & Taylor, M. J. (2005). At what stage of neural processing do perspective depth cues make a difference? *Experimental Brain Research*, *170*, 457–463.
- Silver, M. A., & Kastner, S. (2009). Topographical maps in human frontal and parietal cortex. *Trends in Cognitive Science*, *13*, 488–495.
- Snyder, L. H., Grieve, K. L., Brotchie, P., & Andersen, R. A. (1998). Separate body- and world-referenced representations of visual space in parietal cortex. *Nature*, *394*, 887–891.
- Song, C., Schwarzkopf, D. S., & Rees, G. (2013). Variability in visual cortex size reflects tradeoff between local orientation sensitivity and global orientation modulation. *Nature Communications*, *4*, 2201 (online).
- Szczepanski, S. M., & Kastner, S. (2013). Shifting attentional priorities: Control of spatial attention through hemispheric competition. *Journal of Neuroscience*, *33*, 5411–5421.

- Szczepanski, S. M., Konen, C. S., & Kastner, S. (2010). Mechanisms of spatial attention control in frontal and parietal cortex. *Journal of Neuroscience*, *30*, 148–160.
- Vallar, G., Lobel, E., Galati, G., Berthoz, A., Pizzamiglio, L., & Le Bihan, D. (1999). A fronto-parietal system for computing the egocentric spatial frame of reference in humans. *Experimental Brain Research*, *124*, 281–286.
- Walter, E., & Dassonville, P. (2008). Visuospatial contextual processing the parietal cortex: An fMRI investigation of the induced Roelof effect. *Neuroimage*, *42*, 1686–1697.
- Walter, E., Dassonville, P., & Bochsler, T. (2009). A specific autistic trait that modulates visuospatial illusion susceptibility. *Journal of Autism and Developmental Disorders*, *39*, 339–349.
- Witkin, H. A., & Asch, S. E. (1948). Studies in space orientation. IV. Further experiments on perception of the upright with displaced visual fields. *Journal of Experimental Psychology*, *38*, 762–782.
- Zaehle, T., Jordan, K., Wüstenberg, T., Baudewig, J., Dechent, P., & Mast, F. W. (2007). The neural basis of the egocentric and allocentric spatial frame of reference. *Brain Research*, *1137*, 92–103.