

ATTENTIONAL AND NEURAL MANIPULATIONS OF VISUOSPATIAL  
CONTEXTUAL INFORMATION

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## DISSERTATION ABSTRACT

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A critical function of the human visual system is to parse objects from the larger context of the environment, allowing for the identification of, and potential interaction with, those objects. The use of contextual information allows us to rapidly locate, identify, and interact with objects that appear in the environment. Contextual information can help specify an object's location within the environment (allocentric encoding) or with respect to the observer (egocentric encoding).

Understanding how contextual information influences perceptual organization, and the neural systems that process a complex scene, is critical in understanding how contextual information assists in parsing local information from background. In the real world, relying on context is typically beneficial, as most objects occur in circumscribed environments. However, there are circumstances in which context can harm performance. In the case of visual illusions, relying on the context can bias observers' perceptions and cause significant motor errors. Studying the illusory conditions under which perceptual/motor functions are "fooled", or breakdown, can provide valuable information about how the brain computes allocentric and egocentric frames of reference.

The following studies examine how attentional (Chapters II & III) manipulations of visuospatial context affect components of observers' egocentric reference frames (e.g.,

perceived vertical or subjective midline) and how neural manipulations (Chapter IV) can modulate observers' reliance on contextual information. In Chapter II, the role of attentional control settings on contextual processing is examined. Chapter III addresses the question of how visuospatial shifts of attention interact with an egocentric frame of reference. Finally, Chapter IV examines the functional role of superior parietal cortex in the processing of egocentric contextual information.

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## CHAPTER I

### CONTEXT, ILLUSIONS AND ATTENTION

In day-to-day interactions with objects within the visual world, an observer is required to make many judgments about the local properties of the objects, to allow for both the appropriate selection of an object for further interaction, and for coordinating the movements required for the interaction. For example, if the observer is searching for a ripe piece of fruit, its color and shape is an important cue for selection, and information about its location, size and orientation are important cues for guiding and shaping the hand for an appropriate grasp. These characteristics are not considered in isolation, though. Instead, the observer processes additional contextual information from the scene, to supplement the information provided directly by the local properties. Under typical circumstances, this contextual information is beneficial – context acts as a critical processing aid and allows for accurate motor responses and perceptual judgments. Under certain circumstances, though, this contextual information can be misleading, causing illusions that distort perception of the local properties. As a scientist, illusions are more than just interesting examples of the way in which brain processing can go wrong. More importantly, they provide a means by which we can gain insight into the mechanisms by which the brain uses contextual information to supplement the local information that it uses to perform a task, by studying the conditions in which the process fails.

This dissertation will broadly focus on the manner in which the brain forms a representation of visual space, using illusions and experimental paradigms that provide attentional and neural manipulations of egocentric frames of reference in human observers. Classic theories of visual attention and contextual processing will be reviewed to introduce the broader focus of this work. Chapter II will examine how an observer's attentional control settings can modulate contextual processing in a visual illusion. Chapter III will examine whether (and how) spatial shifts of attentional interact with an observer's egocentric frame of reference. Chapter IV employs a noninvasive neural manipulation to examine the role of a sub-region of the posterior parietal cortex in processing the contextual information that is used to determine an object's orientation in space. Finally, Chapter V discusses the larger implications of this research and avenues for future investigation.

### **Classes of visual illusions**

Contextual information can influence perceptual organization at multiple levels of the visual hierarchy. As early as the retina and primary visual cortex, the mutual inhibition that exists between neurons heightens orientation and contrast sensitivity (e.g., Jones et al., 2001; Ichida et al., 2007). Contextual influences also operate at object recognition stages of visual processing, for example, that allow the grouping of contours that provide the coherent outline of a human face (Hasson et al., 2001). Even an observer's perception of space is affected by the context of a visual scene, with, for example, the edges of a doorframe providing contextual information that contributes to an observer's perception of gravitational vertical (Asch & Witkin, 1948).

Illusions are often divided into two broad categories (see Figure 1). Illusions classified as “local” in nature are regarded as occurring in early sensory-level regions (e.g., retina or primary visual cortex), and are caused by the mutual inhibitory interactions between neighboring populations of neurons (Bair, Cavanagh, & Movshon, 2001). Alternatively, “global” level illusions are believed to influence perceptual processing at higher, more elaborate stages of visual processing, for example, in posterior parietal cortex or the parahippocampal place area (Walter & Dassonville, 2008; Murray, Boyaci, & Kersten, 2006). The fact that global-level illusions occupy a high level of visual abstraction puts this class in the unique position of being capable of modulating feedforward sensory inputs through recurrent connections.

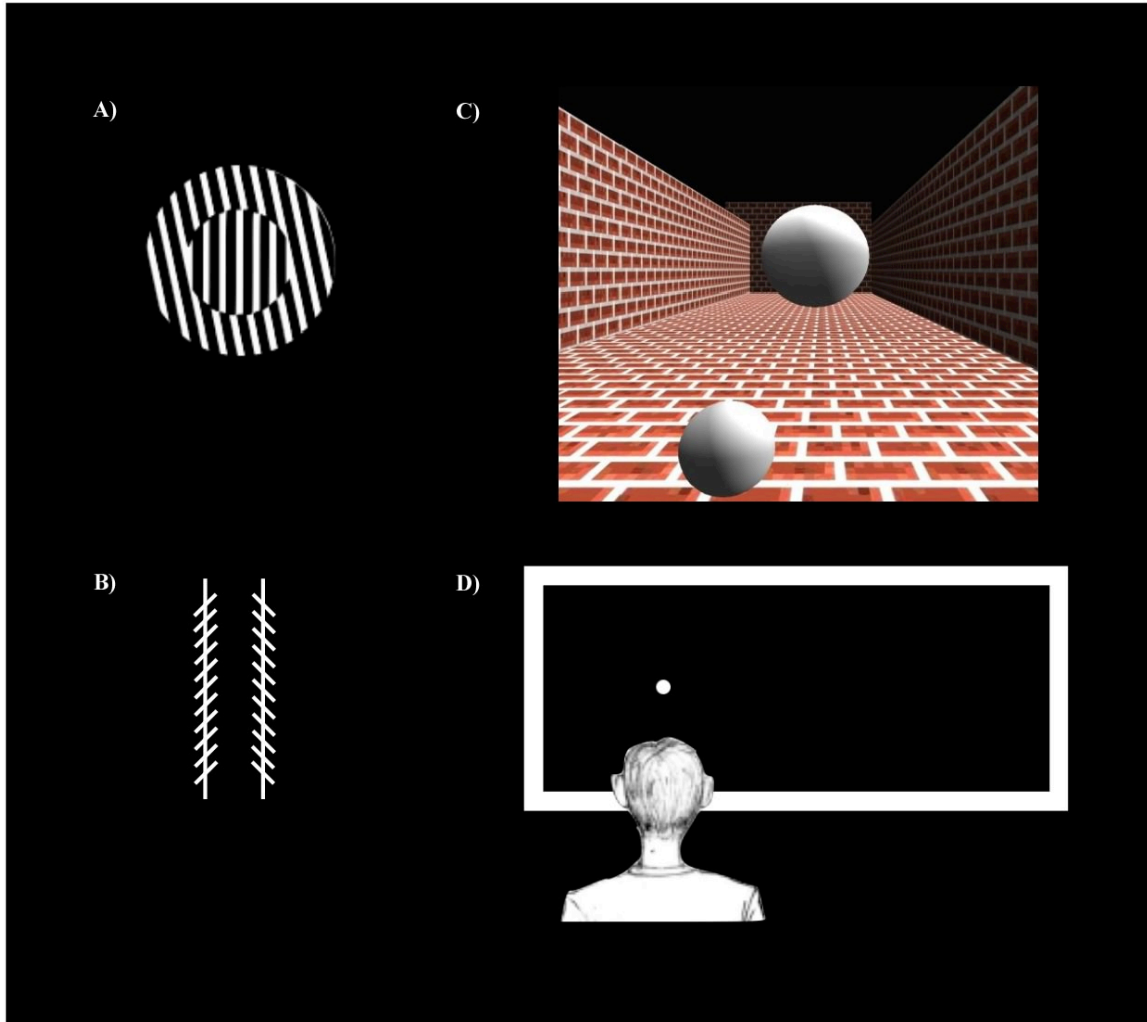


Figure 1: Examples of local (A & B) and global (C & D) contextual manipulations. A) Simultaneous tilt illusion. B) Zöllner illusion. C) 3D rendering of the Ponzo illusion. D) Induced Roelofs effect. (See text for description of illusory effects.)

A subset of illusions are caused by contrast interactions between target elements and adjacent context that share similar features (Blakemore et al., 1970). The simultaneous tilt (STI) is a classic example of an orientation illusion driven by local-level contextual manipulation (Figure 1A). In the STI, observers are asked to make a judgment regarding the orientation of a circular grating of lines, importantly; this central grating is surrounded by an annulus of lines that are also tilted (e.g., typically  $\pm 15^\circ$  from gravitational vertical). Observers typically perceive the central grating as tilted slightly in the direction opposite the annulus (Gibson & Radner, 1937). For example, a central grating that is vertically oriented ( $0^\circ$  tilt) will be perceived as tilted to the right, when flanked by a left-tilted annulus (see Figure 1A). The perceptual effects in the STI are likely caused by the mutually inhibitory interactions between the populations of visual neurons encoding the orientations of the central and surrounding elements (Blakemore et al., 1970). This same explanation could also explain the Zöllner illusion (Figure 1B).

An example of a global-level contextual manipulation is the induced Roelofs effect. In this paradigm, a large rectangular frame is presented to an observer in otherwise complete darkness, positioned so that the center of the frame is shifted several degrees to the right or left of the observer's midsagittal plane. A small target is presented inside the frame and the observer must report the location of the target with respect to perceived midline (Figure 1D). When the target is inside a right-shifted frame, participants typically report the target as lying to the left of its actual location (see Roelofs, 1934; Bridgeman, Peery, & Anand, 1997). Conversely, a left-shifted frame causes a rightward pattern of localization errors. The induced Roelofs effect is driven by a distortion of the observer's egocentric reference frame (Dassonville & Bala, 2004a; Dassonville et al., 2004b), with

the offset frame pulling the observer's perception of midline in the direction of the frame shift. Thus, the target mislocalization occurs when its position is encoded within this biased reference frame. For example, in the presence of a right-shifted frame, a target that lies at the participant's objective midline will appear to lie to the left of straight-ahead when encoded with respect to a right-shifted apparent midline.

The Ponzo illusion (Ponzo, 1912) is another example of an illusion that is driven by distortions of the observer's perception of space. However, it differs from the Roelofs effect in that it is driven by pictorial depth cues (see Figure 1C), including orientation, occlusion, shape from shading/contour, and linear perspective cues, depending on the specific experimental manipulation. Some or all of these cues are present in the context and act to distort the observer's sense of perceived depth (but see Prinzmetal, Shimamura, & Mikolinski, 2001). In Figure 1C, the distortion of apparent depth causes the observer to perceive the top sphere as further away in the scene. This illusion of apparent depth has a secondary effect on the perceived size of the rear sphere in the image, causing it to be perceived as larger than the near sphere.

A global contextual manipulation related to the Roelofs and Ponzo illusions is the rod-and-frame illusion (RFI, Witkin & Asch, 1948). In the original formulation of the RFI, a large frame and enclosed rod were presented to the observer in otherwise complete darkness (Figure 2). The frame was tilted off of gravitational vertical (typically by 15°). Participants are asked to rotate the rod until they perceive it as vertical. Witkin & Asch (1948) found that the tilted frame caused the rod to be perceived as being tilted in the opposite direction (that is, a counterclockwise tilt of the frame would cause the rod to be

perceived as being rotated somewhat clockwise, so that the rod would need to be tilted somewhat in the direction of the frame offset in order to be perceived as vertical).

Subsequent research manipulated the size of the frame, as well as the orientation of the observer relative to the frame, to elucidate the mechanism(s) that cause the RFI (Bischof, 1974; Goodenough et al., 1979). The presence of the large tilted frame serves to distort the observer's perception of vertical, with perceived vertical being rotated in the direction of the frame tilt. The rotated frame is believed to cause this distortion by providing a biased visual cue to the vertical direction that combines with the vestibular cues that are derived from the otoliths organs in the utricle and saccule of the inner ear. The RFI is similar to the Roelofs effect, in that the frame in both serves to distort the observer's egocentric frame of reference – this distortion of perceptual space then biases subsequent orientation or location judgments.

### **Individual differences in contextual processing**

Witkin & Asch (1948) employed the rod-and-frame illusion in an early attempt to quantify perceptual biases and individual differences in contextual processing. Using several instantiations of the rod-and-frame test, Witkin observed a range of individual differences in observers' susceptibility to the effects of the frame, with some observers showing large errors, while others showed none. Witkin observed that individuals fell along a continuum in terms of their reliance on the context of the frame. A small number of individuals were highly susceptible or immune to the effect of the frame, with the majority of people falling between these two extremes.



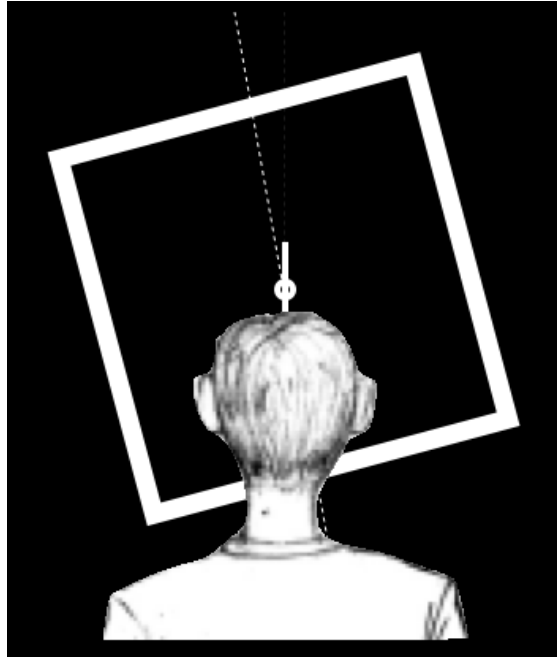


Figure 2: Rod-and-frame task. Participant is asked to adjust the orientation of the central rod so that it is aligned with gravitational vertical. The left-tilted frame rotates the observer's subjective vertical in the direction of the frame tilt, causing the observer to perceive the rod as right-tilted.

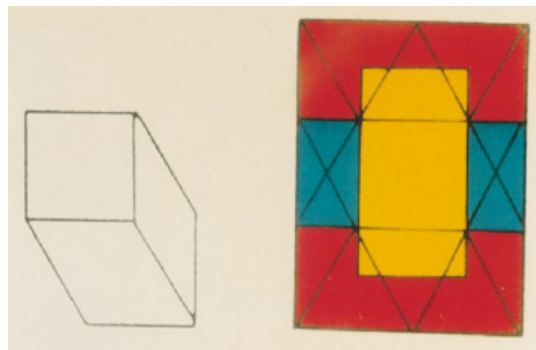


Figure 3: Embedded Figures Task. Participants must find the simple figure (left) within the complex figure (right) and report its location.

In subsequent work, Witkin (1950) developed a disembedding task to study the cognitive processes that are involved in finding camouflaged visual targets. The Embedded Figures Task (Figure 3) required participants to locate a simple geometric shape that was presented within the gestalt of a much more complex image. While the individual components of the target shape are easy to see, the overall shape of the target is hidden within the perceptual organization of the background pattern. Again, Witkin noted a broad range of individual differences in participants' abilities to locate the target shape. Some individuals could find the target item seemingly effortlessly, while others could not complete a single trial in the allotted time.

Individual differences in RFI and EFT performance were taken as evidence for differences in contextual processing biases. While both tasks differ in their details, they are both similar in that the context (i.e., the frame in the RFI, or the complex gestalt in the EFT) must be ignored in order to achieve optimal performance. To efficiently perform the EFT, participants must effectively ignore the gestalt of the complex image to locate the target shape. Individuals that are more reliant on visual contextual information would have difficulty performing the EFT, because they do not effectively ignore the extraneous features of the complex shape that are obscuring the target shape. Similarly, an individual that is reliant on contextual information would also show an increased susceptibility to the RFI, due to a heightened processing of the illusion-inducing frame. With these ideas in mind, Witkin & Goodenough (1981) examined the behavioral relationship between EFT performance and RFI susceptibility and found an inverse relationship between the two. Specifically, individuals who excelled at the EFT were

typically less susceptible to the illusory effects of the tilted frame, leading to a smaller distortion of perceived vertical.

Individual differences in RFI and EFT led Witkin to develop the theory of Field Dependence/Independence (FDI) in the early 1940's (see Witkin & Goodenough, 1981, for a review). The early formulation of FDI was an attempt to characterize an individual's perceptual processing capabilities as active processes, rather than passive computations that were constant across the population. Witkin's idea that an observer's perception of an image was influenced by a "cognitive style" unique to that individual ran counter to the commonly held beliefs of experimental psychology at the time. The theory proposed that perceptual processing abilities fell along a continuum, with two "cognitive styles" that occupied the extreme ends of this distribution. Field-dependent individuals were thought to be more reliant on contextual information, with these individuals having a greater tendency to integrate objects with the surrounding context. Because of this tendency, these individuals would be particularly susceptible to the RFI and distracted in the EFT. In contrast, field-independent individuals would tend to focus on local details and ignore context. A field-independent individual would therefore excel at the EFT and show decreased susceptibility to visual illusions.

The individual differences approach of FDI to psychological functioning spread through a multitude of research disciplines, including child development, perceptual functioning, neuropsychology, educational policy, and personality/socialization (Wapner & Demick, 1991). While it is now generally thought that the attempts to interpret FDI as being relevant to these other disciplines were overblown, the more specific finding of a relationship between RFI susceptibility and EFT performance continues to be interpreted

as indicating a general tendency to make more or less use of the context presented within various visual tasks. More recent work has examined the individual differences in the susceptibilities to a wider array of illusions (Walter, Dassonville, & Boschler, 2009). The results from that study have caused a more complex image to emerge. Whereas FDI would predict positive correlations in the susceptibilities to all visual illusions driven by contextual processing, this was not the case. Instead, the susceptibilities to the RFI, Ponzo, and Roelofs illusions were found to be positively correlated within one factor, susceptibilities to another set of illusions (i.e., the Ebbinghaus and Müller-Lyer illusions) formed a second, independent factor. The primary distinction between these factors seemed to be the level of processing at which the illusions cause their effect, with the first factor containing those illusions that were driven by global levels of context (and, even more specifically, distortions of the observer's egocentric reference frame), and the second factor containing those illusions that had their effects at more local levels of processing.

### **Components of visual attention**

The use of contextual information in visual processing is critical for judgments of spatial attributes of objects, visual search, and implicit learning (Chun & Jiang, 1998; Brockmole, Castelhano, & Henderson, 2006; Davenport & Potter, 2004). Relying on environmental cues, or internal knowledge of contextual regularities is beneficial in real-world situations. The inherent reliability of contextual information can then be used to effectively guide attention within a cluttered scene. However, examining behavior in the presence of illusion-inducing context can provide a chance to see how attention interacts

with, or potentially contributes to certain visual illusions. A portion of the studies included in this dissertation will examine how the attentional goals of an observer influence their reliance on context and how shifts of attention interact with illusory context.

Attentional selection of candidate objects within the environment is computationally important, because the volume of information contained in a typical visual scene far exceeds the processing capacity of the central nervous system. Furthermore, the majority of the sensory information impinging on the sensory receptors is not needed for the individual's current behavior goals. The current framework that attention can operate in reflexive or goal-driven modes dates back to early formulations attributed to William James (1890/1950). Building off of James' early ideas, recent models of visual attention assume that these modes of attention are largely space-based (but see also Chen, 2012); these models assume that attention moves to various locations in the environment, and any information that falls within the focus of attention is selected for further processing (Jonides, 1980, 1984).

An early demonstration of the perceptual consequences of focusing attention came from Eriksen & Hoffman (1974) who showed that providing participants with advance knowledge of where a target would appear allowed them to shift the focus of attention, which facilitated their detection of a visual target. Subsequent work by Eriksen & Eriksen (1974) examined how distracting information affected processing within the window of attention. Using a flanker paradigm, participants were asked to respond to a target letter that was flanked by incongruent or congruent distractor letters. Congruent distractors were the same letter as the central target letter, while incongruent items needed to be

ignored to efficiently perform the task. There was a significant cost when the flanker items were incongruent, compared to when they were neutral or congruent. As the flankers were moved farther away from the central target letter, the distracting effects of the flankers decreased, further supporting a strong spatial component of attention selection. Specifically, when the flankers are close the target items, attentional resources may involuntarily spill over to those items and process their identity, causing a response conflict when the distractors are incongruent.

The development of the spatial cueing paradigm (Posner, Snyder, & Davidson, 1980a; Posner, 1980b) was used to examine how stimulus attributes and mental set interacted in attentional selection in space. These paradigms were also critical in elucidating temporal differences in the modes of attentional selection. In this task, observers are asked to detect the presence of a peripheral target that is preceded by a spatial cue. In one condition, the cue is a non-predictive, exogenous peripheral onset that could appear at the subsequent location of the target (valid cue), or a non-target position (invalid cue). Posner showed a reaction time benefit for targets that appeared in previously cued locations of the visual field. In contrast, participants were slower to respond to invalidly cued locations, compared to neutral cues, because of the need to reorient attention from the initial cued position. The onset cues showed a rapid profile of facilitation (~ 50-200 milliseconds post-cue) that quickly turned to inhibition around 300 ms post-cue.

The attentional cue in the spatial cueing paradigm can also be spatially predictive of the target's location. In this endogenous condition, a central arrow indicates the likely location of the target item. In some respects, this cue form causes behavioral effects

similar to those observed with exogenous cues, but differences do exist between the two. Predictive cues showed a slower time course of facilitation, with facilitation occurring ~250-300 milliseconds after cue onset, without any subsequent inhibition. The facilitative effect of the cue lasts as long as the observer chooses to maintain the attentional focus at that location. This led Posner to propose an empirical distinction between two forms of selective attention. In one mode, attention behaved in a reflexive manner, what was termed exogenous attention. In this mode, the allocation of attention is driven by salient events in the environment, followed by a rapid disengagement and reorientation of attention to a new location. Alternatively, selective attention could be driven by the demands of the task (endogenous attention), with the decision to exercise control over attention being made by the voluntary actions of the observer.

Volitional control ability is not the only piece of empirical evidence that differentiates exogenous and endogenous modes of selection. Despite early psychophysical work providing clear support for Posner's model, early imaging studies demonstrated that cortical circuits involved in voluntary and reflexive shifts of attention are largely overlapping. However, recent studies have further refined this functional overlap, demonstrating that distinct sub-regions of posterior parietal cortex are transiently active during voluntary vs. reflexive attentional shifts (Serences et al., 2005; Serences & Yantis, 2006). The time courses of facilitation and inhibition also differ prominently between reflexive and voluntary shifts of attention (Müller & Rabbitt, 1989; Posner & Cohen, 1984; Klein, 2000). The perceptual consequences of selection differ between the modes of attention, for example endogenous attention has been found to selectively decrease contrast detection thresholds (Yeshurun, Montagna, & Carrasco, 2008). Prinzmetal,

McCool, & Park (2005) have suggested that endogenous and exogenous selection operate at different stages of information processing. The authors demonstrate in several experiments that endogenous selection influences tasks designed to measure the accuracy of a representation, as well as the speed with which a response is executed (i.e., reaction time). Reflexive orienting of attention, on the other hand, only influences response speed. They propose that these two modes of attention are controlled by different mechanisms, and serve different functional purposes, such that, endogenous shifts of attention affect the fidelity of perceptual representations, while exogenous shifts of attention influence decision-level stages of processing,

In the subsequent experiments, a spatial cueing manipulation will be adopted to examine the question of how these two modes of attention might affect an egocentric reference frame in a visual illusion.

### **Involuntary attentional capture**

Following Posner's seminal work on temporal differences in attentional selection, the focus of attention research turned to the specific stimulus properties that can reflexively attract attention. The use of peripheral onset cues in the early cueing experiments suggested that abrupt onsets (i.e., luminance transients) might have a unique ability to reflexively attract attention. Yantis & Jonides (1988, 1990) employed visual search experiments to demonstrate that abrupt onset targets were detected rapidly in a cluttered display. Additionally, abrupt onset items were also found to be particularly distracting when searching for a non-onset target. The propensity for onsets to capture attention was argued to be ecologically adaptive, because onsets could signal the appearance of new



objects in the environment (for example potential prey, or a looming predator). Subsequent work controlling for luminance transients in the search displays, demonstrated that the appearance of new objects (see Yantis & Hillstrom, 1994) in the environment capture attention in a purely bottom-up manner, completely independent of the observer's goals.

In a cluttered visual environment, perceptual salience can be signaled along a variety of dimensions (e.g., color, orientation, or shape). The importance of these bottom-up factors in determining attentional selection has been reflected in most modern models of attentional control (Itti & Koch, 2000; Kim & Cave, 1999; Nothdruft, 1993). Theeuwes (1991, 1992, 1994) provided evidence that salient features, not just new objects, capture attention in a purely bottom-up manner. Theeuwes developed a visual search task in which participants searched for a target item in the presence of two salient singletons. One singleton was the target item and the other was an irrelevant distractor. Theeuwes (1992) asked participants to search a circular array composed of color circles or diamonds. Each shape contained an oriented line segment; participants were to report the orientation of the line that appeared in the singleton shape (e.g., the diamond). In the distractor condition, an additional color singleton was presented in the search array. Search performance slowed significantly when the irrelevant singleton was present, even though observers were clearly using a top-down set to search for the shape singleton. When the salience of the color singleton was reduced, the distractor item no longer interfered with visual search. Based on these findings, Theeuwes concluded that salient singletons, regardless of their feature dimension, capture attention automatically and independent of top-down goals.

The unique ability of new objects and salient features to capture attention generated a great deal of research in the field of attentional control (Yantis & Egeth, 1997; Theeuwes & Godjin, 2001; Yantis, 2000). This bottom-up view of attentional control was challenged by Folk et al. (1992) who noted that the distractors used in the early onset work shared stimulus properties with the targets. In a concrete example, Folk et al. noted that Remington et al. (1992) used targets that were defined by onsets, however the distractor items were also defined by abrupt onsets. If an observer is tuned to search for onset items, distractor items that possess this same characteristic might cause involuntary capture based on the task demands. To convincingly argue that onsets reflexively capture attention, the stimulus properties of the target and distractors must be unique. Folk et al. (1992) used a variant of the capture paradigm where observers were asked to detect one of two stimulus properties (e.g., color or onsets) in the presence of the other distractor property. They found that onset distractors were particularly disruptive when searching for an onset target, however distractors defined by color had little effect. Similarly, when observers were looking for a red target, there was no evidence of attentional capture by onset distractors. This led Folk et al. (1992) to propose the contingent-capture hypothesis. This hypothesis argues that top-down attentional control settings dictate susceptibility to capture. Specifically, the more overlap a target attribute has with the properties of distractors, the more likely attention will be involuntarily captured.

### **Neural substrates of attention and contextual processing**

The first neuroimaging studies of spatial attention used well-characterized psychophysical manipulations of spatial attention to examine the neural substrates of

goal-driven and reflexive shifts of attention (Corbetta et al., 1993, 1995). Corbetta et al. (1993) used both endogenous and exogenous cues to examine activation patterns when peripheral locations in the visual field were selected. They observed that two primary regions of cortex are recruited when visuospatial shifts of attention are executed, with these activations centered in the superior parietal and superior frontal cortices. The superior parietal regions were largely recruited when stimuli were selected based on the observer's goals and stimulus salience. Importantly, these activations occurred independent of an overt behavioral response. In contrast, the frontal regions were active only when behavioral responses were executed to peripheral stimuli, demonstrating that these regions coordinate motor responses after attentional selection. Subsequent human imaging further supported the model that a frontal-parietal circuit coordinated visuospatial shifts of attention (Anderson et al., 1994; Nobre et al., 1998; Gitelman et al., 1996).

While these groundbreaking studies laid the foundation for modern research studying the neural substrates of attention, they were not without limitations. For example, modern imaging technology far exceeds previous techniques in numerous domains, including spatial resolution/localization and analysis capabilities. Corbetta et al. (1993, 1995) observed that largely homologous regions of posterior parietal cortex, mostly in the right hemisphere, were active during peripheral shifts of attention. This pattern of activation was observed for attention shifts driven by the cognitive goals of the observer, and by salience; these results are consistent with parietal cortex acting as a domain-general control center for visuospatial shifts of attention. Recent studies have further refined this model, by demonstrating that distinct sub-regions of parietal cortex and frontal eye fields

are modulated by voluntary and stimulus-driven shifts of attention (Kincade et al., 2005). A series of recent studies – spanning object-, space-, and feature-based manipulations of attention – demonstrate that voluntary and stimulus-driven attentional shifts recruit distinct circuits in posterior parietal cortex (Yantis et al., 2002; Liu et al., 2003; Serences et al., 2004; Shomstein et al., 2004). Across all studies, voluntary shifts of attention activated superior and medial parietal lobule, while more ventral regions of inferior parietal sulcus were active during stimulus-driven shifts.

A survey of the current neuroimaging literature suggests potential links between the neural circuits that control visuospatial attention, and those recruited in visuospatial judgments and the processing of visuospatial context. Spatial attention is inextricably linked with all studies of visual perception, as any experimental manipulation necessitates selection of task-relevant information. Vallar et al. (1999) had participants perform a task in which they indicated when a bar, moving laterally on screen, traversed the perceived midline. They observed significant activation in a network of frontal and parietal regions when participants had to judge the location of the bar relative to midline, compared to a control experiment in which the participant determined the location of the target in allocentric coordinates. The strongest activations were observed in the right superior parietal lobule and inferior parietal sulcus – regions that have been implicated in the control of voluntary and reflexive visuospatial attention (Corbetta et al., 1993, 1995; Anderson et al., 1994; Nobre et al., 1998; Gitelman et al., 1996).

Walter & Dassonville (2008) adapted the induced Roelofs effect for use with fMRI, to determine the brain regions that are recruited when individuals make location judgments in the presence of the Roelofs-inducing frame. In separate blocks of trials,

participants reported the location of the target (presented either with or without the context of a Roelofs-inducing frame), or they performed a control task that involved judgments of the target's color. The localization task, when compared to the color task, was accompanied by an increased level of activation in a frontoparietal network similar to that seen by Vallar et al. (1999). However, there was a significantly greater activation, primarily right-lateralized, in the superior parietal lobule (SPL) when participants reported the location of the target that was presented in the context of the Roelofs inducing frame, compared to the same localization task with no frame present. A similar parietal region was seen to be involved in the processing of the illusion-inducing context of the Müller-Lyer illusion (Weidner & Fink, 2006). Together, these findings indicate a possible role for right SPL in processing visuospatial contextual information. This region shows some overlap with attentional control areas, centering largely in the superior parietal lobule and intraparietal sulcus. However, contextual manipulations do not show the frontal recruitment observed by Corbetta et al. (1993, 1995) and Kincade et al. (2005).

### **Empirical studies of visuospatial contextual processing**

The experiments of Chapters II & III will explicitly address the role of visual attention in modulating, or even serving to drive, the induced Roelofs effect. Recent work by Bridgeman & Lathrop (2007) has demonstrated that the induced Roelofs effect can be obtained under conditions in which the inducing frame is not consciously perceived due to inattention blindness. This result implies that the effects of the illusion are driven solely within levels of visual processing that are immune to attentional modulations. However, while Bridgeman and Latham demonstrate that the Roelofs effect can be

obtained with an unperceived frame, it is unclear from their data whether the *magnitude* of the Roelofs effect was modulated by this manipulation of awareness. Experiments in Chapter II of this dissertation directly test whether attentional set can influence susceptibility to the Roelofs effect.

While the consequences of the Roelofs effect on perception and action are well characterized, research examining the mechanism responsible for the distortion of subjective midline is lacking. Walter and Dassonville (2006) found a robust Roelofs effect with a stimulus consisting only of one end of the frame – the effect was present as long as there was an imbalance between the stimuli in the left and right halves of the visual display. These results, coupled with the results of Bridgeman & Lathrop (2007) have helped define the characteristics of stimuli able to cause the effect; however, none has explored its underlying mechanisms. In Chapter III, the role of shifts of attention and visual field asymmetries is examined in the Roelofs effect.

Finally, Chapter IV uses a non-invasive brain stimulation method in humans to characterize the contextual processing role of a candidate cortical region of interest. Illusion susceptibility in the rod-and-frame and simultaneous tilt illusions is directly compared within-subjects after neural computation in this target region is temporarily disrupted. The results support a specific contextual processing role for this region, independent of potential attentional disruptions induced by the stimulation procedure.

## CHAPTER II

### ATTENTIONAL CONTROL SETTINGS MODULATE SUSCEPTIBILITY TO THE INDUCED ROELOFS EFFECT

Although one's percept of the world is seemingly flawless, manipulations of visual context can sometimes fool the visual system, revealing clues about the mechanisms used by the brain to organize our perceptual environment. In one such example, the presentation of a large rectangular frame that is offset from the observer's objective midline causes a distortion of the perceived, or subjective, midline (Roelofs, 1935). Under these conditions, when observers are asked to indicate the direction that is perceived to be straight-ahead, they report their midline as being shifted in the direction of the offset frame (Brecher, Brecher, Kommerell, Sauter, & Sellerbeck, 1972; Brosgole, 1968; Dassonville & Bala, 2004a; Dassonville, Bridgeman, Bala, Thiem, & Sampanes, 2004; Werner, Wapner, & Bruell, 1953). In turn, this distortion of the observer's representation of visual space causes errors when judging the location of the frame (the Roelofs effect, Roelofs, 1935) or the location of a target presented inside the frame (the induced Roelofs effect, Bridgeman, Peery, & Anand, 1997; Dassonville & Bala, 2004a; Dassonville et al., 2004).

Although a distortion of the observer's subjective midline is understood to drive the Roelofs illusions (however, see also de Grave, Brenner & Smeets, 2002, 2004; Dassonville & Bala, 2004b), the mechanism by which the offset illusion-inducing frame

causes this distortion is unclear. One way to begin to dissect this mechanism is by investigating the level of visual processing in which the frame has its effect. Recent work by Bridgeman & Lathrop (2007) has demonstrated that the induced Roelofs effect can be obtained under conditions in which the inducing frame is not consciously perceived. Using a version of the classic inattention blindness paradigm developed by Mack & Rock (1998), participants had to make a target location judgment in a paradigm that was made attentionally demanding by the presence of an additional perceptual task (a length discrimination judgment). On a small subset of trials, an offset Roelofs-inducing frame was presented while participants were performing the two tasks. When questioned after the trial, more than half (54%) of participants reported that they did not perceive the frame; nonetheless, perception of the target's location was biased by the unperceived frame, suggesting that this contextual information is integrated even under circumstances in which it never reaches perceptual awareness. Indeed, the analysis of Bridgeman and Lathrop indicated that awareness of the frame was insufficient to even modulate the magnitude of the effect. In sum, these results suggest that the contextual information of the Roelofs-inducing frame exerts its effects early in sensory processing.

Similar to the findings of Bridgeman & Lathrop (2007) with the induced Roelofs effect, Moore & Egeth (1997) demonstrated that the Ponzo and Müller-Lyer illusions could be evoked even without awareness of the illusion-inducing contextual information (see also Chan & Chua, 2003; Lamy, Segal, & Ruderman, 2006). However, other studies have typically indicated that, in spite of this, the magnitude of illusory phenomena can be modulated by attention within the visual display. For example, the magnitude of the Müller-Lyer illusion can be modulated using paradigms that cause observers to focus



their attention on one of two sets of illusion-inducing wings that are presented simultaneously (Coren & Porac, 1983; Goryo, Robinson, & Wilson, 1984; Tsal, 1984; Predebon, 2004). Furthermore, Predobon (2006) demonstrated that the common finding of illusion decrement in the Müller-Lyer illusion, or the decrease in illusion magnitude over the course of an experiment, is best accounted for by the observer's adoption of an attentional set to ignore the illusion-inducing context, indicating that an observer's internal goals can modulate illusion susceptibility. These studies, and others that have examined the rod-and-frame (Daini & Wenderoth, 2008) and Ebbinghaus illusions (Shulman, 1992), indicate that attentional selection is capable of modulating the illusory effects of contextual elements within the visual image.

The report by Bridgeman & Lathrop (2007) that the magnitude of the Roelofs effect was not modulated by the awareness of the inducing frame seems to run counter to the many reports that attention can modulate effect sizes in a wide range of illusions. It may be that the Roelofs effect is truly different from these other illusions, with its effects driven solely within levels of visual processing that are immune to attentional modulations. Alternatively, it is possible that the Roelofs effect can in fact be modulated by attention, but that this effect escaped detection due to the low statistical power inherent in the type of between-subject comparison of single-trial measures of illusion susceptibility that Bridgeman and Lathrop performed. In the present study, we perform a more direct test of the ability of attention to modulate the magnitude of the induced Roelofs effect.

## Experiment 1

If top-down attentional selection does in fact play a role in the Roelofs effect, we might expect the magnitude of the illusion to be modulated by manipulations known to affect spatial attention. As an example, the contingent involuntary orienting hypothesis suggests that involuntary shifts of attention are contingent on top-down control settings that are created based on task expectancies and/or demands (Folk, Remington, & Johnston, 1992). Indeed, a number of paradigms have been used to demonstrate that an attentional distractor has a much larger impact when it is of the same color as the expected target (Folk et al., 1992; Folk & Remington, 1999; Folk, Leber, & Egeth, 2002, 2008; Folk & Remington, 2006).

In the present study, we modified the standard induced Roelofs task to determine whether the magnitude of the illusion could be modulated by feature-based attentional selection. Participants were instructed to search for and report the location of a target (e.g., a red dot) presented inside an offset rectangular frame. The target item was presented amongst three distractor items of different colors, so that, in order to achieve an optimal performance, participants would be required to maintain an attentional set that would filter out the irrelevant colored items. The color of the offset, Roelofs-inducing frame was manipulated so that on some trials it matched the participants' top-down attentional settings. If it is true that the Roelofs effect can be modulated by attentional filtering, the magnitude of the illusion would be expected to be larger on those trials in which the target and frame colors match, but smaller on trials in which the frame is of a different color.

## Methods

*Participants.* Twenty University of Oregon undergraduates with normal or corrected-to-normal vision volunteered to participate for course credit. Participants provided informed consent prior to their participation, with all procedures approved by the Institutional Review Board of the University of Oregon.

*Apparatus.* Participants were seated in a dark room with the head steadied by a chin and forehead rest positioned approximately 90 cm from the plane of a translucent projection screen (137 cm x 102 cm). Stimuli were back-projected (Electrohome Marquee 8500 projector with a refresh rate of 60 Hz) onto the screen, and centered at eye-level. Eye position was monitored continuously during experimental trials, using an Eye-Link 1000 eye-tracking system (SR Research Systems), operating at a 250-Hz sample rate. Manual responses were collected as button presses on a game pad connected to the host computer.

*Stimuli.* At the start of each trial, a white fixation point (RGB values: 255, 255, 255; 0.9° in diameter) appeared 10° above eye-level at the center of the screen. A large rectangular frame (25° horizontal x 12.5° vertical, 1° thick), was positioned so that it was centered at eye-level, 5° to the left or right of the participants' midsagittal plane. Inside the frame, one target (defined by color; see below) and three distractors (0.5° in diameter) appeared in random locations within an invisible 7 x 3 array of possible locations (Figure 4). Positions within this array were -4.5, -3, -1.5, 0, 1.5, 3, and 4.5° from the participant's midsagittal plane, and -1.5, 0 and 1.5° from eye-level. Targets and distractors appeared in randomly-selected locations within the array with equal

probabilities, such that any small display imbalances (and any resulting Roelofs-like effects) caused by their presentation would cancel out over the course of the experiment.

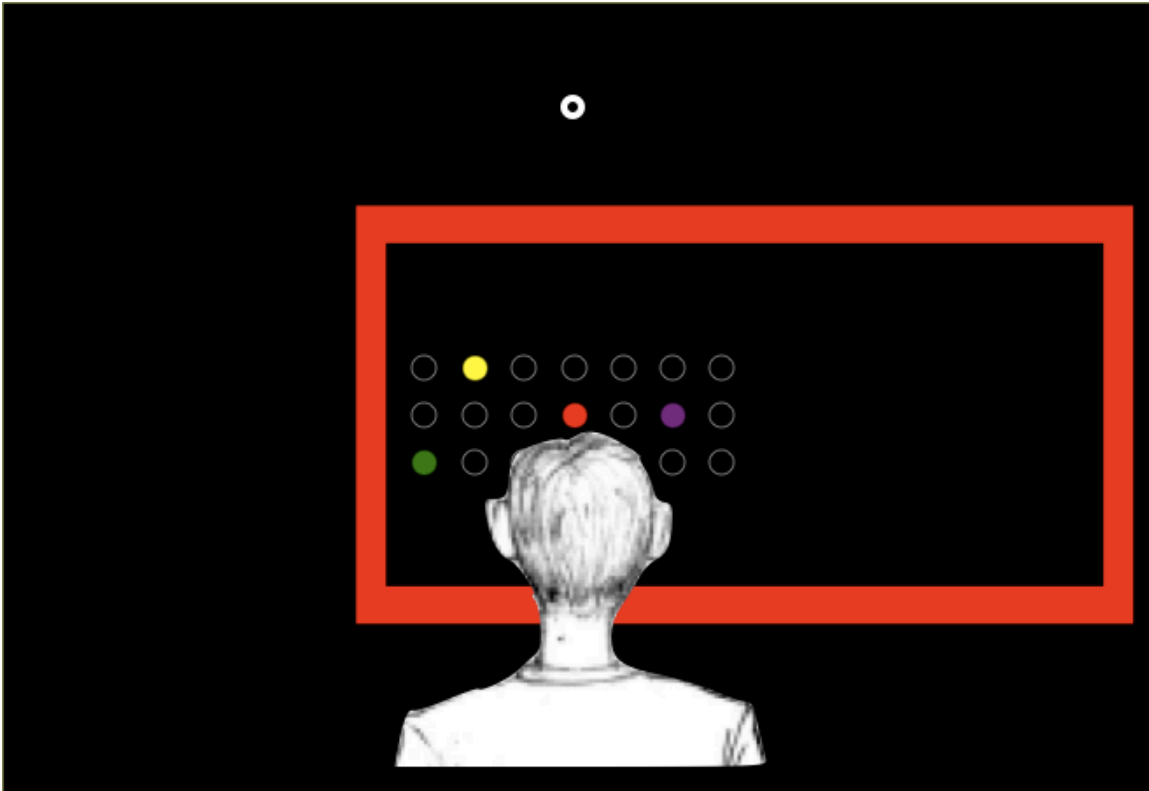


Figure 4: Sample display from Experiment 1. Spatial schematic of visual display; while the display is drawn to scale, the cartoon observer is not. The array of possible target/distractor locations (gray circles) was not visible to participants, and the fixation point was extinguished before frame, target and distractor onset. In this *set-color* trial, the participant had the task of reporting the location of the red target (left or right of straight-ahead) presented amidst yellow, purple and green distractors within a red frame (here offset to the participant's right).

Participants were asked to report only the location of the target, which could be distinguished by its red color (RGB: 255, 0, 0) for half of the participants (randomly assigned), or blue (RGB: 0, 200, 255) for the others. The distractors were green (RGB: 0, 210, 0), yellow (RGB: 196, 196, 0), and purple (RGB: 218, 121, 255) on each trial. The

color of the Roelofs-inducing frame varied randomly from trial-to-trial, either red (RGB: 255, 0, 0), blue (RGB: 0, 200, 255), or yellow (RGB: 196, 196, 0). All frame, target, and distractor colors were matched for luminance ( $0.2 \text{ cd/m}^2$ ).

For participants searching for a red target, the red, blue, and yellow frames comprised the *set-*, *different-*, and *distractor-color* conditions, respectively. Specifically, when searching for a red target, the red frame was the same color as the to-be-reported target (*set-color* condition). Likewise, the yellow frame comprised the *distractor-color* condition because yellow was one of the three distractor colors, whereas blue never appeared as a distractor color and constituted the *different-color* condition. Conversely, for participants that searched for a blue target, the red frame constituted the *different-color* condition, the blue frame constituted the *set-color* condition and the yellow frame constituted the *distractor-color* condition. Equal numbers of *set-*, *distractor-* and *different-color* trials appeared in the experimental trials.

*Procedure.* Each trial began with the presentation of the fixation point. Participants initiated the trial by moving the eyes to the fixation point, and then pressing a button on the game pad with the left thumb. The fixation point was extinguished immediately, and after a 400-ms delay, the rectangular frame was illuminated, followed 100 ms later by the target/distractor array. The frame and target/distractor array were then simultaneously extinguished, with a total frame duration of 200 ms and a target/distractor duration of 100 ms. Participants were instructed to report the location of the target, while ignoring the irrelevant frame and distractors. Participants responded with a button press to indicate the target's location with respect to straight-ahead, with a press of the left index finger

indicating a target to the left, and a press of the right index finger indicating a target to the right.

Throughout each trial, participants were required to maintain fixation within an invisible, circular fixation zone (2.5° radius<sup>1</sup>) that surrounded the fixation point in the center of the screen. Trials during which blinks occurred, or during which the eyes moved outside of the fixation zone (even after the fixation point was extinguished), were discarded and repeated at the end of the experimental block. This resulted in a total of 504 valid experimental trials completed by each participant. Prior to the experimental trials, participants performed 40 practice trials, for which performance was not analyzed.

*Data analysis.* For each combination of target location, frame location and frame color, the perceived location of the target was quantified as the proportion of trials in which the participant reported the target as being located to the right of straight-ahead (Figure 2). Since the induced Roelofs effect caused by a frame shifted left or right of midline is known to affect only a target's perceived azimuth, trials were collapsed across the different target elevations. Psychometric functions were then fit to this data to determine the point of subjective equality (*PSE*, the location at which the targets were equally likely to be judged left or right of straight-ahead), using the equation:

$$\text{proportion "Right" responses} = (1-\text{amp})/2 + (\text{amp} \times e^{((\text{tarpos}-\text{PSE})/\tau)})/(1+e^{((\text{tarpos}-\text{PSE})/\tau)}),$$

---

<sup>1</sup> To prevent the fixation point from serving as a possible allocentric cue to target location, it was extinguished 500 ms before target presentation. The larger-than-typical fixation zone was required to offset the increased task difficulty that resulted from the requirement to maintain fixation even after the fixation point was extinguished. Possible effects of small eye movements away from the fixation point are examined in the Results section of Experiment 1.

where  $tarpos$  was the actual target location,  $PSE$  was the point of subjective equality,  $\tau$  was the slope of the psychometric function, and  $amp$  was the amplitude of the psychometric function (the best-fit  $PSE$ ,  $\tau$  and  $amp$  values were determined iteratively using a least-squares algorithm in Microsoft Excel). The amplitude parameter was included to account for the finding that the floor and the asymptote of the psychometric functions often did not reach 0 and 1 in some participants. This effect may have occurred due to an occasional inability of the participant to correctly isolate the target from the distractors. To quantify the magnitude of the Roelofs effect in each color condition, the  $PSE$  for the left-frame condition was subtracted from that of the right frame condition, with this total effect size statistically compared across color conditions.

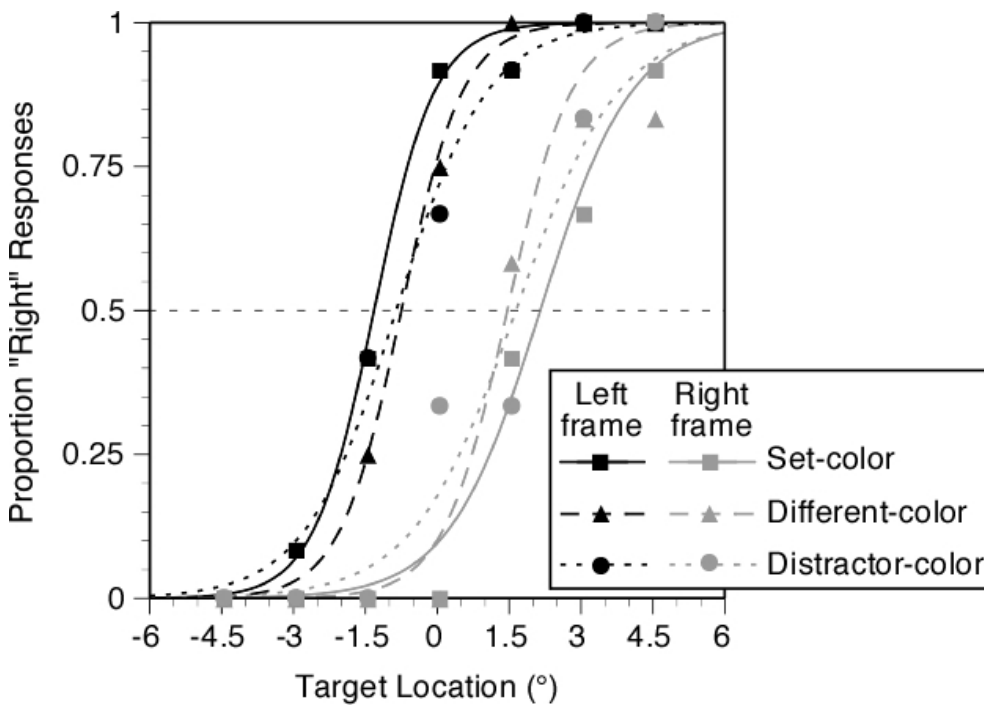


Figure 5: Typical results from a single participant in Experiment 1. Best-fit psychometric functions are plotted for each frame offset (e.g., left and right) and each color condition. The point at which each function surpasses a proportion of 0.5 indicates the point of subjective equality (PSE) for that condition.

## Results

Figure 5 shows the typical pattern of results from a single participant, with left-shifted frames increasing the likelihood that particular targets are reported as being to the right of straight-ahead, and vice-versa. Although the overall magnitude of the induced Roelofs effect in each color condition (Figure 6, Table 1) differed significantly from zero [*set-color*:  $t(19) = 6.024, p < .0001$ ; *different-color*:  $t(19) = 4.609, p < .0001$ ; and *distractor-color*:  $t(19) = 5.043, p < .0001$ ], a repeated-measures ANOVA revealed a significant main effect of frame color [ $F(2, 38) = 6.751, p = .003$ ]. Planned comparisons indicated that the Roelofs effect for the *set-color* condition was significantly larger than that for the *different-color* [ $t(19) = 3.485, p = .002$ ], and *distractor-color* conditions [ $t(19) = 3.191, p = .005$ ], while the effects for the *different-* and *distractor-color* conditions did not significantly differ [ $t(19) = -0.651, p = .523$ ].

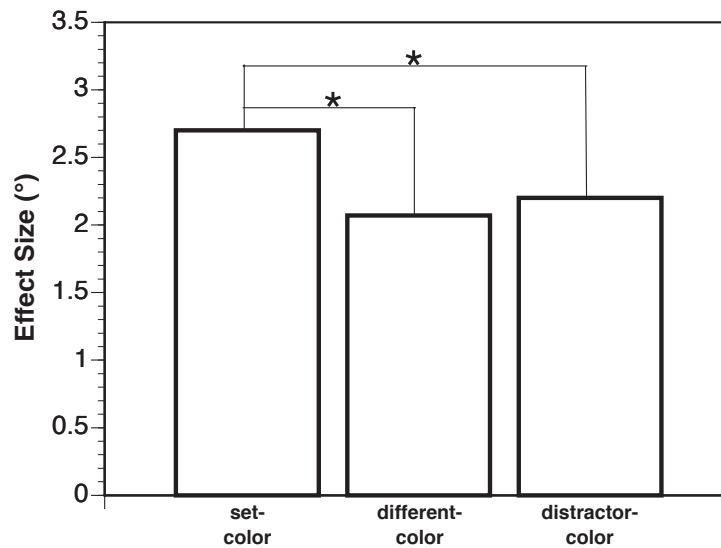


Figure 6: Mean induced Roelofs effect size (calculated by subtracting the PSE for the frame left condition from that of the frame right condition) for each of the three frame color conditions in Experiment 1. Asterisks indicate  $p < .05$ .



To test for differences in the slope ( $\tau$ ) and amplitude ( $amp$ ) values across the psychometric functions for the different color conditions, separate repeated-measures ANOVAs were conducted with frame color as the sole factor, and slope and amplitude (collapsed across the right and left frame conditions) as the dependent variables (Table 1). The main effect of frame color was not significant for slope ( $F(2, 38) = 1.38, p = .262$ ), but did reach significance for the amplitude ( $F(2, 38) = 5.08, p = .01$ ), with a smaller overall amplitude in the *different-color* frame condition. Planned comparisons indicated the amplitude was significantly smaller in the *different-color* condition compared to the *set-color* and *distractor-color* conditions ( $t(19) = 2.26, p = .03$ ;  $t(19) = -2.99, p = .007$ , respectively). Amplitude in the *set-color* and *distractor-color* conditions did not significantly differ ( $t(19) = -.79, p = .439$ ).

Table 1: Roelofs Magnitude, Slope & Amplitude Parameters (mean  $\pm$  se) for Different Trial Conditions in Experiments 1 & 2.

Experiment	Condition	Roelofs ( $^{\circ}$ )	Slope ( $^{\circ}/^{\circ}$ )	Amplitude ( $^{\circ}$ )	
1	Set-color	2.80 $\pm$ 0.44	12.90 $\pm$ 1.41	0.90 $\pm$ 0.03	
	Different-color	2.13 $\pm$ 0.45	10.09 $\pm$ 1.25	0.84 $\pm$ 0.04	
	Distractor-color	2.30 $\pm$ 0.45	12.20 $\pm$ 1.59	0.92 $\pm$ 0.03	
2	Distractors-present	Set-color	2.53 $\pm$ 0.59	11.46 $\pm$ 0.95	0.97 $\pm$ 0.01
		Different-color	2.26 $\pm$ 0.63	10.83 $\pm$ 0.95	0.96 $\pm$ 0.01
	Distractors-absent	Set-color	2.77 $\pm$ 0.59	7.71 $\pm$ 0.90	0.99 $\pm$ 0.01
		Different-color	2.30 $\pm$ 0.56	6.56 $\pm$ 1.01	0.99 $\pm$ 0.01

*Eye-tracking analyses.* To ensure that the patterns of mislocalization seen for the different color conditions were not caused by differing tendencies to break fixation and make small eye movements within the invisible fixation zone, we compared the eye position at target onset for each combination of frame position and color using a fully-factorial ANOVA. Importantly, eye position was unaffected by frame position, frame color or their interaction [ $F(1, 18) = 2.89$ ,  $F(2, 36) = .35$ ,  $F(2, 36) = .005$ , respectively, all n.s.].

## **Discussion**

The results of Experiment 1 demonstrate that a top-down attentional set, in this case an attentional set tuned to color based on a contingent task, can modulate the magnitude of the induced Roelofs effect. Specifically, when participants searched for a target item of a certain color, the presentation of a frame of that same color caused a larger shift in perceived straight-ahead, compared to the significantly smaller shift that occurred when the frame color did not match the participants' attentional set (e.g., yellow frame when searching for a red target). These findings are consistent with a contingent-capture account of attention as proposed by Folk et al. (1992), with the attentional set serving to enhance the effects of frames with colors that match the expected target, or diminish the effects of non-target-colored frames through attentional filtering.

In the paradigm of the present study, the target item for which participants searched was always presented among three distractor items, defined by their yellow, purple, and green colors. Given this limited range of distractor colors, one might expect that if feature-based filtering did occur, the filter might be specifically tuned to filter out those

colors. On the other hand, it is possible that the attentional set served to filter out all non-target colors, including those that were not typically included among the distractors. In this latter possibility, one would expect the magnitude of the Roelofs effect for the *different-color* condition to resemble that of the *distractor-color* condition. Indeed, the effect in the *different-* and *distractor-color* conditions did not significantly differ, while both were smaller than for the *set-color* condition, indicating that the attentional set acted broadly by either filtering all non-target colors, or enhancing only the target color, or both.

Is it possible that different rates of guessing could account for the difference in the magnitude of the induced Roelofs effect measured in the different color conditions? One could argue that in the *set-color* trials, the frame would serve as a potent distractor due to its color. This would then draw attentional resources away from the target, causing participants to “miss” the target and base their responses on guesswork. If that was the case, one would expect psychometric functions with decreased slopes (i.e., greater  $\tau$  values) and smaller amplitudes for the *set-color* trials. However, this pattern of results was not seen in the data (Table 1), indicating that a higher rate of guessing could not account for the results.

Although our findings are consistent with an attentional set that can modulate the perceptual consequences of the Roelofs-inducing frame, an alternative explanation should be considered. Specifically, it is possible that the similar target and frame colors in the *set-color* condition might have led to an enhancement of the Roelofs effect due to a perceptual grouping of the target and frame. Experiment 2 was designed to address this alternative perceptual grouping account of these results.

## Experiment 2

In order to argue that feature-based attentional processing can modulate the magnitude of the induced Roelofs effect, it is important to rule out the possibility that the findings of Experiment 1 were the result of the visual system's tendency to perceptually group objects of the same color. The Gestalt psychology principle of *similarity* suggests that when objects have similar characteristics, for example color or shape, they tend to be grouped together at a perceptual level (Koffka, 1935). Previous work has demonstrated that this Gestalt grouping tendency is capable of modulating illusory effects in, for example, the Müller-Lyer illusion, where the illusion is strongest when the horizontal segment of the figure is of the same color as the illusion-inducing wings (Goryo et al., 1984).

To dissociate these two possibilities, Experiment 2 employs a color-contingent paradigm similar to that of Experiment 1, but includes occasional probe trials in which only a single target is presented (i.e., *distractors-absent* trials), with the participant required to report the location of this solitary target *regardless of its color*. Because the *distractors-present* trials are more numerous than the relatively rare *distractors-absent* trials, and because the sequence of trial types is unpredictable, the attentional set maintained by the participant to assist in the *distractors-present* trials should be operational during the *distractors-absent* trials as well. If this attentional set concomitantly modulates the effects of a Roelofs-inducing frame, then this effect should also be apparent in the *distractors-absent* trials regardless of the actual color of the target. On the other hand, if the results from Experiment 1 depict a tendency for a larger Roelofs effect to occur when the target and frame can be perceptually grouped due to like colors,

one would similarly expect a larger effect in the *distractors-absent* trials only when the target and frame are the same color and not when they are different colors.

## Methods

*Participants.* Twenty-one University of Oregon undergraduates with normal or corrected-to-normal vision volunteered to participate for course credit. Participants provided informed consent prior to their participation, with all procedures approved by the Institutional Review Board of the University of Oregon.

*Apparatus.* The apparatus was identical to that used in Experiment 1.

*Stimuli and procedure.* The majority of trials (75%, dubbed here *distractors-present* trials) were identical to those described in Experiment 1, with participants asked to report the locations of red targets presented among green, yellow and purple distractors, in the presence of frames that were either red (*set-color*) or blue (*different-color*). In the remaining 25% of trials (*distractors-absent* trials), the stimulus contained only a solitary blue target within a red (*set-color*) or blue (*different-color*) frame, with no distractors present. Participants were instructed that when a lone target appeared inside the frame, regardless of color, they were to report the location of the target just as they did in *distractors-present* trials.

In the experiment, participants performed four blocks of 224 trials each, resulting in 896 total trials (672 *distractors-present* trials and 224 *distractors-absent* trials, presented in random order). Participants were informed that the majority of the trials would be *distractors-present* trials, and were instructed to report the location of the red target item in these trials. When no distractors were present, participants were told to report the

location of the single target item, regardless of its color. Prior to performing the experimental trials, participants performed 40 practice trials. All eye-tracking and rejection procedures were identical to Experiment 1.

*Data analysis.* Analysis methods were identical to those of Experiment 1.

## Results

A significant induced Roelofs effect was evident in all task conditions (Figure 7, Table 1; *set-color/distractors-present*:  $t(20) = 4.404, p < .0001$ ; *different-color/distractors-present*:  $t(20) = 3.69, p = .001$ ; *set-color/distractors-absent*:  $t(20) = 4.819, p < .0001$ ; *different-color/distractors-absent*:  $t(20) = 4.183, p < .0001$ ). A repeated-measures ANOVA, including frame color and distractor presence as factors, revealed a significant main effect of frame color [ $F(1, 20) = 15.406, p = .001$ ], indicating a larger Roelofs effect when the frame color matched the attentional set. However, there was no significant main effect of distractor presence [ $F(1, 20) = .984, p = .333$ ], nor any interaction between frame color and distractor presence [ $F(1, 20) = .785, p = .386$ ]. Planned comparisons revealed that the effect in the *set-color/distractors-present* trials was larger than in the *different-color/distractors-present* trials ( $t(20) = 2.618, p = .016$ ), replicating the results of Experiment 1. Importantly, a similar difference was seen in the *distractors-absent* trials, with a larger Roelofs effect for the *set-color* condition compared to the *different-color* condition ( $t(20) = 2.768, p = .012$ ).

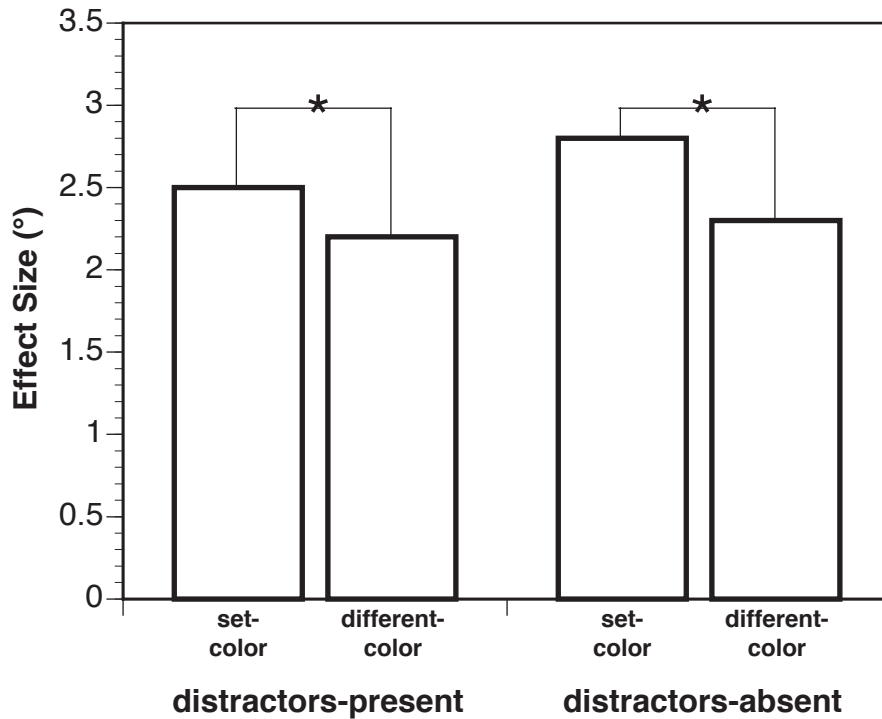


Figure 7: Mean induced Roelofs effect size for each of the four trial conditions in Experiment 2. Asterisks indicate  $p < .05$

As in Experiment 1, we analyzed the slope ( $\tau$ ) and amplitude ( $amp$ ) values of the psychometric functions using a repeated-measures ANOVA, with frame color and distractor presence as factors (Table 1). The main effect of frame color was not significant for slope ( $F(1, 19) = 1.51, p = .235$ ) or amplitude ( $F(1, 19) = .01, p = .917$ ). However, there was a significant main effect of distractor presence for both slope and amplitude ( $F(1, 19) = 24.36, p < .001$ ;  $F(1, 19) = 9.88, p = .005$ , respectively), but frame color and distractor presence did not significantly interact for either parameter ( $F(1, 19) = .11, p = .744$ );  $F(1, 19) = .08, p = .776$ ).

## Discussion

In the *distractors-present* trials, a larger Roelofs effect was found when the color of the frame matched the participants' attentional set (i.e., *set-color/distractors-present* trials, where the frame was red as participants anticipated having to search for a red target), compared to trials in which the frame was of a different color (i.e., *different-color/distractors-present* trials). This replicates the findings from Experiment 1, but does not itself resolve the confound that prompted Experiment 2, since this difference in effect size could be attributed either to the fact that the frame matched the color of the attentional set, or that it matched the color of the target, allowing for an enhanced perceptual grouping of the two.

The *distractor-absent* trials are key in resolving this confound, since the targets on these trials are of a different color (blue) than that of the attentional set (red). Thus, on *set-color/distractor-absent* trials, the frame matched the color of the attentional set, but did not match the color of the target; the opposite pattern was true for the *different-color/distractor-absent* trials. The finding that the Roelofs effect was significantly larger for the *set-color/distractor-absent* trials indicates that it was the match between the frame color and the attentional set that allowed for an enhanced Roelofs effect, not the match between frame and target colors.

Given the expected effects of the distractors, it was not surprising to see an increased rate of guessing in the trials in which they were present, as indicated by significant decreases in amplitude and slope (i.e., increased  $\tau$  values) of the psychometric functions in the *distractors-present* as compared to the *distractors-absent* conditions. However, there were no main effects of frame color on the amplitude and slope, nor were there any



interactions involving frame color, indicating that the differences in the Roelofs effect across the color conditions were not caused by different rates of guessing.

### **General Discussion**

Our results demonstrate that feature-based attentional processes are capable of modulating the magnitude of the induced Roelofs effect – when participants were instructed to search for a specific target color amongst distractor items, an offset frame with a color that matched the participants’ attentional set caused a larger Roelofs effect than one with a different color. Thus, although the Roelofs effect can be obtained without a conscious awareness of the inducing frame (Bridgeman & Lathrop, 2007), it is possible to modulate the effect with top-down processes in the form of attentional set. Given this, it is somewhat surprising that Bridgeman & Lathrop found no significant difference in the magnitude of the illusion when comparing participants that did perceive the frame with those that did not. However, this null result in their analysis can possibly be attributed to a lack of statistical power in their test – given large individual differences in susceptibility to the illusion (Walter, Dassonville, & Boschler, 2009), a between-subjects test (using only a single measure of susceptibility from each participant) would lack the desired sensitivity.

The current findings demonstrate that the Roelofs effect is similar in some respects to the Müller-Lyer illusion, which is also not completely reliant on conscious awareness of the contextual elements that evoke the illusion (Moore & Egeth, 1997; Chan & Chua, 2003; Lamy et al., 2006), but has been shown to be modulated by attentional effects (Coren & Porac, 1983; Goryo et al., 1984; Tsal, 1984; Predebon, 2004, 2006). Although

the phenomena of visual illusions are often regarded as windows into the low-level processes of the visual system, later stages of visual processing, such as feature- and space-based attentional selection, can influence illusion susceptibility. Conceptual and semantic information has also been shown to modulate the magnitude of the Ebbinghaus illusion (Coren & Miller, 1974; Coren & Enns, 1993; Rose & Bressan, 2002; but see also Choplin & Medin, 1999), providing further evidence of the extent to which top-down processing can affect the impact of contextual information in perception. However, the effect of top-down processing is not without limits: observers trained to recognize line segments as being fragments of intact rectangular frames viewed in previous training sessions, nonetheless showed an induced Roelofs effect appropriate for the line segment rather than for the intact frame that it represented (Walter & Dassonville, 2006).

An aspect of this work that remains unclear is the manner in which the attentional modulation of the Roelofs effect is brought about. Under a filtering account, attention would serve to decrease the impact of distractors and frames that have colors that do not match the attentional set (i.e., an attentional cost to unattended stimuli), while a frame with a color matching the attentional set would pass through the filter and have its normal impact. In contrast, it is also possible that the perceptual salience of a frame that matches the attentional set may actually be exaggerated by its ability to capture attention (i.e., an attentional benefit to attended stimuli), giving it a larger-than-normal impact compared to frames with different colors. Of course, it is also possible that both costs and benefits play important roles. Undoubtedly, the relative sizes of these costs and benefits will be just as difficult to tease apart in the realm of contextual processing as they have been in other aspects of attentional processing.

The findings of the current study indicate that the magnitude of the induced Roelofs effect (Bridgeman et al., 1997; Dassonville & Bala, 2004a; Dassonville et al., 2004) can be modulated by attentional processing, but it remains to be shown whether the same can be said of the original Roelofs effect (in which it is the frame itself that is mislocalized; Roelofs, 1935). We have argued elsewhere (Dassonville & Bala, 2004b) that the induced and original effects are driven by the same mechanism; if true, then we would expect similar attentional modulations for both. However, de Grave et al. (2002, 2004) have argued that different mechanisms underlie the two effects. If that is the case, then there is the possibility that our current findings will not hold for the original Roelofs effect.

The Roelofs effect demonstrates the brain's tendency to use the locations of salient objects in the visual scene as cues to the structure of perceptual space. Although, in the limited viewing conditions used to demonstrate the Roelofs effect, these cues can lead to illusory perceptions, it can be conjectured that, when viewing a well-lit scene, the sum of these cues provide generally accurate information for the construction of a reasonably faithful representation of space. Given this, the present finding that top-down attentional processing can modulate the effects of contextual cues can be inferred to apply not only to the illusory conditions associated with the Roelofs effect, but also to the more typical use of contextual information for constructing a representation of space while viewing well-lit scenes.

## CHAPTER III

### THE ROELOFS EFFECT DOES NOT REFLECT SPATIAL DISTORTIONS CAUSED BY SHIFTS OF VISUOSPATIAL ATTENTION

When an observer makes a judgment about an object's orientation or location, contextual information from the visual scene is typically used to help refine the judgment (Asch & Witkin, 1948). However, if the contextual information contained within the scene is misleading, visual illusions can occur. In a classic example, Roelofs (1935) presented an observer with a large rectangular frame positioned so that one edge of the frame was aligned with the observer's objective midline. To the observers, though, this was not how it appeared -- when asked to adjust the frame so that the edge was directly ahead, the observers shifted the frame even further in the direction of the offset. Roelofs' early experiments revealed that the presence of the large rectangular frame causes a distortion of the observer's subjective midline, with the midline biased in the direction of the offset frame (Brecher et al., 1972; Brosgole, 1968; Werner, Wapner, & Bruell, 1953). A direct demonstration of this effect can be achieved by simply asking observers to point or make a saccadic eye movement to straight ahead in the presence of an offset frame. The observer's motor response typically deviates toward the center of the frame (Dassonville & Bala, 2004; Dassonville et al., 2004). In a recent adaptation of the classic Roelofs illusion, observers are asked to make a perceptual report of the location of a visual probe presented within the offset rectangular frame (i.e., the *induced* Roelofs

effect; Bridgeman, Peery, & Anand, 1997). The frame-induced distortion of subjective midline causes participants to systematically mislocalize the probe as being displaced in a direction opposite the frame offset (Dassonville & Bala, 2004). For example, a right-shifted frame will cause a deviation of the apparent midline to the right, which, in turn, causes the enclosed target to appear to lie further to the left.

The primary focus of research on the Roelofs illusion, and the related induced Roelofs effect, has focused on understanding the consequences of a biased subjective midline on perception and action. However, research that explicitly examines the mechanism responsible for the distortion of subjective midline is lacking. Bridgeman and Latham (2007) demonstrated that an offset frame would cause the effect even when it was presented under conditions that would cause the frame to go unperceived due to inattention blindness. It has also been shown that the effect can be obtained using stimuli other than the large rectangular frame that is typically used to demonstrate the phenomenon. Walter and Dassonville (2006) found a robust Roelofs effect with a stimulus consisting only of one end of the frame – the effect was present as long as there was an imbalance between the stimuli in the left and right halves of the visual display. But while these studies have further defined the characteristics of stimuli able to cause the effect, none has explored its underlying mechanisms. What is it about an imbalanced visual image that causes a distortion in the observer's subjective midline?

The Roelofs effect is typically tested under visually impoverished conditions. Observers are placed in total darkness and the frame is the primary visual contextual information in the environment. The onset of the frame is a very abrupt and salient perceptual event, one that would likely cause immediate attentional capture. One intuitive

hypothesis is that the onset of the frame acts to automatically capture attention. The shift of attention toward the frame could, in turn, pull the observer's subjective midline in the same direction. Links between shifts of attention and egocentric reference frames have not been empirically tested. However, hints in the attention localization literature suggest that these links could exist.

Past research has demonstrated that the accuracy of an attempt to locate a briefly presented target item decreases when covert attention is directed away from the target (Newby & Rock, 2001; Tsal, 1999; Tsal & Bareket, 1999; Butler, 1980). Tsal & Bareket (1999) observed that not only did target localization vary when attention was shifted in the visual field, target reports also tended to systematically deviate away from the locus of attention, in the direction of the horizontal meridian. In addition, clinical evidence suggests that the current locus of spatial attention can act as an egocentric reference frame that the brain uses to encode the location of objects. McCloskey & Rapp (2000) describe a patient who perceives objects as being in their mirror image locations with respect to the locus of attention (i.e., an object to the right of the attentional locus is mislocalized to the left; see also Rhodes & Montgomery, 1999, 2000; Flevaris et al., 2001).

Potential anatomical links between the control of visuospatial attention and the computation of egocentric reference frames can be drawn from the neuroimaging literature. Vallar et al. (1999) had participants perform a task in which they indicated when a bar, moving laterally on screen, traversed perceived midline. The researchers observed a significant activation in a network of frontal and parietal regions when participants had to judge the location of the bar relative to midline, compared to a control

experiment where the bar's location was reported within an allocentric reference frame. The strongest activations were observed in in the right superior parietal lobule and inferior parietal sulcus – regions that have been implicated in the control of voluntary and reflexive visuospatial attention (Corbetta et al., 1993, 1995; Anderson et al., 1994; Nobre et al., 1998; Gitelman et al., 1996). In a recent study, Walter & Dassonville (2008) adapted the induced Roelofs effect for use with fMRI, to determine the brain regions that are recruited when individuals make location judgments in the presence of Roelofs-inducing frame. In separate blocks of trials, participants reported the location of the target in the presence of the offset frame, or performed a control task that involved a color judgment. During the target localization task, a significant, primarily right-lateralized activation was observed in the superior parietal lobule (SPL), indicating a possible role for right SPL in processing visuospatial contextual information.

Recent psychophysical work (Lester & Dassonville, 2011) has also shown that the midline distortion observed in the induced Roelofs effect can be modulated by an observer's attentional goals. Using a modified color-contingency paradigm (see Folk, Leber, & Egeth, 2005), participants reported the location of a target item (e.g., a red target, presented amidst distractors of other colors) presented inside the offset frame. The magnitude of the midline distortion was largest when the frame matched the color of the target item. While this study was designed to examine attentional filtering for colors and not to explicitly measure discrete shifts of attention, the attentional modulation raises the possibility that shifts of visuospatial attention may influence individuals' perception of straight-ahead.

In the current study, we explore the possibility that the distortion of the apparent midline associated with the Roelofs effect is driven by an attentional shift in the direction of the offset frame. Specifically, we examine whether shifts of visuospatial attention, using a modified Posner cueing paradigm (Posner, 1980; Posner, Snyder, & Davidson, 1980), affect perceived straight-ahead. On the majority of trials, participants performed a letter identification task that was preceded by a spatial cue that was either spatially non-predictive (Experiments 1 & 3) or predictive (Experiment 2) of the letter's subsequent location. Accuracy in the identification task allowed for an assessment of the cues' effectiveness in attracting the observer's spatial attention across trials. However, on occasional, unpredictable trials, the letter was replaced with a visual probe whose location was to be reported by the participant. An assessment of the performance in the localization task allowed for a determination of whether the earlier cue and resulting shift of attention are capable of causing a distortion of the participant's spatial reference frame

If spatial shifts of attention are the underlying cause of the Roelofs effect, we predict that that participant's subjective midline will be yoked with the locus of spatial attention. Specifically, when attention shifts to the left visual hemifield, subjective midline will be pulled to the left, causing the participant to report the location of the visual probe as lying further to the right than it really is; the opposite effects would occur with a rightward attention shift. In contrast, if subjective midline is not drawn to the locus of attention, localization performance should not be significantly affected by the shift of attention. This pattern of findings would indicate that the imbalanced visual display used to generate the Roelofs effect does so through a mechanism that is independent of any shifts of attention.



## Experiment 1

### Methods

*Participants.* Fourteen University of Oregon undergraduates with normal or corrected-to-normal vision volunteered to participate for course credit. Participants provided informed consent prior to their participation, with all procedures approved by the Institutional Review Board of the University of Oregon.

*Apparatus.* Stimuli were back-projected onto a translucent screen (137 cm x 102 cm), using an Electrohome Marquee 8500 projector with a screen refresh rate of 60 Hz. Manual responses were collected using a keyboard connected to the host computer. Stimuli were centered at eye-level while participants were seated in a completely-darkened room. Participants' eye position was monitored on-line using an Eye-Link 1000 eye-tracking system (SR Research), operating at a 250-Hz sampling rate. Using a tower-mounted tracker setup, participants sat comfortably with their heads steadied by chin and forehead rests, approximately 90 cm from the plane of the presentation screen. Eye position was monitored continuously during experimental trials; trials during which an eye movement or blink occurred were discarded and repeated at the end of the experimental block. Participants were required to maintain fixation within a fixation zone throughout the trial, even after the fixation point was extinguished at the start of the trial (the fixation point was removed so that it could not be used as an allocentric localization cue). A relatively large fixation zone ( $2.5^\circ$  radius) was used to allow for the possible small movements of the eye that occur during fixation in complete darkness, especially with covert attention focused in the periphery (Hafed & Clark, 2002, Engbert & Kliegl, 2003; Laubrock, Engbert, & Kliegl, 2005; but see Horowitz et al., 2007). However, it is

possible that small eye movements within the fixation zone might themselves cause a mislocalization of the visual probes (see, for example, Henriques et al., 1998). For this reason, eye position was included as a variable in all regression analyses of the probe localization data.

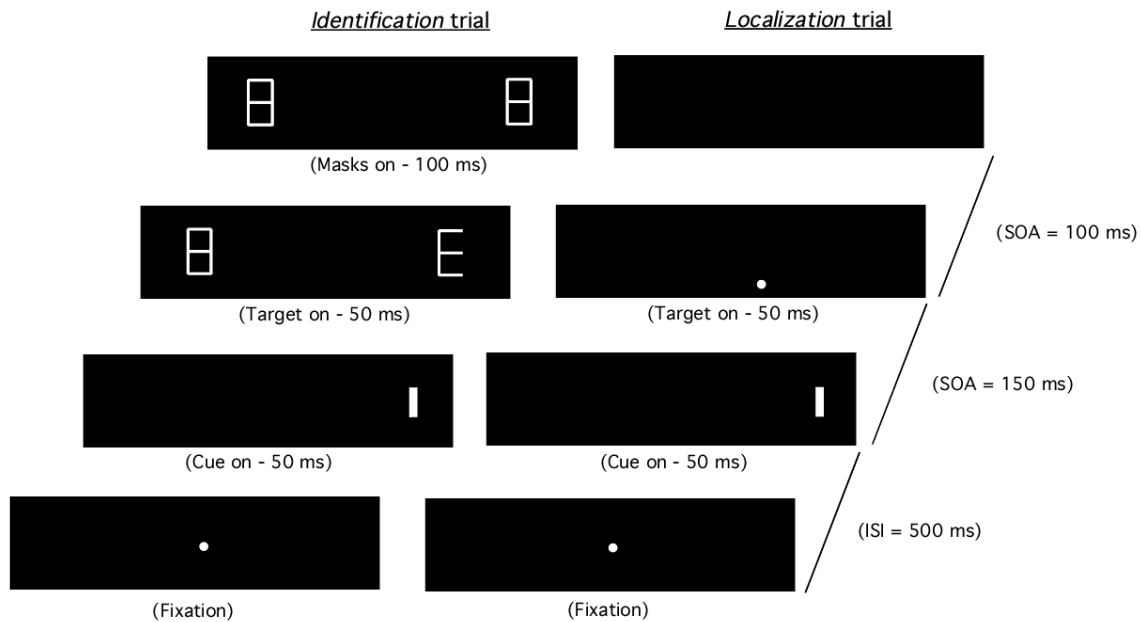


Figure 8: Sample trials of the letter identification (left) and probe localization tasks (right) from Experiment 1. The identification trial is an example of the validly cued condition, in which the cue and target letter appear in the same spatial position. In localization trials, participants reported the perceived location of the visual probe within an array of previously learned probe positions (not seen). All timing procedures were identical across the tasks, except the masks were not presented in the localization trials. The exogenous cue was never predictive of the subsequent target position in either task.

*Probe localization training.* Prior to beginning Experiment 1, each participant completed a short period of training (100 trials) in which they learned an array of five possible locations ( $8^\circ$  below fixation, and  $-3^\circ$ ,  $-1.5^\circ$ ,  $0^\circ$ ,  $1.5^\circ$  and  $3^\circ$  from midline) for the visual probe that would be used in the later localization trials. Each trial began with the

presentation of a central white fixation point ( $1^\circ$  in diameter); participants fixated this point and pressed the spacebar when they were ready to begin a trial. After a 200 ms ISI, a small white probe ( $1^\circ$  in diameter) appeared in one of the five possible locations for 1 s. Participants were asked to report the perceived location of the probe by pressing one of five corresponding keys on the keyboard with the fingers of the right hand keyboard key (thumb on the right arrow key for a probe in the  $-3^\circ$  location, index finger on the “1” of the number pad for the probe at the  $-1.5^\circ$  location, middle finger on the “2” for the probe at the  $0^\circ$  location, ring finger on the “3” for the probe at the  $1.5^\circ$  location, and little finger on the Enter key of the number pad for the probe at the  $3^\circ$  location).

Feedback (2 s duration, starting 500 ms after the keyboard response) was included to help participants learn the probe array more quickly and accurately. If participants indicated the correct position of the probe, the word “Correct” appeared just above fixation. If they reported the incorrect location, “Incorrect” appeared along with the true position of the probe, to assist in learning the probe positions. Feedback was visible for 2 seconds before the fixation point reappeared and participants were free to begin the next trial. Average accuracy for the training period was 81% (SE = 2.70) and significantly above chance ( $t(13) = 11.43, p < .001$ ), demonstrating that participants successfully memorized the locations of items in the probe array.

*Stimuli and experimental procedure.* Each participant completed 21 practice trials to gain familiarity with the task, followed by 252 experimental trials. The majority of the experimental trials (144 of 252 trials) were *letter identification* trials, in which participants reported the identity of a target letter that followed an attentional cue. The remaining trials (108 of 252) were *probe localization* trials, in which participants

reported the location of a visual probe in the same manner that was learned in the earlier localization training (previous section). Attention and localization trials appeared in a random order, with no advance warning to indicate the type of trial to expect. Both types of trials included a non-predictive attention cue that could appear to the left or right of fixation, or bilaterally. Participants were informed of the non-predictive nature of the cue and were instructed to ignore it and concentrate on either identifying the target letter or reporting the location of the visual probe, whichever appeared in the course of a trial. Participants were instructed to emphasize accuracy in their responses, rather than speed.

Letter identification trials. Every trial (Figure 8, left) began with the presentation of a central fixation point ( $1^\circ$  diameter). Participants initiated the trial by moving the eyes to the fixation point, and then pressing the keyboard spacebar with the left hand. The central fixation point then disappeared; after a 500 ms ISI, a small peripheral cue ( $0.8^\circ$  in width x  $2.5^\circ$  in height) appeared for 50 ms. This exogenous cue appeared randomly on the left or right,  $19^\circ$  from fixation, or bilaterally. Following the peripheral cue (150 ms SOA), a single target letter (E or H) and a figure-8 ( $3^\circ$  x  $6^\circ$ ) were presented (50 ms duration) simultaneously,  $15^\circ$  from fixation. After a 50 ms ISI, two visual masks (figure-8,  $3^\circ$  x  $6^\circ$ , 100 ms duration) appeared to obscure any residual visual information.

Participants were instructed to report the identity of the target letter by pressing one of two keys with their left hand (“x” with their index finger if the letter was an H, “z” with their middle finger if the letter was an E). Trials were categorized according to the locations of the exogenous cue and target letter. For valid cue trials, the exogenous cue and target letter appeared on the same side of fixation. In invalid cue trials, the cue and

target letter appeared on opposite sides of fixation. Neutral cue trials included bilateral exogenous cues.

Probe localization trials. Localization trials (Figure 8, right) began in an identical fashion as the identification trials, with a fixation point that was followed after 500 ms by the appearance of an attentional cue presented 19° left or right of the fixation point, or bilaterally. However, no letter targets or visual masks followed the attentional cue. Instead, following the attentional cue (150 ms SOA), a small white circular probe (1° diameter) appeared in one of the possible probe locations (8° below fixation, and -1.5°, 0° or 1.5° from midline) that were learned during the earlier training procedure (see the localization training, above). However, unlike the training period and unbeknownst to the participants, probes in the experimental trials could appear only in the central three locations of the array of locations, to accommodate possible mislocalizations due to the prior attentional cue and minimize the occurrence of probes that appeared further right (or left) of the rightmost (or leftmost) locations in the learned array. To end the trial, participants reported the location of the probe using the key press procedure they had learned in the earlier training.

## Results

A repeated-measures ANOVA of the accuracies in the letter identification trials (Figure 9) demonstrated that there was a significant main effect of cue validity ( $F(2, 26) = 7.50, p < .005, \eta^2 = .37$ ), with valid cues ( $M = 74.3\%$  correct,  $SE = 4.46$ ) resulting in a significantly greater accuracy in letter identification, compared to the neutral ( $M = 69.0\%$ ,  $SE = 4.27$ ) and invalid cues ( $M = 65.3\%$ ,  $SE = 3.29$ ). Separate contrasts revealed that

valid cues led to a significantly greater accuracy compared to the neutral ( $t(13) = 3.77, p < .005$ ) and invalid cues ( $t(13) = 2.45, p < .05$ ); however, accuracy for neutral cues was not significantly greater than that for invalid cues ( $t(13) = -1.65, p = .124$ ).

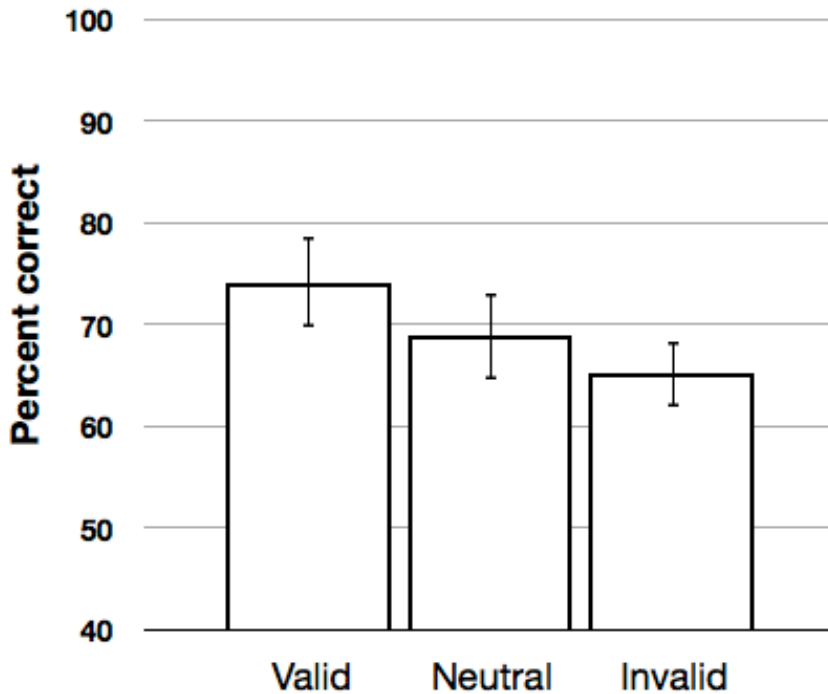


Figure 9: Percent correct in the letter identification task of Experiment 1. Errors bars represent standard error estimates for each cue condition.

To isolate the effects of the attentional cue on the ability to determine the location of the visual probe in localization trials, the perceptual reports of probe location were assessed with respect to the independent variables of probe location, eye position at target offset, and cue location using a block-wise multiple regression (with the independent variables entered in that order). Eye position was included as a factor to rule out the

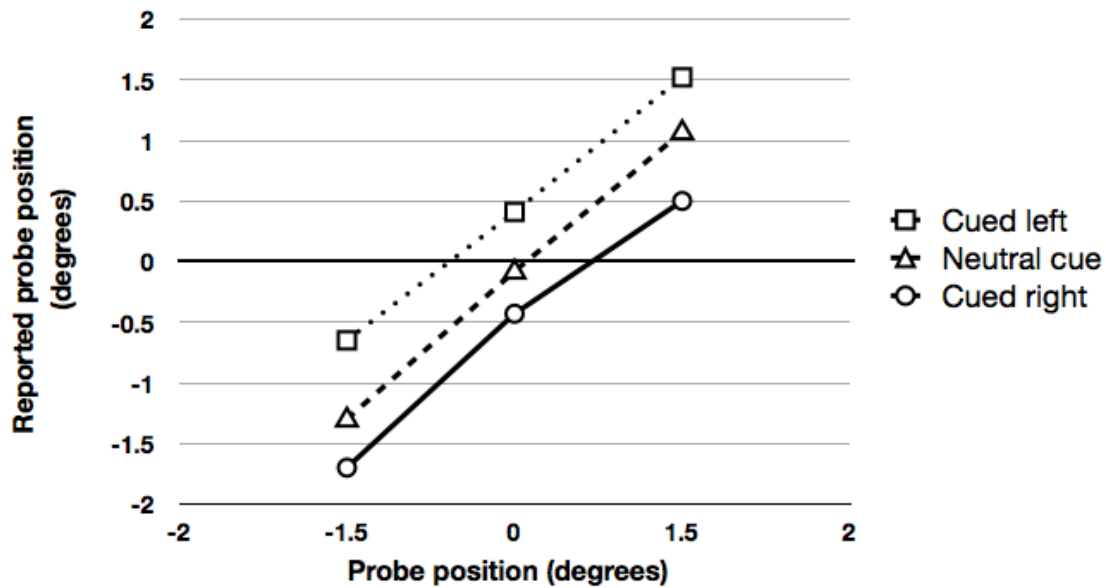


Figure 10: Perceived probe location in the localization task of Experiment 1, plotted with respect to the actual probe location (negative values indicate locations to the left of fixation). Data is plotted separately for the right cue, left cue and neutral cue conditions.

possibility that any apparent cue effects were not simply caused by the cue's tendency to evoke small eye movements (within the  $2.5^\circ$  radius of the fixation window). As expected, probe location was the largest predictor of perceived location, accounting for approximately 43% of the variance ( $R^2 = .43$ ,  $\beta = .659$ ,  $t(1510) = 34.02$ ,  $p < .001$ ). Eye position at target offset was only a marginally significant predictor of perceived location ( $R^2 = .008$ ,  $\beta = .033$ ,  $t(1509) = 1.71$ ,  $p = .09$ ), accounting for less than 1% of the variance. Importantly, even after accounting for the variability associated with probe location and eye position, the factor of cue position was a significant predictor of the perceived location of the probe ( $R^2 = .08$ ,  $\beta = -.278$ ,  $t(1508) = -15.48$ ,  $p < .001$ ), accounting for approximately 8% of the variance in the reported probe location. The mean reported

difference in the location of the probe (right cue – left cue conditions) was  $0.94^\circ$ , with probes reported in the opposite direction as the peripheral cue (Figure 10).

## **Discussion**

In Experiment 1, exogenous attentional cues were used to cause reflexive shifts of attention. Subjects then reported the identity of a subsequent letter (identification trials) or the location of a visual probe (localization trials) in randomly intermixed trials. The pattern of results in the identification trials clearly indicated that the attentional cues were effective at summoning attention, allowing for more accurate identification of the target letter after valid cues. In the localization trials, the presence of the attentional cues led to biases in the participants' reports of probe location, with the probes reported to occupy locations shifted in the direction opposite the exogenous cue.

In the induced Roelofs effect, a large frame presented in a location offset from the observer's objective midline has the tendency to cause the apparent midline to become deviated in the direction of the frame (Dassonville & Bala, 2004; Dassonville et al., 2004). This bias in the apparent midline subsequently causes a pattern of errors in probe localization, with the probe perceived to be shifted in the direction opposite the frame shift. The effects of the lateralized attentional cue in the current experiment strongly mirror (in direction and magnitude) the biased perceptual reports observed in the Roelofs literature, suggesting that the effects are one and the same. This serves as a replication of the findings of Walter and Dassonville (2006), who showed that stimuli much smaller than the typical large frame are able to induce the effect.



The results of Experiment 1 also support the hypothesis that shifts of visuospatial attention can bias an observer's apparent midline and possibly serve as the underlying cause of the Roelofs effect. However, there is an alternative explanation that must be entertained. While the paradigm of Experiment 1 did successfully manipulate the distribution of visuospatial attention, it involved the use of displays that were unbalanced in their visual content, with an attentional cue that was presented either to the left or right of the visual display. It may be that it is the mere presence of an unbalanced display may be sufficient to distort participants' subjective midline, independent of any effects that display may have on attentional deployment. This alternative explanation is examined in Experiment 2, in a paradigm that generates shifts of attention without the use of unbalanced visual displays.

## **Experiment 2**

The deployment of visuospatial attention is influenced by visual information that falls broadly into two categories: 1) events within the visual environment (i.e., stimulus-driven or exogenous orientation of attention), and 2) the goals/intentions of an observer (i.e., goal-driven or endogenous orientation) (Posner, 1980). In Experiment 1, a classic stimulus-driven manipulation of attention was employed. In Experiment 2, shifts of spatial attention were achieved by providing participants with advance knowledge of the likely position of a target letter. Specifically, a centrally presented endogenous cue indicated the probable location of the target, so that participants could orient spatial attention accordingly. If the perceived location of a visual probe is affected by attentional shifts that are not accompanied by unbalanced visual displays, it would provide strong

supporting evidence that the Roelofs effect is driven by a shift of attention toward the illusion-inducing offset frame.

## **Methods**

*Participants.* Seventeen University of Oregon undergraduates with normal or corrected-to-normal vision volunteered to participate for course credit. Participants provided informed consent prior to their participation, with all procedures approved by the Institutional Review Board of the University of Oregon.

*Apparatus.* The apparatus was identical to that in Experiment 1.

*Probe localization training.* To familiarize themselves with the array of 5 possible probe locations, participants completed a training procedure identical to that of Experiment 1. Average accuracy was significantly greater than chance ( $M = 78.9\%$  correct,  $SE = 1.82$ ;  $t(16) = 15.83$ ,  $p < .001$ ).

*Stimuli.* All stimuli were identical to Experiment 1, except for the attentional cue. A predictive cue (75% valid) was presented in the center of the display screen after the offset of the fixation point. The endogenous cue consisted of two chevrons ( $2.5^\circ \times 2.5^\circ$ ) that pointed either to the left (i.e.,  $\ll$ ) or right (i.e.,  $\gg$ ) target position, to indicate the likely position of the subsequent target letter. In neutral trials, the chevrons ( $2.5^\circ \times 2.5^\circ$ ) pointed to both target positions (e.g.,  $\diamond$ ).

*Experimental procedure.* All procedures were identical to Experiment 1, except where noted. Participants completed 37 practice trials and 296 experimental trials. The majority of the experimental trials were identification trials (222 of 296 trials), with the remaining localization trials (74 of 296).

Letter identification trials. In valid trials (75% of the attention trials), the tips of the chevrons indicated the correct location of the target letter. In invalid trials (12.5%), the incorrect target location was indicated. In neutral trials (12.5%), the chevrons pointed to both locations (e.g.,  $\langle \diamond \rangle$ ), indicating that the target was equally likely to appear at either location. Participants were informed of these probabilities and were encouraged to shift attention in the direction indicated by the cue, because a target letter was likely to appear at that location. An 850 ms SOA elapsed between the onset of the cue and the target letter.

Probe localization trials. The localization trials were identical to those of Experiment 1, except for the use of the endogenous attentional cues and the longer SOA (850 ms) described above for the letter identification trials. The endogenous cue was never predictive of the location of the localization probe.

## **Results**

In the identification trials (Figure 11), a main effect of cue validity was again observed ( $F(2, 32) = 20.20, p < .001, \eta^2 = .56$ ), with participants having a significantly greater accuracy in reporting the target letter when it was preceded by a valid cue ( $M = 79.0\%$  correct,  $SE = 1.85$ ) compared to invalid ( $M = 61.23\%$ ,  $SE = 2.54$ ;  $t(16) = 5.84, p < .001$ ) and neutral cues ( $M = 70.84\%$ ,  $SE = 2.26$ ;  $t(16) = 3.64, p < .005$ ). The invalid cue also led to a significant behavioral cost, with a decreased accuracy following invalid cues compared to the trials with neutral cues ( $t(16) = -3.17, p < .005$ ).

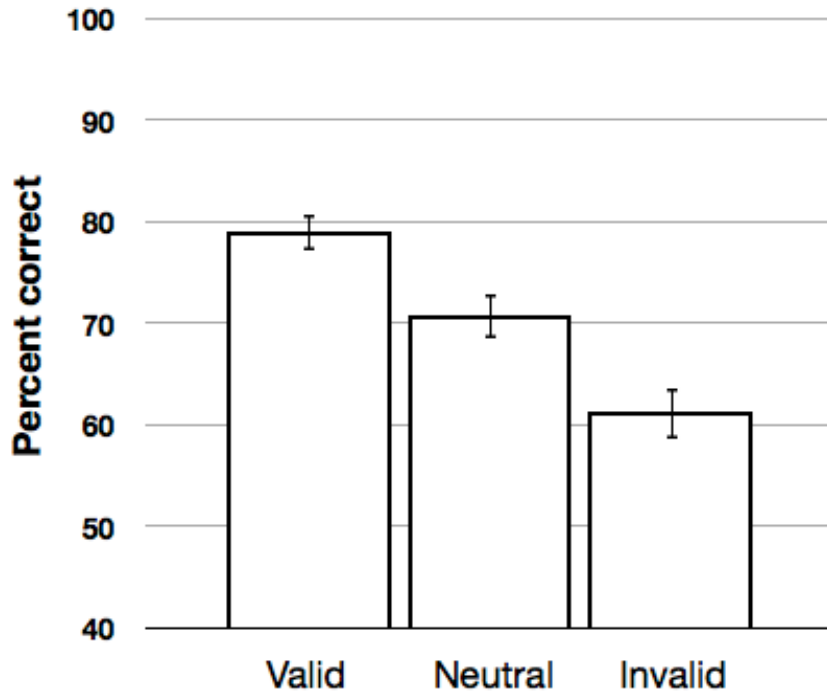


Figure 11: Percent correct in the letter identification task of Experiment 2. Errors bars represent standard error estimates for

For the localization task, a block-wise multiple regression was again conducted, using probe location, eye position at target offset, and cue location as independent variables (with the variables entered in this order). Probe location accounted for approximately 76% of the variance in participants' responses ( $R^2 = .76$ ,  $\beta = .874$ ,  $t(1220) = 62.96$ ,  $p < .001$ ). Eye position was also a significant predictor of perceived probe location ( $R^2 = .01$ ,  $\beta = .041$ ,  $t(1219) = 2.92$ ,  $p = .004$ ), although it accounted for a much smaller proportion of the variance (1%). In addition, cue location was a significant predictor of target report, even when eye position was taken into account ( $\beta = .032$ ,  $t(1218) = 2.27$ ,  $p < .05$ ), but it accounted for an even smaller proportion of the variance (0.001%). The mean reported difference in the location of the probe (right cue – left cue conditions) was

0.13°, with probes reported in the direction of the locus of attention (Figure 12). It should be noted that not only was this distortion of perceived probe location much smaller than that seen with the exogenous cues of Experiment 1 or the typical Roelofs effect, the bias was in the opposite direction as well, with probes reported to be shifted toward the attended location after endogenous cues but away from the attended location after exogenous cues.

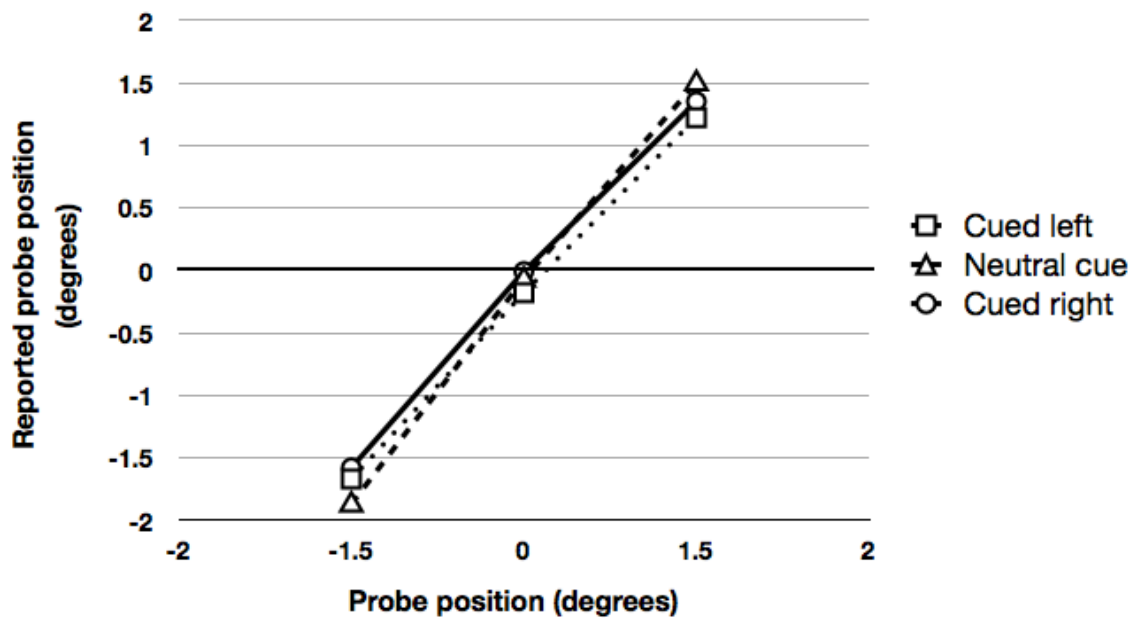


Figure 12: Perceived probe location in the localization task of Experiment 2, plotted with respect to the actual probe location (negative values indicate locations to the left of fixation). Data is plotted separately for the right cue, left cue and neutral cue conditions.

Since the effect of the endogenous cues on probe localization was so small, with borderline significance, we sought additional evidence that the effect was real. Given the individual differences that exist in the magnitude of the validity effect, one might expect to find a correlation between the magnitude of the validity effect and the associated bias in the probe localization task. Indeed, there was a significant positive correlation ( $R^2 = .45, p = .003$ ; Figure 13) between the validity effect in the identification trials (% correct valid – % correct invalid) and the perceptual bias from the localization trials (mean error with left cue – mean error with right cue). This result indicates that the more effectively the participant used the cue to orient attention, the more biased was their perception of the probe's location.

## **Discussion**

In Experiment 2, endogenous central cues were used to elicit shifts of spatial attention. Performance in the letter identification task demonstrated that participants successfully oriented attention to the cued location, with valid cues leading to increased accuracy in identifying the letters, and invalid cues leading to decreased accuracy.

The endogenous shift of attention was also accompanied by a bias in the perceptual reports of probe location in the localization trials, even after accounting for the bias in the reported probe locations caused by differences in eye position. When participants attended to the cued location in the right (or left) visual hemifield, participants on average, reported the visual probe to be further to the right (or left) compared to when attention was in the other hemifield. While this effect was quite small (and barely apparent in the plot of the data in Figure 12), it was statistically significant, and was replicated in a

number of other endogenous cueing tasks in our laboratory (unpublished observations). Furthermore, the magnitude of the mislocalization caused by the endogenous cue was significantly correlated with the strength of the cueing effect – participants that showed a greater cueing effect reliably showed a greater mislocalization.

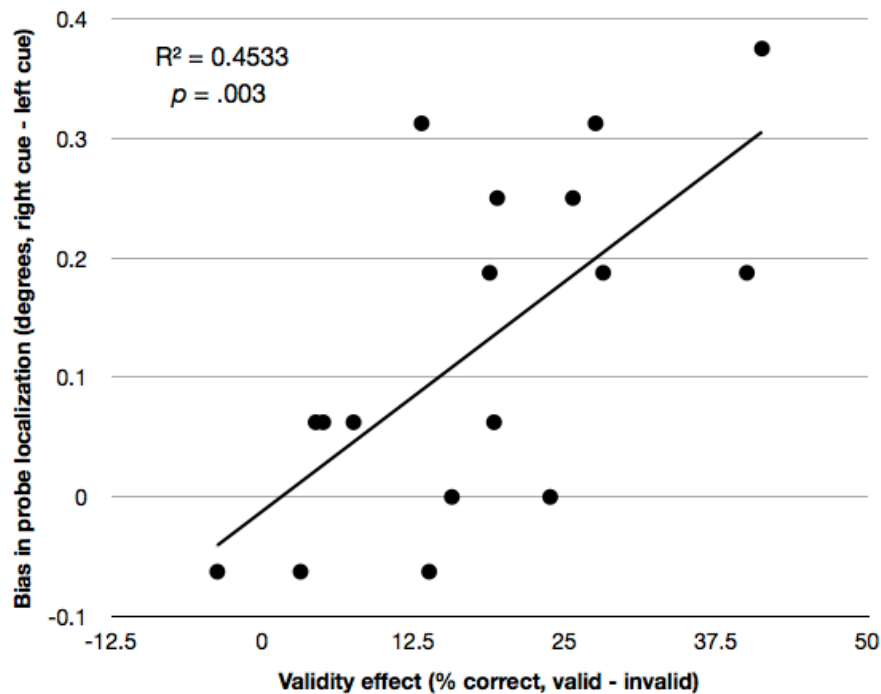


Figure 13: Relationship between cueing effect and the distortion of perceived probe location in individual participants. Cueing effect was calculated as the difference in accuracy (percent correct) between valid and invalid cues, with positive values indicating a benefit for validly cued locations. The magnitude the distortion in perceived probe location was calculated as the difference in the average perceived probe location for the right cue and left cue conditions.

Although other studies have reported varying degrees of perceptual mislocalization when attention is directed to peripheral locations in the visual field, the typical results in the literature differ somewhat from those presented here. In particular, whereas we found that the perceived location of the probe was attracted toward the locus of attention, most

previous reports have shown a perceptual repulsion away from the locus of attention (e.g., Suzuki & Cavanagh, 1997; Pratt & Turk-Browne, 2003; Pratt, & Arnott, 2008; see also Bocianski, Müsseler, & Erlhagen, 2008, 2010; Fortenbaugh & Robertson, 2011). However, the details of our paradigm differed in many ways from those of these other studies. An exploration of the differences that lead to either a perceptual repulsion or attraction would be a worthy endeavor.

Although the mislocalizations seen in Experiment 2 are reliable, they are very different in magnitude and direction than the mislocalizations typically obtained with the induced Roelofs effect, in which observers report the probe as being shifted in a direction *opposite* that of the offset frame that induces the effect. The mislocalization caused by endogenous shifts of attention, then, provide evidence against the general hypotheses that shifts of attention serve to distort the observer's apparent midline, and that the Roelofs effect is driven by a reorienting of attention toward the center of the inducing frame. It may be, though, that important differences exist in the way that the apparent midline is affected by exogenous and endogenous shifts of attention, with the apparent midline susceptible to distortions caused by exogenous but not endogenous shifts. Indeed, if the Roelofs-inducing frame causes a reorienting of attention, it is of an exogenous nature. Further, the results of Experiment 1 are consistent with, but do not definitively support, the idea that exogenous shifts of attention lead to a distortion of apparent midline. Experiment 3 attempts to eliminate the confounds that existed in Experiment 1 in order to more precisely measure the effects of both an exogenous reorienting of attention and the imbalanced visual display inherent in the Roelofs effect.



### Experiment 3

This series of experiments was undertaken to test the hypothesis that the distortion of the observer's midline that underlies the Roelofs effect is caused by a shift of attention to the center of the offset inducing frame. While Experiment 1 demonstrated that a small exogenous attentional cue does indeed induce a Roelofs-like effect, Experiment 2 suggested that it was not attentional shifts per se that cause the effect. However, since Experiment 1 tested the effects of an exogenous cue and Experiment 2 tested the effects of an endogenous one, it could be that the difference in outcomes points to differences in the effects of exogenous versus endogenous shifts of attention, with only exogenous shifts able to cause a bias in the apparent midline. Therefore, we have not yet established whether the Roelofs effect is driven directly by the visual field asymmetry that is inherent in the offset inducing frame, or instead due to the resulting attentional shift that such an asymmetry might evoke. To distinguish between these possibilities, it is necessary to devise a paradigm that successfully dissociates the visual field asymmetry from the resulting shift of attention that might occur.

In Experiment 3, a visual field asymmetry was created by presenting to participants an array of 8 circles that was offset to the left or right of straight ahead (Figure 14). Although this offset array is somewhat different than the typical Roelofs-inducing rectangular frame, it is expected that the resulting asymmetry in the visual field will still be capable of causing a Roelofs effect when participants attempt to determine the location of a visual probe presented below the array. In a letter identification task, participants were instructed to report the identity of a letter that was a specific color (e.g., red). The letter always appeared inside one of two possible circles in the offset array. On

some trials, the spatial position of the letter was preceded by a non-predictive cue that matched the color of the letter (e.g., one red circle in the offset array). Previous work has demonstrated involuntary attentional capture to the location of this type of irrelevant cue, because the color of the cue matches the observer's attentional settings (Folk et al., 1992; Folk & Remington, 1999; Folk, Leber, & Egeth, 2002, 2008; Folk & Remington, 2006). If this type of color-contingent exogenous shift of attention can override the attention grabbing effects of the offset array of circles, we predict that the perceived location of the visual probe should be modulated by the location of the colored cue. Alternatively, if the Roelofs effect is driven directly by sensory imbalances in the visual field and is therefore unaffected by shifts of attention, we would predict no effect of the cue – instead, the probe's perceived location should be modulated by the location of the offset array of circles.

## **Methods**

*Participants.* Eighteen University of Oregon undergraduates with normal or corrected-to-normal vision volunteered to participate for course credit. Participants provided informed consent prior to their participation, with all procedures approved by the Institutional Review Board of the University of Oregon.

*Apparatus.* The apparatus was identical to that of Experiments 1 & 2.

*Localization training.* Participants first completed the identical localization training procedure described in the previous experiments, except the probe was positioned approximately 11° below fixation. Average accuracy was significantly greater than chance ( $M = 81.78\%$  correct,  $SE = 1.89$ ;  $t(17) = 15.98$ ,  $p < .0001$ ).

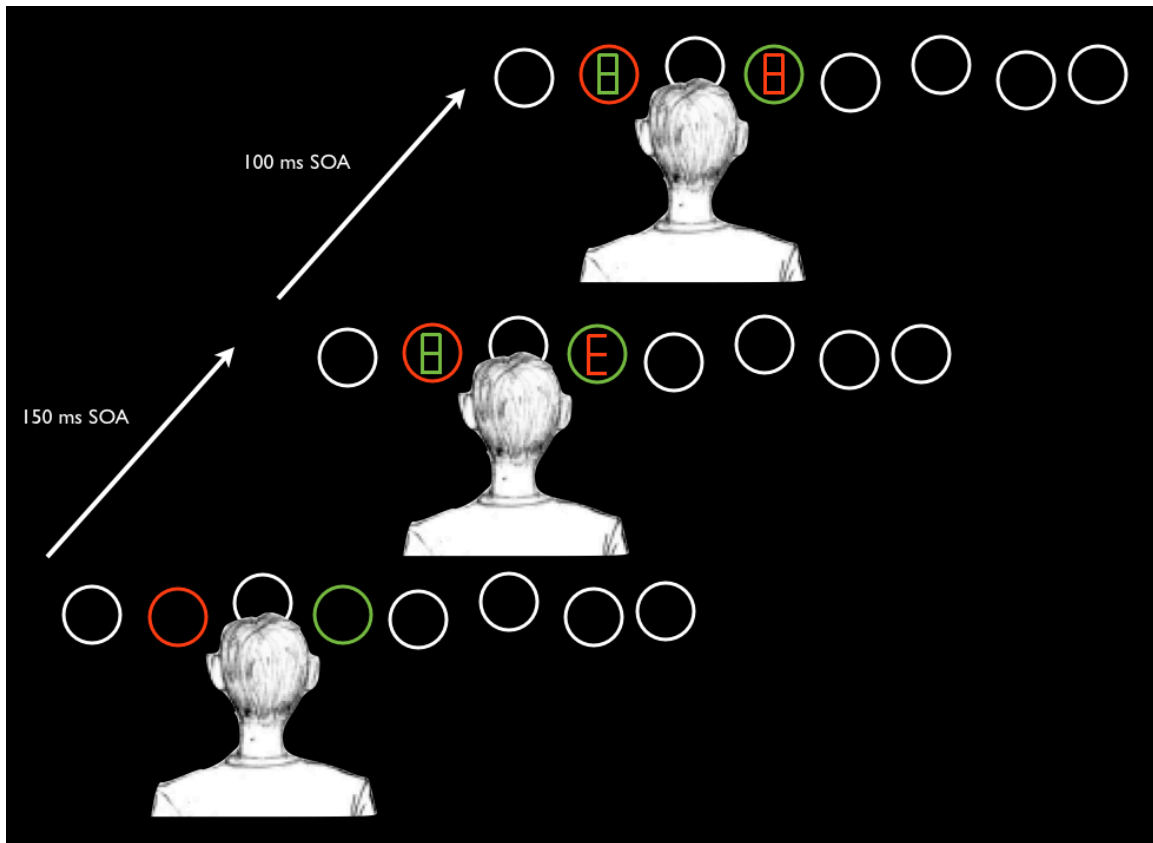


Figure 14: Example of a valid array – invalid cue trial in the identification task from Experiment 3. The fixation point (not shown) was presented at eye-level, centered on the participant’s objective midline. The observer was always positioned roughly halfway between the two possible target letter locations. The array of circles shifted (left or right) around those positions throughout the experiment. In the localization task (not shown), the target and distractor letters and masks did not appear; instead, a small visual probe appeared below the array.

*Experimental procedure.* Participants completed 20 practice trials and 252 experimental trials. Participants were instructed that there would be two tasks in the experiment; a *letter identification task* (comprising 144 of the 252 trials) and a *probe localization task* (108 trials). Participants never had to perform both tasks in a single trial; they were told the two tasks would be randomized throughout the experiment, with no prior warning to indicate which trial type to expect. In the letter identification task, participants were asked to report the identity of a target letter (an E or H) that would

appear simultaneously with a figure-8 distractor, with the letter always of one color (the target color, red or green, counterbalanced across subjects) and the distractor always of another (the distractor color, green or red). In addition, they were told that the target letter could appear inside either of two colored circles (one red, the other green), and that the color of the circles were not predictive of the letter position or its identity. For the remaining localization trials, participants were told that the letter would not appear, but would be replaced by a visual probe whose position should be reported just as it had been in the earlier localization training procedure.

Every trial began with the presentation of a central fixation point (white,  $1^\circ$  diameter) in the center of the screen. Participants initiated the trial by moving the eyes to the fixation point, and then pressing the spacebar on a keyboard with the left hand. After 250 ms, an array of horizontally arranged circles ( $n = 8$ , each  $5.4^\circ$  in diameter, with a stroke width of  $0.3^\circ$ ) was then presented  $5.5^\circ$  below fixation (Figure 14). The circles were displaced laterally  $8.3^\circ$  from one another, on average, with an additional jitter factor in the horizontal and vertical dimensions ( $\pm 0.06$  to  $1.1^\circ$ , randomly selected each trial) so as to preclude their use as stable allocentric cues across trials. The entire array subtended approximately  $63^\circ$ , with the center of the array offset  $14^\circ$  to the left or right of objective midline, such that the majority of the circles fell in one visual hemifield on any given trial. On a minority of trials (96 of 252 trials), all circles in the array were white; in the remaining trials (156 trials), circles in the array were white, with the exception of one that was of the target color and one that was of the distractor color. When they appeared, the two colored circles were always in the array positions immediately flanking the participant's objective midline, and were not jittered in their positions (however, the

constant change in the locations of the other circles, and in the entire array, gave the strong subjective impression that these colored circles were also jittered). It was expected that the circle having the target color would act as an exogenous cue that attracted the participant's attention, since its color matched that of the target letter for which the participant was searching.

Letter identification trials. After the circle array was presented (150 ms SOA), a target letter (E or H,  $2.7^\circ$  by  $4.2^\circ$ , of the target color) appeared inside one of the circles that flanked the participant's objective midline. A single non-target figure-8 distractor ( $2.7^\circ$  by  $4.2^\circ$ , in the distractor color) was presented in the corresponding circle in the other hemifield. After 75 ms, both the target letter and distractor were extinguished, followed after a 25 ms ISI by the presentation of two figure-8 masks (16 ms duration). Subsequently, all stimuli were extinguished, and participants ended the trial by pressing one of two keys with the left hand to indicate the identity of the target letter ("x" with their index finger if the letter was an H, "z" with their middle finger if the letter was an E). After a 500 ms intertrial interval, the fixation point reappeared and participants were free to begin the next trial.

For the identification trials, trials were categorized according to whether the circle array and cue circle locations were consistent with the location of the target letter. Trials in which the target letter appeared inside the circle with the matching color (i.e., both were of the target color) were categorized as valid cue trials. Invalid cue trials were those in which the target letter appeared in the circle with the distractor color. Neutral cue trials contained no colored circles; that is, all the circles were a uniform white. Similarly, trials in which the circle array was offset to the same side as the target letter (e.g., both were to

the right of fixation) were categorized as valid array trials. Trials in which the circle array was offset in the direction opposite the target letter were considered invalid array trials.

Probe localization trials. Localization trials began in the same manner as the identification trials, and were identical through the presentation of the circle array. However, after a 150 ms SOA from array onset, a localization probe (0.5° diameter, 75 ms duration, with the same color as the target letter in the identification trials) was presented instead of a target letter. The probe appeared 11° below fixation, randomly in one of the central three possible probe positions learned earlier in the localization training (-1.5°, 0°, or 1.5° from participant's midline). After the probe was extinguished, participants pressed one of five buttons with the right hand to indicate the perceived position of the probe. After a 500 ms intertrial interval, the fixation point reappeared and participants were free to begin the next trial.

In the localization trials, trials were categorized according the locations of the circle array (right array or left array) and the location of the circle with the target color (right cue, left cue or neutral cue).

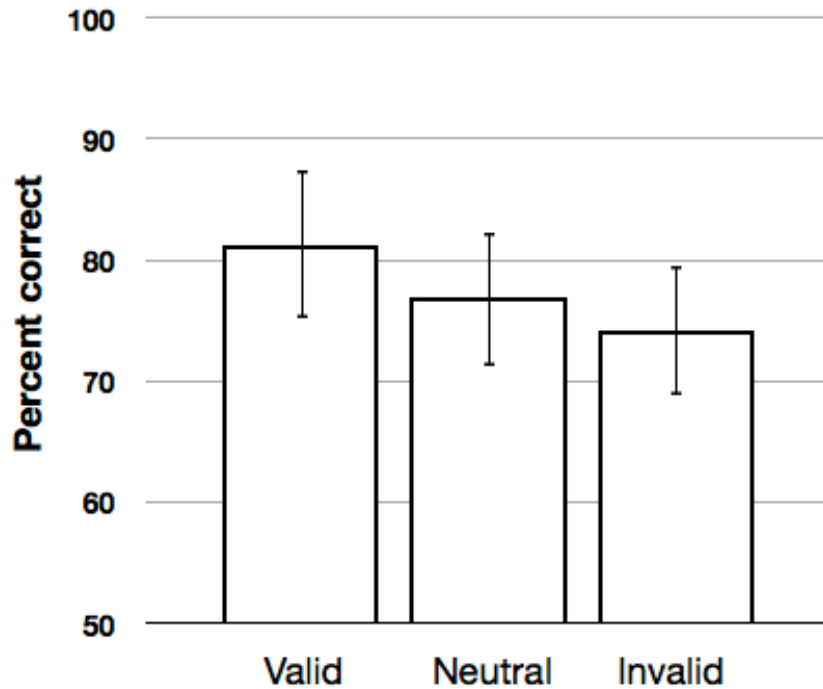


Figure 15: Percent correct in the identification task of Experiment 3. Errors bars represent standard error estimates for each cue condition.

## Results

In an assessment of letter identification accuracy, a repeated-measures ANOVA with factors of cue and array validity revealed a significant main effect ( $F(2, 34) = 5.95, p = .006, \eta^2 = .849$ ) of cue validity. In contrast, there was no significant effect of array validity ( $F(1, 17) = .04, p = .843, \eta^2 = .054$ ), and the interaction between cue and array validity also did not reach significance ( $F(2, 34) = 1.58, p = .221, \eta^2 = .311$ ). Because the factor of array validity had no significant effect on identification accuracy, we collapsed across this factor in subsequent analyses. Accuracy (Figure 15) in the valid color cue condition ( $M = 81.3\%, SE = 3.0; t(17) = 3.30, p = .004$ ) was significantly greater than in the invalid cue condition ( $M = 74.2\%, SE = 2.7$ ), and marginally greater than in the

neutral cue condition ( $M = 76.9\%$ ,  $SE = 2.8$ ;  $t(17) = 2.09$ ,  $p = .052$ ). The difference between the invalid and neutral cue conditions did not significantly differ ( $t(17) = -1.39$ ,  $p = .183$ ).

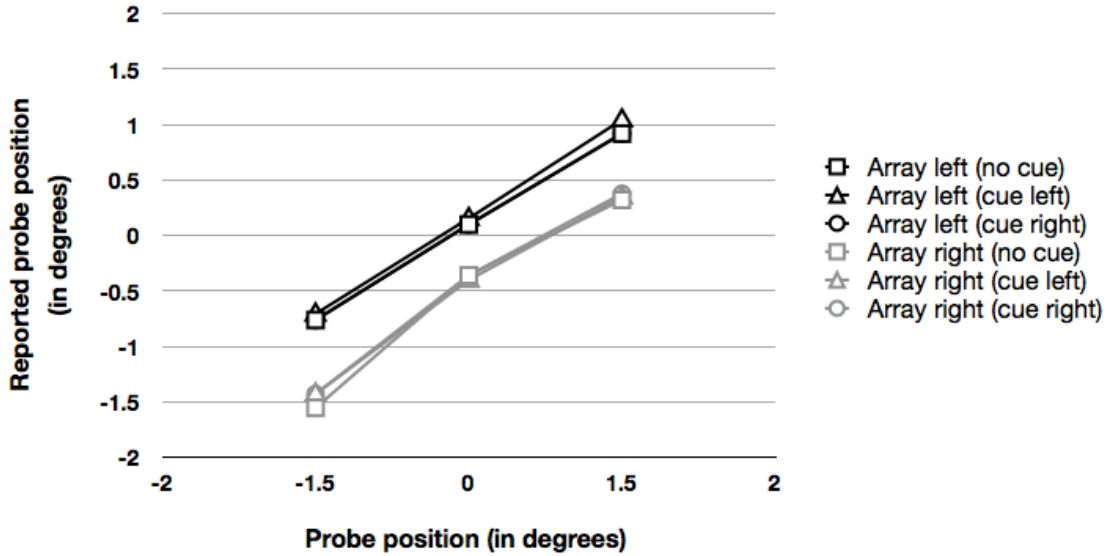


Figure 16: Perceived probe location in the localization task of Experiment 3, plotted with respect to the actual probe location (negative values indicate locations to the left of fixation). Data is plotted separately for the different combinations of cue and array locations. Data from the neutral cue conditions are obscured by data from the left cue and right cue conditions within each of the array conditions.

We performed a separate multiple regression analysis of the probe localization trials (Figure 16), with the factors of probe position, array location, and cue location entered in a block-wise fashion (in that order). Not surprisingly, the factor of probe location had the greatest effect on the perceived location of the probe ( $R^2 = .357$ ,  $\beta = .597$ ,  $t(1942) = 34.59$ ,  $p < .0001$ ). In addition, array location significantly affected the perceived location of the probe ( $R^2 = .064$ ,  $\beta = -.253$ ,  $t(1941) = -14.66$ ,  $p < .0001$ ). The mean reported difference in



the location of the probe, across the three cue conditions (array right – array left conditions) was  $0.61^\circ$ , with probes reported in the opposite direction as the shifted array (Figure 16). However, the factor of cue location had no significant effect on the reports of probe location ( $R^2 < .0001$ ,  $\beta = -.009$ ,  $t(1940) = -.545$ ,  $p = .586$ ).

## **Discussion**

In letter identification task of Experiment 3, accuracy was significantly affected by the location of the target-colored circle that preceded the presentation of the target letter. If this cue validly indicated the subsequent target letter location, accuracy increased. This finding demonstrated that the manipulation of attentional set effectively captured attention, drawing the locus of attention toward the cue that shared the target's color. Importantly, accuracy was unaffected by the location of the circle array, indicating that the color-contingent manipulation of attention was effective at overriding any attentional attraction that the offset array might of otherwise had.

While the letter identification accuracy was affected by the location of the color cue and not the location of the circle array, there was an opposite pattern of performance in the probe localization task. Specifically, the perceived location of the probe was modulated by the location of the offset circle array, but not by the location of the color cue. The bias in localization caused by the offset array mirrored the typical Roelofs effect, with the probe's location reported to be shifted in the direction opposite the array offset. The fact that the probe localization was unaffected by the exogenous shift of attention aimed at the color cue indicates that reflexive shifts of attention do not cause a distortion

of the observer's apparent midline, and therefore must not serve as the mechanism that drives the Roelofs effect.

### **General Discussion**

In three experiments we examined the affect of orienting visuospatial attention on observers' perception of spatial location. Experiment 1 demonstrated that non-predictive exogenous cues are capable of causing a Roelofs-like effect, demonstrating that the Roelofs effect is not dependent on the use of the typical large inducing frame. However, the results of Experiment 1 did not conclusively demonstrate that it was a shift of attention that caused the distortion, since the imbalanced visual display might have been sufficient enough to drive the distortion independent of any shift in the locus of spatial attention. Experiments 2 used a central endogenous cue that prompted a shift of attention without the use of an imbalanced visual display. The resulting endogenous shift of attention was found to be capable of inducing a distortion of the perceived location of a visual probe, but this distortion was clearly different (much smaller in magnitude, and in the opposite direction) from the typical Roelofs effect. Finally, the paradigm of Experiment 3 used a color-contingent attentional manipulation to successfully dissociate a shift in attention from an imbalance in the visual display. The results provide clear evidence that it is the imbalance of the visual display and not any accompanying shift of attention that drives the Roelofs effect.

Comparing the results of Experiments 2 and 3 seems to indicate a difference in the effects of endogenous and exogenous shifts of attention on perceived space, with exogenous shifts causing no distortion in the perceived location of a visual probe while endogenous shifts cause the probe's perceived location to be attracted to the new locus of

attention. (Experiment 1 is of little value in this comparison, since any effect of the exogenous shift of attention was confounded by the Roelofs effect driven by the imbalanced display.) We offer three possibilities for this discrepancy. First, it is possible that neither type of attentional shift causes a distortion of the perceived probe location, and the apparent distortion seen in Experiment 2 is simply a type I statistical error. However, while the effect is quite small, we have replicated it several times in the lab, using variations of the paradigm presented here in Experiment 2 (unpublished observations). Furthermore, an examination of the individual differences in performance in the identification and localization tasks in Experiment 2 revealed that the magnitude of the distortion in the localization task was proportional to the magnitude of the validity effect in the identification task, a relationship that would not be expected if the apparent distortion in the localization task was merely a type I error. For these reasons, we do believe that the distorting effect of endogenous shifts of attention is real.

Second, it is possible that exogenous shifts of attention cause a distortion similar to that of endogenous shift, but the perceptual consequences were not detected in Experiment 3 due to a type II statistical error. Indeed, the effect would be expected to be quite small, using the effect seen with the endogenous shift in Experiment 2 as a guide, and it may have been overpowered by the much larger Roelofs effect caused by the offset array of circles.

Third, it may be that exogenous and endogenous shifts of attention really do differ in their abilities to cause distortions of the perceived probe location. Exogenous and endogenous shifts of attention are similar in a variety of ways; for example, there is partial functional overlap in the brain regions that control reflexive and voluntary shifts

of attention (Corbetta et al., 1993, 1995; Anderson et al., 1994; Nobre et al., 1998; Gitelman et al., 1996). However, they also differ in many respects. While early imaging studies provided evidence for broad overlap between cortical circuits involved in voluntary and reflexive shifts of attention, recent studies have demonstrated that distinct sub-regions of posterior parietal cortex are transiently active during voluntary vs. reflexive attentional shifts (Serences et al., 2005; Serences & Yantis, 2006). Reflexive and voluntary shifts of attention also differ prominently in their time courses (Müller & Rabbitt, 1989; Posner & Cohen, 1984; Klein, 2000), and their perceptual consequences (Yeshurun, Montagna, & Carrasco, 2008). Prinzmetal, McCool, & Park (2005) have suggested that endogenous and exogenous manipulations of attention likely affect different stages of processing, proposing that endogenous shifts of attention affect perceptual representations, while exogenous shifts of attention influence decision-level stages of processing. If this distinction is true, it could provide a basis for the difference in the spatial distortions that can be attributed to the two.

Although the results presented here indicate that the Roelofs effect is caused by an imbalance between the left and right visual fields independent of any shifts of attention, it remains to be determined how the imbalance causes the underlying distortion of the observer's apparent midline. One possibility is that the visual system uses the middle of the full extent of the visual field as a cue to form a representation of the direction that the head is facing, for use as the origin for an egocentric reference frame. This visual cue would not be used exclusively, since it is clear that vestibular and proprioceptive cues would also contribute (as evidence by the fact that observers are still capable of making egocentric judgments about a object's location even when that object is perceived in

otherwise complete darkness). Under normal viewing conditions, the visual field is reliably symmetrical around the observer's objective midline, and would serve as a useful cue to form veridical representations of straight-ahead. However, this cue would prove to be less reliable when the observer is in an impoverished visual environment, when imbalances in the visual field would become more prominent, resulting in the Roelofs effect.

## CHAPTER IV

### RIGHT SUPERIOR PARIETAL LOBULE IS A SELECTIVE PROCESSOR OF EGOCENTRIC CONTEXTUAL INFORMATION

When an observer makes a judgment about an object's spatial attributes, such as location, orientation or size, the specific attribute is not considered in isolation, but is instead judged within the context provided by the entire visual scene. Depth cues, for example, provide information about the distance between the observer and the object of interest, which in turn allows for an appropriate use of the object's retinal size as a cue in the assessment of its actual size (Gregory, 1963). Similarly, when attempting to determine the orientation of an object, the edges of building walls, doors, etc., can provide visual cues of the observer's own orientation in space so that deviations from a normal upright posture can be taken into account (Asch & Witkin, 1948). While this use of egocentric visuospatial context is typically beneficial to the observer's judgment, misleading contextual information can lead to illusions, with, for example, the well-known Ponzo and rod-and-frame (Fig. 1A) illusions driven by distortions of perceived depth and orientation, respectively.

#### **Experiment 1**

Recent imaging work has demonstrated that egocentric contextual information from the Ponzo illusion can modulate perception through the effects of feedback connections

from higher levels of visual processing to earlier levels, such as area V1 (Murray, Boyaci, & Kersten, 2006; Fang et al., 2008). However, the anatomical origin of this feedback signal remains a mystery. Walter & Dassonville (2008) used fMRI to explore the cortical regions involved in processing the contextual information that leads to the induced Roelofs effect, an illusory shift in the perceived location of a target induced by an underlying distortion of the observer's perception of straight-ahead (Bridgeman, Peery, & Anand, 1997; Dassonville & Bala, 2004a; Dassonville et al., 2004). A greater activation was observed in the superior parietal lobule (SPL), predominantly in the right hemisphere, when participants made location judgments within the illusion-inducing context, compared to trials in which the same judgment was made with targets presented in isolation.

Although these results suggest that right SPL plays a role in processing the contextual cues that contribute to our perception of visual space, another possibility must be acknowledged. When viewing an illusory stimulus, the observer often understands that the visuospatial context is misleading and should therefore be ignored in order to achieve optimal performance in the task. The activation in right SPL observed by Walter & Dassonville (2008) may therefore reflect an active attempt by the observer to suppress the contextual information, in an attempt to mitigate its illusory effects. To test these alternatives, we used slow repetitive transcranial magnetic stimulation (rTMS) to temporarily disrupt the processing of this parietal region in healthy observers. If right SPL plays a direct role in processing egocentric contextual information, rTMS should cause a *decrease* in illusion susceptibility. Alternatively, if right SPL plays a role in

suppressing the effects of misleading contextual information, one would expect an *increase* in illusion susceptibility after rTMS.

## **Methods**

*Participants.* Participants (n = 12, 3 female, ages 18 – 34) gave their informed, written consent to participate in the study, as per the Institutional Review Board of the University of Oregon.

*Anatomical scans.* Each participant completed an initial magnetic resonance imaging (MRI) session to collect anatomical scans for use in guiding the transcranial magnetic stimulation (TMS). T<sub>1</sub>-weighted images were acquired at the Lewis Center for Neuroimaging at the University of Oregon. MR images were acquired using a 3T head-only MRI scanner (Siemens Magnetom Allegra, Erlangen, Germany), with a phased array head-coil and a standard MPRAGE sequence (TR = 2.5 s, TE = 4.38 ms, TI = 1.1 s, 176 slices, 1 mm thickness, 0 mm gap, FOV = 256 x 256 x 100 mm), yielding an in-plane anatomical resolution of 1 x 1 x 1 mm. To ensure that the laterality of the images would be correctly interpreted, participants were scanned with a small marker (0.5 ml centrifuge tube filled with a nickel sulfate solution) taped to the right side of the forehead.

*Anatomical registration.* Following completion of the anatomical scan, the image of each participant's brain was warped to a common MNI space using *Brainsight* neuronavigation software (Rogue Research Inc.). This transformation was performed by demarcating the AC/PC line in the individual scans; a bounding box was then adjusted to encompass the entire cortex. Four external anatomical references (the tip of the nose, the bridge of the nose, and right and left tragal notches) were registered in each individual's



scan for use in guiding the stimulator in subsequent TMS sessions. The Talaraich coordinates corresponding to the BOLD activations observed by Walter and Dassonville (2008) were used to delineate target sites in the left and right superior parietal lobules (MNI: -14, -68, 57 and 19, -66, 57, respectively) after first converting to MNI coordinates (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).

*TMS sessions.* Each experiment consisted of three TMS sessions separated by a minimum of one week. In each session, a single cortical site (right SPL, left SPL or vertex) was stimulated, with site order counterbalanced across participants in both experiments. Each session began with a pre-TMS baseline run of the experimental task (see *Experimental Task* section, below), lasting approximately 10-15 minutes.

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) 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 TMS session was then set to 110% of this resting motor threshold.

Participants were seated comfortably, with a chin rest stabilizing the head. Using the *Brainsight* frameless stereotaxic system, the anatomic reference frame was calibrated for individual participants, using the tip of the nose, the bridge of the nose and tragal notches as landmarks. The magnetic coil was subsequently guided to the appropriate cortical region of interest and locked into place using an adjustable arm. The position of the coil

was monitored on-line by the experimenter, with the coil never deviating more than two mm from the target anatomical site. Ten minutes of low-frequency (1-Hz) repetitive TMS (rTMS) were then administered, with the pulses controlled by LabView (National Instruments) experimental software. Recent work examining the effects of TMS on cortical excitability show that low-frequency rTMS reduces cortical excitability, effectively inhibiting the underlying neural tissue for several minutes (Fitzgerald, Fountain, & Daskalakis, 2006; Maeda et al., 2000). After the 10 min stimulation period, participants promptly completed a post-TMS run of the experimental task.

### **Stimuli and Procedure**

*Rod-and-frame illusion (RFI)*. Stimuli were presented on a CRT monitor operating at a resolution of 1024 x 768 (refresh rate = 60-Hz). To remove any environmental (i.e., allocentric) cues that might aid the participants in their task, the brightness and contrast of the monitor were reduced so that the edges of the screen were not visible. In addition, the monitor was placed within a large wooden box (painted black), with a blackout curtain draped over the open end. Participants viewed the monitor from 24 inches away, with the blackout curtains draped over their head and shoulders to prevent stray light from providing cues.

At the beginning of the first TMS session, participants completed 16 practice trials of the RFI task (see Figure 17A). Each trial began with a centrally presented fixation point (.5° in diameter). Participants pressed the spacebar on a keyboard to begin each trial. After a 200 ms delay, a tilted rod (0.17° wide and 4.8° long) was presented for 500 ms, centered on the fixation point. The rod was oriented -6, -4, -2, -1, 1, 2, 4, or 6° from

vertical, with negative values indicating leftward tilts. Participants reported whether the top of rod was tilted right or left by pressing one of two keys (J or F) on the keyboard. Feedback was then presented for 500 ms, indicating the correct response (i.e., “right” or “left”).

Following the practice block, participants completed 270 experimental trials. Each trial began with a central fixation point ( $0.5^\circ$  in diameter). Participants initiated a trial by pressing the spacebar. In a portion of the trials ( $n = 180$ ), a large tilted frame (with each edge subtending  $19^\circ$  of visual angle, tilted  $15^\circ$  to the left or right of gravitational vertical) was then presented for 400 ms. After a delay of 300 ms from frame onset, a tilted rod ( $-6, -4, -2, -1, 0, 1, 2, 4, \text{ or } 6^\circ$  from gravitational vertical) was flashed for 100 ms, with the frame and rod extinguished simultaneously. The remaining 90 trials were identical, except that the rod was presented in isolation (that is, no frame was presented). As in the practice trials, participants ended the trial by reporting the orientation of the rod with a keypress. Trials with and without the frame were presented in random order, and no feedback on performance was provided to the participants.

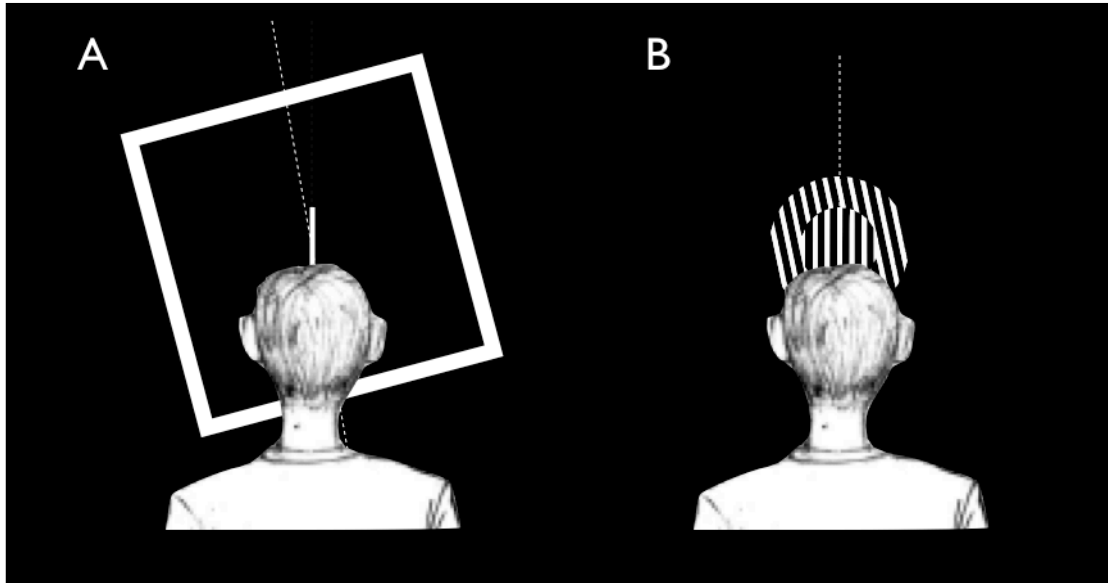


Figure 17: Experimental tasks. A) Visual display for evoking the rod-and-frame illusion (Experiment 1), in which a square frame tilted away from gravitational vertical distorts an individual's perception of subjective vertical (dashed line, not seen by observer). When the observer assesses the rod's orientation, the biased perception of vertical typically causes the rod to appear to be tilted 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 due to local contrast effects in early visual processing, without distorting subjective vertical (dashed line).

*Data analysis.* For each combination of rod and frame tilt in the RFI trials, the perceived location of the rod was quantified as the proportion of trials in which the participant reported the central stimulus as being oriented to the right of gravitational vertical (Figure 18A). Psychometric functions were then fit (Microsoft Excel, using a least-squares algorithm) to this data to determine the point of subjective equality (PSE, the orientation at which the rod was equally likely to be judged as being tilted left or right of vertical), using the equation:

$$\text{proportion "Right" responses} = e^{((\text{rodtilt}-\text{PSE})/\tau)} / (1 + e^{((\text{rodtilt}-\text{PSE})/\tau)}),$$

where *rodtilt* was the orientation of the rod, *PSE* was the point of subjective equality, and *tau* was the rate of change of the psychometric function. To quantify the magnitude of the illusion, the PSE for the left-tilt condition was subtracted from that of the right-tilt condition, with this total effect size statistically compared across conditions.

In Experiment 1, participants ( $n = 12$ ) reported the orientation of the rod in a version of the rod-and-frame illusion (Figure 17A; Witkin & Asch, 1948), with illusion susceptibility quantified as the difference between the point of subject equality (PSE, the orientation at which participants reported the rod as being tilted clockwise and counterclockwise with equal probability) for left- and right-tilted frames (Figure 18A). Participants completed a baseline block of RFI trials, followed by 10 minutes of 1-Hz rTMS, and then a final RFI block to assess the effects of the stimulation. Three regions of interest were targeted with rTMS in separate sessions: right SPL, and two control sites – a mirror site in left SPL and vertex.

## Results

A repeated-measures ANOVA revealed a significant interaction ( $P = 0.02$ , d.f. 2, 22) between stimulation site and block, (pre- vs. post-TMS), with no significant main effects. A significant decrease in illusion susceptibility was found following right SPL stimulation (Figure 18B), compared to vertex ( $P = 0.04$ ) and left SPL ( $P = 0.01$ ), suggesting that right SPL plays a role in processing the egocentric contextual information provided by the tilted frame. The slopes of the psychometric functions (a measure of task

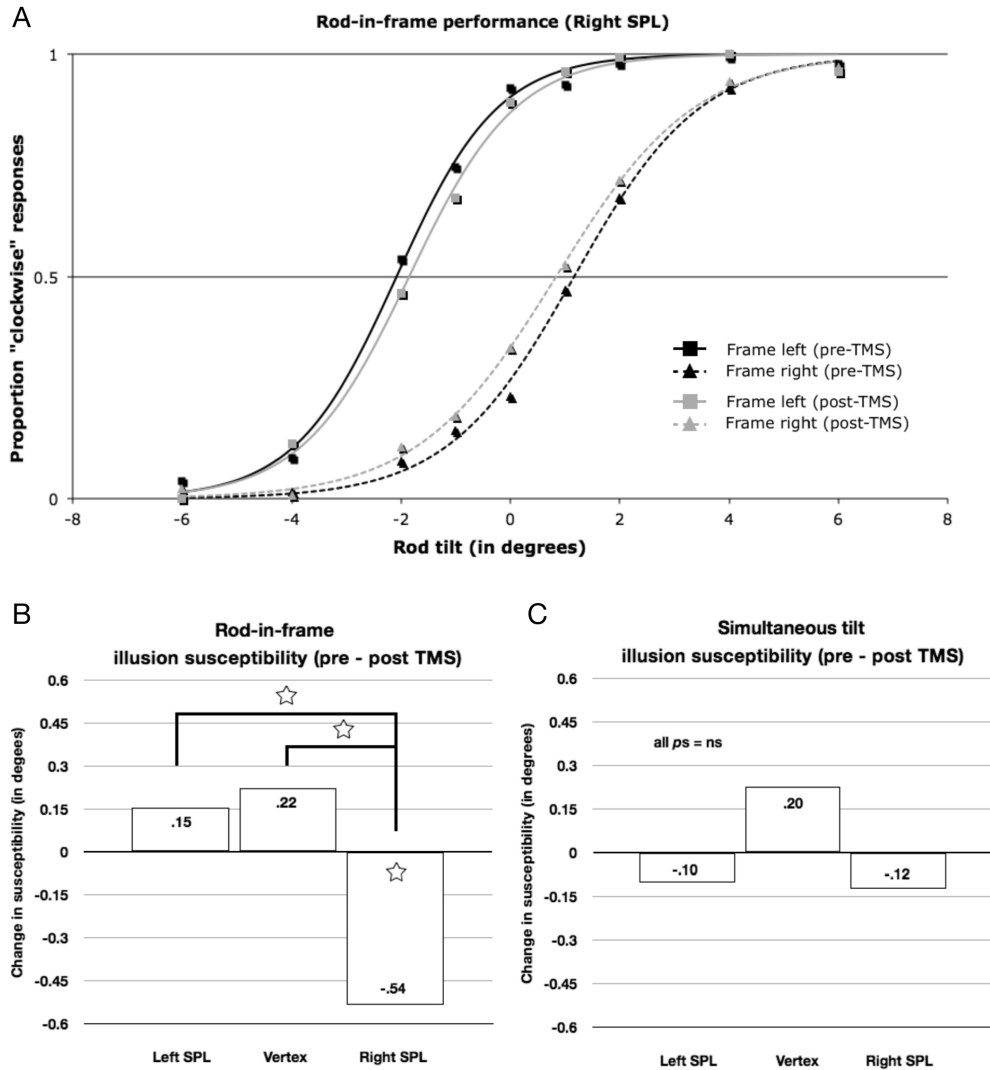


Figure 18: Results of Experiments 1 & 2. A) Average results from the right SPL stimulation site in Experiment 1, showing the proportion of trials in which each rod orientation was reported to be rotated clockwise from vertical. Best-fit psychometric functions are shown for each frame tilt (i.e., left and right) in both pre- and post-TMS blocks. The point at which each function surpasses a proportion of 0.5 indicates the point of subjective equality (PSE) for that condition, with illusion susceptibility in each block assessed as the difference in PSE for right- and left-tilted frames. B) Total change in rod-and-frame susceptibility (pre- minus post-TMS) for each cortical region of interest in Experiment 1. TMS at only the right SPL site caused a significant change in

difficulty) did not significantly change after TMS ( $P$ 's  $> 0.10$ ), ruling out the possibility that TMS simply minimized the distracting influence of the frame. In addition, there were no significant changes in illusion susceptibility or task difficulty for any stimulation site ( $P$ 's  $> 0.11$ ) during trials in which the rod was presented in isolation (i.e., with no accompanying frame), indicating that the effects of TMS acted specifically to modulate the participants' use of the egocentric contextual information provided by the frame.

## Experiment 2

If right SPL is a selective processor of egocentric context, susceptibility should be unaffected in illusions in which the inducing context affects early, local levels of visual processing, as in the simultaneous-tilt illusion (Figure 17B; Gibson & Radner, 1937). In Experiment 2, participants completed a version of the simultaneous-tilt illusion in an rTMS paradigm otherwise identical to that of Experiment 1.

### Methods

*Participants.* The same participants as Experiment 1 participated in Experiment 2.

### Procedure and apparatus

*Simultaneous tilt illusion (STI).* The apparatus was identical to that of Experiment 1. At the beginning of the first TMS session, participants completed 16 practice trials of the STI task (see Figure 18B). Each trial began with a centrally presented fixation point ( $0.5^\circ$  in diameter). Participants pressed the spacebar to begin each trial. After a 200 ms delay, a circular patch of a tilted grating ( $3.2^\circ$  of visual angle in diameter) was presented for 500

ms, centered on the fixation point. Across the grating, red and black bars ( $0.26^\circ$  in width) alternated in a square wave pattern. The grating was tilted  $-5, -3, -1, 1, 3,$  or  $5^\circ$  from vertical, with negative values indicating leftward tilts. Participants reported whether the grating was tilted right or left by pressing one of two keys (J or F) on the keyboard. Feedback was then presented for 500 ms, indicating the correct response (i.e., “right” or “left”).

Following the practice block, participants completed 210 experimental trials. Each trial began with a central fixation point ( $0.5^\circ$  in diameter). Participants initiated a trial by pressing the spacebar. In a portion of the trials ( $n = 140$ ), an outer annulus of oriented bars ( $5^\circ$  outer diameter,  $3.2^\circ$  inner diameter, with red and black bars of  $0.26^\circ$  in width alternating in a square wave pattern, tilted  $15^\circ$  to the left or right of gravitational vertical) was presented for 700 ms. After a delay of 200 ms from annulus onset, the inner grating (tilted  $-4, -2, -1, 0, 1, 2,$  or  $4^\circ$  from gravitational vertical), with the annulus and inner grating extinguished simultaneously. The remaining 70 trials were identical, except that the inner grating was presented in isolation (that is, no outer annulus was presented). As in the practice trials, participants ended the trial by reporting the orientation of the inner grating. Trials with and without the inner grating were presented in random order, and no feedback on performance was provided to the participants.

## **Results**

A repeated-measures ANOVA revealed no significant main effects or interactions ( $P$ 's  $> 0.30$ ; Figure 18C), suggesting that the effects of rTMS on right SPL are specific to the use of egocentric contextual information.



## **General Discussion**

The results of the present study go beyond those of a previous imaging study that demonstrated right SPL to be activated during a localization task in which observers are influenced by egocentric contextual information (Walter & Dassonville, 2008). Here, the use of rTMS allows for an examination of the causal relationship between this activation and subsequent perception, with the finding that right SPL participates directly in the processing of egocentric context in the formation of visual representations of space. The lateralization of this function is not surprising given previous research demonstrating the right hemisphere's role in processing visual information at a global level (Han et al., 2002; Volberg & Hubner, 2007), and making location judgments within an egocentric reference frame (Walter & Dassonville, 2008). Given these findings, right SPL should be considered a viable candidate for the origin of the feedback signal that provides a modulatory effect on neural activity in early visual areas according to the egocentric context provided by the visual scene (Murray, Boyaci, & Kersten, 2006).

## CHAPTER V

### GENERAL CONCLUSIONS

This dissertation has focused on how environmental cues interact with visuospatial attention in the creation and maintenance of egocentric reference frames. As an observer navigates the visual world, objects and landmarks can be encoded in a variety of reference frames. They may be encoded egocentrically, for example, relative to the position of the eyes in their orbits, or relative to the orientation of the trunk. Objects are also localized relative to one another, in allocentric (world-centered) coordinates. The redundancies inherent in these multiple coordinate systems provide a means of increasing the accuracy and precision of perceptual and cognitive judgments, and they provide flexibility when an observer must navigate and interact with the world.

In our day-to-day interactions with the environment, it is difficult to dissociate the characteristics of the egocentric and allocentric reference frames. However, it is possible to isolate the reference frames through the use of experimental manipulations that provide impoverished visual cues, effectively limiting the number and types of cues available. In the paradigms used in Chapters II and III, for example, participants were first asked to learn the locations of individual probes that were presented in complete darkness, with no other visual stimuli that could provide cues to their locations within an allocentric coordinate system. Thus, the probes' locations are learned in an egocentric reference frame, and subsequent distortions of that egocentric reference frame (that is, distortions

of the apparent midline) by an imbalanced visual display led to mislocalizations of the visual probes. Likewise, the paradigm of Chapter IV caused distortions of the egocentric reference frame (specifically, distortions of perceived vertical) through the use of the rod-and-frame illusion.

### **Attentional set and the induced Roelofs effect**

Visual context can operate at multiple levels of the visual processing hierarchy. One way to understand the visual processing responsible for a visual illusion is to delineate the specific level in the processing hierarchy that is involved. In an extreme example, it has been shown that contextual information can influence perception even in the absence of awareness (Bridgeman & Lathrop, 2007; Moore & Egeth, 1997; Chan & Chua, 2003; Lamy, Segal, & Ruderman, 2006). On the other hand, illusory effects can also be modulated by top-down processes, as when they are minimized by explicitly instructing participants to ignore the context (Coren & Porac, 1983; Goryo, Robinson, & Wilson, 1984; Tsal, 1984; Predebon, 2004, 2006).

The paradigm of Chapter II was designed to test whether feature-based attentional settings might interact with the bottom-up processing of the visual context provided by a Roelofs-inducing frame. The results were consistent with the larger attentional capture literature, demonstrating that distractor items (in this case, the Roelofs-inducing frame) are most disruptive when they have featural overlap with task-relevant targets (Folk et al., 1992; Bacon & Egeth, 1994; Folk et al., 2002, 2008). The studies presented in Chapter II demonstrate that the induced Roelofs effect can be modulated by attentional control settings. Importantly, these findings cannot be attributed to low-level perceptual grouping

effects. When the frame matched the task-relevant target color, an exaggerated distortion of midline was observed. Attentional control settings, and their affect on attentional capture have traditionally been studied at relatively high levels of cognitive functioning (e.g., visual search) (Leber & Egeth, 2006). The results demonstrate that attentional set is also capable of modulating the visual system's weighting of low-level egocentric contextual information.

### **Locus of attention and subjective midline**

Early work examining the effects of attention on localization abilities demonstrated that spatial localization of a target item becomes more variable when covert attention is shifted to another location (Newby & Rock, 2001; Tsal, 1999; Tsal & Bareket, 1999; Butler, 1980). In addition, clinical evidence exists that suggests the current locus of spatial attention can act as an egocentric reference frame (McCloskey & Rapp, 2000).

In the induced Roelofs task, the rectangular frame is a very large and salient object and it is typically the only visual reference available to the observer. Chapter III presented the hypothesis that these characteristics of the Roelofs-inducing frame cause it to reflexively capture attention, and it is this shift of attention that triggers a concomitant shift in subjective midline (additional evidence for this idea is provided by previous work showing that a small peripheral distractor is sufficient to cause a distortion of subjective midline; Walter & Dassonville, unpublished observations). The Roelofs effect has been observed when the frame is visible for prolonged periods of time, demonstrating that shifts of attention and subjective midline are not invariably yoked (Roelofs, 1934).

However, transient frame presentations may attract attention (and, with it, the apparent midline) because no external visual information is present to anchor subjective midline.

In Chapter III, this hypothesis was tested using modified versions of a spatial cueing task (Posner, 1980a, 1980b). Exogenous (reflexive) cues showed a pattern of responses consistent with subjective midline shifting with the locus of attention (Experiment 1). An endogenous (predictive) cue was then used to control for physical imbalances in the visual field (Experiment 2). The pattern of results did not support the hypothesis that midline shifted with the locus of visuospatial attention. Experiment 3, which pitted a visual display that was imbalanced toward one hemifield with a shift of attention into the other hemifield, provided further evidence that shifts of attention do not cause the distortions of subjective midline associated with the Roelofs effect. The results of these studies support the conclusion that the Roelofs effect is driven not by shifts of attention, but instead by asymmetries in the visual field.

Why, then, do these asymmetries cause a distortion in the apparent midline? The importance of symmetry across the visual field is consistent with the idea that the entire visual field acts as an environmental reference under normal circumstances. As an observer views the world in typical, well-lit conditions, the right and left hemifields form a complete visual field that is usually centered around the observer's apparent midline. Under those conditions, the middle of the visual field would provide a useful cue to indicate straight ahead, which could be combined with proprioceptive and vestibular cues. In the Roelofs paradigm, on the other hand, the entire extent of the visual image is defined by the offset boundaries of the inducing frame, whose center would serve as a misleading cue for straight ahead.

### **Contextual processing in right superior parietal lobule**

Neurophysiological studies have demonstrated that posterior parietal regions represent the locations of objects in the visual field within many different egocentric reference frames in a multiplexed fashion (Nitz, 2006; Rogers & Kesner, 2006; Brochie et al., 1995; Crowe, Averbeck, & Chafee, 2008). The single-unit animal literature suggests that parietal cortex is critical in performing the computations required to create and maintain a representation (or representations) of personal and external space.

Research in humans suggests a further dissociation in processing specificity between the parietal hemispheres. Several recent studies have demonstrated that the cerebral hemispheres differ in their sensitivity to global vs. local-level visual information (Hubner & Volberg, 2005; Hubner, Volberg, & Studer, 2007; Fink et al., 1996). Behavioral, hemodynamic, and electrophysiological studies, using hierarchical stimuli (e.g., a large letter S, composed of small E's) all point to the right hemisphere acting as a selective processor of global contextual information.

Relatively little research has examined how the hemispheres may differ in their processing of contextual information used for egocentric and allocentric spatial computations. Walter & Dassonville (2008) provided initial evidence that similar hemispheric differences exist when global contextual information is used in a localization judgment. They observed that a largely right-lateralized region of the superior parietal lobule was active when observers were judging the location of a target relative to midline, in the presence of illusion-inducing context. However, the exact function of the activation was unclear – it may have been that the rSPL was itself involved in processing the global context, thereby causing the distortion of subjective midline. On the other hand, it was

also conceivable that this activation reflected inhibitory operations that may have been part of the participants' attempts to minimize the effects of the illusion.

To dissociate these functions, the experiments of Chapter IV used 1-Hz repetitive TMS to temporarily suppress neural activity in the rSPL. Observers performed the rod-and-frame task before and after TMS, allowing us to examine potential behavioral changes due to TMS. After TMS, observers were less susceptible to the effects of the illusion, indicating that the rSPL typically plays a role in processing the context provided by the rotated frame. Importantly, no effect of TMS was observed in the simultaneous tilt illusion, which is driven by mechanisms operating at a lower level of visual processing (i.e., primary visual cortex). These results coupled with previous fMRI findings (Walter & Dassonville, 2008) suggest that the rSPL is a selective processor of egocentric visual context.

### **Future Directions**

These initial studies pose several interesting questions for future investigations. What is the potential role of feature priming in the attentional modulation of the Roelofs effect seen in Chapter II? Is the small but significant mislocalization observed in the endogenous cue experiment of Chapter III caused by a distortion of subjective midline, albeit one that is very different, and much smaller in magnitude, compared to that of the Roelofs effect? Is the region in right superior parietal lobule that is sensitive to the context provided by the Roelofs and rod-and-frame stimuli a domain-general processor of egocentric context? Finally, Chapter IV suggests that illusions of egocentric context and illusions of contrast can be dissociated at the neural level using TMS. If the context in the

rod-and-frame and simultaneous tilt are processed in separate areas of the visual system, would differences in the time course of these illusions also be observed?

### **Filtering vs. priming in contingent capture**

The results of Chapter II were interpreted within a contingent capture framework of visual search. The original formulation of contingent capture argued that the creation of a top-down set selectively tuned the attentional system for specific target properties. Critically, it was assumed that non-relevant features are simply filtered out (Folk et al., 1992). A contentious issue in the attentional capture literature has centered on the role of a top-down set under conditions of spatial uncertainty. Folk et al. (1992) argued that top-down set affected the *selection* stage of processing, whereby stimuli sharing properties with the observer's set are automatically selected. In contrast, recent work from Belopolsky, Schreif, & Theeuwes (2010; see also Lamy & Egeth, 2003; Lamy, Egeth, & Leber, 2004) suggests that attentional set facilitates search by *suppressing* non-relevant features, allowing for rapid disengagement from other salient irrelevant stimuli. The suppression hypothesis does not assume that ignored features cannot capture attention – salient distractors can capture attention – but attention is rapidly disengaged because of the current attentional set. Thus, the role of an attentional set acts at the disengagement stage, rather than the attentional selection stage. The results of Chapter II could be interpreted as indicating that attention may have acted to decrease the salience of the non-set frames causing them to have a smaller-than-normal effect on midline. Alternatively, non-set frames may have had a normal influence on midline, but the effect of the set-matching frame was exacerbated because of the feature overlap with the target. Thus, our



results can be interpreted under either the *selection* or an *inhibition* hypothesis of contingent capture. The critical difference between the two is the stage of attentional selection in which the effect of the offset frame is modulated.

A particularly important question is the possible role of intertrial priming in the results of Chapter II. The original precueing studies asked participants to search for a target defined by a specific feature (e.g., a color or an onset) that was constant for the duration of the experiment (Folk et al., 1992, 1994). To prevent attentional capture by irrelevant singletons, the observers should actively maintain the attentional set on a trial-by-trial basis. However, the active maintenance of a top-down template may not be necessary when the relevant feature is invariant across trials.

Maljkovic & Nakayama (1994) investigated an effect they termed *priming of popout*. They demonstrated that when participants had to search for a red target among green distractors (or vice versa), repeating a target (but not the response) facilitated search, even though the likelihood of a feature repetition was chance. Priming of popout was argued to be a form of automatic priming that is immune to top-down control. Maljkovic & Nakayama (1994) argued that the search facilitation is likely due to changes in low-level feature weightings that operate throughout the entire search display (Kristjánsson, 2002).

In both experiments of Chapter II, participants were instructed to search for a target of a specific color. The relevant color was counter-balanced across subjects, but the relevant color did remain constant for each participant. The initial establishment of a top-down set is critical for task performance, however visual selection during later stages of the experiment may be due to adjustments in the weights of the target and distractor

features, rather than active attentional filtering (Meeter & Olivers, 2006; Olivers & Humphreys, 2003; Olivers & Meeter, 2006). Adjusting feature weights could then guide visual selection in a bottom-up manner, allowing the maintenance of the attentional set to be abandoned.

It is possible that both intertrial priming and top-down set played a role in Experiments 1 & 2 of Chapter II. The relative contributions of these two processes could be examined by cueing participants to adopt a specific attentional set (e.g., report blue) before each trial. This would require participants to rapidly reconfigure their attentional set on a trial-by-trial basis. If top-down set is involved, a capture effect should be replicated whenever the frame matches the current relevant target color. Critical trials would be those in which the set is switched, but the subsequent frame matches the previously abandoned attentional set. For example, assume after having previously searched for a red target in trial  $n-1$ , trial  $n$  required the observer to search for a blue target. Under these circumstances, intertrial priming would predict an exaggerated affect of a red frame on trial  $n$  due to the repetition of the feature that had been searched for in trial  $n-1$ . An intertrial priming account also predicts that the irrelevant frame should become more disruptive across repetitions because the weights will be adjusted over several trials.

### **Attentional shifts and subjective midline**

The results of Chapter III demonstrate that the Roelofs effect is caused by visual field imbalances, and not spatial shifts of attention. An obvious question for future investigation is the nature of the target mislocalization observed with endogenous cues in

Experiment 2 of Chapter III. It can be reasonably concluded from the attentional cueing studies that the induced Roelofs effect is caused by low-level imbalances in the visual field (i.e., the lateralized peripheral cue); this asymmetry then serves to distort subjective midline, as was demonstrated in Experiments 1 and 3. However, the question remains, why was localization performance affected by endogenous shifts of attention, which caused the target to be perceived as being shifted toward the cued location (that is, with a leftward shift of attention, the target was perceived to be to the left of its actual position - an effect in the opposite direction of the typical Roelofs effect)?

The pattern of results observed in Experiment 2 differs from that of other attentional mislocalization reports in the literature. Suzuki & Cavanagh (1997) provided evidence that the locus of attention can repulse the perceived location of a target – the attentional repulsion effect (ARE). Using a paradigm very different from ours, their participants performed a vernier acuity task while attention was directed to the periphery, which caused a small repulsion in the target's perceived position (with a leftward shift of attention, the target was perceived to be to the right of its actual position). The results of Chapter III cannot be attributed to variance due to eye movements, as this variance was removed during the analyses. It may be that the mislocalizations seen with endogenous cues were caused by a distortion of the midline, with the midline repelled in a direction opposite the shift of attention. To investigate this possibility, participants could be asked to make a pointing movement or a saccade to perceived midline after the offset of the endogenous cue (in a task analogous to that of Dassonville & Bala, 2004). While this would be a step toward directly measuring the distortion of subjective midline, there are potential concerns with this design. In particular, the size of the mislocalization caused by

the endogenous cue was very small compared to the typical Roelofs effect, increasing the chance of a type II statistical error even if the effect is real. Second, a shift of visuospatial attention would undoubtedly accompany the motor response of the participant (Sheliga, Riggio, & Rizzolatti, 1994). This additional shift of attention may disrupt the distortion of midline caused by the attentional cue. For example, a the planning of a pointing movement toward the perceived target location may evoke concomitant shift of attention, which could distort the effect caused by the initial attentional cue.

### **Contextual processing in the rSPL**

Recent work by Walter and Dassonville (2012) has demonstrated that relatively distinct regions of parietal cortex (superior parietal lobe and precuneus) are recruited when an observer performs a search for a target object obscured by extraneous contextual information (the Embedded Figures Task, or EFT; see Figure 3). To successfully solve the search task and locate the target shape, the effects of the irrelevant contextual information in the complex image must be suppressed. Interestingly, performance in the EFT has been shown to correlate with an observer's susceptibility to various visual illusions, like the rod-in-frame illusion (Witkin & Asch, 1948) and the Roelofs effect (Walter & Dassonville, unpublished observations). These behavioral interrelationships predict that the same brain structures affected by the context of the EFT also process the illusion-inducing contextual information provided in the rod-in-frame and the Roelofs illusions. Indeed, Walter & Dassonville (2008) showed that the illusion-inducing contextual cues of the Roelofs effect activated the same parietal regions that were active in the EFT.

Although Walter and Dassonville (2012) found a specific region of the parietal cortex that was activated by the contextual information in the EFT, it is still unclear what this activation represents. One possibility is that this brain region is itself involved in processing the contextual information, directly causing less-than-optimal search performance. On the other hand, it is possible that this region is involved in suppressing the effects of the context, which would be critical in the participant's attempts to perform well in these difficult tasks.

A potential extension of the rod-and-frame TMS study of Chapter IV involves the use of TMS to investigate the specific role that this parietal region plays in the EFT. TMS disrupts neural processing in a brain area of interest by generating a very focal, but powerful magnetic pulse over the scalp of a normal, healthy individual, which temporarily disrupts the stimulated area of the brain. If this parietal region were directly involved in processing the contextual information provided in the EFT displays, then disrupting this area would be expected to increase EFT performance. On the other hand, if this region were involved in actively suppressing the effects of the context, TMS would be expected to decrease search performance.

TMS is a valuable tool for addressing questions of functionality in the brain, however individual variations in cortical anatomy (i.e., sulcal and gyral folding) can limit its generalizability across subjects. Therefore, when performing TMS studies, it would be useful to perform a functional localizer scan within the target group of subjects, and then test the same subjects in the subsequent TMS protocol. This allows null findings to be interpreted with more confidence – if TMS has no effect on EFT performance, it could be

reasonably concluded that the rSPL is not involved in processing the context present within the complex image.

Functional magnetic imaging work examining size constancy has demonstrated that the contextual information present in the Ponzo illusion can modulate perception through feedback connections from higher levels of visual processing to earlier levels, such as area V1 (Murray et al., 2006; Fang et al., 2008). However, the anatomical origin of this feedback signal remains a mystery. The Ponzo illusion, like the rod-and-frame and Roelofs illusions, is driven by a distortion of the observer's perception of space. Previous research has shown that susceptibility to the Ponzo, rod-and-frame and Roelofs illusions are correlated; individuals who experience a greater distortion of perceived vertical and perceived straight-ahead in the rod-and-frame and Roelofs illusions, respectively, also show a larger overestimation of object size in the Ponzo illusion (Walter & Dassonville; 2009). Given these findings and the results of Chapter IV, right SPL should be considered a viable candidate for the origin of the feedback signal that provides a modulatory effect on neural activity in early visual areas, according to the egocentric context provided by the visual scene.

To explore the nature of this feedback, participants would complete a version of the Ponzo illusion, in which they must judge the size of two spheres in the presence or absence of the illusion-inducing context. If the Ponzo illusion is driven by feedback from the right SPL, a reduction in illusion susceptibility would be predicted after rTMS to right SPL, compared to a control site at vertex. Task performance would not be expected to change when the illusory context is absent.

## **Temporal differences in visual illusions**

Studies examining differences in the time course of contextual influences on visual processing have increased in the animal literature (Bair, Cavanaugh, & Movshon, 2003). However, similar issues have not been systematically addressed in humans. In particular, the temporal effects of illusory context on visual perception remain untested (see Danckert et al., 2002). The studies conducted in Chapter IV demonstrate that the context of the tilted frame in the RFI is processed, at least in part, in the right posterior parietal lobe. In contrast, the simultaneous tilt is thought to be caused by inhibitory interactions between orientation sensitive columns in primary visual cortex. If these illusions are operating at different levels of the visual hierarchy, differences in the time course of the illusory-inducing context might be observed.

A future avenue for study could vary the time between the onset of the context (e.g., the rotated frame) and the reported stimulus (e.g., the rod). For example, the onset of the frame could precede the onset of the rod in some trials, and lag behind the rod in others. Using a variety of stimulus onset asynchronies would allow for a careful mapping of the time course of the illusion. Illusions occurring early in the visual system, like the simultaneous tilt, may only occur when the context is presented before, or in conjunction with the central grating. Alternatively, the RFI may have effects over a larger temporal window due to rapid and sustained feedback from posterior parietal cortex. Future studies could probe the time courses of “global” and “local” visual illusions to characterize when contextual cues are bound with the target stimulus. Employing converging paradigms will serve to strengthen the case for dissociable contextual processing modules in the human visual system.

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