THE TIME COURSE OF THE INTEGRATION OF VISUAL INFORMATION INTO THE EGOCENTRIC REFERENCE FRAME

by

JEFFREY MICHAEL PETERSON

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Student: Jeffrey Michael Peterson

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This dissertation has been accepted and approved in partial fulfillment of the requirements for the Doctor of Philosophy degree in the Department of Psychology by:

Paul Dassonville	Chairperson
Ulrich Mayr	Core Member
Margaret Sereno	Core Member
Terry Takahashi	Institutional Representative

and

Kate Mondloch	Interim Vice Provost and Dean of the Graduate School

Original approval signatures are on file with the University of Oregon Graduate School.

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DISSERTATION ABSTRACT

Jeffrey Michael Peterson

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An important function of the visual system is to identify and localize objects within our environment. This task is often facilitated by accounting for the broader visual context in which the object is embedded. However, the modular nature of visual processing and the various neural transmission delays across the visual cortex suggests that the analysis of an object and its context might proceed in an asynchronous fashion.

The experiments presented in this dissertation were designed to assess the time course by which visual context is integrated with the egocentric reference frame. We presented observers with the tilted frame of the rod-and-frame illusion, which, once integrated with the egocentric reference, induces a bias in subjective vertical. To determine the latency between the presentation of the frame and its initial effect on subjective vertical, we assessed participants' perception of vertical at various times before and after the onset of the tilted frame.

Chapter II describes two experiments in which perceived vertical was assessed with an orientation judgment of a briefly flashed rod. This experiment produced the surprising result that the perceived orientation of a rod presented *before* frame onset was biased by the direction of the frame's tilt. We proposed a differential latencies model to

account for this result. Specifically, that the latency between the presentation of the rod and the completion of the orientation judgment is longer than the delay between the onset of the frame and its initial effect on perceived vertical. Experiment 2 in this chapter provides a test of this model. Chapter III describes a similar experiment; however, subjective vertical was assessed with a vertically-directed saccadic eye movement. The earliest effect of the tilted frame was observed in saccades initiated 100 ms after frame onset.

The results of our experiments suggest that contextual visual information is rapidly integrated within the egocentric reference frame, where it subsequently shapes our perceptual judgments and guides our actions. The speed of this integration suggests that visual context relevant to global orientation is processed during the initial feedforward sweep of activation ascending the visual hierarchy.

CURRICULUM VITAE

NAME OF AUTHOR: Jeffrey Michael Peterson

GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of Oregon, Eugene
University of North Dakota, Grand Forks

DEGREES AWARDED:

Doctor of Philosophy, 2020, University of Oregon
Master of Science, 2016, University of Oregon
Bachelor of Science, 2011, University of North Dakota

AREAS OF SPECIAL INTEREST:

Cognitive Neuroscience
Sensorimotor Integration

PROFESSIONAL EXPERIENCE:

Graduate Teaching Fellow, University of Oregon, Eugene
2014-2020

Decision Research, Inc., Eugene
2018-2020

GRANTS, AWARDS, AND HONORS:

Distinguished Teaching Award, University of Oregon, 2020

Gregores Research Award, University of Oregon, 2016

Magna Cum Laude, University of North Dakota, 2011

PUBLICATIONS:

Peterson, J. M., & Weatherly, J. N. (2011). Comparing three strategies of motivating gambling behavior in the laboratory environment. Analysis of Gambling Behavior, 5(1), 28-34.

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TABLE OF CONTENTS

Chapter Page

LIST OF FIGURES

LIST OF TABLES

Table Page

CHAPTER I

INTEGRATING VISUAL CONTEXT FOR PERCEPTION AND ACTION

To interact with an object in our environment, it is necessary to estimate its various spatial features. For example, to reach out and grasp the coffee mug on my desk, it is useful to have a visual estimate of the mug's size, its location with respect to my hand, and the orientation of its handle. Incorporating the broader visual context that surrounds the object tends to improve the accuracy of these estimates by establishing a reliable spatial frame of reference (Conti & Beaubaton, 1980; Krigolson & Heath, 2004; Hay & Redon, 2006). In fact, vision is such a reliable source of spatial information that it is used to calibrate the metrics of other sensory modalities (Brainard & Knudsen, 1993; Pavani, Spence & Driver, 2000; Zwiers, Van Opstal, & Paige, 2003; Röder, Kusmierek, Spence, & Schicke, 2007; Gori, Sandini, Martinoli, & Burr, 2014; Héroux, Law, Fitzpatrick, & Blouin, 2015). In some cases, however, the visual context can be misleading and our reliance upon it creates situations where our perception of a feature does not cohere with its objective measurement: a visual illusion.[1]

When offered for public consumption, illusions are often presented as an oddity or intriguing quirk. They are skillfully employed at funhouses or so-called "mystery spots", where objects appear to roll uphill or tourists maintain postures that seem to defy

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[1] There is some debate about whether it is useful to characterize such situations as "illusory"; see for example, Purves, Wojtach, & Lotto (2016).

gravity. Some illusions inspire such controversy that they “break the internet” (e.g., #TheDress). For a vision scientist, however, illusions can be useful tools. With careful manipulation, they can reveal the principles upon which the brain forms our perceptions (Eagleman, 2001). In this sense, illusions provide a means to stress test the perceptual system, to learn how it works by studying the conditions where it fails.

Cognitive and neural science often compare the brain to an information processor. If we consider information to be the reduction of uncertainty (Shannon, 1948), then a primary function of the brain is to reduce the uncertainty about the external world and our relation to it. To perform this function, the brain must rely on imperfect sources of information: sensation and memory. Stimulation arriving from the environment is filtered through our sensory apparatus, the sensitivities of which have been tuned by evolution to detect the limited bandwidths of energy most pertinent to our fitness. Once transduced, the information is represented by populations of noisy neuronal activity. This coarse and, often, ambiguous sensory representation is supplemented with our expectations and existing knowledge to create an internal model that represents the most likely state of the world (Land, 2014; Nienborg & Roelfsema, 2015). This framework suggests that, despite the typically unified and unambiguous experience we enjoy from moment-to-moment, our perception results from a probabilistic process; it is the product of numerous unconscious inferences unfolding over time.

Though our uncertainty about the external world is reduced by the information processing of the brain, it cannot be eliminated. One might consider an illusion to be the result of one (or more) of these perceptual inferences arriving at an incorrect conclusion and, thereby, distorting the brain’s internal model of the world. By examining when, during the course of perceptual and cognitive processing, an illusion causes such a distortion, we can learn more about the time course by which information becomes available to the brain for it to form estimates and make decisions about what is going on in world “out there.”

This dissertation is focused on the time course by which visual context is integrated with the brain’s representation of egocentric space. The experiments described herein used a visual illusion to distort an observer’s perception of vertical. The latency between the presentation of this illusion and its subsequent effect on perception and action were measured in order to draw inferences about when the brain utilizes contextual visual information to update its representation of our spatial orientation. Chapter I provides an introduction to illusions driven by visual context, consequences for perception and action, and considerations for the time course of contextual integration. Chapter II describes two experiments that measured the time course of visual integration by assessing perceptual estimates of vertical before and after an illusion-induced distortion of egocentric space; a model accounting for our observations is then proposed and tested. In Chapter III, the time course by which this egocentric distortion influences actions, specifically saccadic eye movements, is assessed. Finally, Chapter IV synthesizes the results of our experiments and considers the broader implications of this research, including new questions that it raises.

Visual Context and Global Orientation

Attempts have been made to create a taxonomy of visual illusions (e.g., Coren et al., 1976; Gregory, 1991). While the specific groupings formed by these analyses depend upon the dimension of comparison that is emphasized (e.g., geometric, physiological, functional, etc.), a distinction is often made between illusions driven by so-called “local effects” and those driven by “global effects”. In general, an illusion that is induced by the interaction between neighboring elements within the stimulus configuration is referred to as being driven by local effects. The simultaneous tilt illusion (STI; Figure 1 A), is a classic example of one such illusion. In the STI, the perceived orientation of the central grating is biased by the orientation of the grating in the surrounding annulus. At a neuronal level, the STI is thought to be driven by lateral inhibitory interactions between neurons in primary visual cortex (V1) that have adjacent receptive fields and similar orientation tunings (Carpenter & Blakemore, 1973; Clifford, 2014).

In contrast to local orientation effects, global orientation illusions occur even when the elements within the figure are spatially distant. Some of these global effects result from a distortion of the observer’s egocentric frame of reference. Broadly, a frame of reference can be defined as the criteria by which the location of an object is described. The critical distinction between one frame of reference and another is the point upon which the system is anchored. Within an egocentric frame of reference, an object’s location may be specified with respect to the direction of gaze, the head, or the body midline. Despite the different anchors, each is an instance of an egocentric reference frame because the description of the object’s location will vary as the position/orientation of the observer changes. By contrast, the location of one object could be described relative to a second object. Such a frame of reference is described as world-centered or allocentric. The origin of an allocentric frame of reference is anchored to some point other than the observer and the relations specified therein are invariant to changes in the location of the observer.

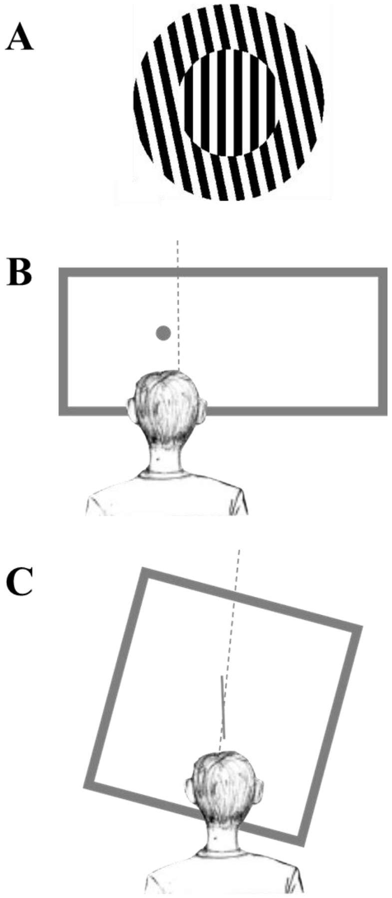


Figure 1: A) The simultaneous tilt illusion: the perceived orientation of the central grating is biased in the direction opposite the grating in the tilted surround. B) The Roelofs effect: a frame offset from the observer's objective midline biases their perceived midline (dashed line) in the direction of the frame's offset. A target presented at the objective midline is perceived as shifted in the direction opposite the frame. C) The rod-and-frame illusion: a tilted frame biases the observer's perception of vertical (dashed line) in the direction of the frame's tilt. A truly vertical rod is perceived as tilted in the direction opposite the frame. Note: the magnitude of the bias depicted in B & C has been exaggerated for illustrative purposes.

One illusion that distorts the egocentric reference frame is the Roelofs effect (Roelofs, 1935; Figure 1 B). When an observer, seated in otherwise complete darkness, is presented with a large frame that has been offset from their objective midline, their perception of straight-ahead becomes biased in the direction of its offset (Dassonville, Bridgeman, Bala, Thiem & Sampanes, 2004). This misperception can be revealed by asking the observer to direct their gaze straight-ahead (Dassonville & Bala, 2004), for example. Because of this bias in perceived straight-ahead, the observer will judge a target enclosed within the frame to be shifted in the direction opposite the frame's offset, an effect known as the induced Roelofs effect (Bridgeman, Dassonville, & Lester, 2018). For example, if the observer is presented with a target that is aligned with straight-ahead, but their perceived midline has been biased to the right by a rightward shifted frame, the observer will report that the target lies to the left of straight-ahead.

Similar egocentric distortions can occur if the frame is tilted. When the frame is rotated on its horizontal axis such that the top is pitched toward the observer, their perceived eye level is biased upward; conversely, if the top of the frame is pitched away from the observer, their perceived eye level is biased downward (Matin & Fox, 1989; Stoper & Cohen, 1989). If instead the frame is tilted clockwise (CW) or counterclockwise (CCW) with respect to vertical, the observer's perception of vertical becomes biased in the direction of the frame's tilt. This effect is a demonstration of the rod-and-frame illusion (Figure 1 C; Witkin & Asch, 1948) and is discussed in more detail below.

Not surprisingly, there is evidence that global orientation illusions are driven by different neuronal mechanisms than those described for local effects. The distortion of perceived straight-ahead that is driven by the Roelofs effect is correlated with activation in the right superior parietal lobe (SPL; Walter & Dassonville, 2008). Repetitive transcranial magnetic stimulation of the right SPL reduced the magnitude of the RFI, while the magnitude of the STI remained unaffected (Lester & Dassonville, 2014). The observation of Lester and Dassonville (2014) suggests that the activity in SPL observed by Walter and Dassonville (2008) was not merely a coincidence and that the neurons there likely play a role in the integration of contextual visual information to update the egocentric frame of reference.

The Rod-and-Frame Illusion

A global orientation illusion of particular interest to the work contained in this dissertation is the rod-and-frame illusion (RFI; Witkin & Asch, 1948). In the original demonstration of this illusion, participants were seated in a darkened room and presented with a large luminous frame that had been rotated from gravity-defined vertical. The participant’s task was to adjust the orientation of a rod enclosed within the frame until it appeared to align with vertical. The authors observed that rod orientation settings tended to err in the direction of the frame’s tilt, suggesting that the frame had biased the observer’s perception of vertical. For example, when surrounded by a frame rotated in the CW direction, a truly vertical rod would be perceived as tilted in the CCW direction. Therefore, the participant needed to rotate the rod CW to bring it in line with perceived vertical. A popular variant of this task consists of presenting an oriented rod to the participant and simply asking them to report whether the rod was tilted CW or CCW from vertical (a two-alternative forced choice). The orientation of the rod is iteratively adjusted across many trials in order to estimate the observer’s perception of vertical.

Subsequent research with the RFI has investigated the various stimulus parameters that induce the illusion, such as the visual angle subtended by the frame (Ebenholtz, 1977; Ebenholtz & Benzschawel, 1977; Spinelli et al., 1991), the degree of the frame’s tilt (Beh, Wenderoth, & Purcell, 1971; Wenderoth & Beh, 1977), and size of the gap separating the ends of the rod from the edges of the frame (Coren & Hoy, 1986; Antonucci et al., 1995). From this research, two complementary mechanisms have been proposed to drive the illusion.

The first is a local orientation contrast mechanism that creates a perceptual repulsion effect, pushing the perceived orientation of the rod away from the orientation of the frame's edges. This is the same mechanism proposed to underlie the STI, described above. Evidence for its role in the RFI comes from studies that have manipulated the distance between the edges of the rod and edges of the frame. As this distance increases beyond the range that neighboring receptive fields in V1 are able to interact, the magnitude of the RFI decreases (Coren & Hoy, 1986; Antonucci et al., 1995). Therefore, it is thought that the influence of local contrast effects may be most prominent in versions of the task that employ a small frame, where spatial constraints necessitate the proximity of the rod to the edges of the frame.

As the distance between the rod and frame increases, the magnitude of the illusion is reduced, but not abolished. As mentioned above, the larger frame size places the rod and the frame in regions of the visual field that are beyond the range of local inhibitory interactions. The remaining effect that is observed in the presence of the large frame must therefore be driven by some other mechanism. It is proposed that this second mechanism involves a competition between the visual and the vestibular systems. Stimulation of the visual periphery (where the large frame is presented) has been demonstrated to affect an observer's estimate of gravitational vertical (Dichgans, Held, Young, & Brandt, 1972; Dichgans & Brandt, 1974). Studies with the RFI have demonstrated that the large frame induces a bias in perceived head orientation (Ebenholtz & Benzschawel, 1977; Sigman, Goodenough, & Flannagan, 1978). The large frame also evokes a vestibular-ocular reflex, an ocular counter-roll (i.e., torsion) in the direction of the frame's tilt, as would be appropriate for a real head tilt in the direction opposite the frame's rotation (Crone, 1975;

Goodenough, Sigman, Oltman, Rosso, & Mertz, 1979). Importantly, these studies did not observe a bias in perceived head orientation or ocular torsion when testing the small frame version of the RFI (side length < 12°). Although the degree of ocular torsion cannot fully account for the magnitude of the illusion (Goodenough et al., 1979), the presence of this relationship demonstrates the interaction between vision and the vestibular senses in the large frame version of the RFI.

To summarize, although the observable perceptual effect is similar for the small- and large-frame versions of the RFI (i.e., the perceived orientation of the rod is biased in a direction opposite the frame's tilt), they are driven by complementary mechanisms. When the frame is small, the illusion is primarily driven by local orientation contrast effects, similar to those described for the STI. When the frame is large, the illusion is created predominantly by a competition between visual and vestibular cues, biasing perceived head orientation and distorting the egocentric frame of reference. The overall illusion magnitude associated with a particular frame size is likely a combination of these two effects, with their relative contribution proportional to the size of the frame (Spinelli et al., 1991).

The simplicity and replicability of the RFI lends itself to investigations within the artificial environment of a laboratory. However, the influence of visual context on perceived vertical has also been demonstrated for more ecological situations, such as when viewing natural landscapes or cityscapes (Singer, Purcell, & Austin, 1970; Haji-Khamneh, & Harris, 2010). Thus, it has been proposed that the RFI is likely to be an instantiation of a more general spatial constancy mechanism (Ebenholtz, 1977). Spatial constancy refers to the apparent stability of the visual world despite movement of the eyes, head, and body. In principle, this constancy could be maintained by accounting for movements of the body represented in somatosensory, vestibular, and efference copy signals. While such cues certainly play a role in spatial constancy, these signals are often slow or imprecise. Our experience of the covariance between visual surface orientations and the direction of gravity (Coppola et al., 1998; Girshick, Landy, & Simoncelli, 2011), paired with the high spatial resolution of vision, make visual cues a reliable heuristic to estimate one's orientation. Given our knowledge that edges in the environment tend align with gravity-defined vertical and horizontal, it may be reasonable for the brain to infer that the projection of a large tilted frame on the retina (as in the RFI) means that the head is tilted. Such ecological accounts have been suggested for other phenomena such as size contrast and the Müller-Lyer illusion (Howe & Purves, 2004, 2005).

Visual illusions, perception, and action

Despite the perceptual biases induced by a rotated or translated visual context, actions directed toward the remembered location of targets embedded within these contexts are generally accurate. This has been demonstrated for grasping movements directed toward the rod in the RFI (Dyde & Milner, 2002) and pointing movements directed toward targets surrounded by the Roelofs frame (Bridgeman, Peery, & Anand, 1997) or projected onto a pitched-from-vertical plane (Li & Matin, 2005). These apparent dissociations between perception and action have been used to support the Two Visual Streams hypothesis of visual processing (Goodale & Milner, 1992; Milner & Goodale, 1995). The hypothesis derives its name from anatomical and functional observations of visual processing in primate cortex. After its arrival in primary visual cortex, the visual processing pathway bifurcates, with one stream projecting dorsally into the parietal lobe and the other stream projecting ventrally into the temporal lobe. Mishkin, Ungerleider, and Macko (1983), suggested a division of labor between these streams such that the ventral stream is predominantly involved in object recognition while the dorsal stream is specialized for spatial vision (a division of “what” vs “where,” respectively). In their Two Visual Streams hypothesis, Miller and Goodale (1995) further proposed that the ventral stream is responsible for conscious visual perception whereas the dorsal stream is unconscious and processes vision for action (a division of “action” vs “perception”, respectively). It was proposed that this distinction accounts for the immunity of actions to visual illusions. Several studies have called the Two Visual Streams hypothesis into question, however (for reviews, see Schenk & McIntosh, 2010; Medendorp, de Brouwer, & Smeets, 2018).

An alternative account to describe the apparent dissociation of perception and action with a subset of illusions was presented by Dassonville and Reed (2015) in what the authors referred to as the Two-Wrongs model. Briefly, if the location of a target is encoded within a distorted map of space, an action guided within that same map will reach the target accurately, as the errors that guide the action perfectly offset the errors of encoding. As applied to the Roelofs effect, for example, the presence of a frame offset to an observer’s left will bias the perceived midline to the left. Consequently, a target lying directly straight ahead will be perceived as being to the right of the midline. In order to point to the target’s location, the observer must direct their hand to a location that is to the right of perceived straight ahead, which, in this example, has been biased to the left. Thus, the error encoded in the perceived location of the target is offset by the error of decoding the location for a pointing movement. The net result is a cancellation of errors and an accurate motor localization, despite an inaccurate perceptual localization.

In a multi-lab collaboration, Dassonville, Bridgeman et al. (2004) used the Roelofs effect in a series of experiments to test different predictions of the Two Visual Streams and Two Wrongs models. In one of their experiments, participants were presented with the Roelofs frame and instructed to point directly straight-ahead. In these conditions, the Two Visual Streams hypothesis predicts that pointing movements will be accurate, as actions should be immune to visual illusions. However, the authors observed that pointing movements were biased in the direction of the frame's offset. The authors also reported that the magnitude of the bias in a participant's pointing error was positively correlated with the magnitude of the bias in their perceptual report; this correlation suggests that the two forms of estimation rely on the same underlying frame of reference. This interpretation is in line with a common-coding theory of perception and action (Hommel, Müsseler, Aschersleben, & Prinz, 2001).

This result has been generalized to several other context illusions. When presented with the tilted frame of the RFI, a vertically-directed saccade (Dassonville & Reed, 2015; Morgan, Grant, Melmoth, & Solomon, 2015) or an outstretched hand aligned to perceived vertical (Li, Matin, Bertz, & Matin, 2008) are biased in the direction of the frame's tilt. Taken together, these results demonstrate the susceptibility of motor guidance to visual illusions that distort the egocentric frame of reference and lend support to the Two Wrongs model.

Processing Latencies in Visual Perception

The bifurcation of the visual pathway into the dorsal and ventral streams, as discussed above, is evidence of the distributed processing of visual information across the cortex. The macaque visual system, for example, has been estimated to have at least 30 functionally discrete regions (Gilbert, 2013). Localization of function is not unique to the visual system; it is a fundamental property of cortical organization (Maunsell & Newsome, 1987; Grill-Spector & Malach, 2004). However, this division of labor raises an intriguing question: how are individual features, which are analyzed in distinct cortical regions, bound together such that we perceive them as belonging to a single object? A further complication arises when one considers that the latency with which visual stimulation arrives at a given region depends upon that region’s location within the processing hierarchy (Schmolesky, et al., 1998; Martin et al., 2019). This question is referred to as the binding problem (or temporal binding problem, when referring specifically to nature of processing delays).

While influential theories have proposed mechanisms by which the binding problem might be overcome (e.g., Treisman & Gelade, 1980; Harris, Harrar, Jaekl, & Kopinska, 2010), some studies indicate that the brain does not fully resolve the temporal binding problem. Under certain conditions, two physically asynchronous events can be perceived as synchronous. Moutoussis and Zeki (1997) asked participants to compare when a moving stimulus changed color relative to when it changed its direction of motion. Participants viewed a small square stimulus as it alternated in color (red vs green) and, at the same rate, alternated in its direction of motion (up vs down). Although the two features alternated at the same rate, the phases of their alternation were offset to varying degrees. For example, if the phases were aligned, the target might be green for the extent of the upward motion and red for the extent of the downward motion. If the phases were offset by 90°, the stimulus might begin its upward motion as green, then, halfway through the movement, change to red for the rest of the upward motion and remain red for the first half of the downward motion. For several different levels of phase offset, participants indicated which color was predominantly associated with each direction of motion. Interestingly, participants were most likely to indicate a given color-direction association when the change in color lagged the change in direction by ~80 ms. The authors interpreted their results as indicating that the cortical regions responsible for making color information available to perception completed their analyses approximately 80 ms faster than the regions responsible for processing the direction of motion.

Subsequent research has created a more complex picture of this differential latencies model. For example, the magnitude of the perceptual asynchrony between color and motion is affected by the angular deviation of the change in direction of motion (Arnold & Clifford, 2002). A 180° direction reversal, as used by Moutoussis and Zeki (1997), produces the largest asynchrony, whereas less dramatic changes in direction (e.g., 45°) produce smaller asynchronies. The magnitude of the asynchrony is also affected by the relative salience of the alternating features (Adams & Mamassian, 2004) as well as stimulus luminance (Bedell et al., 2006). These studies suggest that the magnitude of perceptual asynchrony for changes in color and motion is not absolute, but depends upon the characteristics of the stimuli involved. Differential latency models have also been proposed to account for other phenomenon, such as the flash-lag effect (Whitney, Murakami, & Cavanagh, 2000; Öğmen, Patel, Bedell, & Camuz, 2004) and visual-proprioceptive integration (Cameron, de la Malla, López-Moliner, 2014)

The studies discussed above assessed the perceived simultaneity of two events in order to make inferences about their relative processing latencies; however, the results of those studies do not necessarily tell us anything about the delay between a single event and our subsequent perception of it. Because neuronal transmission is not instantaneous (the conduction velocity along a myelinated axon is ~75-120 m/s), there is some measureable delay between when an event occurs and when the neural activity corresponding to our perception of the event is evoked. Most regions within visual cortex are activated within ~120 ms after the onset of a stimulus (Raiguel, Lagae, Gulyàs, & Orban, 1989; Nowak, Munk, Girard, & Bullier, 1995; Lamme & Roelfsema, 2000). However, the relationship between activity in a given region and its role in perception has been difficult to assess.

For example, in a task where participants decided whether a briefly flashed image contained an animal or an inanimate object, EEG responses to the different image categories were differentiated as early as 150 ms post-stimulus (Thorpe, Fize, Marlot, 1996), a latency related to task performance, not simply to correlations between low-level image properties (VanRullen & Thorpe, 2001). Although, the activity observed at this time likely contributed to the eventual perceptual choice, this result does not necessarily entail that the participant was aware of the categorical distinction (or even that the categorization process was completed) 150 ms post-stimulus. Similar ambiguities exist when estimating latencies with electrophysiological recordings; even if it is known that a region is casually related to the perception of a given feature, the high density of recurrent connectivity throughout the visual hierarchy makes it difficult to assess at what point perception of the feature is generated. It may be possible to make inferences about the relative contributions of feedforward and feedback activity to perception by applying transcranial magnetic stimulation (TMS) to a region of interest at varying post-stimulus delays (Scharnowski et al., 2009; Tapia & Beck, 2014; Zeng, Fink, & Weidner, 2020). However, it can be difficult to assess the extent to which TMS completely, or only partially, disrupts the targeted region. In addition, the disruption caused by TMS likely propagates for some distance beyond the targeted region, limiting its spatial resolution. Finally, behavioral methods that rely on introspection to estimate the timing of perception (e.g., Libet, 2004) are prone to biases and illusions that are difficult to detect and control. Given the advantages and disadvantages of these different methodologies, progress in estimating the latency of perception will likely come from mixed-methods approaches.

The Time Course of Context Integration

The quality and quantity of information the visual system extracts from a scene varies during the course of viewing, even in situations where the image is static. The global precedence effect is a classic demonstration of how information in different levels of a hierarchical stimulus become available to perception with different latencies (see Kimchi, 1992, for review). Navon (1977) presented participants with compound letter stimuli, such as those presented in Figure 2 A. Large, global letters were comprised of smaller, local letters. The identity of the letter at the global level could be the same (congruent) or different (incongruent) from that at the local level. When participants were instructed to identify the letter at the local level, their responses times were longer than when they were instructed to identify the letter at the global level; this became known as the global precedence effect. Navon (1977) also reported an interaction between task instruction and congruency such that participant response times were longest when they were instructed to identify the letter at the local level when it was incongruent with the letter at the global level. It is thought that the global letter is processed with a degree of automaticity such that it interferes with identification the local letter. Sripati and Olson (2009) provided neurophysiological evidence for the global precedence effect by observing that neurons in inferotemporal cortex of monkey respond approximately 30 ms faster to the global structure of a hierarchical shape stimulus than to its local structure.

In addition to its influence on the latency of recognition, visual context can bias our perception of an object's features, as discussed above for various context-induced illusions. If the latency associated with processing the global elements of an image differs from the latency of processing its local elements, then the influence context has on an embedded object might change over the course of viewing the image. In terms of a visual illusion, this would suggest that the magnitude of a context-induced illusion might vary as visual processing of the image unfolds.

Reynolds (1981) demonstrated that the perception of illusory edges produced by a Kanizsa triangle is subject to the amount of time allowed to process the image. The Kanizsa triangle consists of three pac-man shaped circles arranged such that the open wedges appear to form the vertices of a triangle (Figure 2 B). Illusory edges are perceived between the pac-men, as if a white triangle were laid atop three solid circles. In his task, Reynolds presented the pac-men for 50 ms followed by a masking stimulus to prevent further visual processing; the delay between the stimulus and the mask varied between

50-150 ms. When the mask followed the stimulus by 50 ms, participants reported seeing the pac-men, but not the illusory triangle. With delays of 100-125 ms between stimulus and mask, participants could report seeing both the pac-men and the illusory triangle. This result demonstrates that our perception of an object can change over the course of visual processing, even in situations where the image remains static.

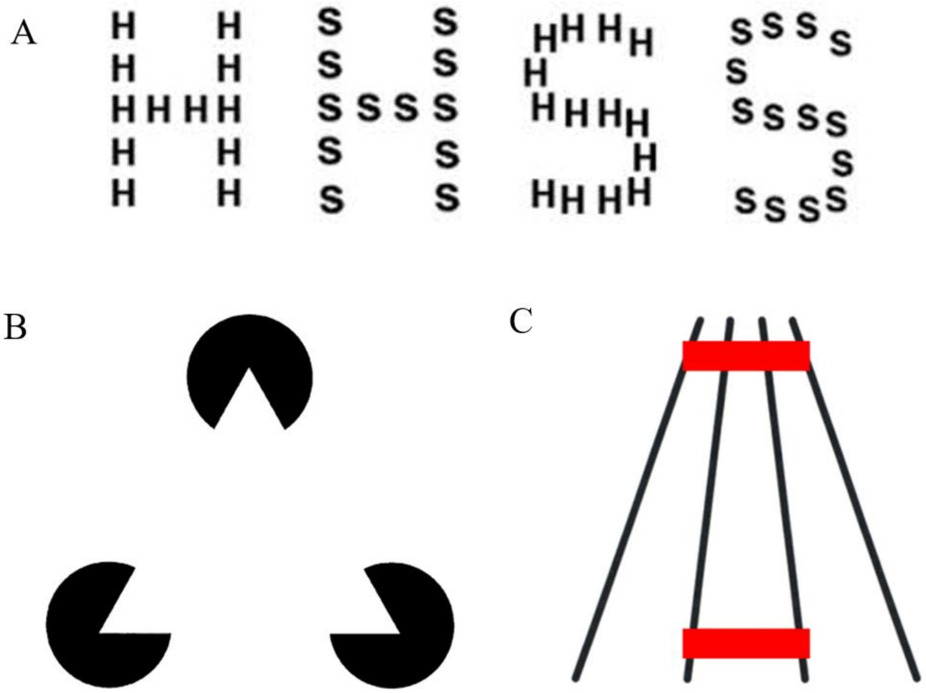


Figure 2: A) Compound letter stimuli, similar to those used by Navon (1977); B) the Kanizsa triangle; C) the Ponzo illusion: horizontal bars are the same length, despite perception that the upper bar is longer.

The time course of various illusions has been investigated, including, the STI (for review see Schwartz, Hsu, & Dayan, 2007), Poggendorff (Sugita, Hidaka, & Teramoto, 2018), Müller-Lyer (van Zoest & Hunt, 2011; de Brouwer, Brenner, Medendorp, & Smeets 2014), Ponzo (Plewan, Weidner, and Fink, 2012; Schmidt & Haberkamp, 2016), RFI (Corbett, Handy, & Enns 2009; Lopez, Mercier Halje, & Blanke, 2011), and White's illusion (Robinson & de Sa, 2008). The following discussion considers studies that have investigated the temporal aspects of the Ponzo illusion (a discussion of studies that have investigated the time course of the RFI is included in Chapter II).

The simplest version of the Ponzo illusion consists of two (or more) converging line segments that serve as the context (Figure 2 C). An object presented near the point where the segments converge is perceived to be larger than an identical object presented near the point where the segments divergence. It is thought that the Ponzo illusion is the product of size constancy mechanisms (Gregory, 2015). Briefly, the converging lines are interpreted by the visual system as parallel lines receding in depth. If two target stimuli (e.g., the horizontal bars) are perceived to be located at different depths but the image they cast on the retina is the same size, then the target that is further away must also be larger.

Plewan, Weidner, and Fink (2012) investigated the minimum duration for which a target stimulus needed to be visible for it to be influenced by the surrounding context of the Ponzo illusion. In a series of experiments, the authors presented the target stimulus for various durations, ranging from 10 ms to 250 ms, within the context of a Ponzo display. The participants' task was simply to press a button as soon as they detected the target. Plewan et al. (2012) assessed changes in reaction time to determine whether the context interacted with the target. Because reaction times are inversely correlated with the perceived size of a stimulus (Osaka, 1976; Sperandio, Savazzi, Gregory, & Marzi, 2009; Sperandio, Savazzi, & Marzi, 2010), Plewan et al. reasoned that the minimum target duration that caused a reduction in reaction time would indicate the amount of time needed to integrate the target with the surround. The authors reported that a reduction in

RT was observed only when targets were visible for at least 40 ms. The authors interpreted their results as indicating the contextual modulation of perceived size requires that the target stimulus be visible within the context for at least 40 ms.

Schmidt & Haberkamp (2016), used a response priming paradigm to test the effectiveness of a briefly (12 ms) flashed Ponzo display. A test image containing two flanker lines of different lengths was presented to participants. The participants' task was to judge which of the two flankers was longer. Preceding the test image was a Ponzo stimulus that contained flankers of equal length. The Ponzo stimulus would only serve as an effective prime (i.e., reduce RTs for the test) if the flankers were integrated with the context of the illusion. To map out the time course of the priming effect, the test stimulus followed the prime by delays ranging from 12-600 ms. The authors reported a priming effect of the Ponzo stimulus that grew in magnitude up to prime-test delays of ~130 ms. The authors suggested that because the effect of the illusion continued to grow over this longer duration, the Ponzo illusion is mediated by slower mechanisms than feedforward processing and suggest feedback processes as a likely candidate.

The fact that the Ponzo stimulus served an effective prime when it was only visible for 12 ms is surprising given the results of Plewan et al. (2014). Schmidt and Haberkamp (2016) validated their results by demonstrating the brief presentation of the Ponzo display induced an illusion as measured with traditional psychophysical methods. Schimdt and Haberkamp suggested the discrepancy between their results and those of Plewan et al. "might be explained by the differences between measuring response times to the illusion versus the influence of the illusion on response times" (p. 282). Why this relationship is non-transitive, however, is unclear.

The suggestion by Schmidt and Haberkamp (2016) that the Ponzo illusion relies on the establishment of recurrent feedback is consistent with the broader literature (Fang, Boyaci, Kersten & Murray, 2008; Murray, Boyaci & Kersten, 2006). The time course suggested by Schmidt and Haberkamp (2016) is also similar to a recent EEG study that reported that the distance cues required for size constancy are incorporated into our estimate of the object's size ~150 ms post-stimulus (Chen, Sperandio, Henry, & Goodale, 2019). In addition, the application of TMS over lateral occipital cortex was most effective at reducing the magnitude of the Ponzo illusion when applied 150 ms post-stimulus (Zeng, Fink, & Weidner, 2020). Overall, these studies suggest that the visual system is capable of rapidly extracting cues from the environment in order to estimate the features of a target object.

In the chapters that follow, we present experiments that were designed to assess the time course by which visual context is integrated with the egocentric frame of reference to update an observer's perceived orientation in space. To do so, we presented participants with the tilted frame of the RFI and assessed subjective vertical at various times before and after the onset of the tilted frame. In Chapter II, subjective vertical was assessed using a perceptual judgment of an oriented rod. In Chapter III, subjective vertical was assessed using a short, vertically-directed saccade. Finally, Chapter IV discusses some general conclusions from these experiments as well as their broader implications.

CHAPTER II

DIFFERENTIAL LATENCIES SCULPT THE TIME COURSE OF CONTEXTUAL EFFECTS ON SPATIAL PERCEPTION

Our perception of an object's features, including its size, location, and orientation, are influenced by the visual context in which the object is embedded. In day-to-day experience, incorporating the surrounding visual context tends to improve the accuracy of such assessments. For example, estimates of location are improved for visual (Conti & Beaubaton, 1980; Toni, Gentilucci, Jeannerod, & Decety, 1996), auditory (Shelton & Searle, 1980), tactile (Kennett, Taylor-Clarke, & Haggard, 2001), and proprioceptive (van Beers, Sittig, & van der Gon Denier, 1996) targets when they are presented within a broader visual context. In some cases, however, the context can be misleading, creating conditions where the perceptual estimate of a feature does not cohere with its objective measurement.

The rod-and-frame illusion (RFI, Witkin & Asch, 1948) is a classic demonstration of the role visual context plays in assessing an object's orientation. When an observer, in otherwise complete darkness, is presented with a large frame that has been tilted with respect to vertical, the observer's perception of vertical becomes biased in the direction of the frame's tilt. Consequently, the perceived orientation of a truly vertical rod enclosed within the frame becomes biased in the direction opposite the frame's tilt. Compared to illusions driven by interactions between local stimulus features (e.g., the simultaneous tilt illusion), the large frame of the RFI creates a bias in global orientation. The presentation of the tilted frame in the retinal periphery competes with vestibular cues to distort the observer's egocentric reference for vertical (Ebenholtz & Benzschawel, 1977; Goodenough et al., 1979; Alberts, de Brouwer, Selen, & Medendorp, 2016).

The spatial parameters that induce the RFI have been studied extensively, including: the visual angle subtended by the frame (Ebenholtz, 1977; Ebenholtz & Benzschawel, 1977; Spinelli et al., 1991), the magnitude of its rotation (Beh, Wenderoth, & Purcell, 1971; Wenderoth & Beh, 1977); the spatial proximity between the ends of the rod and edges of the frame (Coren & Hoy, 1986; Antonucci et al., 1995); as well as the visual salience and spatial frequency of the stimuli (Nyborg, 1972; Ebenholtz, 1985). In contrast, the temporal characteristics of the RFI have received considerably less attention. Given the processing delays inherent to neuronal transmission, there is undoubtedly some latency between when the frame is presented to an observer and when it first affects perceived vertical.

Lopez, Mercier, Halje, & Blanke (2011) used evoked potentials to compare the time course of a visual vertical judgment to that of a control task (judging which of two tilted lines was thicker). The authors reported that the visual vertical task specifically evoked activity over temporo-occipital cortex approximately 75-105 ms post-stimulus (i.e., after rod presentation); the duration of this activity was shorter when verticality judgments were made with a frame present compared to when the frame was absent. The authors also reported a more distributed activation over temporo-occipital and parieto-occipital cortex ~260-290 ms post-stimulus. Lopez et al. (2011) interpreted the earlier activation as related to the allocation of attention to and perceptual processing of the rod's orientation, and that the frame's influence on the duration of this activity may reflect the integration of visual context in these early sensory processes. The later activation was attributed to a process of comparing the rod’s orientation to an internal reference of vertical.

Lopez et al. (2011) did not find an evoked potential map that specifically reflected the influence of the tilted frame on behavior, however. It is possible that the relatively small behavioral effect (perhaps due to the relatively small frame used in this study, 9° side length) limited their ability to detect activity specific to the frame. In addition, although the authors compared orientation judgments made with and without a frame, in conditions where the frame was present, it remained visible for the duration of the testing block. The persistent visibility of the frame precluded their ability to estimate the latency between the onset of the frame and its subsequent effect on perceived vertical. Although their study is informative regarding the time course of an orientation judgment in the presence of visual context, it does not provide an estimate of the afferent processing delay of the frame itself.

In a series of behavioral experiments, Corbett, Handy, and Enns (2009) varied the onset of a tilted frame with respect to the appearance of an oriented rod. Rather than use the traditional point of subjective equality (PSE) to assess the magnitude of the illusion, the authors examined manual response times (RTs) to infer whether the tilted frame had influenced the orientation judgment. The authors’ rationale was that, when the rod and frame are tilted in the same direction, the bias in perceived vertical should make the orientation judgment more difficult; in turn, RTs should increase. Similarly, when the rod and frame are tilted in opposite directions, the illusion should facilitate the orientation judgment and reduce RTs.

In their second experiment, the tilted frame appeared and remained visible for various durations prior to the presentation of the rod. Corbett et al. (2009) reported that the frame needed to be present for at least 800 ms prior to the onset of the rod in order to affect RTs (note: synchronous rod-frame presentations also produced an effect, but this was interpreted as being driven by perceptual grouping). The authors interpreted this result as evidence of a relatively slow effect of the tilted frame on perceived vertical. However, this result was not replicated in a third experiment where the illusion magnitude was measured with the PSE. Here, the authors reported a significant RFI when the frame preceded the onset of the rod by only 400 ms. In fact, the magnitude of the RFI in the 400 ms condition did not differ from that of a condition where the frame preceded the rod by 1600 ms. This suggests that the frame’s effect on perceived vertical may have reached a maximum already 400 ms after its onset. The authors cite the discrepancy between the results of their experiments as evidence for the appropriateness of implicit measures (e.g., RT) rather than explicit measures (e.g., PSE) when assessing the time course of an illusion. Implicit measures, it was argued, are more sensitive; though, the authors provide no evidence that this was the case nor why it should be expected.

Experiment 1

The aim of this first experiment was to provide a clearer picture of the time course by which the tilted frame of the rod-and-frame-illusion affects perceived vertical. To that end, we employed a variation of the traditional two-alterative forced choice paradigm. Participants judged whether an oriented rod was tilted to the left or right of vertical; however, a temporal mismatch was imposed between the presentation of the rod and the onset of the frame, creating several levels of a rod-frame stimulus onset asynchrony (SOA) condition. As the RFI is, by definition, a perceptual effect, the perceptual report required by the PSE provides the most direct measure of the illusion. Therefore, we used the PSE to estimate the observers' perceived vertical at each level of SOA. In contrast to the longer rod duration used by Corbett et al. (2009; 100 ms) and Lopez et al. (2011; 200 ms), the rod presented in our experiment was flashed very briefly (~5 ms). This punctate stimulus presentation was intended to constrain when the perceptual judgment occurred. The briefer rod duration also allowed for a finer temporal sampling of perceived vertical as it transitioned from an accurate representation to one that was fully affected by the tilted frame.

Methods

Participants. Twenty undergraduate students (M = 18.5 years, *SD* = 1; 17 women; 17 right-handed) were recruited from the Human Subjects Pool at the University of Oregon to participate in this study. All participants had normal or corrected-to-normal vision and provided informed consent prior to their participation. The study lasted approximately one hour and participants received course credit for their time. All procedures were approved by the University of Oregon Institutional Review Board.

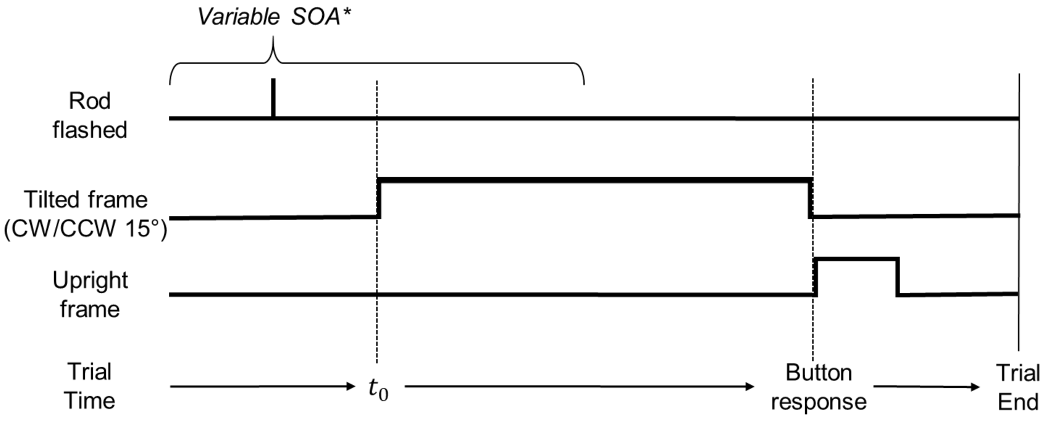
Apparatus. The experiment took place in a small testing room (250 x 160 x 300 cm). Aside from the visual stimuli presented during the course of the experiment, the room was completely dark, with walls, ceiling and objects within the room either painted black or draped in black cloth. Participants were seated approximately 86 cm from a flat, semi-translucent screen (137 x 102 cm; Polacoat Ultra projection screen with a DA-100 diffusion coating, Da-Lite, Warsaw, IN, USA) on which visual stimuli were back-projected (60 Hz retrace rate; Electrohome Marquee 8500 CRT, Niagara Falls, Ontario, CAN). The experimental procedure was programmed using Experiment Builder (SR Research, Kanata, ON, CAN), which ran on a host computer that controlled the presentation of visual stimuli. A forehead and chin rest were used to stabilize the head. Eye position was monitored throughout the experiment using an eye tracker in a tower configuration (EyeLink 2000, SR Research). Eye tracker calibration was established at the beginning of the session for each participant and maintained for the duration of the experiment. If calibration drifted, the researcher suspended the experiment and initiated a recalibration protocol. Participants used a handheld gamepad controller (SideWinder, Microsoft Corp.) to interact with the experiment (e.g., trial initiation, response submission).

Stimuli. All visual stimuli were red (RGB: [255 0 0]). Prior to the start of each trial, a circular fixation point (0.5° diameter) with a black pinhole center was presented centrally and at eye-level. The fixation point remained visible for the duration of the trial. After trial initiation, a large, square frame appeared (35.9° side length; 1° stroke width) with its center aligned on the fixation point. The frame was tilted 15° clockwise (CW) or counterclockwise (CCW) from vertical. The tilted frame remained visible until the end of the trial, at which time it was replaced with an upright frame (0° tilt) of the same dimensions for 500 ms; this was done to prevent possible carryover effects of the tilted frame between trials.

An oriented rod (7° length; 0.2° stroke width) was briefly presented at various times with respect to the onset of the tilted frame. The rod was presented centrally and at eye level such that it was bisected by the fixation point. The rod could assume an orientation rotated between –20° and 20° from vertical. The specific orientation of the rod on a given trial was determined using an adaptive staircasing procedure (see below). Programmatically, the duration of the rod's visibility was set to one retrace of the projector (16.67 ms). However, due to the fast decay rate of red phosphor in the CRT projector, it was possible to achieve a much shorter presentation time. After 5 ms, the luminance of the rod is reduced to 99.9% of its peak intensity; for convenience, we round our estimate of the rod's duration to 5 ms. The relative onset times and duration of the stimuli were confirmed by measurement with a light-sensitive diode and digital oscilloscope (WaveForms, Digilent, Inc).

Auditory feedback was provided to inform the participant whether their response had been submitted successfully or the trial had been rejected. A trial was rejected if a blink was detected, the eye departed an invisible circular boundary (4° diameter) surrounding the fixation point, or if a response was not provided within 4000 ms after the presentation of the rod. Rejected trials were reattempted at a later point in the experiment. No feedback was given regarding the accuracy of the participant's response.

Procedure. The participant's task in the experiment was to indicate whether a briefly flashed rod was tilted CW or CCW from vertical. Participants were told to respond as quickly and as accurately as possible. To familiarize themselves with the procedure, participants completed a block of 16 practice trials prior to beginning the experimental block. Practice trials were identical to the experimental trials with the exception that only upright frames were presented.



*Rod flashed @ t -200, -133, -100, -67, -33, 0, 33, 200

Figure 3: Stimulus presentation sequence for experiment 1. The onset of the tilted frame is used as a temporal reference (t_0). The rod could appear at various SOAs with respect to frame onset (–200, –133, –100, –67, –33, 0, 33, & 200 ms; negative SOAs denote rods presented before frame onset. Note: stimulus onset times and durations are not depicted to scale.

Each trial began when the participant directed their gaze to the fixation point and pressed a button on the gamepad with their left thumb; participants were instructed to maintain their fixation for the duration of the trial. After a 500 ms delay, the tilted frame appeared. The tilted frame remained visible until the participant submitted a response. On each trial, an oriented rod was briefly flashed (~5 ms duration). The presentation of the rod was varied such that it could appear before (negative SOAs), simultaneous with (0 ms SOA), or after (positive SOAs) the onset of the tilted frame (Figure 3); in total, eight levels of the rod-frame SOA condition were used (–200, –133, –100, –67, –33, 0, 33, and 200 ms). After the presentation of the rod, the participant used the gamepad to indicate whether they had perceived the rod as tilted CW or CCW from vertical by pulling the right or left trigger button, respectively. After the participant’s response was recorded, the tilted frame was replaced with an upright frame of the same dimensions for 500 ms. At this point, the trial concluded and the participant was free to initiate the next trial. Every 400 trials, the participant received on-screen instructions to take a one-minute break, after which, the experiment resumed (participants could take additional breaks by delaying the button press that would begin the next trial). The levels of each condition (2 frame tilts x 8 rod-frame SOAs) were randomly interleaved during experimental trials.

Staircasing Procedure. To maximize the number of trials with rods presented at or near the PSE, the orientation of the rod on a given trial was determined using a 1-up/1-down staircasing procedure. Each rod-frame SOA x frame-tilt condition was associated with two interleaved staircases, one initiated with rods tilted 20° CCW and initially approaching vertical in a CW direction, the other with rods tilted 20° CW and initially approaching vertical in a CCW direction. With each trial in the staircase, the orientation of the rod advanced toward perceived vertical until the participant indicated that the orientation had passed vertical. This was indicated, for example, when a rod initially approaching vertical from the left was first reported as being tilted to the right of vertical. The staircase then reversed and the rod’s orientation began to approach subjective vertical from the opposite direction in subsequent trials. The staircase procedure continued in this manner until 12 reversals were recorded, at which point the staircase closed. The experiment concluded when each of the 32 staircases (8 SOAs x 2 frame tilts x 2 staircase directions) recorded 12 reversals. This resulted in participants completing, on average, 710 (*SD* = 40) valid trials.

Analysis. For each participant, the PSE was calculated in each rod-frame SOA x frame-tilt condition. Here, the PSE is the orientation at which the participant would be equally likely to judge the rod as CW and CCW; the PSE is therefore taken as an estimate of the participant's subjective vertical. The PSE was calculated by fitting a psychometric function to the participant's responses within each SOA x frame-tilt condition (data from the two associated staircases were combined). The function took the following form:

$$f(x) = \frac{1}{1 + e^{-k(x - x_0)}} \qquad \text{eq. (1)}$$

where *x* is the rod orientation, x_0 is the PSE (i.e., the inflection point), and *k* is the slope. The parameters x_0 and *k* were fit using a custom least-squares optimization routine written in R (R Core Team, 2018). The magnitude of the RFI at each SOA was then determined by subtracting the PSE of the CCW-tilted frame condition from the PSE of the CW-tilted frame condition; this yielded an RFI magnitude at each SOA for each participant. The RFI magnitudes were then submitted for group-wise comparisons.

To facilitate a comparison between the results of our study and those of Corbett et al. (2009), we also examined RTs. First, trials were coded as congruent or incongruent, depending on whether the rod and the frame were rotated in the same or opposite directions, respectively; trials with vertically aligned rods were removed from this particular analysis. Only trials where the participant responded correctly were assessed. As with Corbett et al., we predicted that RTs would be longer for congruent trials than for incongruent trials.

Results

The primary results of this experiment are depicted in Figures 4 & 5. First, the magnitude of the RFI at each SOA was tested against zero (i.e., no effect), with significance levels adjusted for multiple comparisons. The –200 ms condition trended toward but failed to reach significance (*t*(19) = 2.91, *p.adj* = .07), suggesting that the tilted frame did not systematically affect the perceived orientation of rods presented 200 ms before frame onset. The difference in PSEs was significant in the –133 ms SOA (*t*(19) = 29.4, *p.adj* < .001, 95% CI[0.88, 1.99]), indicating that the perceived orientation of rods presented 133 ms *before* frame onset were affected by the direction of the frame's tilt, in spite of the fact that the rod, with its 5 ms duration, was no longer visible 128 ms before the frame appeared. The magnitude of the RFI at each subsequent SOA was also significantly greater than zero (Table 1).

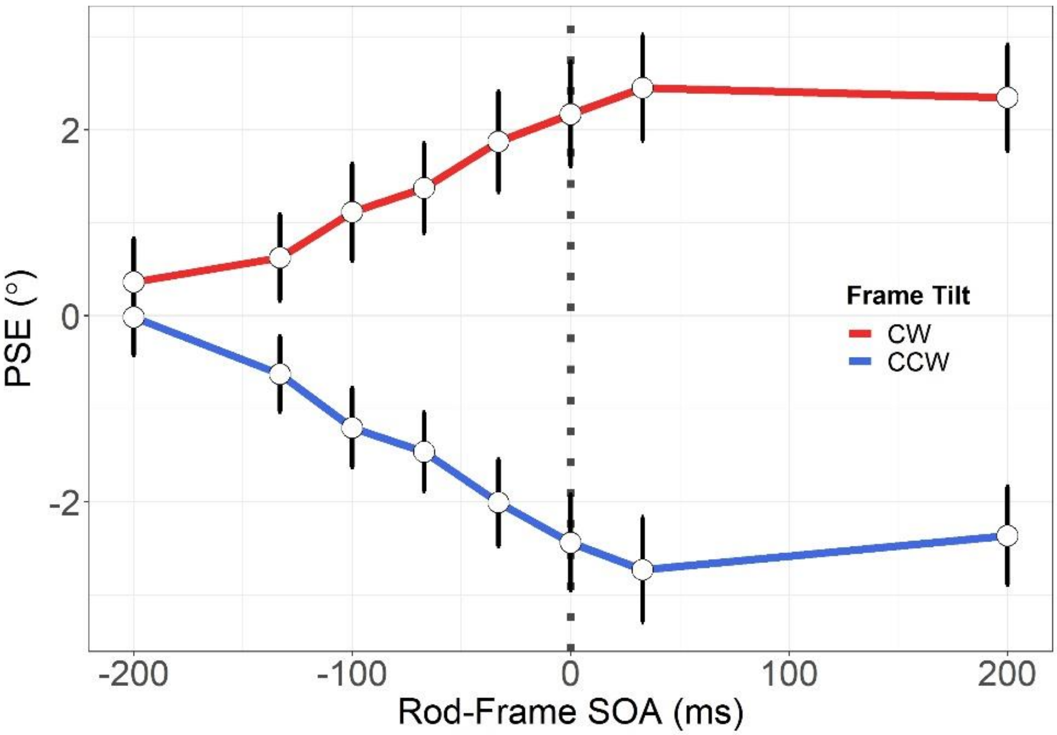


Figure 4: Mean point of subjective equality (PSE) for all participants at each SOA for both directions of frame tilt. A negative PSE indicates a CCW bias; a positive PSE indicates a CW bias. Error bars are +/– 1 SE

Table 1: Summary of experiment 1 results. Data reported as mean (*SD*). Boxed results denote RFI magnitudes that significantly differed from zero after Bonferroni correction; in all cases, p < .001. Note: although the 95% CI for –200 does not include zero, the adjusted p-value was greater than 0.05.

SOA	**PSE**		**RFI Magnitude**	**95% CI**
	CCW Frame	*CW Frame*		
–200	–0.12 *(1.75)*	0.31 *(1.97)*	0.43 *(0.66)*	[0.12, 0.74]
–133	–0.68 *(1.66)*	0.75 *(2.02)*	1.44 *(1.19)*	[0.88, 1.99]
–100	–1.19 *(1.82)*	1.06 *(2.25)*	2.25 *(1.91)*	[1.36, 3.15]
–67	–1.52 *(1.89)*	1.42 *(2.14)*	2.94 *(1.88)*	[2.06, 3.81]
–33	–2.08 *(2.11)*	1.92 *(2.42)*	4.00 *(2.44)*	[2.86, 5.15]
0	–2.46 *(2.30)*	2.25 *(2.38)*	4.71 *(2.64)*	[3.47, 5.94]
33	–2.79 *(2.37)*	2.40 *(2.47)*	5.19 *(3.05)*	[3.76, 6.62]
200	–2.49 *(2.36)*	2.37 *(2.54)*	4.86 *(2.94)*	[3.48, 6.24]

Figure 5 depicts a general trend for the RFI magnitude to increase with each SOA. To characterize the growth of the illusion over time, the RFI magnitude values were first submitted to a one-way repeated measures ANOVA with rod-frame SOA as the within-subject factor. Results are reported with Greenhouse-Geisser corrections as the assumption of sphericity was not met. There was a significant effect of SOA (F(1.88, 35.72) = 48.59, p < .001, η_g^2 = 0.36), suggesting that, indeed, the magnitude of the RFI differed between SOA levels. To estimate the initial onset of the illusion, the RFI magnitude at each SOA was compared to the magnitude at –200 ms, where no significant effect was observed. Even after correcting for multiple comparisons, the RFI magnitude was significantly larger at every SOA than it was at the –200 ms SOA. The fact that the magnitude of the illusion was already significant at the –133 ms SOA suggests that the initial effect of the tilted frame on subjective vertical probably occurred sometime earlier, between 200 and 133 ms before frame onset (a different set of SOAs was used in experiment 2, below, to better isolate this earliest effect). To determine when the illusion reached a plateau, the RFI magnitude at each SOA was compared to the magnitude at the 200 ms SOA. The RFI for the 200 ms SOA did not significantly differ from the 0 or 33 ms conditions, but it did significantly differ from each of the even earlier SOAs. Examining the pattern of mean RFI magnitudes (Table 1), these results suggest that the distortion of subjective vertical grew steadily with each SOA, reaching a plateau in the 0 ms condition, where it maintained a similar magnitude for the 33 and 200 ms SOAs.

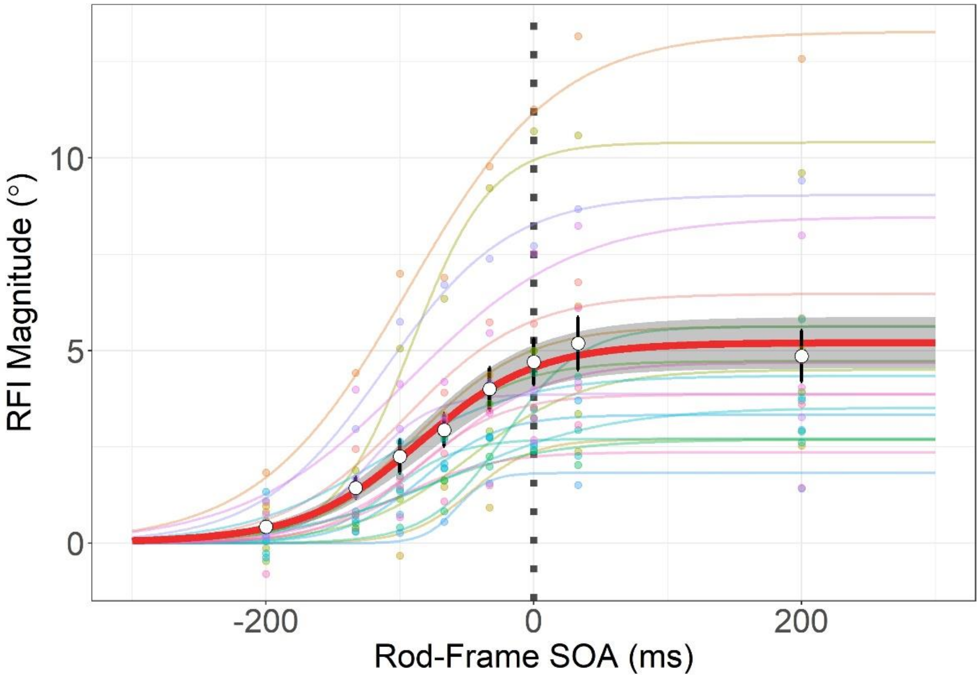


Figure 5: RFI magnitude as a function of rod-frame SOA. The RFI is the difference between PSEs of CCW- and CW-tilted frames (Figure 4). White circles are the mean RFI at each SOA. Data from individual participants are color coordinated. Error bars and shaded region are +/– 1 standard error.

For the analysis of RTs, we compared the mean response time of congruent trials (i.e., rod and frame tilted in the same direction) to incongruent trials (i.e., rod and frame tilted on opposite directions) at each SOA for each participant. The RT difference between congruent and incongruent trials was submitted to a one-way repeated measures ANOVA with rod-frame SOA as the within-subjects factor. The ANOVA was significant ($F(2.36, 44.76) = 5.13$, $p = .007$, $\eta_g^2 = .09$). After adjusting for multiple tests, the only significant pairwise comparison was between the –100 ms and 0 ms SOAs ($t(19) = –3.82$, *p.adj* = .032). Comparisons between the –100 ms SOA and the –67 ms (*p.adj* = .057), –33 ms (*p.adj* = .073), and 33 ms (*p.adj* = .078) SOAs trended toward significance, however. When compared against zero (i.e., no effect), only the 0 ms SOA condition neared significance $t(19) = 2.99$, *p.adj* = .06).

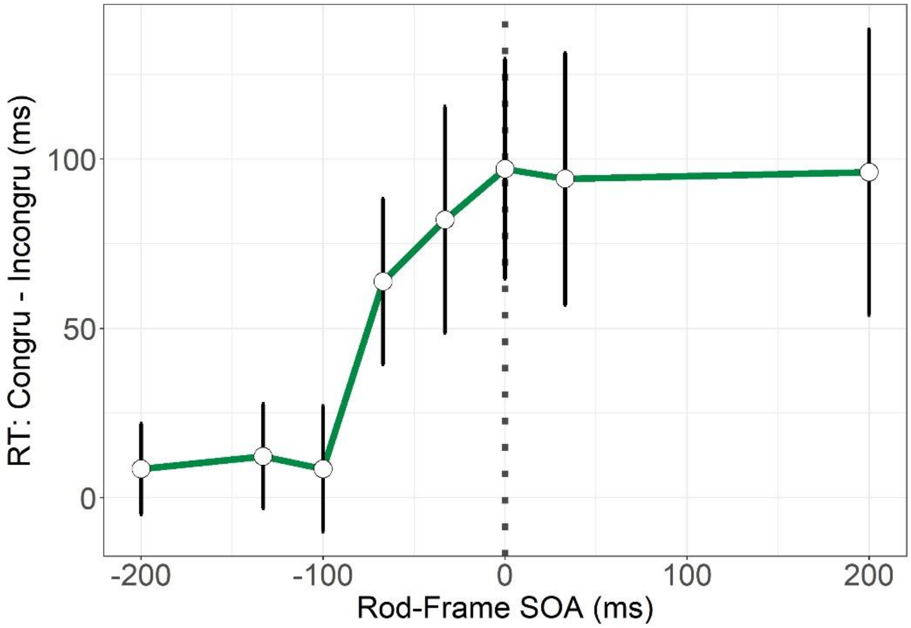


Figure 6: Mean RT difference between congruent and incongruent trials at each SOA. Error bars are +/– 1 SE.

Visually, the time course trends present in the RT differences (Figure 6) were similar to those in the RFI magnitude (Figure 5), though the statistical trends differed in important ways. The illusion as measured by the PSE was already significantly different from zero at –133 ms SOA; however, the RT difference did not change until the –67 ms SOA (even then, not significantly so). The effect measured by PSE was significant at every SOA greater than –200 ms, whereas the effect measured by RT only neared significance for the 0 ms SOA. Nonetheless, when comparing the individual differences in effect sizes across participants, there was a moderate positive correlation between the magnitude of the RT difference and the magnitude of the RFI such that larger RFI magnitudes were associated with larger RT differences between congruency conditions ($t(158) = 5.99$, $r = .43$, $p < .001$). This relationship suggested that those participants who were more susceptible to the tilted frame also tended to experience a greater contrast in difficulty between congruent and incongruent trials.

Discussion

The aim of this experiment was to provide a description of the time course by which visual context is integrated into the egocentric frame of reference. To do so, we used a modified version of the RFI in which subjective vertical was assessed with the perceptual judgment of a briefly flashed rod that was presented at various times with respect to the onset of the tilted frame. The perceived orientation of rods presented 200 ms before frame onset were not systematically affected by the direction of the frame’s tilt; conversely, the perception of rods presented 200 ms after frame onset demonstrated a full effect of the illusion. Between these extremes, the illusion grew in magnitude, with the earliest observable effect detected in the –133 ms SOA condition, and reaching a plateau for rods presented simultaneously with frame onset.

It is worth restating two points regarding the present methodology. First, the rod was only presented for ~5 ms and, in the negative SOA conditions, its visibility never overlapped with that of the tilted frame. Second, the frame orientation condition was randomly interleaved across experimental trials, making it impossible for participants to anticipate the direction of the frame's tilt on a given trial. Thus, finding that the perceived orientation of a rod was affected by a frame that appeared 133 ms later might seem somewhat paradoxical. We suggest that a differential latencies model offers a plausible explanation for these results.

Differential latency models rely on two canonical observations about cortical processing. First, distinct cortical regions specialize in the analysis of specific stimulus properties; for example, neurons in V4 and MT respond preferentially to color and motion, respectively. Second, these regions carry out their respective analyses in parallel. However, the latency with which a region receives its initial input and, subsequently, completes its analysis, varies depending upon the region's location within the visual processing hierarchy (Schmolesky, et al., 1998; Lamme & Roelfsema, 2000, Martin et al., 2019). The presence of these differential processing latencies has been offered to account for the perceived synchrony of physically asynchronous events (Bartels, & Zeki, 1998; Zeki, 2001). For example, to perceive that a change in the color of a stimulus had occurred simultaneously with a change in its direction of motion, the change in color must physically precede the change in direction (Moutoussis & Zeki, 1997; Arnold, 2005); the exact magnitude of this effect depends on other factors such as task and attention (Nishida & Johnston, 2002; Clifford, Arnold, & Pearson, 2003; Enns & Oriet, 2004). Although the present experiment was not concerned with the perceived simultaneity of the rod and the frame, differential processing latencies may still have perceptual relevance for our task.

Consider that the observed PSEs (Figure 4) do not correspond to the subjects' perceived vertical at the *precise* moment the rod was flashed; instead, the PSE more likely reflects the perception of vertical at the time the orientation judgment was made. These two events, the rod presentation and the orientation judgment, are separated in time by afferent and cognitive processing delays. During this intervening time, it is possible for another stimulus to appear and, subsequently, perturb the internal frame of reference. That is, although the rod was presented at a time when the representation of vertical was unbiased, the assessment of its orientation was completed at a time when the reference frame had become distorted. To the outside observer, it would appear as if the reported orientation of the rod was predictively affected by the perturbing stimulus. Specifically, a differential latencies account of our data suggests that the delay between the onset of the frame and its initial effect on subjective vertical is shorter than the delay between the presentation of the rod and the completion of the orientation judgment.

An illustration of this model is presented in Figure 7. The stages of processing associated with the frame are depicted in Figure 7 A. The onset of the tilted frame is followed by an afferent processing delay (t_{frame}) before it drives a change in subjective vertical (w_{frame}) as it is integrated into the egocentric frame of reference. We assume this bias does not occur instantaneously but unfolds over time. The onset of w_{frame} is defined by the initial distortion of subjective vertical; its offset is defined by the time when the distortion reaches a plateau.

Figure 7 B depicts the processing stages that take place during the rod orientation judgment. The presentation of the rod is followed by an afferent processing delay (t_{rod}) as well as a period during which the orientation judgment is performed (w_{rod}). Here, w_{rod} is depicted as a diffusion process, where the evidence required to complete the judgment is accumulated during a sampling window until a decision boundary is reached (Usher & McClelland, 2001; Gold & Shadlen, 2007; Ratcliff & McKoon, 2008). Although we did not set out to test any specific diffusion or race-to-threshold models, considering the decision process in these terms helps to interpret the current data. Once a decision is reached, efferent processes are initiated (t_{resp}), resulting in an overt response.

The interaction between these processes as they occur in three hypothetical trials is depicted in Figure 7 C. The orientation judgment of the rod presented in trial X is completed in temporal proximity to the initial distortion of perceived vertical (i.e., the beginning of w_{frame}), causing a small, observable effect in the perceptual report. This SOA, where we first detect the effect of the frame, represents the difference between the afferent processing delay of the frame (t_{frame}) and the latency with which the rod orientation judgment is completed ($t_{rod} + w_{rod}$). The earliest SOA where the RFI magnitude was greater than zero was the –133 ms condition. However, given that the –200 ms SOA trended on significance (and in light of results to be presented in experiment 2, below), it is reasonable to assume the earliest effect of the frame lies somewhere between the –200 ms and –133 ms SOAs. For convenience, we round this estimate to 150 ms. That is, $t_{frame} - (t_{rod} + w_{rod}) = -150$ ms.

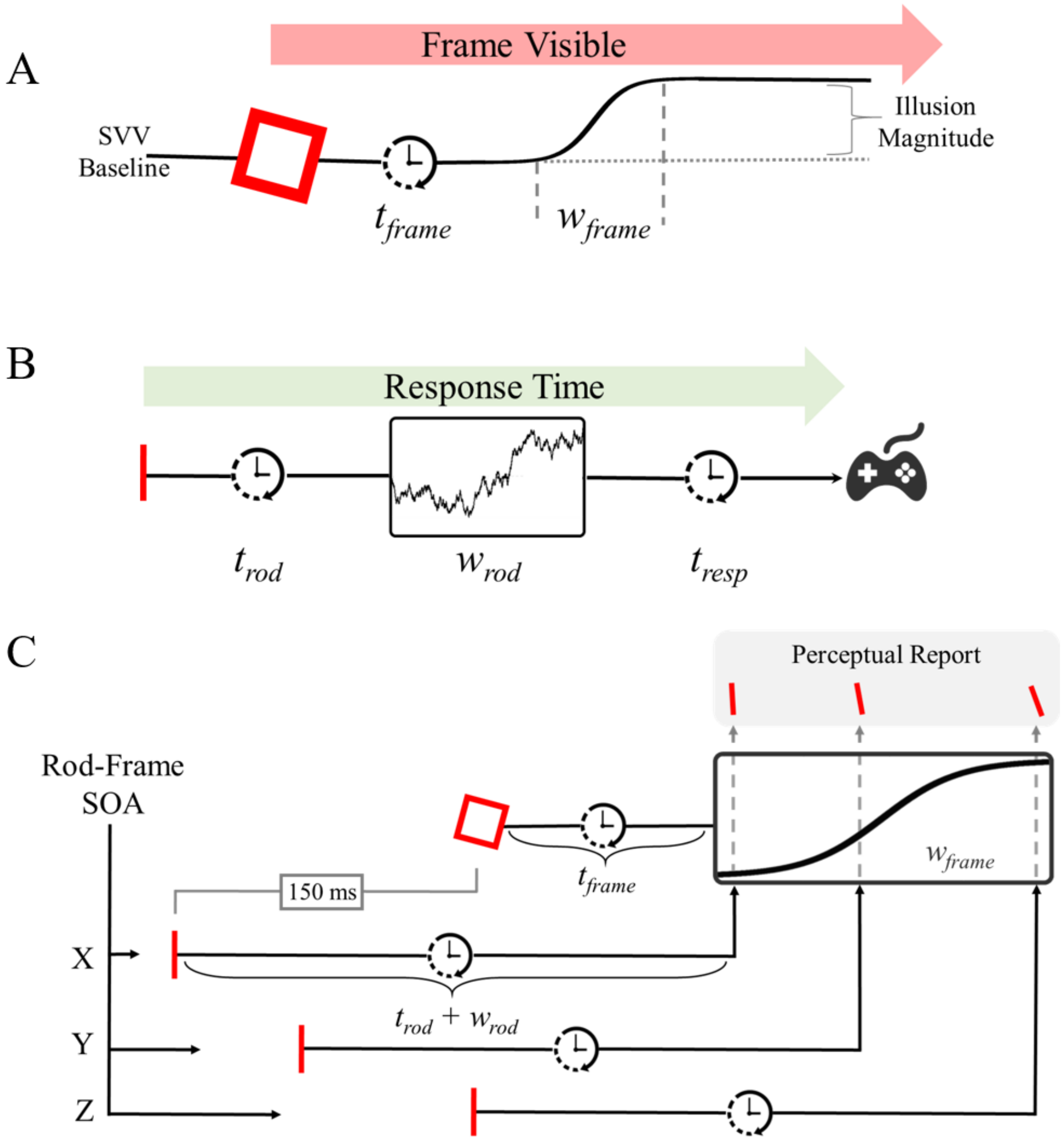


Figure 7: Relevant processing components for the frame (A) and the rod (B); see text for details (SVV: subjective visual vertical). C) Three trials with different SOAs (X, Y, Z). The delayed completion of the orientation judgment causes the rod to be compared (grey, dashed arrows) with subjective vertical at different points of its ongoing distortion (w_{frame}). Note: the rate of change in subjective vertical (w_{frame}) is hypothetical. Also, the magnitude of the bias depicted in the perceptual report has been exaggerated for illustrative purposes.

In trial Y, the rod is presented nearer (< 150 ms) to frame onset. The orientation judgment for this trial is completed at a time when the distortion of the reference frame has increased and causes a larger bias in the perceptual report. The orientation judgment of a rod presented simultaneously with the frame, as in trial Z, is completed at a time when the change in subjective vertical has reached a plateau; the perceptual report therefore demonstrates the maximum effect of the illusion. This delayed sampling of the change in subjective vertical, we propose, gives rise to the apparently predictive nature of the time course observed in this first experiment.

Within this framework, the magnitude of the RFI depends upon the extent to which there is temporal overlap between w_{rod} and w_{frame}; this degree of overlap was manipulated with the SOA condition. No effect of the tilted frame was observed when the rod was presented 200 ms before frame onset, indicating that the orientation judgment was completed while the reference frame was still unbiased (w_{rod} ended before w_{frame} began). On the other hand, the full effect of the illusion was observed when the rod was presented simultaneously with or after frame onset. In these cases, the orientation judgments were completed at a time after the egocentric distortion had reached its plateau (w_{rod} began after w_{frame} ended). Between these extremes, the orientation judgment (w_{rod}) overlaps with the ongoing distortion of the reference frame (w_{frame}). In these cases, the rod's orientation would be assessed within a reference frame that is partially distorted, which, we propose, leads to the intermediate RFI magnitudes observed between the –133 ms and 0 ms SOAs.

Our results suggest that the latency with which the tilted frame affects subjective vertical is shorter than the latency with which the orientation judgment is completed.

What factors might contribute to the temporal processing advantage of the frame? First, it is likely that low-level stimulus characteristics contributed to the differences in processing latencies. For example, the frame had a much greater surface area than the rod and therefore had a higher overall luminance. The frame was also visible for a longer duration than the rod. Increased luminance and duration have both been associated with faster reaction times (Raab & Fehrer, 1962; Hildreth, 1973, 1979; Pins & Bonnet, 1996) and therefore, presumably, faster processing times. Second, the frame was presented in the retinal periphery, where processing speeds have been demonstrated to be faster than in central vision, where the rod was presented (Carrasco, McElree, Denisova & Giordano, 2003). The increased processing speed in the retinal periphery is thought to be due to a greater ratio of M to P ganglion cells (Azzopardi, Jones, & Cowey, 1999); in macaque, the speed of conduction and integration along the magnocellular pathway has been demonstrated to be approximately 20 ms faster than the parvocellular pathway (Schmolesky et al., 1998). Finally, it is important to emphasize that the comparison of relevance is between the afferent processing delay of the frame (t_{frame}) and the latency of the rod orientation judgment ($t_{rod} + w_{rod}$). Thus, in addition to the afferent processing advantages of the frame (i.e., its luminance, duration, eccentricity), the decision component associated with the rod further increases the differential between the latencies relevant in the present task.

Our results contrast with the conclusions of Corbett et al. (2009), who reported that the frame is required to be visible for at least 800 ms to affect subjective vertical. We clearly observed an effect of the frame despite it never being visible for 800 ms prior to the presentation of the rod. Important methodological differences between our study and those of Corbett et al. caution against a direct comparison of our results. First, the frame used in our study was larger than that used by Corbett et al. (35.9° vs 12.4°, respectively). Frame size is thought to modulate the extent to which the illusion is driven by local contrast effects versus visuo-vestibular interactions (Ebenholtz & Benzschawel, 1977; Sigman, Goodenough, & Flannagan, 1978; Coren & Hoy, 1986; Antonucci et al., 1995). Thus, the time courses observed in our two studies may have been produced by a different weighting of these effects.

Second, the rod used by Corbett et al. (2009) was visible for 100 ms and appeared at one of two orientations (8° CW or CCW of vertical). The rod in our task was visible for ~5 ms and was usually oriented near the PSE, making the orientation judgment in our task more difficult. Both a shorter stimulus duration and increased task difficulty are associated with longer response times (Hildreth, 1979; Ulrich, Rinkenauer, & Miller, 1998). Indeed, the RTs in our study were ~200 – 300 ms longer than those reported by Corbett et al. Sequential sampling models of perceptual decision making suggest that the increase in RT associated with a difficult discrimination is driven by a longer period of evidence accumulation (Ratcliff & McKoon, 2008). A longer period of evidence accumulation in our study may have provided a longer window of opportunity for the frame to influence the orientation judgment, which would influence the time course we observed in the perceptual report.

A final distinction between our studies was the choice of outcome variable. While we used the PSE to measure the time course in the change of subjective vertical, the conclusions of Corbett et al. (2009) are based on RT differences between congruent and incongruent trials. Although we noted a general trend in the mean RT differences that was similar to the trend in RFI magnitude, the large amount of variability in RT limited our ability to make any confident comparisons between the two time courses. It is our position that the PSE offers a more suitable means to assess the time course of the change in subjective vertical, especially given these changes appear to be subtle and occur within a relatively narrow window of time.

In experiment 2, we test a prediction of our differential latency model. Specifically, that by increasing the latency with which the rod orientation judgment is completed, the observed time course should shift earlier in time, ahead of frame onset. That is, the first observable effect on subjective vertical should occur at an even earlier SOA than was observed in experiment 1.

Experiment 2

The differential latency model proposed to account for the results of experiment 1 suggests that the apparently predictive effect of the frame is due to a relatively shorter latency of the frame's initial effect on perceived vertical compared to the latency at which the rod orientation judgment is completed. Specifically, $t_{frame} - (t_{rod} + w_{rod}) = -150$ ms. A prediction of this model is that altering the afferent processing latency of the rod will shift the observed time course of the illusion. For example, reducing the afferent processing delay of the rod (i.e., t_{rod}) should decrease the duration by which the observed effect temporally precedes frame onset; that is, the observed time course would shift later in time, toward frame onset. Conversely, increasing the duration of t_{rod} should increase the duration by which the observed effect precedes frame onset and shift the time course earlier, away from frame onset.

One means of altering the processing time of a visual stimulus is to modify its luminance. Low luminance stimuli are associated with longer response times in both simple and choice reaction time tasks (Lappin & Disch, 1972; Pins & Bonnet, 1996). A portion of this additional response time is due to increased afferent processing time; the phototransduction of a low intensity stimulus occurs more slowly than for a high intensity stimulus (Kuffler, 1953; Lennie, 1981). Evidence from visual evoked potentials suggest that the delays incurred by low luminance stimuli extend beyond the retina and affect processing latencies throughout the visual hierarchy (Kammer, Lehr, & Kirschfeld, 1999; Brisson, Robitaille, & Jolicœur, 2007). Stimulus intensity does not appear to affect the latency of motor processes during response selection, however (Miller, Ulrich, & Rinkenauer, 1999).

In experiment 2, we test our differential latencies model by comparing the RFI time course for rods in high (5.8 cd/m^2) and low (0.3 cd/m^2) luminance conditions. Piéron (1914) described the relationship between stimulus intensity and RT as a power function, where low luminance stimuli are associated with longer RTs. Although initially defined for simple RTs, Pins and Bonnet (1996) demonstrated that Piéron's law also holds for a variety of choice RT tasks, including a line orientation judgment. Using the parameters fit by Pins and Bonnet (1996) to their orientation task, we estimated that the mean RT in our task would be 49 ms longer for the low luminance condition.

In addition to longer RTs, a reduction in rod luminance should produce specific effects in the RFI time course. Reducing the luminance of the rod should incur a longer period of afferent processing and thereby delay the completion of the orientation judgment. This, in turn, should augment the temporal disparity between ($t_{rod} + w_{rod}$) and

t_{frame}, shifting the time course away from frame onset (Figure 8). Specifically, we expected that the first observable effect in the low luminance condition would occur at an earlier SOA than the first observable effect in the high luminance condition. Because of the shifted time course, we also expected to observe a larger RFI magnitude in the low luminance condition for SOAs corresponding to the rising phase of the time course (e.g., –100 ms SOA).

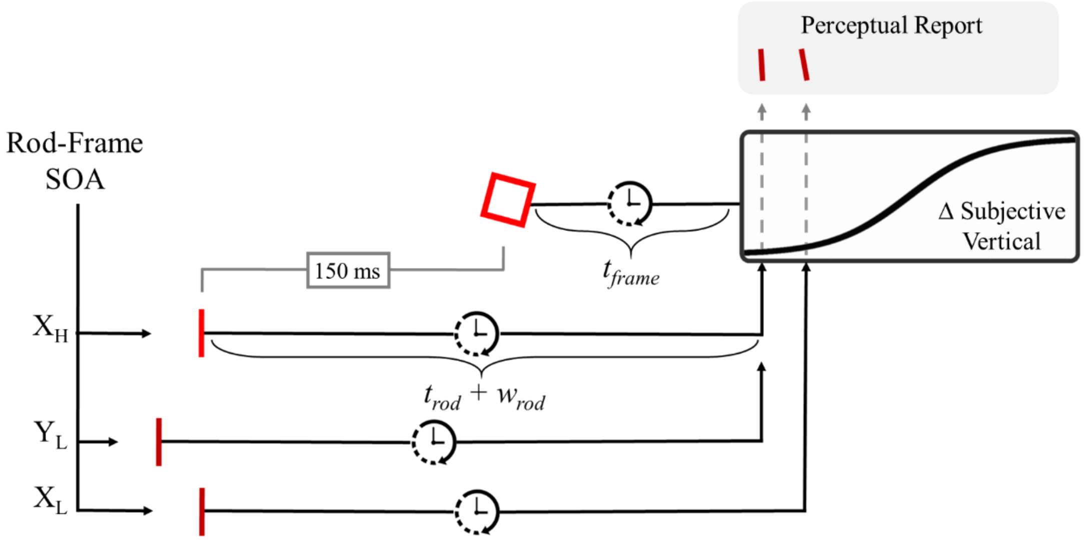


Figure 8: Model of predicted results for experiment 2. Compared to the high luminance condition (X_H), low luminance conditions (X_L, Y_L) are associated with a longer delay before completion of the orientation judgment. Our predictions for this experiment are 1) that the first observable effect will be earlier for the low than for the high luminance condition (X_H vs Y_L); and 2) for a given SOA between –133 and 0 ms, the low luminance condition will have a larger RFI magnitude than the high luminance condition (X_H vs Y_L).

Methods

Participants. Forty undergraduate students (M = 19.1, *SD* = 1.1 years; 21 women; 33 right handed) were recruited from the University of Oregon Human Subjects Pool to participate in this study, none of whom had participated in experiment 1. All participants had normal or corrected-to-normal vision and provided informed consent prior to their participation. The study lasted approximately one hour and thirty minutes. Participants were compensated with course credit for their time. All procedures were approved by the Institutional Review Board of the University of Oregon.

Apparatus & Stimuli. The apparatus used were identical to that of experiment 1. In addition to the stimuli described in experiment 1, a rod-luminance condition with two levels (high x low) was included. Luminance levels were measured with a chroma-meter (CS-100A, Konica Minolta). The rod in the high luminance condition was the same level of brightness as that in experiment 1 (5.8 cd/m^2); the rod in the low luminance condition was reduced by 95% (0.3 cd/m^2), but still above the threshold of detection.

Procedure. Trials in experiment 2 proceeded identically to those in experiment 1. As in experiment 1, the onset of the rod was varied with respect to the onset of the frame. To ensure that participants could complete the entire protocol within a reasonable amount of time, the number of levels in the rod-frame SOA condition was reduced from eight to six (–200, –150, –100, –50, 0, 100 ms). The orientation of the rod on each trial was determined using a staircasing procedure, as described for experiment 1. Two interleaved staircases were used for each frame tilt (CW, CCW) x rod luminance (high, low) x SOA (–200, –150, –100, –50, 0, 100 ms) condition; these conditions were randomly interleaved across experimental trials. The experiment concluded when 12 response reversals were recorded in each staircase. This resulted in participants completing, on average, 1095 (*SD* = 75) valid trials. Participants received a one-minute break after every 400 trials (participants could take additional breaks by delaying the button press that would begin the next trial).

Analysis. For each participant, the PSE in each frame tilt x rod-luminance x SOA condition was determined using eq. 1, fitting the parameters x_0 and k to the participants' responses in each frame tilt x rod luminance x SOA condition (data from the two associated staircases were pooled). The RFI magnitude was then determined for each SOA x rod-luminance condition by subtracting the PSEs of CCW- from CW-tilted frames. This produced two RFI time courses for each participant, one associated with each level of rod luminance. To characterize these time courses, a second logistic function was fit. The function took the following form:

$$f(x) = \frac{L}{1 + e^{-k(x-x_0)}} \qquad \text{eq. (2)}$$

here, x is the rod-frame SOA; x_0 is the inflection point of the sigmoid; k is the slope; and L is the upper asymptote, corresponding to the maximum illusion magnitude. Previous research demonstrated that altering the luminance of the RFI stimulus does not reduce the magnitude of the illusion (Nyborg, 1972, 1974). Therefore, we did not expect the parameter L to differ between high and low luminance conditions and so it was fit to both conditions simultaneously; that is, for a given participant, the value of L was the same for both the high and the low luminance conditions. A paired-samples t-test indicated that the RFI magnitude did not differ between high and low luminance conditions for the 100 ms SOA condition (mean difference = 0.07°, $t(39) = 0.46$, $p > .05$), supporting this analysis decision. Figure 9 depicts the results of this fitting procedure for a single participant.

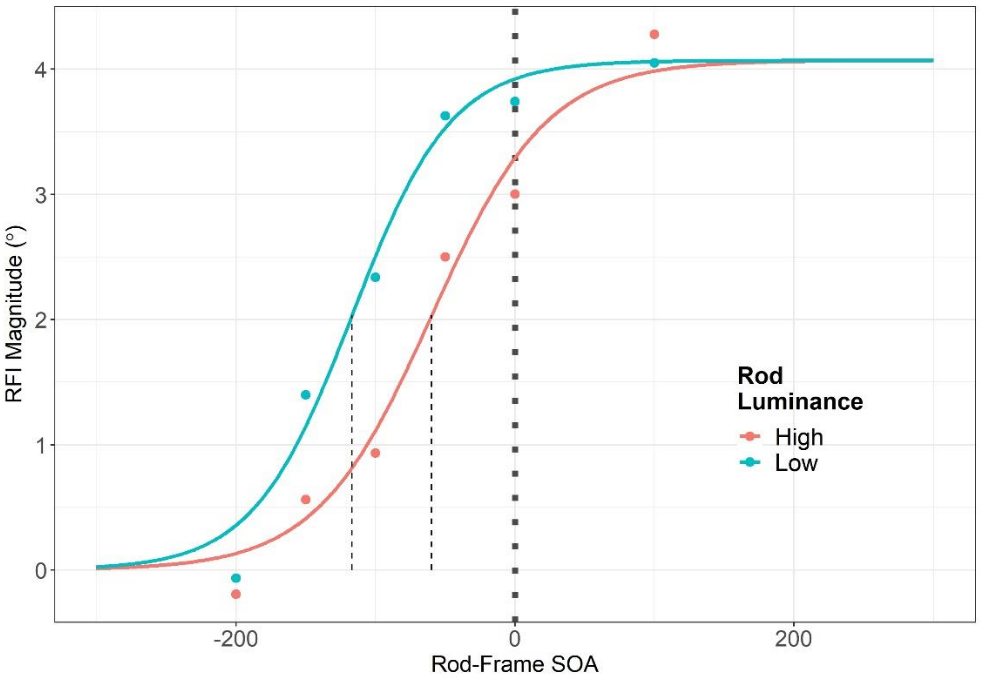


Figure 9: Sigmoids fit to the RFI time courses for high (orange) and low (turquoise) luminance conditions for a single subject. Short dashed lines indicate the midpoint (x_0) of each sigmoid. Here, the low luminance time course was shifted 57 ms earlier in time relative to the high luminance time course.

The parameters of equation 2 were fit using a custom least-squares optimization routine written in R (R Core Team, 2018). The quality of each fit was assessed by regressing the observed RFI magnitude at each SOA onto the magnitude predicted by the fitted model. Participants with an R^2 value less than 0.5 (corresponding to a *p*-value greater than 0.1) were removed from subsequent analyses. Rejected data were visually inspected to confirm the poor fit. Four participants were removed based on this criterion, leaving 36 participants for the final analysis. The removal of these data did not change the overall pattern of significance but allowed for greater confidence in our estimate of the difference between luminance conditions.

Results

We first tested whether the low luminance condition was associated with longer RTs, as predicted by the results of previous studies (Lappin & Disch, 1972; Pins & Bonnet, 1996). A paired samples t-test indicated that RTs for the low luminance condition were, on average, 33 ms slower than RTs for the high luminance condition (Low: *M* = 845.6 ms, *SD* = 117.9; High: *M* = 812.3, *SD* = 115.7; *t*(36) = 9.44, *p* < .001, 95% CI[26.1, 40.4]). Although this difference was in the predicted direction, the 95% confidence interval surrounding the estimate did not include 49 ms; this suggests the difference in RT between luminance conditions was smaller than that predicted by Pieron's law using the parameters determined by Pins and Bonnet (1996).

RFI values were then submitted to a two-way repeated measures ANOVA with SOA and rod luminance as within-subjects factors; Greenhouse-Geisser corrections were applied where the assumption of sphericity was not met. The main effect of SOA was significant (*F*(1.78, 62.17) = 154.1, *p* < .001, η_g^2 = .36). All pairwise comparisons of the RFI magnitude between levels of SOA were also significant. In addition, the RFI magnitude was significantly greater than zero at each SOA (Figure 10). Examining the pattern of means in Table 2 indicates that the perceived orientation of rods presented before frame onset were affected by the direction of the frame's tilt and that this effect grew in magnitude with each subsequent SOA. These results replicate the main findings of experiment 1.

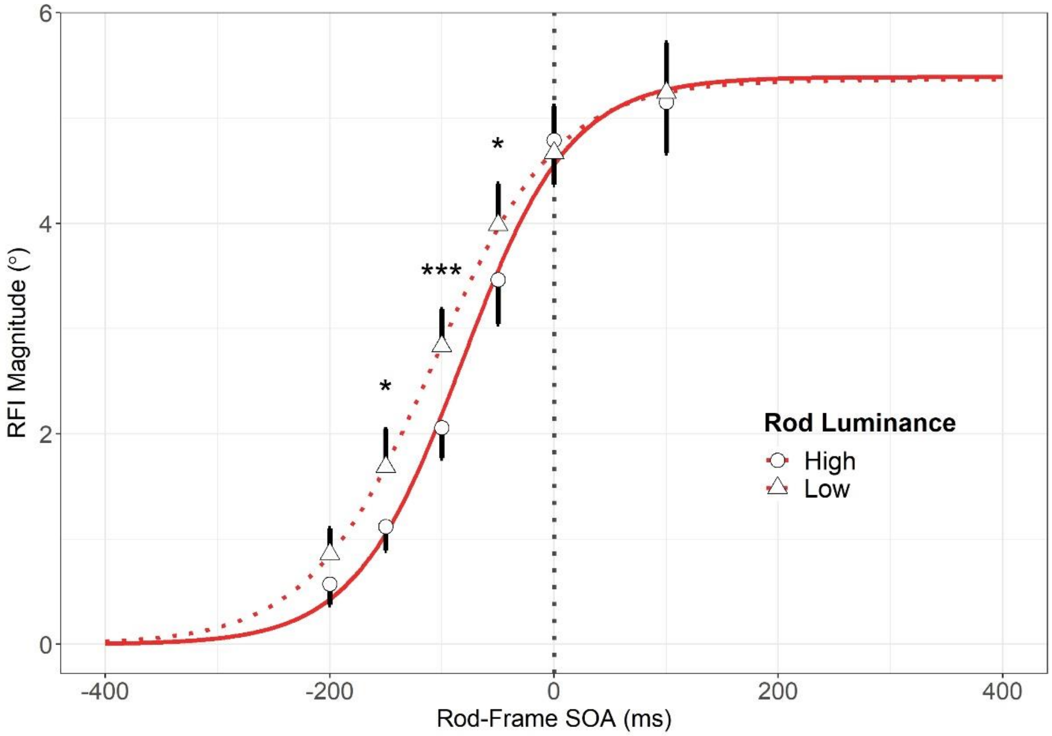


Figure 10: The RFI time courses for high (solid line, open circles) and low (dashed line, open triangles) luminance conditions. Asterisks denote significant differences in illusion magnitude between luminance levels for individual SOAs. Error bars are mean +/– 1 SE. To improve visibility, only the upper or lower extent of the error bars are depicted.

The main effect of rod luminance was also significant (*F*(1, 35) = 22.92, $p < .001$, $\eta_g^2 = .006$). The average RFI magnitude for the low luminance condition was larger than that for the high luminance condition (Low: $M = 3.21°$, $SD = 2.76$; High: $M = 2.86°$, $SD = 2.75$). In addition, the interaction between SOA and rod luminance was significant (*F*(3.60, 125.65) = 4.32, $p = .004$, $\eta_g^2 = .005$), suggesting the difference in illusion magnitude between luminance conditions depended on SOA. To characterize this interaction, the simple effect of rod luminance was assessed at each level of SOA. The effect of rod luminance was significant for the –150 ms SOA (*F*(1, 35) = 8.29, *p.adj* = .04, $\eta_g^2 = .03$), –100 ms SOA (*F*(1, 35) = 29.64, *p.adj* < .001, $\eta_g^2 = .04$), and the –50 ms

SOA ($F(1, 35) = 8.66$, $p.adj = .03$, $\eta_g^2 = .01$). In each case, the RFI magnitude was higher in the low luminance condition. The main effect of rod luminance was therefore largely driven by the differences in RFI magnitude at these SOAs.

Table 2: Summary of experiment 2 results. Data reported as mean (*SD*). All RFI magnitudes were significantly greater than zero. Boxes highlight SOAs where RFI significantly differed between high and low luminance conditions.

SOA	**High luminance**			**Low luminance**		
	PSE		**RFI Magnitude**	***PSE***		**RFI Magnitude**
	CCW tilt	*CW Tilt*		*CCW Tilt*	*CW Tilt*	
–200	–0.91 *(1.70)*	–0.33 *(1.64)*	0.57 *(1.19)*	–1.13 *(1.88)*	–0.27 *(1.55)*	0.86 *(1.43)*
–150	–1.08 *(1.84)*	0.04 *(1.61)*	1.12 *(1.38)*	–1.61 *(2.03)*	0.08 *(1.87)*	1.69 *(2.13)*
–100	–1.69 *(2.16)*	0.37 *(1.60)*	2.06 *(1.77)*	–2.17 *(2.11)*	0.67 *(1.75)*	2.83 *(2.09)*
–50	–2.43 *(2.18)*	1.04 *(1.88)*	3.46 *(2.53)*	–2.81 *(2.20)*	1.17 *(1.74)*	3.99 *(2.32)*
0	–3.19 *(2.33)*	1.60 *(1.66)*	4.79 *(2.55)*	–3.13 *(2.59)*	1.54 *(1.65)*	4.67 *(2.66)*
100	–3.41 *(2.51)*	1.74 *(1.84)*	5.15 *(2.88)*	–3.42 *(2.49)*	1.82 *(1.91)*	5.24 *(2.84)*

The results of the ANOVA suggest that the time course of the perceptual report was affected by rod luminance. To characterize the magnitude of this effect for each participant, sigmoidal functions (eq. 2) were fit to the RFI time courses associated with the high and low luminance conditions. Figure 9 depicts these fits for a single participant. Note that the inflection point of the sigmoid fit to the low-luminance condition was shifted earlier in time relative to the inflection point of the sigmoid fit to the high-luminance condition. Across all participants, the inflection points of the sigmoids fit to the low luminance condition were significantly lower (i.e., earlier in time) than those fit to the high luminance condition (Figure 11, top; mean difference = –24.5 ms, $t(35)$ =

5.32, *p* < .001, 95% CI [15.13, 33.78]). Compared to the time course associated with high luminance rods, the time course of low luminance rods was shifted earlier in time, away from frame onset. The slope of these sigmoids (as quantified by the space constant, *k* in eq. 2) did not significantly differ between luminance conditions (Figure 11, bottom; *t*(35) = –1.57, *p* = .13).

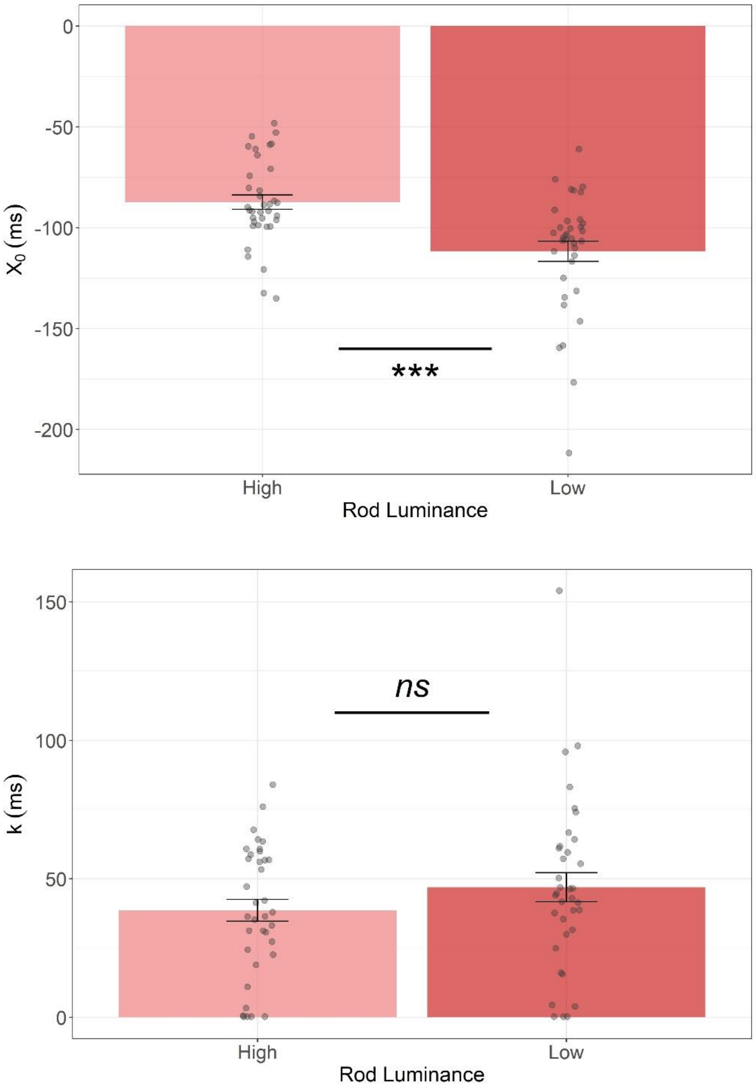


Figure 11: Top: the mean inflection point of the sigmoids fit to high and low luminance RFI time courses. Bottom: mean slope (as quantified by k in eq. 2) of the sigmoids fit to the RFI time courses (lower values of k indicate steeper change over time). Points are data from individual subjects; horizontal jitter was added to improve visibility. Error bars are +/– 1 SE.

It was interesting to note the similarity between the mean shift in time course (24.5 ms) and mean difference in RT (33 ms) between luminance conditions. A paired samples t-test suggested the two did not significantly differ ($t(35) = 1.8$, $p = .07$, 95% CI[–18.7, 1]). A correlation between the individual differences in the two measures trended on, but failed to reach significance ($t(34) = 1.9$, $r = .31$, $p = .06$). The direction of this relationship was such that participants who tended to exhibit a larger shift between the time courses also tended to have a larger RT difference between the luminance conditions.

Discussion

The results from this experiment replicated the main finding of experiment 1: the orientation judgment of rods presented before frame onset were affected by the direction of the frame's tilt. The differential latencies model proposed to account for this effect predicted that increasing the time dedicated to the afferent processing of the rod would augment the temporal disparity between the latency of the frame's effect on subjective vertical (t_{frame}) and the completion of the rod orientation judgment ($t_{rod} + w_{rod}$). Indeed, we observed that the RFI time course associated with the low luminance condition was shifted earlier from frame onset compared to the high luminance condition; the magnitude of the shift was ~25 ms. As further evidence of this shift, the magnitude of the RFI was larger for the low luminance condition at SOAs corresponding to the rising phase of the time course (i.e., –150, –100, –50 ms). The RFI magnitude did not differ between luminance conditions at SOAs where the effect of the frame was either very small (–200 ms) or reaching saturation (0 & 100 ms). Our prediction that the earliest observable effect in the low luminance condition would come at an earlier SOA than that for the high luminance condition was not borne out (the illusion magnitude was significantly greater than zero at all SOAs). However, given the significant shift of the low luminance time course, observing such a difference should be only a matter of testing the appropriate SOA.

The mean difference in RT between high and low luminance conditions was significantly smaller than that predicted by Pieron’s law and the parameters reported by Pins and Bonnet (1996) for their orientation judgment task. Although Pins and Bonnet examined a number of tasks that varied in complexity (e.g., semantic categorization, orientation discrimination, etc.), they did not explicitly test how their parameters might change with varying degrees of task difficulty. Their orientation task, for example, was to discriminate whether a line was tilted 45° CW or CCW from vertical. It is possible that the greater difficulty of our discrimination task (where the staircase procedure caused the tilt of most stimuli to be near the PSE) attenuated an effect that is more prominent when the discrimination is easier. A better description of Pieron’s law and its predictions for the present task requires a dedicated exploration that varies both rod orientation (difficulty) and luminance.

General Discussion

The aim of the experiments described in this chapter was to assess the time course by which visual context is integrated into the egocentric frame of reference. We used a modified version of the RFI in which participants judged the orientation of a rod that was briefly flashed at various times with respect to the onset of the tilted frame. This resulted in a surprising effect where the perceived orientation of a rod presented as much as 150 ms before the frame onset was affected by the direction of the frame's tilt. To account for these observations, we proposed a differential latency model where the latency between the presentation of the rod and the completion of its orientation judgment is longer than the latency between the onset of the frame and its initial effect on subjective vertical. In experiment 2, we tested a prediction of this model. By reducing the luminance of the rod, and thereby increasing the time devoted to its afferent processing, the RFI time course should shift further away from frame onset. Indeed, the results from experiment 2 demonstrated that, compared to the high luminance condition, the time course of the low luminance condition was shifted ~25 ms further away from frame onset.

In the discussion that followed experiment 1, several explanations were offered to account for the temporal processing advantage of the frame that allowed for its apparently predictive effect on the perceived orientation of the rod. A portion of this advantage is likely due to differences in low-level stimulus characteristics, including the higher luminance and longer visible duration of the frame (Raab & Fehrer, 1962; Hildreth, 1973, 1979; Pins & Bonnet, 1996). The frame was also presented in the retinal periphery, where speeded neuronal processing is facilitated along the magnocellular pathway (Azzopardi, Jones, & Cowey, 1999; Carrasco, McElree, Denisova & Giordano, 2003). Given these differences, we suspect that the afferent delay of the rod is longer than the afferent delay of the frame.

Perhaps the most important component that contributes to the differential latencies is the rod orientation judgment (w_{rod}). Although w_{frame} might be considered to serve a somewhat analogous role within the processing stream of the frame, there are important distinctions between the two processes. We assume that w_{frame} does not need to be completed (the illusion does not need to reach its maximum) before an effect on subjective vertical can be detected. This allows for partial distortions of the reference frame to be observed. The completion of w_{rod}, on the other hand, is synonymous with the completion of the orientation judgment; behaviorally (at least in the task presented here), we are unable to observe a "partial judgment." Thus, the tilted frame can begin to affect the orientation judgment as soon as its afferent processing is completed, whereas the orientation judgment is susceptible to interference until the decision window is closed.

We suggest that during the decision window (w_{rod}), the reference frame is sampled continually and an average of these samples is used to assess the rod's orientation. When the decision window overlaps with the ongoing distortion of the reference frame (w_{frame}), the result of such an averaging would be a dampened representation of the underlying change in the reference frame that occurred during the decision window. If this suggestion were correct, then the observed growth rate of the illusion (as depicted in Figures 5 & 10) would underestimate the true rate of change in perceived vertical during w_{frame}. Thus, the observed rate of change in illusion magnitude is susceptible to the duration of the decision window; a longer decision window would produce a flatter time course curve, whereas a shorter window would produce a steeper curve.

In sequential sampling models of perceptual decision-making, evidence accumulation continues until a decision threshold is reached (Huk & Shadlen, 2005; Ratcliff & McKoon, 2008). Increasing the difficulty of a judgment increases the duration of the sampling period because more evidence is required to reach the threshold (Ratcliff

& McKoon, 2008). In the present experiments, task difficulty was modulated by the degree to which the rod's orientation deviated from subjective vertical (and perhaps its luminance, see below). The time course that we reported (Figure 5) was based on the PSE, which, by definition, is the most difficult orientation to discriminate. It is possible that w_{rod} extended for a considerable duration post-stimulus. For example, Scharnowski et al. (2009) demonstrated that feature integration is susceptible to disruption by TMS for a period up to 400 ms post-stimulus.

For difficult orientation judgments, we suspect the decision window extended long enough post-stimulus such that it became susceptible to the effect of the tilted frame. Conversely, rods with a more obvious tilt (e.g., 8°) should be associated with a shorter decision window. Above, we offered this as one potential reason for the discrepancy between our results and those of Corbett et al. (2009). Within our own study, this raises the interesting possibility that the perception of rods with a more dramatic tilt were not affected by the tilted frame at the earliest SOAs; the ease of their discrimination may have allowed for sufficient evidence to be accumulated prior to frame onset. Because the response mode in the present experiment was categorical, we cannot estimate the illusion magnitude on a single trial and are therefore unable to examine this possibility.

It is reasonable to consider that decreasing the luminance of the rod would also increase task difficulty and thereby extend the duration of the decision window, w_{rod}. In turn, one might have predicted that the time course associated with the low luminance condition would be flatter (that is, have a lower slope, or a shorter space constant) than the time course for the high luminance condition. Although the slopes of the high and the low luminance time courses differed in the expected direction, this difference was not significant (Figure 11). It is possible that the luminance manipulation produced too subtle an effect to manifest a significant difference in slopes, given the statistical power of our test. Alternatively, it has been demonstrated that the duration of the sampling window can be adjusted to accommodate the features of the predominant target stimulus, such as its duration (Ossmy et al., 2013). It is possible that interleaving the luminance condition caused participants to adopt a sampling window duration that was a compromise between the optimal durations for the high and low luminance conditions. Had the luminance conditions been administered in a blocked design, we may have observed larger differences in the shape, and possibly the onset, of the time courses.

The relatively fast effect of the frame might seem somewhat surprising given the evidence that regions higher in the visual processing hierarchy (specifically, superior parietal lobule) play an important role in driving global orientation illusions such as the Roelofs effect (Walter & Dassonville, 2008) and the RFI (Lester & Dassonville, 2014). However, the fast processing of the frame is consistent with other studies that have reported rapid scene processing (Fei-Fei, Iyer, Koch, & Perona, 2007; Greene & Oliva, 2009), even when attention is otherwise directed (Groen, Ghebreab, Lamme, Scholte, 2015). It is possible that the frame begins to effect subjective vertical when its evoked activity reaches parietal cortex during the rapid forward sweep of visual information processing. The orientation of the rod might not become available for conscious scrutiny until after feedback from these higher cortical regions is received in regions lower in the visual hierarchy (Lemme & Roelofsema, 2000; Hochstein & Ahissar, 2002). Feedback to lower visual areas has been demonstrated to occur rapidly (Hupé et al., 2000) and global context manipulations, such as the Ponzo illusion, have been demonstrated to modulate the processing of stimuli in lower visual areas (Murray, Boyaci, & Kersten, 2006). The latency of the perceptual effect induced by the Ponzo illusion is consistent with the time course of feedback (Schmidt & Haberkamp, 2016). In the present task, the long sampling window associated with the difficult orientation discrimination may have allowed enough time for reentrant signals from parietal regions that carried the biasing effect of the frame to be established. This interpretation is compatible with the study of Lopez et al. (2011) who reported a modulatory effect of the frame on activity in temporo-occipital cortex that occurred ~75-105 ms after presentation of the rod. Importantly, this influence was present in activity that occurred prior to the orientation judgment, which the authors suggest occurred ~260-290 ms post-stimulus.

Sugita, Hidaka, and Teramoto (2018) described results similar to ours using the Poggendorff illusion (the apparent misalignment of two collinear lines when the segments are partially occluded by an intervening rectangle). These authors reported a perceived misalignment of the briefly presented segments even when the inducing rectangle appeared after the presentation of the segments. Sugita et al. (2018) attribute the effect they observed to an updating of the iconic memory of the line segments. These authors also demonstrated that this updating could occur in nonretinotopic coordinates, an observation consistent with other studies of visual integration (Noory, Herzog, & Ogmen, 2015; Wutz, Drews, & Melcher, 2016). This is an intriguing explanation and one not mutually exclusive with our own. The model we proposed to explain our results emphasizes the differential latencies between the afferent processing delay of the frame and the completion of the orientation judgment. We do not make specific claims about the representation that is judged, whether it is iconic or otherwise. It is possible we have articulated the temporal window during which the iconic memory of the rod is vulnerable to a subsequent distortion of global orientation. Nonetheless, this time course is still dependent upon the afferent delay of the frame and the rate of its distortion.

We have proposed that the increasing RFI magnitude across SOAs is the result of sampling the egocentric reference while the frame-induced distortion is ongoing. Alternatively, the apparent predictive effect of the frame may result from a binding error, such as those observed in rapid serial visual presentation paradigms (e.g., Intraub, 1985). According to this interpretation, although the rod was presented before the frame, it may have been incorrectly bound into the same perceptual representation. As the temporal gap between the presentation of the rod and the onset of the frame decreases, the likelihood that they are bound into the same percept increases. In this case, the RFI magnitude would index the relative frequency of binding errors at each SOA. This account implies that the effect of the frame is all-or-none. For example, should a rod be erroneously bound into the same percept as a frame that appeared 150 ms later, the perceived orientation of that rod would be fully biased (rather than partially, as we suggest). However, because a binding error at this SOA is sufficiently rare, the influence of this single trial would be diluted by averaging it with the greater proportion of trials in which the rod was not bound with the frame. Because participants did not make an analog assessment of the rod orientation, we are unable to estimate the perceived orientation of a rod on a single trial and cannot rule out this binding error account of our results.

A limitation of the present studies is that we cannot provide an estimate of the absolute duration of the frame's afferent processing delay (t_{frame}), only a relative estimate that it is ~150 ms faster than the latency with which the orientation judgment is completed (t_{rod} + w_{rod}). An estimate of when w_{rod} is completed would provide constraints for our estimate of t_{frame}. To address this limitation, future studies could be designed specifically with the aim of applying a sequential sampling analysis to the distribution of RTs. This would allow inferences to be drawn regarding the duration of each processing component that makes up the RT. Alternatively, a compelled response paradigm (Stanford, et al., 2010; Rüter et al., 2013) could be used to estimate the processing time dedicated to the orientation judgment. Adapting the procedure for EEG would provide a means to assess the neural correlates of the decision process with high temporal resolution.

Chapter III describes a modified version of the time course task. Rather than perform a categorical perceptual judgment of an oriented rod, however, participants estimated subjective vertical with a saccadic eye movement. Because we can rely on neurophysiological literature that has estimated the latency between the formation of a saccade goal and the initiation of the saccade, we will be better able to constrain our estimate of the afferent processing delay of the frame. In addition, the analog nature of this response mode will allow us to address other ambiguities inherent to categorical discrimination tasks.

CHAPTER III

ASSESSING THE TIME COURSE OF CHANGES IN SUBJECTIVE VERTICAL USING SACCADE ENDPOINT BIASES

As with the perceptual estimate of a target’s location, the accuracy of a motor estimate tends to be improved when the task is performed within a lighted environment and the target is embedded within a visual background (Conti & Beaubaton, 1980; Honda, 1999; Krigolson & Heath, 2004; Hay & Redon, 2006). Some of this improvement is thought to be due to the use of allocentric landmarks (Byrne & Crawford, 2010; Chen & Crawford, 2020) to create a more robust encoding of the target’s position (cf. Fillimon, 2015). In addition, a visual estimate of the effector’s location, if available, supplements the coarser spatial representations provided by proprioception and allows for increased precision in motor guidance (Ernst & Banks, 2002; McGuire & Sabes, 2009; Cameron, de la Malla, & López-Moliner, 2014). Finally, contextual visual information can be incorporated with vestibular and proprioceptive cues to estimate the body’s orientation in space (Dichgans & Brandt, 1974; Ebenholtz & Benzschawel, 1977; Sigman, Goodenough, & Flannagan, 1978; Mittelstaedt, 1983) which, in turn, influences the egocentric localization of objects (Matin & Fox 1989; Dassonville et al., 2004).

The time course by which visual information confers its benefit to motor guidance has often been studied using correction latency paradigms (Georgopoulos, Kalaska & Massey, 1981; Veerman, Brenner, & Smeets, 2008; Dotan et al., 2019). In these studies, a target (often a reach target) is displaced during an ongoing movement. When the direction of displacement is predictable, response times can be as fast as 110 ms (Soechting & Lacquaniti, 1983). As predictability decreases, response times become longer; for example, with 25% predictability, response times are closer to 210 ms (Boulinguez & Nougier, 1999).

Other studies have demonstrated that the displacement of visual landmarks or background stimuli also influence motor accuracy (Uchimura & Kitazawa, 2013; Fiehler, Wolf, Klinghammer, & Blohm, 2014; Klinghammer, Blohm, Fiehler, 2015). Such displacements have been reported to bias saccadic eye movements in as little as 150 ms (Chakrabarty, Nakano, & Kitazawa, 2017). In these cases, however, the effect of the displaced landmark was interpreted as occurring within an allocentric frame of reference. The time course by which changes in the visual background update the egocentric frame of reference and, in turn, affect motor guidance is less clear. The lack of clarity in this regard is, in part, due to a debate about whether motor estimates are in fact susceptible to such distortions.

When a visual background is misleading, as in various illusions, the perceptual estimate of a target's orientation or location demonstrate predictable biases. For example, in the rod-and-frame illusion (RFI; Witkin & Asch, 1948), a large frame that has been rotated from gravitational vertical causes the observer's perception of vertical to become biased in the direction of the frame's tilt. Consequently, a rod enclosed within the frame is perceived as being rotated in the direction opposite the frame's tilt. In a similar illusion, a large frame that has been offset to the left or right of the observer's objective midline biases the observer's perceived midline in the direction of the frame's offset (the

Roelofs effect; Roelofs, 1935). In turn, the perceived location of a target presented within the frame is biased laterally, in the opposite direction of the frame’s offset.

Despite these context-induced biases of perceived target orientation and position, actions directed toward the target are generally accurate. This apparent immunity of the motor system has been demonstrated for grasping movements directed toward the rod in the RFI (Dyde & Milner, 2002) and pointing movements directed toward targets surrounded by the Roelofs frame (Bridgeman, Peery, & Anand, 1997). This dissociation between perception and action was initially marshalled in support of the Two Visual Streams hypothesis of visual processing (Goodale & Milner, 1992; Milner & Goodale, 1995). According to this hypothesis, vision for action is processed along an unconscious dorsal stream that is immune to illusions, while vision for conscious perception is processed along an independent, illusion-prone ventral stream. Several studies have called this hypothesis into question, however (for reviews, see Schenk & McIntosh, 2010; Medendorp, de Brouwer, & Smeets, 2018).

An alternative account to the Two Visual Streams hypothesis was presented by Dassonville and Reed (2015) in what the authors referred to as the Two-Wrongs model. Briefly, if the location of a target is encoded within a distorted map of space, an action guided within that same map will reach the target accurately, as the errors that guide the action perfectly offset the errors of encoding. Consider the model as it applies to the RFI. A large frame rotated in the counterclockwise (CCW) direction biases an observer’s perception of vertical also in the CCW direction. A truly vertical line enclosed within this frame would be perceived as rotated in the clockwise (CW) direction. In order to align their hand with the perceived tilt of the rod, the observer must orient their hand to a position that is rotated slightly CW of subjective vertical; however, in this example, subjective vertical has been biased in the CCW direction. Thus, when the misperception of the rod's orientation is added to the misperception of vertical, the net result is a cancellation of errors and, ultimately, an accurate motor localization.

A test of the Two Visual Streams and Two Wrongs models can be conducted by asking participants to direct a movement toward perceived vertical (in the case of the RFI) or perceived straight ahead (in the case of the Roelofs effect). The Two Visual Streams hypothesis predicts that such estimates would be accurate. However, when the participant is required to align an outstretched hand (Li, Matin, Bertz, & Matin, 2008) or direct a saccade (Dassonville & Reed, 2015; Morgan, Grant, Melmoth, & Solomon, 2015) toward perceived vertical or straight ahead (Dassonville & Bala, 2004), the motor estimates are biased in the direction predicted by the frame's displacement. Moreover, the magnitude of a participant's perceptual bias has been shown to correlate with the magnitude of their motor bias (Dassonville et al., 2004; Dassonville & Reed, 2015), suggesting that the two forms of estimation rely on the same underlying frame of reference. This interpretation is in line with a common-coding theory of perception and action (Hommel, Müsseler, Aschersleben, & Prinz, 2001). Taken together, these results demonstrate the susceptibility of motor guidance to visual illusions that distort the egocentric frame of reference and lend support to the Two Wrongs model.

The studies reported in Chapter II used the RFI to investigate the time course by which contextual visual information is incorporated into the egocentric frame of reference. In these experiments, subjective vertical was assessed with a perceptual judgment of an oriented rod that was briefly flashed at various times with respect to the onset of a tilted frame. Of our results, most notable was the observation that the perceived orientation of rods presented prior to frame onset were affected by the direction of the frame's tilt. To account for these results, we proposed a model in which the latency between the presentation of the rod and the completion of its orientation judgment (t_{rod} + w_{rod}) is longer than the latency between the onset of the frame and its initial effect on subjective vertical (t_{frame}). Specifically, we estimated that $t_{frame} – (t_{rod} + w_{rod}) = –150$ ms.

While our model suggested a 150 ms difference between the afferent processing of the frame and the latency of the rod orientation judgment, our ability to estimate the absolute time dedicated to either process was limited. Consider what constraints can be placed upon our estimate of t_{frame}, the afferent transmission delay between the presentation of the frame and its initial effect on perceived vertical. A lower bound to the estimate is provided by the onset of the frame itself; the afferent processing of the frame cannot be completed instantaneously nor prior to the presentation of the frame. In Chapter II, rod orientation judgments that were biased by the tilted frame (even partially) had an average RT of 830 ms. For the frame to affect the orientation judgment, its afferent transmission must have been completed. Therefore, the manual RT provides an upper bound to the estimate of t_{frame}. However, because we were unable to dissect this response period into its constituent cognitive processes, we were unable to make a more precise estimate of t_{frame}. If it was known, for example, when during the course of the response time that the perceptual judgment of the rod's orientation was completed, an estimate of t_{frame} could be made.

The present experiment was intended to clarify some of the ambiguity remaining from Chapter II. The design of this experiment is conceptually similar to those described in Chapter II in that subjective vertical was assessed at various time points with respect to the onset of a tilted frame. Here, however, we replaced the perceptual estimate of subjective vertical with a motor estimate. The motor estimate took the form of a short, vertically directed saccadic eye movement that was initiated at various times with respect to frame onset (hereafter, the time of saccade onset relative to the time of frame onset will be referred to as the saccade-frame onset asynchrony) (Figure 12). Specifically, we sought to determine the time course by which the tilted frame affects subjective vertical by assessing the relationship between saccade endpoint bias and the duration of the saccade-frame onset asynchrony.

For our purposes, the appeal of using saccades as a response mode is that it allows us to reference the extensive neurophysiological literature of eye movements. For example, the physical initiation of a saccade lags the formation of its goal, constituting an efferent delay. The latency between the formation of a saccade goal in the frontal eye fields (Dassonville, Schlag, & Schlag-Rey, 1992) and the initiation of the movement toward that goal has been estimated to be ~30 ms (Robinson & Fuchs, 1969; Bruce, Goldberg, Bushnell, & Stanton, 1985). Following the conventions of our model (Chapter II, Figure 7), the efferent delay of the saccade will be referred to as t_{motor}.

We predicted that saccades initiated simultaneously with the frame or prior to its onset, would not demonstrate a systematic bias in their endpoints. In these cases, the saccade goal (formed ~30 ms prior to saccade initiation) would be formed within a frame of reference that had not yet been biased by the tilted frame. Saccade endpoints should remain unbiased for a period after frame onset, until the afferent processing of the frame is complete. After this point, the frame will begin to distort the egocentric reference, and saccade goals formed during this time will reflect that bias. Thus, the shortest saccade-frame onset asynchrony interval for which the saccade endpoints significantly differ between CW- and CCW-tilted frame conditions represents the combination of the afferent processing latency of the frame plus the efferent processing latency of the saccade ($t_{frame} + t_{motor}$). Using the efferent latency cited above (t_{motor} = ~30 ms) will allow us to make a more refined estimate of the afferent processing delay of the frame.

Methods

Participants. Twenty-two undergraduate students (M = 19.3 years, *SD* = 1.4; 14 women; 19 right-handed) were recruited from the Human Subjects Pool at the University of Oregon to participate in this study. All participants had normal or corrected-to-normal vision and provided informed consent prior to their participation. The study lasted approximately one hour and thirty minutes. Participants were compensated with course credit for their time. All procedures were approved by the University of Oregon Institutional Review Board.

Apparatus. The experiment took place in a small testing room (250 x 160 x 300 cm). Aside from the visual stimuli presented during the course of the experiment, the room was completely dark, with wall, ceiling and objects within the room either painted black or draped in black cloth. Participants were seated approximately 86 cm from a flat, semi-translucent screen (137 x 102 cm; Polacoat Ultra projection screen with a DA-100 diffusion coating, Da-Lite, Warsaw, IN, USA) on which visual stimuli were back-projected (60 Hz retrace rate; Electrohome Marquee 8500 CRT, Niagara Falls, Ontario, CAN). The experimental procedure was programmed using Experiment Builder (SR

Research, Kanata, ON, CAN), which ran on a host computer that controlled the presentation of visual stimuli. A forehead and chin rest were used to stabilize the head. Eye position was monitored throughout the experiment using an eye tracker in a tower configuration (EyeLink 2000, SR Research, Kanata, ON, CAN). The location of the eye was sampled at 1000 Hz. The velocity and acceleration thresholds for saccade detection were set to 30°/s and 8000°/s/s, respectively. Eye tracker calibration was established at the beginning of the session for each participant and maintained for the duration of the experiment. If calibration drifted, the researcher suspended the experiment and initiated a recalibration protocol. Participants used a handheld gamepad controller (SideWinder, Microsoft Corp.) to interact with the experiment (e.g., trial initiation, response submission).

Stimuli. All visual stimuli were red (RGB [255, 0, 0]). Prior to the start of each trial, a circular fixation point (0.5° diameter) with a black pinhole center was presented centrally and at eye-level. Participants initiated each trial by directing their gaze to the fixation point and pressing a button on the gamepad controller. After a variable delay, a response circle (6.8° radius, 0.3° stroke width) appeared surrounding the location of the fixation point. The fixation point was extinguished simultaneously with the appearance of the response circle. The appearance of the response circle/disappearance of the fixation point served as a “go-signal” for the participant to initiate a saccade directed to the topmost point of the response circle. A large square frame (35.9° side length; 1° stroke width) was presented at various delays with respect to the delivery of the go-signal such that the saccade was initiated before or after its appearance (Figure 12). On a given trial, the frame could appear in one of three orientations: upright, rotated 15° CW or 15° CCW from vertical. The frame remained visible until the end of the trial, at which time it was replaced with an upright frame of the same dimensions for 500 ms, so as to prevent possible carryover effects of the tilted frame between trials.

Auditory feedback was provided to inform the participant whether their response had been submitted successfully or the trial had been rejected. A trial was rejected if a saccade or blink was detected prior to or less than 150 ms after the delivery of the go-signal or if the gaze location at the end of the trial deviated more than 2° above or below the response circle. Rejected trials were reattempted later in the experiment. No feedback was given regarding the directional accuracy of the participant's response.

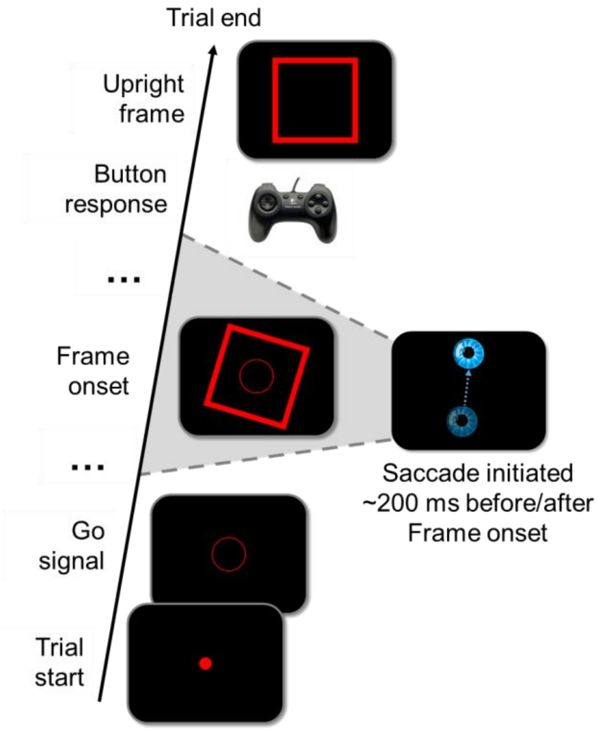


Figure 12: Procedure for saccade task. At the beginning of each trial, the participant directed their gaze to the fixation point. After a variable delay, the go-signal was delivered, instructing participants to initiate their saccade. Frame onset was varied with respect to the go-signal such that the saccade was initiated within a temporal window that extended ~200 ms before and after frame onset. The participant then used the gamepad to submit their response. After which, an upright frame was displayed for 500 ms. Note: figure not drawn to scale.

Procedure. The participant's task in this experiment was to perform a cued saccade from the central fixation point to the top of the surrounding response circle. The "top" of the circle was described to the participant as the location of 12 o'clock, if the response circle were a clock face and, thus, aligned with gravitational vertical. Participants completed a block of 15 practice trials prior to beginning the experimental block. Practice trials were identical to the experimental trials with the exception that only upright frames were presented.

At the beginning of each trial, only the fixation point was visible. Participants initiated the trial by directing their gaze to the fixation point and pressing a button on the gamepad controller. After a variable delay (500-1000 ms), the fixation point disappeared and, simultaneously, the response circle appeared; this served as the go-signal to initiate the saccade. Participants then made a saccade to the top of the response circle. To allow for small corrective saccades, the number of saccades the participant could perform during a single trail was not restricted. When the participant was satisfied with their response (that is, when they were satisfied that their eyes were pointed at the top of the response circle), they pressed a trigger button on the gamepad to end the trial.

On each trial, a large frame (CW-, CCW-tilted, or upright) appeared and remained visible until the participant submitted their response. The appearance of the frame was varied with respect to the delivery of the go-signal such that the saccade would be initiated within a 400 ms interest period that extended from 200 ms before to 200 ms after frame onset. The interest period was divided into 13 epochs of 33 ms; the experiment concluded when the participant completed 15 trials within each epoch for each frame tilt condition (CW-, CCW-tilted, and upright), resulting in 585 valid trials. Because saccade reaction times have inter- and intra-subject variability, a running average of the participant's saccade latency over the previous ten trials was used to adjust the time that the go-signal was delivered and increase the likelihood that a saccade would be initiated within the targeted epoch.

Analysis. Data from all participants were concatenated in DataViewer (SR Research, Kanata, ON, CAN) and a saccade report was generated wherein each row contained data pertaining to a single saccade. Subsequent parsing, cleaning, and analysis were performed with custom routines written in R (R Core Team, 2018). Practice and aborted trials were removed. Trials that contained a blink (1%) were also removed. Saccades were indexed according to the order in which they occurred during the trial (i.e., primary, secondary, tertiary, etc.); saccades that did not leave the fixation window or that ended after the button press to terminate the trial were ignored. Next, the primary reaction time (RT) for each trial was defined as the latency between the go-signal and the onset of the primary saccade; the latency between the go-signal and a given saccade was defined as the saccade RT. Thus, while a trial may have multiple saccade RTs, it only had one primary RT. Trials in which the primary saccade reaction time was less than 150 ms or longer than 600 ms were removed. The saccade-frame onset asynchrony was then calculated for each saccade by subtracting the time of frame onset from the time of saccade onset. Saccades initiated before frame onset had a negative saccade-frame onset asynchrony; saccades initiated after frame onset had a positive asynchrony.

Saccade endpoints were then converted into polar coordinates, with the origin set to the fixation point and zero degrees aligned to vertical. Saccade endpoints that deviated to the left (i.e., CCW) of vertical were coded as negative; endpoints that deviated to the right (i.e., CW) were coded as positive. To correct for idiosyncratic biases in saccade endpoint error, a baseline accuracy was calculated for each participant using the mean endpoint error of all trials in which the saccade was completed prior to frame onset (across participants, the mean baseline accuracy was near vertical, M = –0.6°, *SD* = 4.9°). The baseline for each participant was then subtracted from the endpoint of every saccade in their dataset.

Next, saccades were binned according to their saccade-frame onset asynchrony (bin width = 50 ms). To ensure subsequent analyses were based on a sufficient number of observations, only bins containing at least 1000 observations (across all participants) were included. This resulted in an analysis window that extended from 200 ms before to 350 ms after frame onset. Finally, outliers were identified using an inter-quartile range rule, applied to each frame tilt condition. Saccade endpoints that fell below the first quartile or beyond the third quartile by a magnitude greater than 1.5 times the inter-quartile range were considered outliers and removed. In total, this cleaning process removed 12.7% of trials. The frequencies of the remaining saccades in each of the frame conditions are summarized in Table 3.

Table 3: Frequency table. Trials varied in terms of frame tilt condition and the number of saccades performed by the participant.

	# saccades per trial			
Frame Tilt	1	2	3+	**Total**
CCW	2964	2202	237	5403
CW	3096	2026	240	5362
Upright	3016	2120	232	5368
Total	9076	6348	709	**16133**

To characterize the trends in saccade bias across saccade-frame onset asynchronies, data from each frame tilt condition were fit with a loess regression (Cleveland, 1979) (Figure 13). A benefit of the loess analysis is that it does not require an a priori assumption about the underlying structure of the data. The loess regression uses a sliding smoothing window, where the estimated saccade bias for a specific saccade-frame onset asynchrony is a function of the observations neighboring that point. Neighboring data are weighted according to a tricubic function such that neighbors that are more distal carry less weight in the estimate. The smoothing parameter α (or span), adjusts the number of observations to be included in the smoothing window. A higher α value produces greater smoothing. Although an appropriate span is often selected via subjective visual assessment (Cohen, Cohen, West, & Aiken, 2013), the span for the current analysis was chosen using the following method. Loess regressions were iteratively fit to the data with span size increasing upon each iteration; the initial span was set to 0.05 and increased by steps of 0.05 to a maximum of 1.0. The residuals of each fit were plotted against the corresponding span, resulting in a pattern that resembled a logarithmic growth curve. The inflection of this curve corresponded to a span of 0.4, representing a reasonable compromise between faithfully capturing tends in the data while avoiding under- or overfitting. Figure 13 depicts the fitted loess lines overlaid upon the average saccade endpoint (bin size = 10 ms) as a visual confirmation of the quality of this fit.

Results

The mean primary RT was 246 ms (*SD* = 70 ms). On average, primary RTs for saccades initiated before frame onset were 19 ms shorter than saccades initiated after frame onset (pre-frame: *M* = 237 ms, *SD* = 59 ms; post-frame: *M* = 256, *SD* = 78 ms); this difference was significant ($t(12039) = 15.8$, $p < .001$, 95% CI[17.2, 22.1]). The fact that saccades with longer RTs were more likely to occur after frame onset is not altogether surprising, given the positive skew to RT distributions. (An assessment of the relationship between saccade RT and saccade bias is included below.) For saccades initiated after frame onset, RTs did not vary between frame tilt conditions ($F(2, 7196) = 0.44$, $p > .05$). Other saccade metrics, including duration ($t(12150) = –0.5$, $p > 0.5$), amplitude ($t(12150) = –1.3$, $p > 0.5$), peak velocity ($t(12150) = –1.1$, $p > 0.5$), and time of peak velocity ($t(12150) = –1.0$, $p > 0.5$), were not related to saccade-frame onset asynchrony.

The primary results of this experiment are depicted in Figure 13, showing the saccade bias as it related to the saccade-frame onset asynchrony. This analysis included all saccades (primary, secondary, etc.). Loess lines were fit to the saccade bias within each frame tilt condition, and overlap between the 95% confidence intervals surrounding each fit was used to assess when the curves for CW- and CCW-tilted frames significantly diverged from one another. As expected, saccades initiated prior to frame onset were not affected by the frame tilt condition; this was also true for saccades initiated in the 100 ms immediately following frame onset. The confidence intervals for the curves fit to CW and CCW frame conditions no longer overlapped beginning with saccades that were initiated 100 ms after frame onset. After this time, saccade bias continued to grow. Saccades in the CW-tilted frame condition became progressively more biased in a CW direction; the CCW-tilted frame biased saccades further CCW. Beginning with saccades initiated ~200 ms after frame onset, there was a general tendency for saccade endpoints, regardless of frame condition, to deviate in a CCW direction; this trend appeared to be driven by a CCW bias in the corrective saccades (see below). Figure 14 depicts curve fits for CW and CCW frame conditions after subtracting the trend for the upright frame condition. After ~200 ms, a stable difference was maintained between frame tilt conditions.

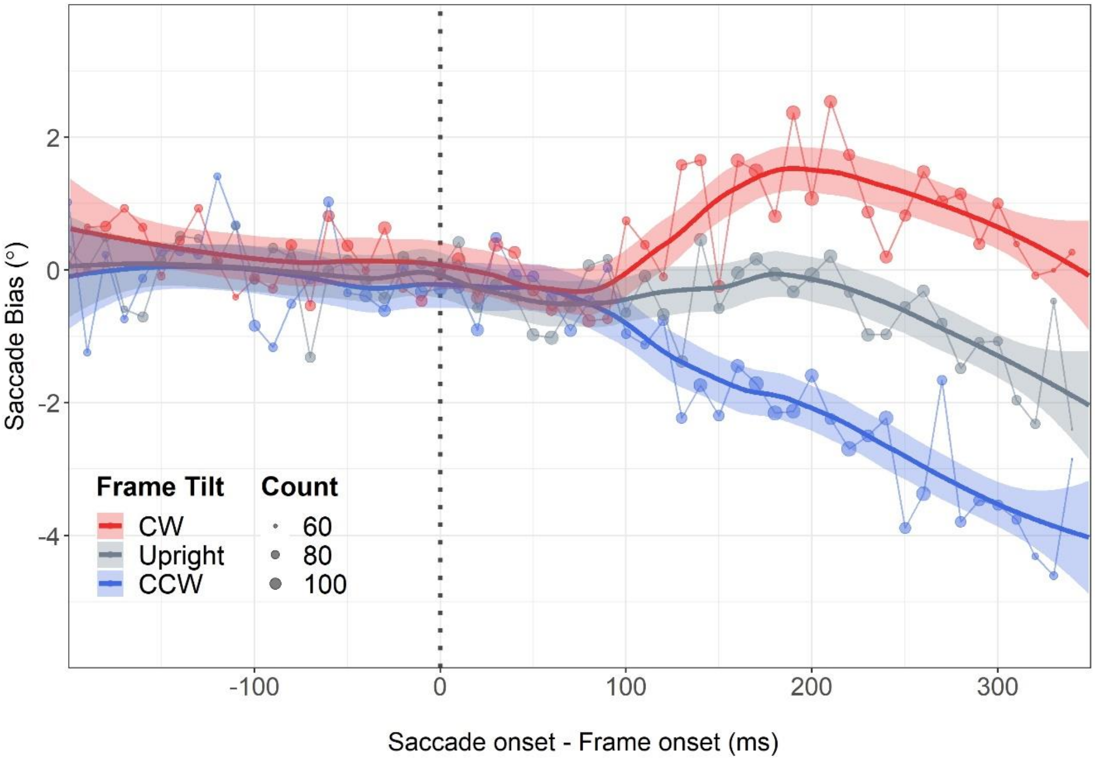


Figure 13: Loess regressions fit to saccade bias as a function of saccade-frame onset asynchrony. Data points are the averaged saccade bias within 10 ms bins. The size of the data point represents the number of observations within the corresponding bin. Note: loess regressions were fit to disaggregated data. Shaded regions are 95% CI.

To supplement the loess analysis, saccades initiated after frame onset were selected and binned according to saccade-frame onset asynchrony (bin width = 10 ms). Within each bin, the saccade endpoints for CW- and CCW-tilted frame conditions were compared using a one-tailed Welch two-sample t-test. After correcting for multiple comparisons, the first saccade-frame onset asynchrony bin to be significantly different between frame conditions was at 130 ms (*t*(194.9) = –5.2, *p.adj* < .001). With one exception (150 ms), comparisons between frame-tilt conditions remained significant for every bin after 130 ms.

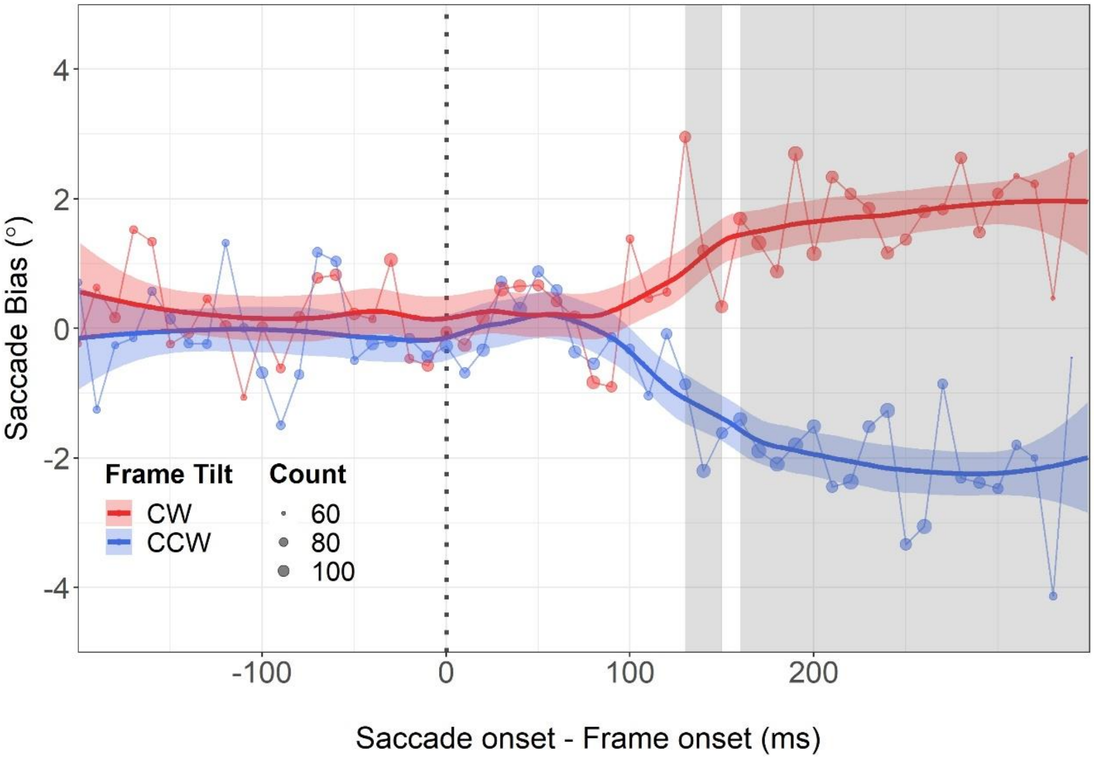


Figure 14: Saccade bias for CW- and CCW-tilted frames after subtraction of the upright frame condition. Grey shading indicates saccade-frame onset asynchronies where saccade biases within 10 ms bins significantly differed between frame conditions (after Bonferroni corrections). Individual data points follow conventions in Figure 13.

Previous studies have suggested a relationship between saccade RT and illusion susceptibility (de'Sperati & Baud-Bovyvan, 2008; van Zoest & Hunt, 2011; see also, de Brouwer, Brenner, Medendorp, & Smeets, 2014). The direction of this relationship is unclear, however. Some studies have indicated that saccades with shorter RTs are less susceptible to illusions and their endpoints are more accurate (de'Sperati & Baud-Bovyvan, 2008). Others studies have suggested the opposite, that short latency saccades are more illusion-prone than longer latency saccades (de Gave & Bruno, 2010; Zoest & Hunt, 2011). Still others found no relationship between saccade RT and illusion magnitude (e.g., Massendari, Lisi, Collins, & Cavanagh, 2018). As noted above, we observed that longer RTs were associated with larger (i.e., positive) saccade-frame onset asynchronies. Therefore, we wanted to assess whether saccade RT could account for the magnitude of saccade bias.

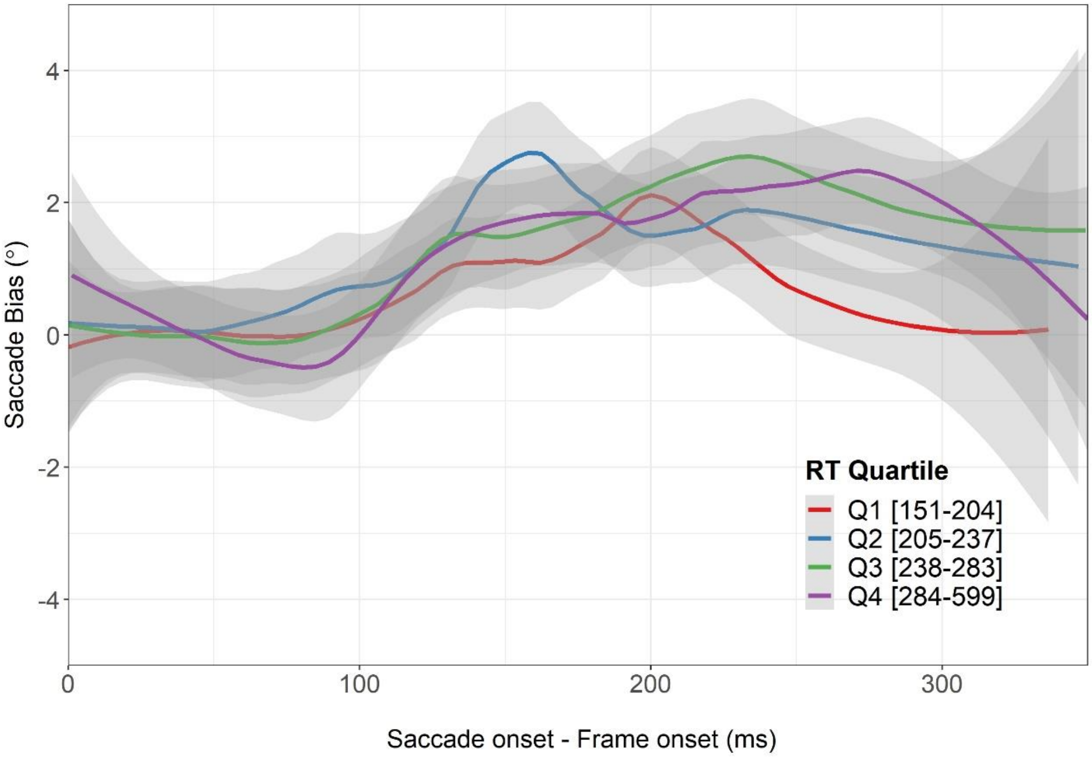


Figure 15: Data were segmented according to a quartile split of primary RT. Saccade bias across saccade-frame onset asynchronies were then plotted for each quartile. Note: saccade bias for the CCW-tilted frame condition was inverted.

For this analysis, only primary saccades that were performed after frame onset were included. To obtain a measure of illusion magnitude that was independent of frame tilt, the saccade endpoints in the CCW frame condition were reflected over the vertical axis. Trials were then grouped according to a quartile split of primary saccade RT. The relationship between saccade bias and saccade-frame onset asynchrony for each quantile is plotted in Figure 15. Data were segmented into 10 ms bins and an ANOVA compared the saccade bias between RT quartiles within each bin. After correcting for multiple comparisons, only the bin corresponding to saccades initiated 240 ms after frame onset trended on significance (*F*(3, 120) = 4.9, *p.adj* = .09). Thus, there is no evidence to suggest that saccade RT affected saccade bias in the present task.

Finally, we wanted to assess the role of corrective saccades. This analysis was limited to primary and secondary saccades. The mean latency between a primary saccade and its corrective saccade was 229 ms (*SD* = 83). Figure 16 A and B depict the saccade bias as a function of saccade-frame onset asynchrony for primary saccades and secondary saccades, respectively. It is interesting to note that, for primary saccades, the difference in saccade bias between frame tilt conditions drops off for saccades initiated ~300 ms after frame onset. Our analysis above suggests this reduction in illusion magnitude is not a consequence of saccade RT, but may instead be due to the visible duration of the stimulus itself (de Brouwer, et al., 2014). This collapse in illusion magnitude is not visible in Figures 13 & 14 because those analyses combined primary and secondary saccades. Secondary saccades initiated at 300 ms were still affected by the tilted frame (Figure 16 B) and served to maintain the steady difference between frame conditions as depicted in Figures 13 & 14. Interestingly, the endpoints of secondary saccades had an overall CCW bias compared to baseline accuracy. Thus, it is likely that the CCW trend present in Figure 13 can be accounted for by the CCW bias in corrective saccades; the reason for this bias in secondary saccades is unclear, however.

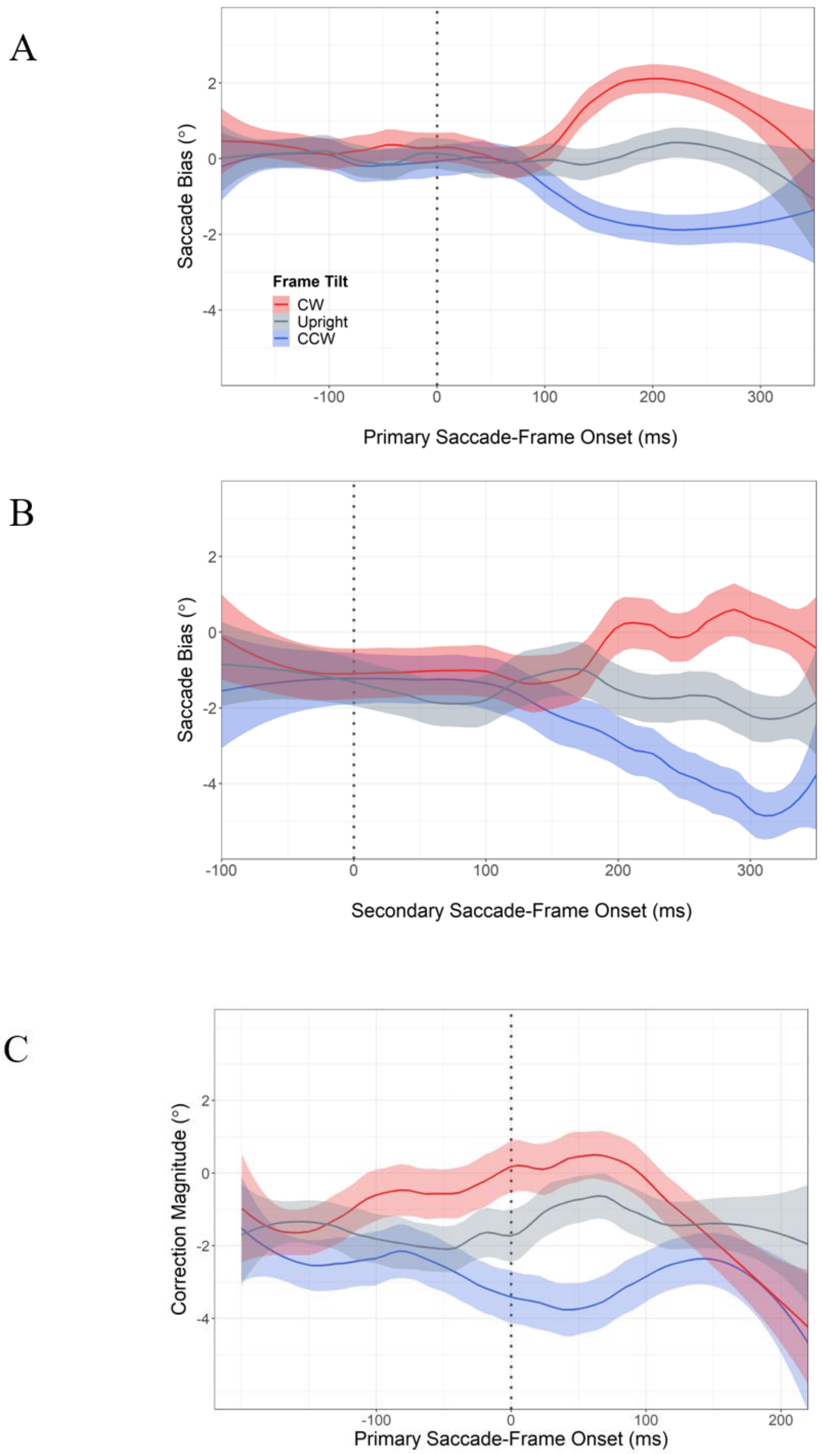


Figure 16: A & B) saccade bias for primary and secondary saccades, respectively; C) the correction magnitude of secondary saccades plotted as a function of the saccade-frame onset asynchrony of their associated primary saccade.

Figure 16 C plots the correction magnitude of secondary saccades with respect to the saccade-frame onset time of their associated primary saccade. When a primary saccade was initiated before frame onset, its secondary saccade was often performed after frame onset. In such cases, the “correction” applied by the secondary saccade was in the direction of the frame’s tilt. The largest corrections occurred for primary saccades that were initiated approximately 50 ms after frame onset. In these cases, the primary saccade was performed while the afferent processing of the frame was still underway; however, the secondary saccade was performed at a time when the afferent processing of the frame was complete and was therefore prone to the illusion. At ~130 ms, the difference in correction magnitude between frame tilt conditions collapses. The endpoint of primary saccades performed at this time were sufficiently biased by the frame’s tilt (see Figures 13, 14, 16 A) and the need for further “correction” was reduced.

Discussion

To investigate the integration of visual context into the egocentric reference frame, we assessed the accuracy of vertically-directed saccades that were initiated at various times with respect to the onset of a large, tilted frame. Replicating previous studies (Dassonville & Reed, 2015; Morgan et al., 2015), we observed that saccade accuracy was biased by the direction of the frame’s tilt. The direction of these errors was consistent with the idea that the tilted frame biases the observer’s egocentric representation of vertical in the direction of the frame’s tilt (Witkin & Asch, 1948). In the presence of a CCW-tilted frame, saccades were biased in a CCW direction relative to saccades performed in the presence of a CW-tilted frame. This result lends further support to models of perception and action in which perceptual and manual estimates of a spatial feature are made from within a common frame of reference (Hommel et al., 2001; Dassonville et al., 2004; Dassonville & Reed, 2015).

The aim of this experiment, however, was to assess the time course by which this frame-induced distortion of the egocentric reference unfolds. On each trial, the saccade could be initiated at varying times before or after frame onset. We limited our analysis to a temporal window extending from 200 ms before to 350 ms after frame onset. Our primary analysis used a loess regression to describe how saccade accuracy changed as a function of saccade-frame onset asynchrony (Figure 13). Unsurprisingly, the endpoints of saccades initiated prior to frame onset were not affected by the direction of the eventual frame's tilt. This was also true for saccades initiated less than 100 ms after frame onset. Recall that an efferent processing delay (t_{motor}) intervenes between the formation of the saccade goal and the initial movement of the eye. Because saccades remained accurate during the 100 ms following frame onset, we reason that the motor endpoint of these saccades was programmed within an unbiased frame of reference, implying that the afferent transmission of the tilted frame (t_{frame}) was still underway. Saccades initiated 100 ms after frame onset were the first to demonstrate a bias in their endpoints. This was indicated by the first point of significant divergence between the loess lines fit to CW and CCW frame conditions. In order to influence saccade trajectories, the afferent processing of the frame must have been completed by the time the goal for these saccades was formed; therefore, $t_{frame} + t_{motor} = \sim 100$ ms. The difference between CW and CCW frame conditions continued to increase until ~200 ms after frame onset; from this, we can infer that $t_{frame} + w_{frame} + t_{motor} = \sim200$ ms. At this point, the difference between the frame tilt conditions remained relatively constant until the end of our analysis window (Figure 14).

One motivation for this experiment was to address some of the ambiguities remaining from the experiments described in Chapter II. In experiments 1 & 2, we assessed subjective vertical using the perceptual estimate of an oriented rod. The rod was briefly flashed at various time points with respect to the onset of the tilted frame. The differential latencies model we proposed to account for the results estimated that the difference between the afferent processing delay of the frame and the delay between the presentation of the rod and the completion of its orientation judgment was ~150 ms = $(w_{rod} + t_{rod}) - t_{frame}$. However, we were unable to make an absolute estimate of these delays. In addition, an alternative account of our data, relying on perceptual binding errors rather than differential latencies, could not be ruled out due to the nature of the two-alternative forced choice response mode used in experiments 1 & 2.

The present experiment employed a design similar to those in Chapter II, but replaced the perceptual judgment with a motor estimate of vertical. The advantage of using saccades as a performance measure was two-fold. First, the analog nature of the saccade allowed us to estimate the frame's effect on subjective vertical for a single trial. Like the perceptual tasks in Chapter II, we observed a steady increase in illusion magnitude, as subjective vertical became increasingly biased in the direction of the frame's tilt. The fact that saccade endpoints during this transition period demonstrated an intermediate effect of the tilted frame makes the binding error account of our perceptual data (which stipulated an all-or-none effect of the tilted frame) less viable. Instead, this observation supports our suggestion that the increasing illusion magnitude is a product of sampling of the reference frame during its continuous transition from an accurate representation of vertical to a biased representation.

The second advantage of using saccades as a performance measure was that an estimate of the efferent delay between the formation of the saccade goal in the frontal eye fields and the initiation of the eye movement has been provided by electrophysiological research (Robinson & Fuchs, 1969; Bruce et al., 1985); this efferent delay is estimated to be ~30 ms. Our results suggested that the endpoint of saccades initiated 100 ms after frame onset were the first to be affected by the direction of the frame's tilt. Using the efferent latency estimate cited above, the motor goal for a saccade initiated at 100 ms was formed at ~70 ms. This suggests that the afferent transmission of the frame (t_{frame}) was completed ~70 ms after its onset, as saccade goals formed at this time began to reflect the frame-induced bias in subjective vertical.

The estimate of 100 ms as the point of divergence between tilted frame conditions was provided by the loess regression. This estimate is sensitive to the chosen level of smoothing, however. Increasing the alpha parameter increases the number of observations included within the smoothing window, which, in turn, narrows the 95% confidence intervals surrounding the fitted curve. For example, performing the analysis using a span of 0.5 (more smoothing) adjusts the estimate of divergence to 95 ms (t_{frame} = 65 ms). Conversely, a span of 0.3 (less smoothing) yields an estimate of 107 ms (t_{frame} = 77 ms). Although these examples represent reasonably large differences in span, the resulting estimate of divergence does not change drastically. Nonetheless, this should be a point of consideration when assessing the degree of confidence to place in our estimate of the frame's afferent processing delay.

We also used a binned analysis to compare saccade biases between frame tilt conditions. Data were segmented into bins of 10 ms and t-tests compared the saccade bias for CW- to CCW-tilted frames within each bin. This analysis suggested that the point of divergence between frame conditions was closer to 130 ms (t_{frame} = ~100 ms). This analysis was more conservative than the loess because the t-test for a given bin was agnostic to the results from adjacent bins. For example, the bin corresponding to 150 ms failed to reach significance despite a significant difference found in the 140 and 160 ms bins (Figure 14). Thus, it is likely that this analysis slightly overestimated the duration of t_{frame}.

Work from Dassonville and colleagues has demonstrated that activation in the right superior parietal lobule (SPL) is correlated with the Roelofs effect (Walter & Dassonville, 2008) and causally related to the RFI (Lester & Dassonville, 2014). Parietal area 7a in macaque has been suggested to be the human homolog to SPL (Konen & Kastner, 2008; Silver & Kastner, 2009). Visual evoked responses in area 7a have been recorded with latencies ranging from 96 – 120 ms (Robinson, Goldberg, & Stanton, 1978; Chafee & Goldman-Rakic, 1998). Recently, Martin et al. (2019) recorded visual response latencies from multiple regions across human visual cortex using electrocorticography (ECOG). These authors reported a visual response latency of 135 ms in SPL1 (a subregion within SPL).

The latency we suggest for the afferent processing delay of the frame is on a similar scale to those cited above, albeit somewhat earlier. The differences between our estimates may be due to differences in stimulus characteristics. For example, Martin et al. used a small target presented at 7° eccentricity, whereas the frame in our task was much larger and presented closer to 18° eccentricity. There is generally a temporal processing advantage for peripheral stimuli (Carrasco, McElree, Denisova & Giordano, 2003) due to the increased ratio of M to P ganglion cells (Azzopardi, Jones, & Cowey, 1999). In addition, Lester and Dassonville (2014) noted an attenuation of the RFI after stimulation of the right SPL with transcranial magnetic stimulation, but not a complete abolishment of the illusion. Thus, it is possible that regions other than SPL, with shorter visual response latencies, are involved in processing the tilted frame and that their recruitment is sufficient to bias saccade trajectories.

Chakrabarty, Nakano, and Kitazawa (2016) described a task similar to our own. These authors used a double-step saccade task in which a background frame was transiently shifted during the presentation of the second saccade target. Saccades directed toward the second target were systematically biased in the direction of the frame shift. Chakrabarty et al. (2016) reported that saccades began to be biased ~150 ms after the frame shift. These authors attributed the effect they observed to an encoding of the saccade target within an allocentric frame of reference. Although, their results might be explained by a distortion of the egocentric reference frame (similar to the Roelofs effect), participants in their study could see other stable visual cues (e.g., the edges of the monitor) which would limit the efficacy of a shifted frame to cause an egocentric distortion.

In our comparison of primary and secondary saccades, we noted a reduction in illusion magnitude for primary saccades initiated ~300 ms after the onset of the frame (Figure 16 A). This reduction in illusion magnitude does not appear to be an effect of saccade RT, however. In their assessment of the time course of the Müller-Lyer illusion, de Brower et al. (2014) also reported a reduction of illusion magnitude as stimulus duration increased, independent of saccade RT. These authors reported large effects of the illusion up to stimulus durations of ~200 ms, with a sudden drop-off in magnitude for stimulus durations of ~300 ms. This timeline is very similar to our own, despite the many differences between the Müller-Lyer stimulus and the tilted frame. To account for their observations, de Brouwer et al. suggested that contextual elements of the stimulus might be processed quickly to assess the gist of a scene (Oliva & Torralba, 2006). As duration increases, more time is allowed for a detailed and accurate visual analysis of the stimulus. This account generally fits our data, with the exception that secondary saccades performed 300 ms after frame onset were also affected by the tilted frame (de Brouwer et al. did not assess corrective saccades). This might suggest that the error signal used to adjust the magnitude of the correction applied by the secondary saccade is derived from a rapid reassessment of the larger visual context of the scene. Future work could investigate whether primary saccades initiated 300 ms after frame onset are followed by corrective saccades that are prone to the illusion or if the diminution of the illusion carries through to the secondary saccades as well.

The results of this study suggest that visual context is rapidly integrated into the egocentric frame of reference and used to guide actions. Given the relevance of visual cues for vital functions, such as maintaining balance and posture (Lee & Aronson, 1974; Fitzpatrick & McCloskey, 1994), the ability to quickly accommodate changes in the visual scene is an adaptive trait. Interestingly, the influence of visual context appears to fluctuate over time; the bias of primary saccades initiated ~300 ms after frame onset was greatly reduced. Our analysis was focused on a narrow window surrounding the time of frame onset so nature of this fluctuation over a longer time scale remains unclear and should be addressed by future research.

CHAPTER IV

GENERAL CONCLUSIONS

Under normal conditions, our subjective experience of vision might have a quality like that of a video camera, capturing the contents of the scene before us with a uniform spatial fidelity across the entire visual field. We can be quickly disabused of this notion with simple demonstrations that reveal the rapid drop off in acuity and color perception for regions just beyond our point of fixation or the presence of a sizable blind spot in each eye. Similarly, the temporal quality of vision is not as uniform as our experience might suggest (Holcombe, 2009); this fact, however, is not as readily demonstrated. Revealing the temporal characteristics of visual processing usually requires carefully controlled manipulations within a laboratory environment.

The experiments described in this dissertation were designed to assess the time course by which contextual visual information is incorporated into an observer's egocentric frame of reference. To do so, we induced a distortion of the observer's internal representation of vertical using the tilted frame of the rod-and-frame illusion (RFI; Witkin & Asch, 1948). The presence of the frame-induced bias of subjective vertical signaled the integration of the visual context with the egocentric reference frame. In separate experiments, we estimated the magnitude of this bias by asking participants to perform either a rod orientation judgment (Chapter II) or a vertically-directed saccade (Chapter III) at various times before and after the onset of the tilted frame.

In Chapter II, participants reported the orientation of a rod that was briefly (~5 ms) flashed at various times before or after the onset of the tilted frame. Experiment 1 in this chapter reported the surprising result that the perceived orientation of a rod presented even 150 ms before the onset of the frame was affected by the direction of the frame's tilt. To account for these results we proposed a differential latencies model (Figure 7) in which the delay between the presentation of the rod and the completion of the orientation judgment ($t_{rod} + w_{rod}$) is longer than delay between the presentation of the frame and its initial effect on perceived vertical (t_{frame}). This model was supported by the results of experiment 2, where the time course associated with low luminance rods (a manipulation that extends the duration of afferent processing) was shifted away from frame onset (i.e., earlier in time) relative to the time course associated with the high luminance condition. The results of these experiments allowed us to compare the latency of the rod orientation judgment to the afferent processing delay of the frame; $t_{frame} – (t_{rod} + w_{rod}) = –150$ ms. However, we were unable to make an absolute estimate of time dedicated to either process.

To address this ambiguity remaining from the perceptual task, we employed an experiment with a similar design, but instead assessed subjective vertical with a saccade directed to the top of a response circle (Chapter III). We reasoned that the latency between the onset of the tilted frame and the initiation of the first saccades to be affected by the direction of the frame's tilt represented a combination of the afferent processing delay of the frame plus the efferent processing delay of the saccade ($t_{frame} + t_{motor}$). The efferent latency between the formation of a saccade goal and the initiation of the eye movement has been previously estimated using electrophysiological methods to be ~30 ms (Robinson & Fuchs, 1969; Bruce et al., 1985). We observed that saccades initiated ~100 ms after the onset of the frame were the first affected by the direction of the frame's tilt. Considering an efferent saccade latency of ~30 ms allowed us to estimate the afferent processing delay of the frame to be, t_{frame} = ~70 ms.

A Rapid Integration of Visual Context

The results of our experiments suggest that contextual visual information is rapidly integrated into the egocentric frame of reference and subsequently used to influence our perception of an object's features and guide our actions. This result aligns well with previous research that has indicated the relatively fast processing of visual context (de Brouwer, Brenner, Medendorp, & Smeets, 2014; Chakrabarty, Nakano, & Kitazawa, 2016; Schmidt & Haberkamp; 2016; Chen, Sperandio, Henry, & Goodale, 2019; Zeng, Fink, & Weidner, 2020). The latency we estimated for the frame's afferent processing delay (~70 ms) is also near the range of latencies reported for visually evoked potentials in SPL (Robinson, Goldberg, & Stanton, 1978; Chafee & Goldman-Rakic, 1998; Martin et al., 2019), a region previously implicated in driving the egocentric distortion caused by the tilted frame (Lester & Dassonville, 2014).

The relatively short afferent processing latency of the frame suggests that its effect on subjective vertical is established during the feedforward sweep of activation through visual cortex (Lamme & Roelfsema, 2000). This interpretation is consistent with other studies that have observed a fast integration of visual context (e.g., de Brouwer et al., 2014; Zeng, Fink, & Weidner, 2020). Oliva and Torralba (2006) proposed a model to describe how processing the visual context of a scene could be mediated by feedforward activation. According to their model, the activation of small receptive fields in low-level visual areas that encode local contour and color information are summated to form the larger receptive fields found in high-level regions, such as inferotemporal and parietal cortex. This summation creates a coarse representation of the distribution of colors, orientations, and contours across the retinal image. Although the authors' primary emphasis was the utility of their model to allow for a semantic-level recognition of a scene, a prerequisite for this type of recognition is the assessment of contours and orientations within the scene. Such a model could account for the rapid afferent processing of the tilted frame observed in our studies.

After the afferent processing of the frame was completed, the distortion in subjective vertical grew in magnitude. The rate of change in subjective vertical observed in the present studies was likely influenced by low-level features of the frame including its size, orientation, and luminance. For example, a frame with a less dramatic tilt (e.g., 8°) would be expected to induce a smaller illusion (Beh et al., 1971; Wenderoth & Beh, 1977); one might expect that the illusion magnitude would reach a plateau more quickly in this case. Similarly, decreasing the luminance of the frame might reduce the rate at which it is integrated with the egocentric reference (as well as increase the latency of its initial effect on perceived vertical); indeed, the results of experiment 2 (Chapter II) indicate the relevance of stimulus energy to the time course of the illusion. Thus, the rate of integration observed in a given task depends, in part, upon the particular characteristics of the stimulus chosen by the experimenter; further research is required to understand the consequences of such manipulations.

After the distortion in subjective vertical had reached its peak, it maintained a relatively stable level of distortion (Figures 10 & 14). In Chapter III, however, we noted that primary saccades initiated 300 ms after frame onset were less affected by the direction of the frame's tilt (Figure 16 A); the stabilization of the illusion magnitude in the saccade task was largely maintained by corrective saccades performed during this time. There was also a small (though, non-significant) reduction in illusion magnitude between the 33 ms and 200 ms SOA conditions in the perceptual task (Chapter II, experiment 1). Previous studies have also reported a reduction in illusion magnitude with increased durations of stimulus visibility (van Zoest & Hunt, 2011; de Brouwer, et al., 2014). Compared to the illusion magnitudes reported here, the magnitudes reported by Dassonville and Reed (2015) was smaller for both their perception and saccade tasks. In their study, the tilted frame appeared prior to the onset of a trial and remained visible until the button response at the end of the trial. This observation supports the notion that a longer visibility of the tilted frame is associated with a lower RFI magnitude. To gain a better understanding of how (or whether) these oscillations in illusion magnitude stabilize over time, the time course of context integration should be assessed over an extended duration in future studies.

Given the relevance of visual cues for posture control (Lee & Aronson, 1974; Fitzpatrick & McCloskey, 1994), the ability to quickly detect and accommodate a change in subjective vertical is highly adaptive. Although much of the research on visual control of balance has been concerned with dynamic visual stimulation (e.g., optic flow), previous work has demonstrated interactions with static images, such as the tilted frame of the RFI. For example, the magnitude of the RFI is modulated by the posture of the observer (Goodenough, Oltman, Sigman, & Cox, 1981; Dyde, Jenkins, & Harris, 2006; Corbett & Enns, 2006). The presence of a large frame has also been shown to influence how standing observers regulate their posture, causing participants to adjust their control strategies when the frame is tilted (Isableu et al., 2010) and stabilizing participants when the frame is upright (Lubeck, Bos, & Stins, 2016). Other studies have reported an interaction between balance control and the extent to which the frame affects rod orientation settings (Luyat, Ohlmann, & Barraud, 1997; Bray et al., 2004), a suggestion that fits well within dynamic sensory reweighting theories of balance control (Assländer & Peterka, 2014; Hwang, Agada, Kiemal, & Jeka, 2014). However, much about the relationship between balance, visual context, and visual perception remains an active field of research.

Assessing Subject Vertical with Perception and Saccades

The experiments described in Chapters II and III had a similar design but for the method by which subjective vertical was assessed. Until this point, we have treated the perceptual judgment and motor estimate as somewhat analogous. The Two Wrongs model (Dassonville & Bala, 2004; Dassonville & Reed, 2015) proposes that the relevant decision criterion (i.e., subjective vertical) is represented within a frame of reference that is common to both tasks. This model is supported by observations that the magnitude of the bias in an individual’s perceptual estimates are correlated with the bias in their manual estimates (Dassonville et al., 2004; Dassonville & Reed, 2015). Given the assumption that the underlying distortion caused by the tilted frame is the same for both tasks, there is no reason to suspect that the afferent processing delay of the frame should depend on the response mode and, therefore, the results from the saccade task could meaningfully constrain the results from the perception task.

To assess the validity of this assumption for the present experiments, we compared the sigmoidal functions fit to the time courses of the perception tasks and the saccade task. To describe the time course of the saccade task using the same conventions as the perception tasks, a logistic function (eq. 2) was fit to the difference between the loess curves associated with the CCW- and CW-tilted frame conditions (i.e., Figure 14). The time course for each experiment is plotted in Figure 17; the midpoint of each sigmoid was aligned to 0 ms to facilitate a comparison of the shape of the time courses. While the growth rate and magnitude of the illusion are similar for the curves fit to the perception tasks, the curve fit to the saccade task has notable differences.

First, the illusion magnitude in the saccade task was approximately 1° smaller than the magnitude in the perception tasks. This difference may be due, in part, to the fact that we recruited a different sample of subjects for each experiment. Although the magnitude of perceptual and motor errors are correlated within a given subject, there is variability between subjects in the overall degree of susceptibility to the tilted frame (Witkin & Goodenough, 1981). It is possible that, by chance, the sample we recruited for the saccade task was less susceptible to the illusion and that they would have demonstrated a similarly reduced illusion magnitude had they participated in the perception task.

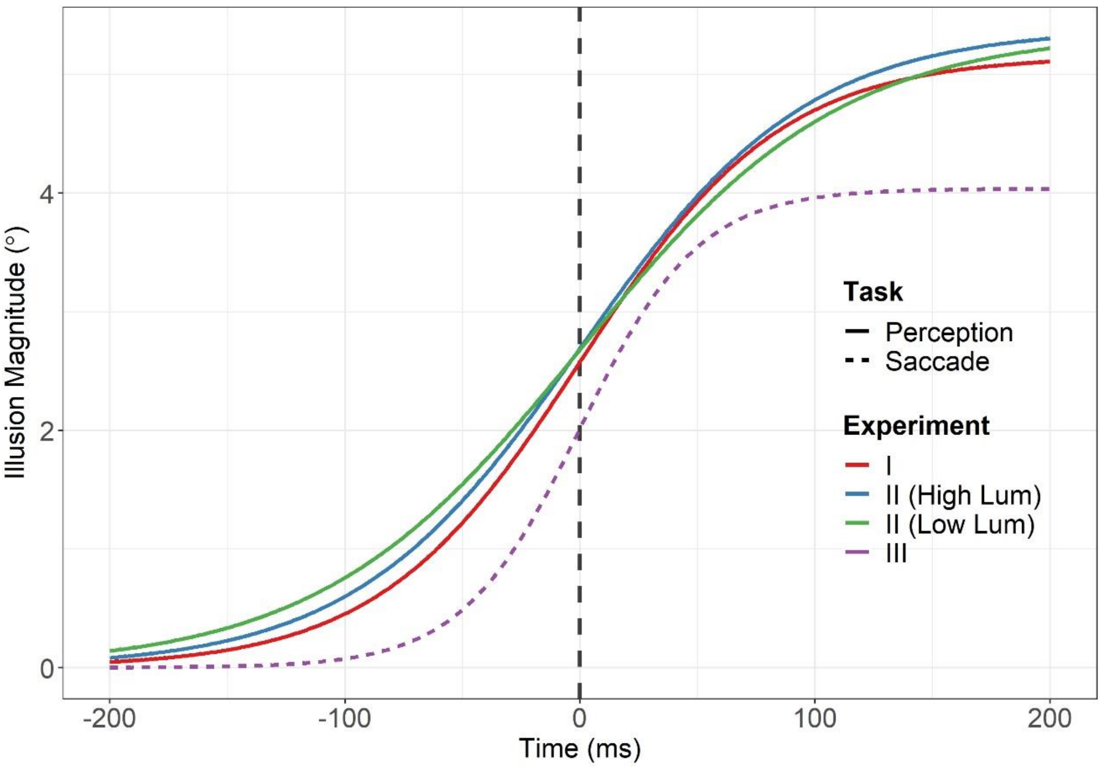


Figure 17: Comparing the growth rate and amplitude of the time courses for the perception and saccade tasks. The midpoint of the time courses are aligned to facilitate a comparison of their slopes. Importantly, 0 ms denotes the midpoint of the sigmoid, rather than time of frame onset, as was the convention in previous figures.

Perhaps a more interesting explanation for the reduced illusion magnitude in the saccade task is related to the dual mechanisms that drive the RFI. As described in Chapter I, the overall magnitude of the RFI is an additive combination of a visuo-vestibular effect and a local orientation contrast effect. The visuo-vestibular effect biases the perceived head orientation (Ebenholtz & Benzschawel, 1977; Sigman, Goodenough, & Flannagan, 1978), distorting the egocentric frame of reference. The orientation contrast effect, created by an interaction between the rod and the edges of the frame (Coren & Hoy, 1986; Antonucci et al., 1995), biases the perceived orientation of the rod but leaves the egocentric reference frame unaffected. The magnitude of the illusion observed in the perception tasks represents a combination of the visuo-vestibular and orientation contrast effects. However, there was no contribution of an orientation contrast effect in the saccade task because no rod was presented in this experiment. Reed and Dassonville (*in preparation*) assessed the relative contributions of visuo-vestibular and orientation contrasts effects for frames of different sizes. When assessing a frame of the same dimensions as the frame used in the present experiments, the authors reported that contrast effects account for ~20% of the overall illusion magnitude. The reduced amplitude observed in the saccade task compared to the perception tasks aligns quite well with the observations of Reed and Dassonville (*in preparation*).

The second notable difference between the time course fit to the saccade task and those fit to the perception tasks is the steeper slope associated with the saccade task; this difference could also be due to the absence of a contrast effect in the saccade task. The saccade task measures the time course of the visuo-vestibular effect, whereas the perception tasks measure the combined time courses of the visuo-vestibular and contrast effects. Because it is unclear when the orientation contrast effect is initiated relative to the visuo-vestibular effect, it is difficult to disentangle their relative contributions to the time course of the perception tasks; this is why, for example, we cannot simply subtract the curve fit to the saccade task from the curve fit to the perception task to estimate the time course of the orientation contrast effect.

In addition to the visuo-vestibular and orientation contrast effects that contribute to the magnitude of the RFI, differences in how the perceptual decision is made and how the saccade goal is formed may cause differences in the growth rate of the illusion as measured by the two tasks. As discussed in Chapter II, the observed growth rate of the illusion depends upon how the reference frame is sampled during the decision window. When the decision window overlaps with the ongoing distortion of the reference frame, the average of the accumulated samples will produce a dampened representation of the actual distortion that occurred during this window. Thus, a longer sampling period would produce a flatter curve (effectively acting as a low-pass filter). In this case, the steeper slope of the saccade task could indicate that the window during which the saccade goal is formed is narrower than the window during which the orientation judgment is made.

The compelled response paradigm offers a potential means to estimate the processing time required for the rod orientation judgment. In this paradigm, a gap of variable duration intervenes between a prompt to perform a discrimination and the presentation of the to-be-discriminated stimuli. Importantly, participants are required to submit a response within a fixed interval after having received the prompt, regardless of the gap duration. With a long gap between the prompt and stimulus onset, the stimuli are only briefly visible and discrimination accuracy is low; with a sufficiently long gap, performance falls to chance. Conversely, with a short gap, the stimuli are visible for a longer duration and discrimination accuracy is improved. Measuring the difference between the gap duration associated with (customarily) 75% accuracy and the gap duration associated with 50% accuracy allows for an estimate of the processing time required to perform the discrimination.

Stanford et al. (2010) used a compelled response paradigm in which monkeys performed a red/green color discrimination. The authors reported that as little as 30 ms of processing time was needed for the monkeys to perform this discrimination. Rüter et al. (2013) used a compelled response paradigm with human participants. These authors reported that a Vernier discrimination (i.e., whether the lower of two collinear line segments is offset to the left or right of the upper segment) could be performed in 63 ms of processing time (importantly, these authors also proposed that an integration period precedes this 63 ms).

It is difficult to draw an inference about the likely duration of processing time required for the rod orientation judgment from the studies reported by Stanford et al. (2010) and Rüter et al. (2013) due to differences in task difficulty; task difficulty is directly related to the duration of processing time (McKoon & Ratcliff, 2008). Nonetheless, a compelled response paradigm could be used to estimate the duration of processing time required to perform an orientation judgment for rods tilted at varying degrees around the PSE. The results of such a study would not only be informative about how much time is allocated to the afferent processing of the rod and to the orientation judgment, but could also be informative in regard to when the judgment is susceptible to the tilted frame.

Importantly, the differences we have observed between the time courses of the perception and saccade tasks is not a challenge to the Two Wrongs model, but instead suggests that the compatibility of the saccade and perception tasks (in their current form) is limited. Future research should employ tasks that allow for a more direct comparison between the saccade and perception tasks. A clear next step is to estimate the time course of the orientation contrast effect. In their study, Reed and Dassonville (*in preparation*) isolated the contributions of the orientation contrast effect from the visuo-vestibular effect using a task in which participants performed a cued saccade to the remembered location of the rod’s endpoint. According to the Two Wrongs model, because the visuo-vestibular effect distorts the egocentric reference frame, the error of decoding the target location for the saccade cancels the perceptual error of target encoding. Therefore, the visuo-vestibular effect does not contribute to motor bias when the action directed toward an external target (i.e., the end of the rod); any remaining saccade bias observed in this task is driven only by orientation contrast effects. This saccade-to-rod task could be modified to resemble the saccade task presented in Chapter III, enabling the time course of the orientation contrast effects to be measured.

In addition, a perceptual judgment task could be designed in which the observer judges whether a target (or "knob") on a briefly flashed circle was positioned CW or CCW of vertical (Figure 18). Such a task would provide a perceptual orientation judgment that is influenced only by visuo-vestibular effects, and not by orientation contrast effects. This experiment, and the one described in the previous paragraph, would allow for separate descriptions of the time course of the visuo-vestibular and the orientation contrast effects and enable a more direct comparison between motor and perceptual estimates of subjective vertical.

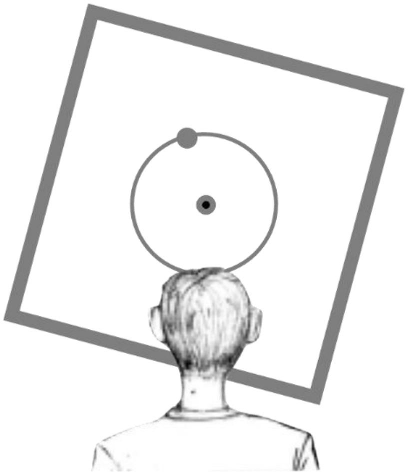


Figure 18: The proposed "knob-and-frame" task. The participant is required to discriminate the location of the knob (CW or CCW from vertical) on a briefly flashed circle. The absence of a rod prevents an orientation contrast effect like that between the rod and the edges of the frame in the RFI. The resulting illusion magnitude will be driven purely by visuo-vestibular effects.

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