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The Effects of Motion on Position Representations
for Perception and Action

By

Anna Kosovicheva

A dissertation submitted in partial satisfaction of the

requirements for the degree of

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in

Psychology

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of the University of California, Berkeley

Committee in Charge:

Professor David Whitney, Chair

Professor William Prinzmetal

Professor Michael A. Silver

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Abstract

The Effects of Motion on Position Representations
for Perception and Action

by

Anna Kosovicheva

Doctor of Philosophy in Psychology

University of California, Berkeley

Professor David Whitney, Chair

Accurately perceiving the locations of objects is essential for successfully interacting with our environment. However, the visual system must constantly contend with motion, both from objects moving through space and on the retina as the observer moves through the environment. Previous work has shown that motion can bias the perceived locations of both moving and non-moving targets, demonstrating that the visual system uses information from motion to update the represented locations of objects. Here, we examined the extent and circumstances under which motion-induced position shifts can influence perception, and whether they can influence action. First, we used psychophysics to demonstrate that motion can influence the location at which low-level adaptation is observed, supporting the idea that motion can bias retinotopic coding of stationary objects at early stages of visual processing. Moreover, we demonstrate that motor responses are not immune to these early influences of motion on position representation. Specifically, we show that position shifts resulting from motion can bias saccade targeting. However, this influence of motion-induced position shifts on saccade targeting does not simply result from perceptual shifts in position. Instead, we demonstrate that the saccade system updates information from motion-induced position shifts before observers are able to consciously perceive these changes. Together, these experiments support the idea that motion exerts an early influence on represented positions and that the saccade system has access to this information before it is perceptually registered.

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Chapter 1: Introduction

In order for us to successfully interact with our environment, our perceptual and motor systems must be able to accurately represent object locations. When crossing a busy street, for instance, it is essential that we are able to accurately represent the locations of approaching cars. Similarly, when playing a game of tennis, we must be able to rapidly update the location of a moving ball. Accurate object localization in these tasks enables us to appropriately direct our motor responses, such as eye movements. This presents a particularly challenging problem for the visual system when there is motion on the retina – either from the objects themselves, or from the observer moving through their own environment. Information that reaches the retina is subject to delays in neural processing, and in the time it takes the brain to process incoming information, objects can shift to new locations. Therefore, it's essential for the visual system to take into account neural processing delays when assigning object position. Here, we examined in detail how the perceptual and motor systems use motion information to update their representations of the locations of objects in our environment.

The need to compensate for neural processing delays suggests that retinal location alone is inadequate for accurate location representation. In fact, a large body of literature has shown that factors other than retinal location, such as frames of reference (Roelofs, 1935), attention (Kosovicheva, Fortenbaugh, & Robertson, 2010; Suzuki & Cavanagh, 1997), eye movements (Cai, Pouget, Schlag-Rey, & Schlag, 1997; Ross, Morrone, & Burr, 1997), memory (Sheth & Shimojo, 2001), and adaptation (Whitaker, McGraw, & Levi, 1997) can influence perceived location. Crucially, the motion of an object can influence the perceived location of another, static object in a different part of the visual field (Whitney & Cavanagh, 2000). This illusion, known as the flash-drag effect, suggests that motion fundamentally biases the represented positions of objects in the visual field. What are the mechanisms involved in this phenomenon, and at what stage of visual processing does it occur? Chapter 2 directly examines whether this influence of motion occurs at a high level of representation, or at early, retinotopic stages of visual processing. To answer this question, we tested whether motion-induced position shifts produced by the flash-drag effect can bias the location at which low-level adaptation is observed. Specifically, the tilt aftereffect is produced by the adaptation of orientation selective cells in primary visual cortex (e.g., Maffei, Fiorentini, & Bisti, 1973; Movshon & Lennie, 1979). If the apparent position shift induced by the flash-drag effect can bias the spatial tuning of the tilt aftereffect, this would suggest that motion biases position coding as early as primary visual cortex. In Chapter 2, we directly test the possibility that motion can bias position coding early in visual processing.

If motion influences early stages of visual processing, it follows that motion-induced position shifts may bias motor responses as well. Not only is it necessary to update represented object positions for perception, but we must also be able to direct our actions appropriately. Chapters 3 and 4 compare the influence of motion on position coding for perception to its influence on action. In Chapter 3, we test whether the saccade system can use position shifts resulting from motion to update saccade target locations by measuring saccades to drifting Gabor targets. In this stimulus, the motion of a sinusoidal grating inside a static Gaussian aperture results in an illusory perceptual shift of its center consistent with the direction of motion (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990). This stimulus allowed us measure whether position shifts resulting from motion can influence saccade landing locations, independent of any physical displacement over time.

Finally, the ability to rapidly respond to position shifts is essential for interacting with our environment. In Chapter 4, we examine how quickly the saccade system can update position information in response to these motion-induced position shifts. Specifically, how soon following a reversal in a drifting Gabor's motion direction do saccades reflect this change? Importantly, how does this lag in saccadic updating compare to temporal delays in updating perceived location? In other words, does the saccade system account for the change in object motion before we have perceived the change? In our example, the car will not wait for our perception of its motion; we may need to act before we perceive the change in the world.

By examining the stage at which motion influences perceptual localization, and the extent and speed with which it influences action, these experiments demonstrate that motion plays an early and critical role in perceptual and saccadic localization. Together, these experiments show that the visual system is highly attuned to motion and balances the need to perceive the positions of moving objects in the world with the need to react to those objects.

Chapter 2: The motion-induced shift in the perceived location of a grating also shifts its aftereffect

One of the most fundamental tasks for our visual system is to localize objects within the visual field. Object localization can be influenced by a number of factors independent of retinal position. For example, eye movements (Cai, Pouget, Schlag-Rey, & Schlag, 1997; Ross, Morrone, & Burr, 1997), spatial attention (e.g., Suzuki & Cavanagh, 1997), frames of reference (Roelofs, 1935), and adaptation (Whitaker, McGraw, & Levi, 1997) have all been shown to produce illusory shifts in perceived position. Notably, a substantial body of literature has shown that object motion can systematically bias perceived location (e.g., Ramachandran & Anstis, 1990; De Valois & De Valois, 1991; Whitney & Cavanagh, 2000). For instance, when a brief stationary flash is presented in alignment with a moving object, the flash appears to lag behind the moving object (Nijhawan, 1994). The motion of an object can also bias the perceived location of another, stationary object within another part of the visual field, a phenomenon known as the flash-drag effect (FDE; Whitney & Cavanagh, 2000). Together, these phenomena demonstrate that motion processing is intrinsically linked to object localization.

However, the stage in visual processing at which this occurs has not yet been established. A number of physiological studies point to changes in receptive field properties as the neural basis of motion-induced mislocalizations. Repeated motion within a static envelope has been shown to produce receptive field shifts within cat V1 (Fu, Shen, Gao, & Dan, 2004). A later study by Sundberg, Fallah, and Reynolds (2006) demonstrated shifts in macaque V4 receptive fields when an illusion was viewed in which an object within an apparent motion display appears shifted from its veridical position. Despite these efforts, the correspondence between the physiological and psychophysical literature is not thoroughly understood, and few attempts have been made to link these effects to object localization in humans. Neuroimaging studies in humans have shown that motion can influence retinotopic coding in primary visual cortex (Whitney et al., 2003, though see Liu et al., 2006), but it is unclear whether changes in retinotopic coding in V1 can account for phenomena such as the flash-drag effect. One approach in examining the neural basis of motion-induced position shifts is to determine whether these distortions can influence phenomena known to occur early in visual processing. Specifically, we examined whether a motion-induced position illusion—the flash-drag effect—can be used to modify the spatial tuning of the tilt aftereffect.

The tilt aftereffect (TAE) refers to an illusory shift in perceived orientation following adaptation to a tilted linear grating (Gibson & Radner, 1937); after a period of adaptation to a left-tilted grating, a subsequently presented vertical grating appears oriented to the right, and vice versa. Neurophysiological studies suggest that adaptation of orientation-selective cells in V1 is the mechanism driving the TAE (e.g., Maffei, Fiorentini, & Bisti, 1973; Movshon & Lennie, 1979). Psychophysical studies in humans have demonstrated that the TAE is selective for location of the adapting grating (Gibson, 1937). This selectivity of the TAE appears to be largely dependent on the match between the retinotopic locations of the adaptor and test stimuli (Boi & Herzog, 2011; Knapen, Rolfs, Wexler, & Cavanagh, 2010), though there were earlier reports of spatiotopic transfer of the TAE across saccades (Melcher, 2005). Intriguingly, Arnold, Birt, and Wallis (2008) demonstrated that the TAE can be influenced by an illusion of perceived size. In their experiment, they manipulated distance cues to influence the perceived size of an adapting

stimulus and showed that the perceptual overlap between the adapting and test grating could bias the direction of the TAE.

It remains unknown whether motion-induced mislocalizations can influence the location at which orientation adaptation occurs, and thereby bias the location of the TAE. This approach provides a basis for understanding the effects of motion on retinotopic coding. If the flash-drag effect can bias the spatial tuning of the TAE, this would suggest that motion can influence retinotopic coding at the same level that orientation adaptation occurs (e.g., V1). Here we used the flash-drag effect to shift the perceived location of an adapting grating away from its retinal location, and then measured the spatial tuning of the TAE. Our results demonstrate a skew in the spatial tuning of the TAE in the direction of the perceived location of the adapting stimulus, indicating that the FDE can affect early, retinotopic spatial coding.

Experiment 1

In Experiment 1, we measured the spatial tuning of the TAE following a flash-drag induced shift in the perceived location of the adapting stimulus. Previous research has demonstrated that presenting briefly flashed circles on top of a large oscillating disk produces a large flash-drag effect (Anstis & Cavanagh, 2011). This procedure allows us to separate the physical location of an adapting stimulus from its perceived location. Experiment 1 consisted of two parts. First, as shown in Figure 2.1, we measured the size of the flash-drag effect individually for each observer using a stimulus similar to the one used by Anstis and Cavanagh (2011). Next, we measured the size of the tilt aftereffect by having subjects adapt to briefly flashed gratings presented repeatedly at the moment of the rotation reversals. We compared the size of the TAE at three locations relative to that of the adaptor: (1) the adaptor's physical (i.e., retinal) location, (2) its perceived location, based on measurements obtained in the first part of the experiment, and (3) an equidistant control location in the opposite direction (its "antiperceived" location).

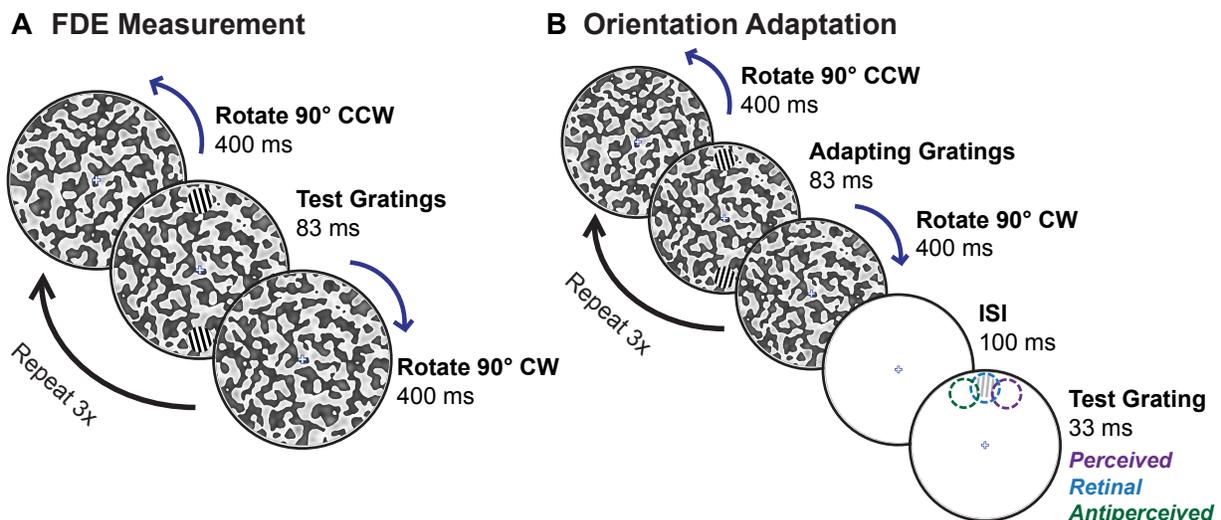


Figure 2.1. Stimulus presentation sequence for the flash-drag measurement (A) and the orientation adaptation (B) portions of Experiment 1.

This design allows a number of predictions regarding the size of the TAE. If there is no effect of motion on the tuning of the TAE, we expect the TAE to be greatest at the retinal location, and to follow a uniform distribution around the adapted location. In other words, the TAE would be equal in magnitude between the perceived and antiperceived locations. Another possible outcome is that the TAE would be greatest at the perceived location, with a decreasing gradient between the retinal and antiperceived locations. This would suggest that the TAE largely depends on the perceived location of the adaptor. A third possibility is that there is a partial influence of perceived location on the spatial tuning of the TAE, with the TAE largest at the retinal location, but larger at the perceived compared to the antiperceived location. The last two of these potential outcomes would support the hypothesis that motion can influence retinotopic coding early in the visual processing stream.

In addition to varying the location of the test stimulus, we examined the possibility that attention to the adaptors may influence the spatial tuning of the TAE. As previous research has demonstrated that voluntary attention modulates both the FDE (Tse, Whitney, Anstis, & Cavanagh, 2011) and the TAE (Spivey & Spirn, 2000), we sought to determine whether any effect of motion on retinotopic coding is attention dependent.

Method

Participants. Eight experienced psychophysical observers (4 female), including one experimenter (GM), participated in the experiment. All subjects reported normal or corrected-to-normal vision. The mean age of the participants was 26 ($SD = 2.4$) with a range of 22 to 29. The experiments were conducted in accordance with the tenets of the Declaration of Helsinki and were approved by the UC Berkeley Institutional Review Board.

Stimuli. Observers were tested individually in a testing booth. Head position was stabilized with a chinrest at a viewing distance of 57 cm. At this distance, 30 pixels subtended 1 degree of visual angle. Stimuli were presented on Dell Trinitron CRT monitor controlled by a Mac Mini. The experiment was written in MATLAB (The MathWorks, Inc.) using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). Stimuli were presented with a resolution of 1024 x 768 and a refresh rate of 60 Hz.

On each trial, observers viewed a patterned disk (10° radius) shown in Figure 2.1 that oscillated clockwise and counterclockwise. The disk pattern was generated by applying a bandpass spatial frequency filter (0.15-0.76 cpd) to a Gaussian white noise image. Each grayscale value in the textured pattern was then wrapped around the median grayscale value (i.e., the new grayscale values were equal to the remainder after dividing by the median value), and the pattern was presented at 80% contrast. Two new patterns were generated for each block of trials that each subject completed, and each pattern was randomly selected with equal probability on a given trial.

Subjects were instructed to fixate on a white cross outlined in blue at the center of the disk, 0.85° long and 0.85° wide, with a line thickness of 0.1° . Each trial began with an initial rotation (either clockwise or counterclockwise) of 90° that lasted 400 ms, followed by an 83.3 ms presentation of two gratings on the stationary disk background at opposite ends of the disk. Each grating consisted of a 1.5 cpd square wave pattern presented at full contrast within a circular aperture 3° wide, centered 8° from the fixation cross. Following presentation of the two gratings, the disk completed a 90° rotation in the opposite direction. This sequence was repeated 3 times on each trial. Trials were separated by an ITI of 500 ms.

Procedure. Experiment 1 consisted of two parts—a flash drag measurement and a tilt aftereffect measurement.

Flash-drag effect measurement. Figure 2.1A shows the stimulus presentation sequence used to measure the flash drag effect. Using a 2AFC method of constant stimuli task, observers were asked to judge whether the top grating was to the left or to the right of the bottom one. The gratings were presented at one of 7 locations relative to the vertical midline of the display shown in Figure 2.1A: -3, -2, -1, 0, +1, +2, or +3 degrees of visual angle. In order to maintain grating positions at opposite ends of the disk, the direction of the top grating shift was always the opposite of that of the bottom one. Both gratings were tilted either 15° to the left or 15° to the right on each trial. The initial rotation of the disk was chosen randomly between counterclockwise and clockwise on each trial.

Tilt aftereffect measurement. On each trial, subjects were presented with the same patterned disk as in the flash drag measurement portion of the experiment. Subjects adapted to two tilted linear gratings that were flashed briefly (83.3 ms) at every other rotation reversal. The flash-drag effect biased the perceived location of the gratings in the direction of the disk's motion immediately following the flash, allowing dissociation between the retinal and perceived location of the adaptor. As previous work has shown that background rotation influences perceived tilt (Hughes, Brecher, & Fishkin, 1972), we controlled for the possibility that the FDE might influence the perceived orientation of the adapting gratings (in addition to shifting their perceived positions). We counterbalanced the initial rotation direction (clockwise and counterclockwise) of the disk with the orientation of the adapting gratings (15° to the left or 15° to the right). The initial rotation direction of the disk was blocked in sets of 280 trials in order to maintain consistent orientation adaptation at the perceived location of the gratings. The rotation sequence was presented 3 times, for a total adaptation duration of 250 ms on each trial.

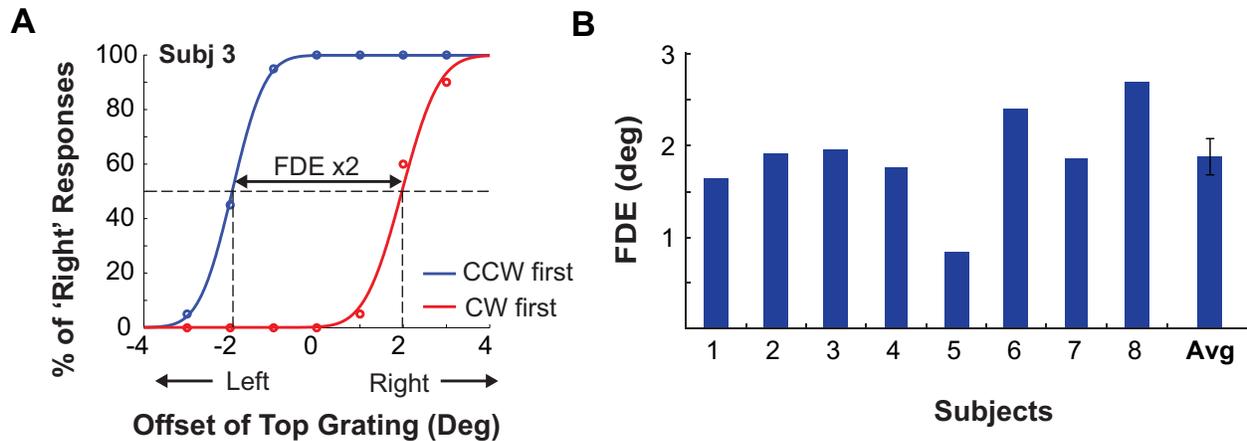
As shown in Figure 2.1B, following an interstimulus interval of 100 ms, brief test gratings (33 ms) were presented at one of three locations—the retinal or perceived location of the adaptor, or an equidistant control location (antiperceived). The retinal location was physically the same as the location of the adapting grating. The perceived location was shifted in the direction of the flash-drag effect by the size of the FDE measured for each observer in the first portion of the experiment. The test grating was a square wave grating similar to the adapting grating and presented at 30% contrast and tilted either -6, -4, -2, 0, +2, +4, or +6° (left to right).

To determine whether any shift in the spatial tuning of the TAE is attention dependent, subjects performed a task in two different attention conditions, presented in separate blocks. Subjects were presented with either: (1) one adapting grating (focused attention condition), with the test grating at its retinal, perceived, or antiperceived location, or (2) two adapting gratings (divided attention condition), with the test grating at the retinal, perceived or antiperceived location of either one of the adaptors, determined randomly on each trial.

Results

Flash-drag effect measurement. The perceptual mislocalization of the adapting grating produced by the flash-drag effect was measured individually for each observer. Subject responses as a function of grating position were fitted with logistic functions using a least squares procedure. As shown in Figure 2.2A, the size of the flash-drag effect is equal to half the difference between the PSEs in the two rotation direction conditions. Figure 2.2B shows the size of the FDE for each observer. To test whether the FDE was significantly greater than zero, we separately bootstrapped the psychometric curves for each motion with 1000 samples. The FDE was then calculated as half the difference between the PSEs. The mean shift was 1.88 degrees of visual angle (SD = .55) across subjects, and the size of the FDE was significantly above zero, $p < .001$. Figure 2.2B shows the size of the FDE for all subjects. All but one subject had a flash-drag

effect larger than the radius of the adapting disk itself (1.5°). For these subjects, there was complete physical separation between the perceived and antiperceived locations of the test gratings.



2.2. (A) Example flash-drag measurement data from one subject. The FDE was measured as half the difference between the PSEs in the two rotation directions. (B) FDE sizes for all subjects in Experiment 1. Error bar represents ± 1 SE.

Tilt aftereffect measurement. The tilt aftereffect was measured in each of three locations for all observers using the equation:

$$TAE = \frac{PSE_{adapt\ right} - PSE_{adapt\ left}}{2} \quad (2.1)$$

Averaged across both attention locations, the mean TAE at the perceived, retinal and antiperceived locations was 0.78 , 1.58 , and 0.56° rotation angle, respectively.

Figure 2.3A shows the size of the TAE at each location collapsed across attention conditions, and 2.3B shows the TAE size between the two attention conditions. We performed nonparametric bootstrap tests to compare the size of the TAE at each test location. Each psychometric curve was bootstrapped separately with 1000 samples and the TAE calculated as half the difference between the PSEs in the two adaptation conditions. Bootstrapped TAE estimates were then averaged across the 8 observers. Averaged across the two attention conditions, the TAE was greater at the retinal compared to the perceived location, $p < .001$, and greater at the retinal compared to the antiperceived location, $p < .001$. A comparison between the non-retinal locations showed that the TAE was larger at the perceived compared to the antiperceived location, $p = .007$. Thus, while the TAE was greatest at the retinal location, it was larger at the perceived compared to the antiperceived location.

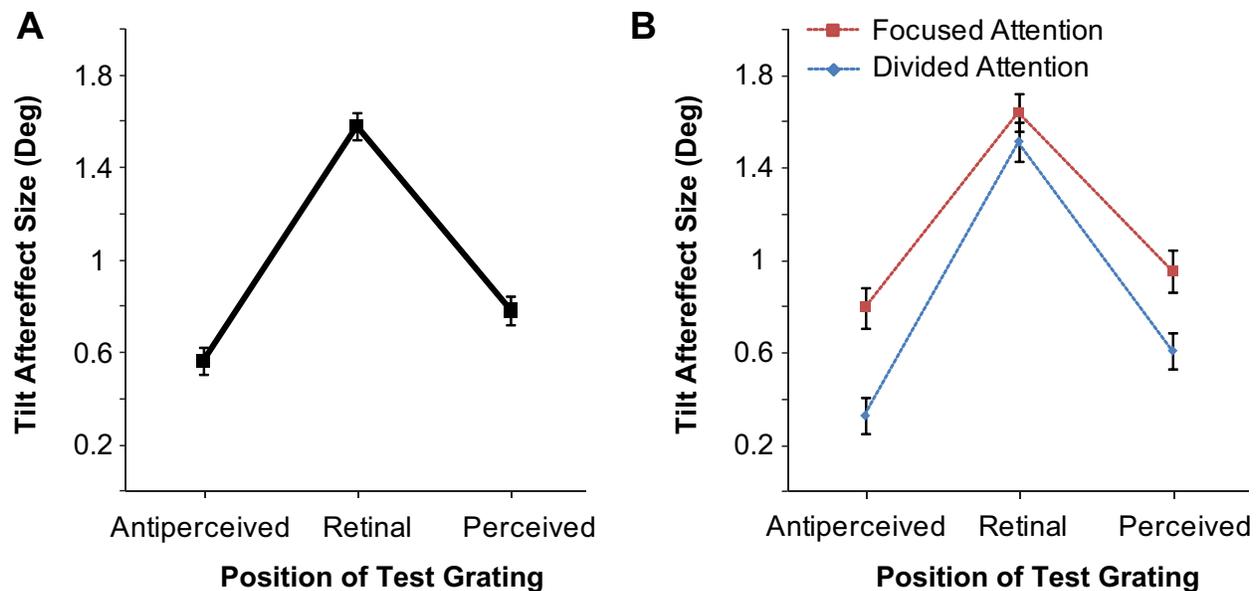


Figure 2.3. (A) Results from Experiment 1 showing the size of the TAE at each of the three test locations. (B) TAE size divided by attention condition. Error bars represent bootstrapped ± 1 SD.

In addition, we compared the magnitude of the TAE between the focused and divided attention conditions at each test location. Previous work has shown that attention modulates the overall magnitude of the TAE (Spivey & Spirm, 2000). Therefore, we might expect individual comparisons of the TAE size between the two attention conditions to show a larger TAE in the focused compared to the divided attention condition. This was confirmed with bootstrap tests showing a greater TAE in the focused as compared to divided attention condition at both the perceived ($p = .006$) and antiperceived locations ($p < .001$), but no difference at the retinal location, $p = .19$. Although we observe an effect of attention condition on the magnitude of the TAE at some locations, our attention manipulation did not modulate the observed skew in the tuning of the TAE. The difference in the TAE between the perceived and antiperceived locations was not significantly different between the two attention conditions, $p = .26$.

Finally, if it is the shift in perceived location of the adaptor that causes the asymmetry in the TAE between the perceived and antiperceived test locations, then we should see a correlation across subjects between the size of the perceived shift and the size of the asymmetry. To test this, we computed the correlation across our 8 subjects between (1) the size of the FDE and (2) the TAE size at the perceived minus the size at the antiperceived location (averaged across the two attention conditions). This analysis yielded a positive correlation between these two measures, $r = .73$, $p = .04$. In other words, subjects who had a larger flash drag effect tended to have a larger difference in the TAE between the perceived and antiperceived locations. In order to correct for absolute differences in the size of the TAE across observers, we re-analyzed this correlation using normalized TAE estimates, calculated as a proportion of each observer's maximum TAE. This correlation, shown in Figure 2.4, was also significant, $r = .85$, $p = .008$. In addition, we calculated Spearman's rank correlation coefficient as a non-parametric measure of the relationship between FDE size and the difference in TAE size, which yielded a similar result, $r_s = .83$, $p = .02$.

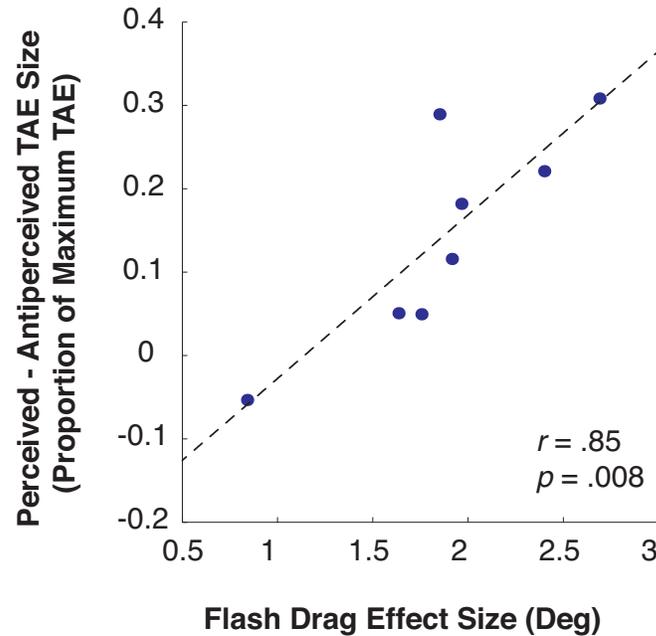


Figure 2.4. Correlation between the size of the FDE (shown in Figure 2.2B) and the difference in TAE size between the perceived and antiperceived locations in Experiment 1. Differences in TAE size are based on values normalized to the maximum TAE for each observer and each point represents one subject.

Discussion

Measurements of the TAE at the perceived, retinal, and antiperceived (control) locations of an adapting stimulus that was shifted by the FDE showed that the largest TAE was observed at the retinal location of the adapting grating, with a smaller TAE measured at the perceived and antiperceived locations. In addition, a comparison between the perceived and antiperceived locations demonstrated that the TAE was significantly greater at the perceived compared to the antiperceived location. This demonstrates that there is a skew in the spatial tuning of the TAE toward the perceived location. An attention manipulation demonstrated that this shift is similar regardless of whether attention is focused at a single adaptor location or distributed across multiple adaptor locations. Furthermore, a between-subjects analysis demonstrated that larger shifts in the perceived location of the adaptor were associated with a greater skew in the tuning of the TAE towards the perceived location of the adaptor.

Given that a greater TAE at the perceived compared to the antiperceived location is indicative of a shift in its spatial selectivity, we attempted a rough estimate of the shift in the underlying spatial tuning function required to produce the observed difference between the perceived and antiperceived locations. With only three data points, we are limited to only the simplest of models and the result can only be seen as suggestive. Given these limits, we fit the data shown in Figure 2.3A to a symmetric inverted-V shaped distribution with a linear decrease in TAE size with increasing distance from its peak. The data can be described by the equation:

$$y = -b \cdot |x - s| + m \quad (2.2)$$

where b represents the slope (equal on both sides), m represents the size of the TAE at its peak, and s represents the shift in the peak of the function from 0. Expressed as a percentage of the size of the FDE, the shift (s) in the underlying distribution of the fitted data was equal to 10.8%. In other words, based on this simple fitting procedure, the observed difference in TAE size between the perceived and antiperceived locations corresponds to a shift in the underlying TAE tuning function equal to approximately 10.8% of the size of the flash-drag effect.

Rather than producing a complete transfer of the spatial tuning to the TAE to the perceived location of the adaptor, the flash-drag effect resulted in a partial shift in its spatial tuning function, with the largest TAE still observed at the retinal location. Importantly, Experiment 1 shows that the location affected by the tilt aftereffect is not entirely dependent on the retinal location of the adapting stimulus and that it can be influenced by the perceived location of the adaptor, perhaps as a mixture of the bottom up and top down effects. In relation to motion processing, this suggests that motion can bias retinotopic coding at early stages of visual processing (i.e., at or before the level at which orientation adaptation is seen).

Experiment 2

One possible explanation for the skewed spatial tuning of the TAE is that motion shifts the retinotopically adapted region. An alternative explanation is that there is a spatially localized attentional modulation (gain) of the TAE closer to the position of the perceived adaptor. This would not require a retinotopic shift in the adapted region, but a change in the allocation of attention, which could in turn increase the size of the TAE at the perceived location, consistent with previous research demonstrating that attention increases the size of the TAE (Spivey & Spirn, 2000). In other words, the flash-drag effect might influence the distribution of top-down attention signals even when subjects are adapted only to the retinal location of the gratings. We therefore conducted an additional experiment to exclude the possibility that the observed results are due to a modulation of the distribution of attention around the adapting stimulus rather than a shift in the locus of adaptation *per se*.

The results from Experiment 1 might suggest that the attention account is unlikely, since a change in the distribution of attention around the adapting stimulus might predict a greater skew towards the perceived location in the focused attention compared to divided attention condition. Nonetheless, individuals can simultaneously attend to multiple items in parallel (e.g., Pylyshyn & Storm, 1988) and distributing attention over two locations might not be accompanied by a substantial reduction in attentional gain relative to focusing attention on one location. Moreover, the idea that the FDE could influence the distribution of attention around the adaptor is supported by a number of studies suggesting an attentional basis for motion-induced position shifts (e.g., Shim & Cavanagh, 2004, 2005). Thus, we directly examined the possibility that attentional gain might selectively boost the size of the TAE at the perceived location relative to the antiperceived location. Experiment 2 was similar to Experiment 1, with the addition of two gratings flanking each adapting grating (Fig 2.5A). The two flanking gratings had the orientation opposite to that of the central grating. The test grating could be presented in one of two possible locations (Fig 2.5C), halfway between the central grating and one of the two flanking gratings.

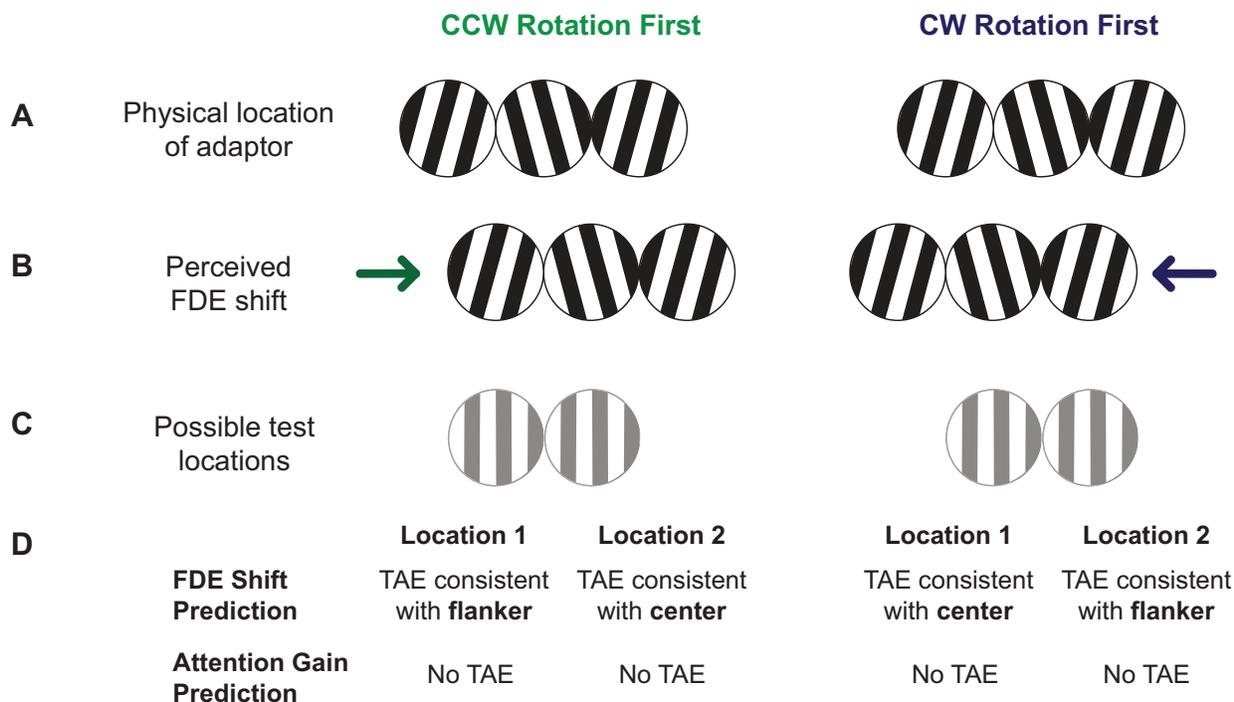


Figure 2.5. Predictions for Experiment 2. Subjects were presented with three adapting gratings, shown in A. The central grating always had the opposite orientation of the two flanking gratings. The two possible test locations (halfway between the central and each flanking grating), shown in C, were identical across the two rotation conditions. The left and right panels show the direction of the flash-drag shift (B) with the initial rotation directions in the CW and CCW directions, respectively. If the results in Experiment 1 were due to a shift in the locus of adaptation from the FDE, we would expect the relative sign of the TAE across the two test locations to switch between the two rotation conditions. An attention gain model would predict no modulation of the TAE, as partial leftward and partial rightward adaptation would cancel out.

Figure 2.5D outlines the two possible sets of results: (1) the expected results if the effect in Experiment 1 is due to a shift in the retinotopically adapted location, and (2) the expected results if the effect can be explained by attention gain. If the FDE produces a shift in the locus of adaptation, we would predict that the sign of the TAE would be modulated by the direction of the FDE. For example, with an initial clockwise rotation, the perceived location of the adaptors is shifted counterclockwise. This would result in a TAE consistent with adaptation to the central grating at one location, and a TAE in the opposite direction at the other location (consistent with adaptation to a flanker). This pattern would reverse when the FDE is in the opposite direction. Attention gain alone would predict that there would be no TAE at either of the two test locations, as adaptation to the left- and right-tilted gratings would cancel out.

Method

Participants. Five observers (3 female), including the author (AK), participated in the experiment. The mean age of the participants was 25 with a range from 23 to 30.

Stimuli. The stimulus was the same as in Experiment 1, with the addition of two flanking gratings, as shown in Figure 2.5. The central grating was tilted either 15° to the left or 15° to the right. The two flanking gratings were tilted by the same amount in the opposite direction from

the central grating. This produced two possible sets of adaptation stimuli with respect to grating orientation: (1) left, right, left or (2) right, left, right (Fig. 2.5A). The three gratings had a radius of 0.95 degrees of visual angle and a center-to-center separation of 1.9° (equal to the size of the mean FDE in Experiment 1), such that they were adjacent to one another. There were two sets of three gratings presented on each trial—one at the top of the display, and one at the bottom of the display, separated by 180° of rotation angle (similar to Fig. 2.1, but with grating triplets at the top and bottom of the rotating disk).

Procedure. The procedure was similar to that in Experiment 1. As before, a test grating was presented 100 ms after the end of the adaptation sequence for 33 ms on each trial randomly at the top or the bottom of the display. For each set of adaptation stimuli, the test grating could appear in one of two locations: either halfway between the central and left grating, or halfway between the central and right grating (Fig 2.5C). There were two possible test locations corresponding to the top of the rotating disk, and two possible test locations corresponding to the bottom of the disk, and results were collapsed across the top and bottom adaptors. As before, the initial rotation direction of the disk was blocked to maintain a consistent perceptual shift in the location of the adaptors across trials.

Results

The size of the TAE was measured at each test location using the procedure outlined in Experiment 1. In order to estimate both the size of the TAE and its direction consistent with the central grating, the size of the TAE was calculated using Equation 2.1, with “adapt left” and “adapt right” referring to the orientation of the central grating. Because the flankers were opposite in orientation to the central grating, positive TAE values correspond to an aftereffect consistent with adaptation to the central grating, and negative numbers correspond to an aftereffect consistent with adaptation to a flanking grating. The size of the TAE was normalized to each observer’s mean TAE across rotation directions at each location, such that the size of the TAE at each location reflects the difference in the TAE between initial CW and CCW rotation.

As shown in Figure 2.6, this analysis yielded a TAE consistent with adaptation to a flanking grating at Location 1 when the initial rotation was CCW and a TAE consistent with the central grating when the initial rotation was CW. This pattern was reversed at Location 2. As in Experiment 1, the data were analyzed by bootstrapping each subject’s responses with 1000 samples. At Location 1, the TAE was greater in the CW-first rotation condition compared the CCW-first rotation, $p = .008$. There was a trend toward the reverse pattern at Location 2, $p = .13$. The difference in the TAE between the initial CW and CCW conditions was significantly different across the two test locations, $p = .004$. This significant interaction demonstrates a reversal in the TAE across rotation conditions between the two test locations.

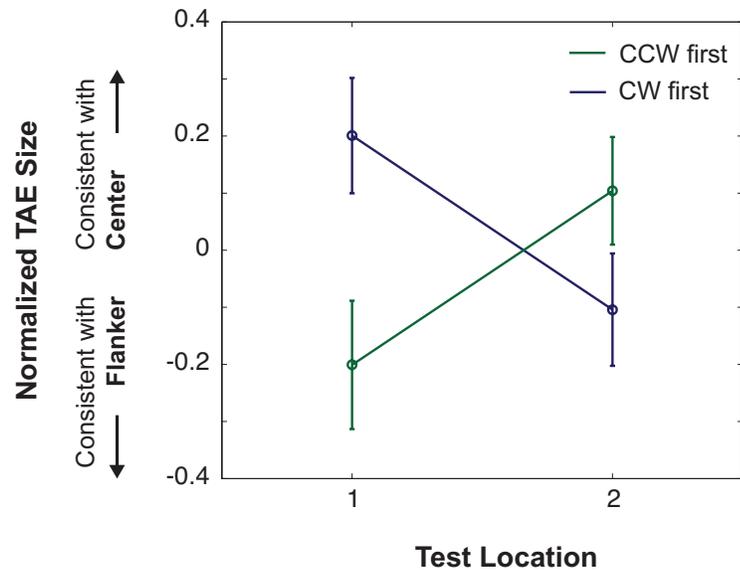


Figure 2.6. Size of the TAE as a function of test location in Experiment 2. Test location 1 corresponds to the perceived location of a flanker with initial CCW rotation and to the location of the central grating with initial CW rotation. Test location 2 corresponds to the perceived location of the central grating when the initial rotation is CCW and to the perceived location of a flanking grating when the initial rotation is CW. Physically, the two test gratings are positioned halfway between the central grating and each flanker. Results show that at test location 1, the TAE is consistent with adaptation to the central grating with initial CW rotation and consistent with adaptation to a flanker with initial CCW rotation. This pattern reverses at test location 2. TAE values are normalized to each subject's mean TAE at each location and error bars represent bootstrapped ± 1 SD.

Discussion

The purpose of Experiment 2 was to determine whether attentional gain could account for the results in Experiment 1. One possible explanation for a skew in the spatial tuning of the TAE towards the perceived location of the adaptor is that top-down attention signals might selectively boost the TAE at the perceived compared to the antiperceived location. We tested for this possibility by adding two flanking gratings on either side of the adaptor and opposite in orientation. With the test locations halfway between the central and flanking gratings, an attention *gain* explanation would predict that partial adaptation to left- and right-tilted gratings would cancel out. On the other hand, if our results are due to a *shift* in the locus of adaptation, we would expect the relationship between TAE size at the two locations to reverse across the two rotation directions. Our results were consistent with the second explanation, suggesting that a selective top-down attentional modulation at the perceived location cannot account for the findings in Experiment 1. Two further experiments were conducted to exclude systematic eye movements as an explanation for our findings.

Experiment 3

The aim of Experiment 3 was to exclude cyclotorsional eye movements as a possible explanation for the findings in Experiment 1. One possibility is that viewing the rotating disk causes the observer's eyes to rotate, which could shift the retinal (and perceived) location of the adapting grating. This could potentially produce a skew in the spatial tuning of the TAE, as

found in 2.3. This explanation is unlikely, as previous work has shown that torsional eye movements cannot account for the position shifts associated with the flash-drag effect (Whitney & Cavanagh, 2000). Nevertheless, we further test the cyclotorsion account in Experiment 3 using our stimulus and design.

In Experiment 3, we attempted to exclude the possibility of cyclotorsion by canceling out the net motion in the stimulus. As shown in Figure 2.7, we presented two disks rotating in opposite directions to eliminate any net motion, making cyclotorsional eye movements unlikely.

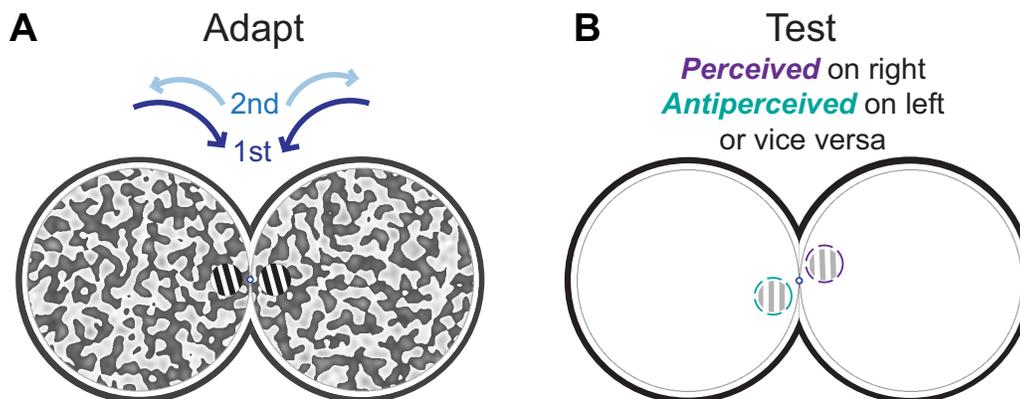


Figure 2.7. Adaptation (A) and test (B) stimuli in Experiment 3. Initial inward, followed by outward rotation (A) produces a flash-drag effect that shifts the perceived location of the adaptor above fixation. In the test display (B), a grating was presented at the perceived location on one side of the disk and at the antiperceived location on the other side of the disk. Subjects were asked to judge which of the two test gratings was tilted more to the right.

Method

Participants. Three observers (1 female), including the author (AK) and one experimenter (GM), participated in the experiment. The mean age of the participants was 26 with a range from 23 to 29.

Stimuli. The stimulus was the same as in Experiment 1, with the following exceptions:

Two rotating disks were presented, one in each hemifield. The radius of each disk was 7 degrees. Subjects fixated on an outlined circle $.25^\circ$ in diameter (blue outline on either side was 0.1°) while the two disks, centered 7 deg to the left and right of fixation, rotated in opposite directions. At every other rotation reversal, two square wave gratings, 1° in radius, 1.5cpd, were presented, centered 1.5° to the left and right of fixation. The gratings were both tilted either 15 to the left or to the right on each trial. The adaptation sequence was otherwise the same as in Experiment 1. This rotation sequence resulted in a flash-drag effect that produced a shift in the perceived locations of the adaptors either above or below the fixation point on any given trial.

Procedure. As in Experiment 1, this experiment consisted of two parts—a flash-drag measurement and a TAE measurement.

Flash-drag effect measurement. We measured the FDE individually for each observer using a procedure similar to that used in Experiment 1. In a 2AFC task, subjects were asked to judge whether the two gratings were above or below the fixation point. The gratings were presented at one of 7 locations relative to the horizontal midline of the display: -1.5 , -1 , -0.5 , 0 , $+0.5$, $+1$, or $+1.5$ degrees of visual angle.

Tilt aftereffect measurement. Following an ISI of 100 ms, subjects were presented with a test stimulus. The test stimulus consisted of two square wave gratings identical to those in Experiment 1. Based on measurements of the FDE for individual observers, the two gratings were positioned such that the test grating on the left side was at the perceived location of the adapting stimulus and the grating on the right side was at its antiperceived location, or vice versa. The tilt of the test grating at the antiperceived location was always 0 degrees, while the tilt of the test grating at the perceived location was varied between -6 and +6 degrees of rotation angle (left to right).

Observers were asked to judge which of the two gratings (left or right) was tilted more to the right. If there is any effect of perceived position on the TAE, one would expect a difference in orientation judgments between the two adaptation directions.

Results

Flash-drag effect measurement. As in Experiment 1, the FDE was measured individually for each observer using the method of constant stimuli. The mean FDE across subjects was 0.61 degrees of visual angle ($SD = 0.11^\circ$), and was significantly above zero, $p < .001$.

Tilt aftereffect measurement. To estimate the difference in the size of the TAE between the perceived and antiperceived locations, we compared orientation judgments between the two adaptation directions. For each adaptation direction (15° to the left and 15° to the right), we calculated the proportion of responses that the test grating at the perceived location was tilted more to the right. This provides an estimate of the difference in the size of the TAE between the perceived and antiperceived locations. For instance, in the adapt left condition, when the test gratings are both vertical, if the grating at the perceived location is judged more right-tilted than the grating at the antiperceived location, this indicates a tilt aftereffect that is larger at the perceived compared to the antiperceived location. The orientation of the test stimulus at the perceived location was varied to obtain two full psychometric functions, one for each adaptation condition.

The difference between the PSEs of the two psychometric functions, shown in Figure 2.8, was bootstrapped for each subject with 1000 samples. Each bootstrapped sample was then averaged across subjects. The difference between the two adaptation directions was significant, $p = .02$.

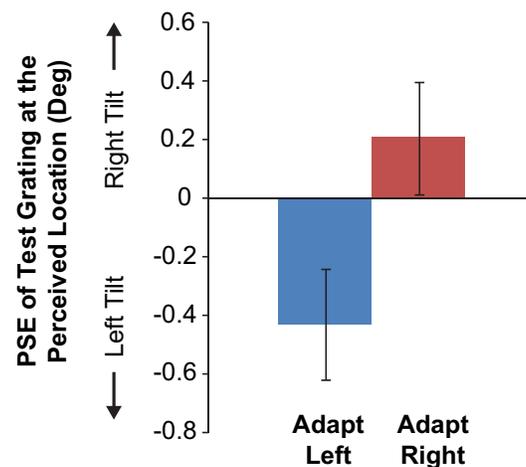


Figure 2.8. Results from Experiment 3. The PSEs (the tilt of the test grating at the perceived location that produces a vertical percept) in the adapt left and adapt right conditions were consistent with the TAE. For instance, adaptation to a left-tilted grating produces a percept of a

rightward-tilted grating when the grating at the perceived location is vertical. A leftward tilted test grating is required to cancel the illusion. Error bars represent bootstrapped ± 1 SD.

Discussion

In Experiment 3, we used a stimulus with balanced retinal motion to exclude the possibility that the perceived location of the adaptor in Experiment 1 was confounded with its retinal location. A comparison of the TAE at the antiperceived and perceived locations demonstrated that the TAE was still greater at the perceived compared to the antiperceived location when the stimulus had balanced rotating motion. However, one further possibility is that vertical and horizontal eye movements may account for the results.

Experiment 4

We conducted a final experiment to exclude eye movements as explanations for the findings in Experiment 3. With the configuration in Experiment 3, it is possible that the stimulus produces vertical eye movements from the downward and upward motion at the center of the stimulus display or perhaps still produces some cyclotorsion if the subject attends to one or the other of the two rotating rings. These various eye movements are unlikely to account for these findings and should have been controlled by the dual rings and by the presence of the stable fixation point. Nevertheless, we can easily measure the effect of eye movements of any kind as they must have an effect that is specific to the eye movement (rotation or translation) and affect the whole visual field independently of the location of the moving texture. Any eye-movement induced effect should therefore be the same on locations overlying the moving texture and appropriate comparison locations that do not overlie the moving texture.

In a dual-task design, subjects were asked to respond to both (1) the positions of two black dots presented above and below fixation, *off the rotating disk*, and (2) the positions of two gratings presented *on top of the disk* as a measurement of the flash-drag effect. If eye movements are the source of the perceived shifts in position, we would expect to find equivalent shifts in position judgments of the two black dots as well as the two gratings as a function of disk-motion direction.

Method

Participants. Three observers (1 female), including the author (AK), participated in Experiment 4. The mean age of the participants was 25 with a range of 23 to 26.

Stimuli. Stimuli were the same as in Experiment 3, with the following exceptions: As shown in Figure 2.9, two black circles were presented 5° above and below fixation (center-to-center) at the same time as the circular gratings. The circular gratings were positioned such that one grating was presented in the same location as in Experiment 3, near the fixation point, while the other was presented on the opposite edge of the disk. The gratings changed configuration randomly from trial-to-trial.

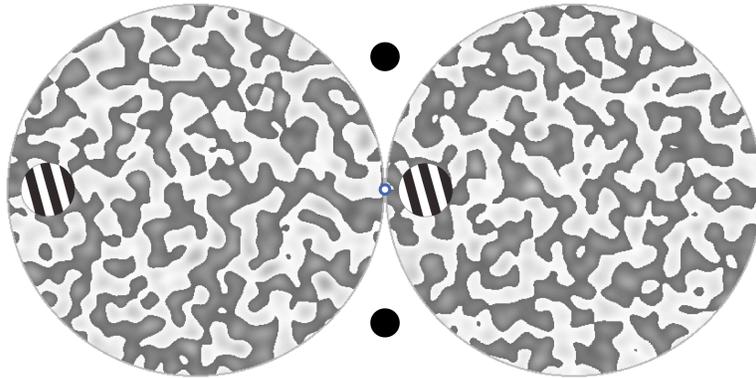


Figure 2.9. Stimulus used in Experiment 4. As in Experiment 3, the disks oscillated inward and outward. At every other rotation reversal, subjects were presented with two square wave gratings on the rotating disks—one close to fixation and one on the opposite end of the adjacent disk. In addition, subjects were presented with two dots, one above and one below the fixation point. At the end of the trial, subjects were asked to judge either (1) whether the top dot was positioned to the right or left of the bottom dot, or (2) whether the outer grating was above or below the inner grating.

Procedure. Two sets of measurements were obtained in parallel in Experiment 4—a measurement of dot position judgments and a flash-drag effect measurement.

Dot position judgments. The relative positions of the two dots were varied from trial to trial. On each trial, the dots were positioned in one of 7 locations relative to the vertical midline: -0.3 , -0.2 , -0.1 , 0 , $+0.1$, $+0.2$, and $+0.3$ degrees of visual angle (from left to right). The bottom dot was shifted by the same amount in the opposite direction from the top dot.

Flash drag effect measurement. In addition, we varied the relative positions of the two circular gratings. The position of the grating near fixation was held constant, and the vertical position of the outer grating was varied on each trial. The outer grating was presented in one of 7 positions relative to the horizontal midline: -3 , -2 , -1 , 0 , $+1$, $+2$, and $+3$ degrees of visual angle (from above to below).

At the end of each trial, subjects were prompted to respond to either the position of the two dots or to the positions of the gratings. In the dot position judgment task, subjects were asked to judge whether the top dot was to the left or to the right of the bottom dot. In the grating position judgment task (flash-drag measurement), subjects were asked to judge whether the more eccentric grating was positioned above or below the grating closer to fixation. Subjects did not know at the start of each trial which judgment they would be asked to make.

Results

Dot position judgments. We compared position judgments of two dots presented above and below fixation between the two disk rotation directions. Figure 2.10A shows the psychometric curve of responses pooled across all subjects as a function of dot position. The mean PSE across the three subjects was $.004$ degrees of visual angle ($SD = .04^\circ$) in the inward-first rotation condition, and $.008^\circ$ ($SD = .03$) in the outward-first rotation condition.

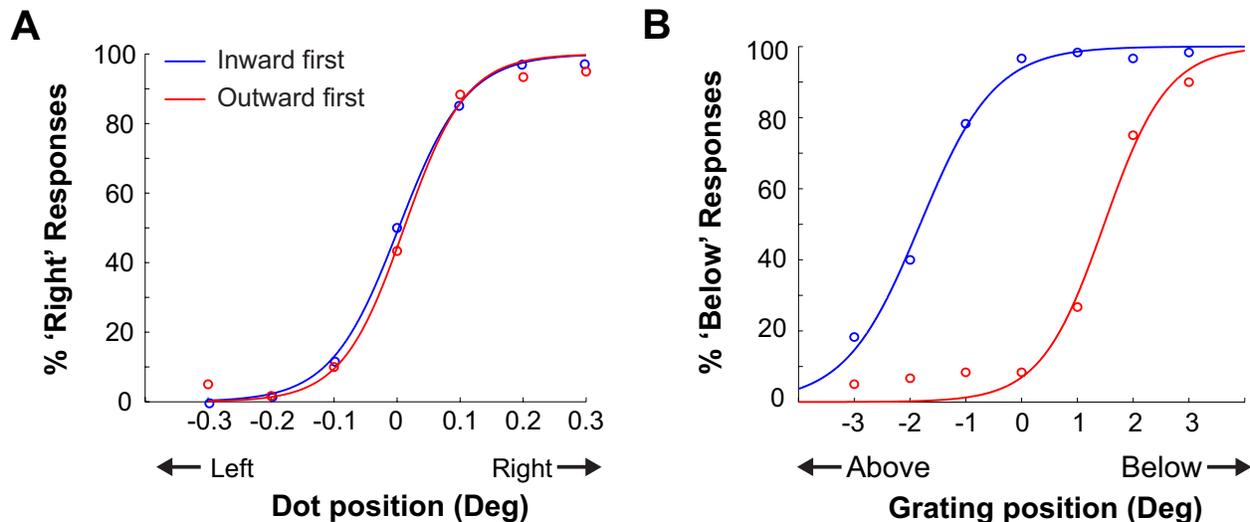


Figure 2.10. (A) Dot position judgment data from Experiment 4. Subjects were asked to judge the positions of two dots above and below fixation. Each curve plots the percent of responses that subjects judged the top dot to the right of the bottom dot for each of the two rotation directions. (B) Grating position judgments from Experiment 4. The curves show the percent of responses that subjects judged the more eccentric grating to be positioned below the grating closer to fixation. The difference between the psychometric functions is consistent with a flash-drag effect. Each psychometric function is pooled across all three observers.

The difference between the two psychometric functions was bootstrapped for each subject with 1000 samples. Each bootstrapped sample was then averaged across subjects. The difference between the two motion directions was not significant, $p = .32$.

Flash drag effect measurement. Using the same flash-drag effect calculation as in Experiments 1 and 2, the FDE was estimated to be equal to half the difference between the PSEs in the two rotation direction conditions. Figure 2.10B shows the psychometric function for all subjects across grating positions. The mean FDE was 1.62 degrees of visual angle ($SD = .38^\circ$) and was significantly greater than zero, $p < .001$. The size of the FDE is comparable to that measured in Experiment 1 (1.88°).

Discussion

In a dual-task design, we obtained separate estimates of the perceived positions of two dots above and below fixation presented off the rotating disks, and of two gratings presented on the rotating disks (Figure 2.9). Results showed that subjects were able to accurately judge the positions of the two dots, and that their perceived locations were not affected by the direction of the disks' rotation. As eye movements due to the disk's rotation should bias position judgments of the dots as much as the gratings, the findings in Experiment 4 demonstrate that eye movements cannot account for the results in Experiment 3.

Moreover, subjects mislocalized the positions of the two gratings presented on the disk consistent with the flash-drag effect, which shifts the perceived locations of the two gratings in opposite directions. For example, with the configuration of gratings shown in Figure 2.9, initial inward (i.e., CW rotation of the left disk) produces both (1) a downward shift in the perceived position of the more eccentric grating and (2) an upward shift in the perceived vertical position

of the grating near fixation. As the FDE requires vertical shifts in opposite directions, vertical eye movements due to the motion near the fixation point are unlikely to produce these results.

General Discussion

We employed a novel method to examine the effects of motion on the spatial profile of low-level adaptation. By presenting adapting gratings shifted in position by the flash-drag effect, we were able to compare the size of the tilt aftereffect at a set of locations around the adaptor. Experiment 1 showed that the tilt aftereffect is greatest at the retinal location of the adapting stimulus, and that it is larger at the perceived location relative to a control (antiperceived) location. This is indicative of a skew in the tuning of the TAE towards the perceived location of the adaptor. Experiment 1 further demonstrated that this effect is no different when subjects divide their attention between two adaptors compared to when there is only one adapting stimulus. Experiment 2 excluded a change in the gain or distribution of attention around the adapting stimulus as an explanation for the findings in Experiment 1. Rather, the results were consistent with a shift in the adapted location, caused by the motion of the disk. Experiments 3 and 4 additionally excluded the possibility that cyclotorsional or vertical eye movements produced a shift in the retinal location of the adaptor, confounding it with its perceived location.

These findings are consistent with previous research showing that the tilt aftereffect does not depend entirely on the physical properties of the adapting stimulus. Specifically, Arnold et al. (2008) found that perceived size could influence the spatial profile of the TAE. Similarly, our results suggest that the spatial location of the TAE is influenced by the perceived location of the adaptor when it is shifted by a motion-based illusion. Given that there is strong evidence that adaptation of orientation tuned cells in V1 underlies the tilt aftereffect (e.g., Maffei, Fiorentini, & Bisti, 1973; Movshon & Lennie, 1979), any shift in the spatial tuning of the TAE away from its retinal location would indicate a change in the spatial coding of the adaptor in early visual cortex. In relation to our findings, this would suggest that motion influences retinotopic coding early in visual processing, which in turn biases the spatial tuning of the TAE. Recent evidence using multivariate analysis of fMRI activation patterns points to similar conclusions (Maus, Fischer, & Whitney, 2009). Together, our results provide evidence that motion can influence retinotopic coding at early stages of visual processing.

One remaining question is why the TAE is not largest at the perceived location of the adaptor. If there was a complete shift in retinotopic coding due to surrounding motion, one would expect the TAE to be largest at the perceived location, second largest at the retinal location, and smallest at the antiperceived location. Instead, the TAE remains greatest at the retinal location, with a skew towards the perceived location of the adaptor. One possibility is that the TAE depends partially on both the perceived and physical position of an adaptor. There is also evidence to suggest that V1 retains coding of physical position to a greater degree than other visual areas (Fischer, Spotswood, & Whitney, 2011). Aftereffects probing later stages in visual processing might exhibit larger shifts toward the perceived location of the adaptor. For instance, as physiological data has shown that motion can produce receptive field shifts in V4 (Sundberg et al., 2006), it is possible that the flash drag effect might produce an even larger shift in the spatial tuning of a color-contingent aftereffect. Future research might examine other types of aftereffects to examine where motion has its effects on spatial representations in visual cortex.

Nonetheless, effects of motion on receptive field profiles have been shown as early as V1 (Fu et al., 2004) and the retina (Baccus & Meister, 2003). In this study, we were able to demonstrate a correspondence between the psychophysical and physiological literature regarding the basis of motion-induced position shifts. Using a psychophysical paradigm, we demonstrated

that motion can influence coding of object features early in the visual processing stream. Future research might be directed towards establishing a more comprehensive connection between these effects and those seen in neurophysiological studies.

Chapter 3: Visual motion shifts saccade targets

Accurate object localization is absolutely crucial for action. Object localization presents a challenge for the saccade system in particular, as the targets of saccades are frequently moving across the retina either because they move or because our heads are moving through the world. Neural processing delays might therefore produce differences between the physical and registered location of a target. In particular, visual input cannot influence saccade programming within the last 80-100 ms before saccade onset (Aslin & Shea, 1987; Becker & Jürgens, 1979; Findlay & Harris, 1984) and the saccade system incurs additional delays due to the time required to execute the eye movement (Carpenter, 1988). Therefore, being able to predict where an object will be is of the utmost importance, and previous work has shown that saccades to moving objects reflect a prediction about the future location of an object (Gellman & Carl, 1991; Keller & Steen Johnsen, 1990; Kim, Thaker, Ross, & Medoff, 1997; Robinson, 1973; Ron, Vieville, & Droulez, 1989).

However, it is an open question what source of information, or combination of sources, might be used to perform this prediction. A number of previous studies have shown that physical changes in the position of an object or the motion of an object can be used to guide saccade targeting. For instance, changes in the position of an object over time might be used as an error signal to predict the future location of the saccade target. This is supported by studies demonstrating that the changing location of the target (for example, in a double-step paradigm) can guide saccade targeting (e.g., Becker & Jürgens, 1979; Deubel, Wolf, & Hauske, 1982; Westheimer, 1954). In addition, previous work has shown that velocity information can be used to anticipate the future locations of saccade targets (e.g., Etchells, Benton, Ludwig, & Gilchrist, 2010; Gellman & Carl, 1991; Keller & Johnsen, 1990; Robinson, 1973; Ron et al., 1989). These results are consistent with neurophysiological studies suggesting that neurons in the frontal eye fields (FEF) encode information about the velocity of saccade targets (Barborica & Ferrera, 2003; Cassanello, Nihalani, & Ferrera, 2008).

In addition to the changes in the position of the target, or the presence of target motion, another possibility is that position information may be updated in the absence of any changes in the target's location. For example, previous work has shown that saccades to targets near a moving object are shifted in the direction of the object's motion, even though the targets themselves do not change their physical location (de'Sperati & Baud-Bovy, 2008; Zimmermann, Morrone, & Burr, 2012). These effects may be similar to the influence of background motion on reaching movements (Gomi, Abekawa, & Nishida, 2006; Saijo, Murakami, Nishida, & Gomi, 2005; Whitney & Goodale, 2005; Whitney, Westwood, & Goodale, 2003). In this case, it is unclear whether the motion shifts the programmed location of the stationary saccade target, or whether the saccade errors are due to the presence of motion in the display.

The aim of the present study, then, was to test whether motion can influence the registered location of the stationary object, which in turn could be used to guide saccade targeting. To do so, we took advantage of a perceptual illusion that shows an influence of motion on object location (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990; see Whitney, 2002 for a review) while independently controlling both the target location and the retinal motion that is present. We presented subjects with drifting Gabor patches to examine whether the shift in registered location holds for saccadic targeting as well as perceptual localization. Prior work has shown that the motion of a sinusoidal grating (i.e., the carrier) within a Gaussian contrast envelope (blurred aperture) results in an apparent displacement of the entire stimulus in the

direction of motion, while the aperture itself remains stationary (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990). As shown in Figure 3.1A, the soft aperture condition results in a shift in the perceived location of the Gabor in the direction of the grating's motion even though the aperture location does not change. However, presenting the same grating within a hard aperture, as illustrated in Figure 3.1B, greatly reduces the size of the illusion (Whitney et al., 2003; Zhang, Yeh, & De Valois, 1993).

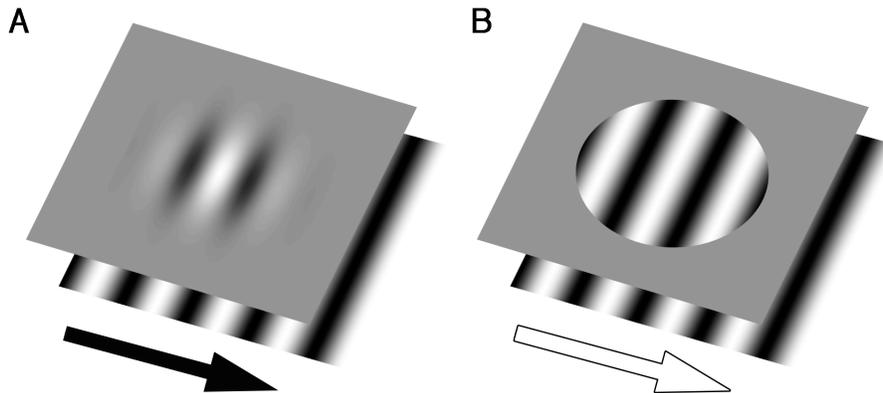


Figure 3.1. (A) Soft aperture stimulus, consisting of a sinusoidal carrier within a static Gaussian contrast envelope. The sinusoid moves continuously to the right while the aperture remains stationary. In this condition, the perceived location of the Gabor is shifted to the right. This illusion is greatly reduced in (B) when the Gaussian envelope is replaced with a hard circular aperture. Critically, the same surface motion is present in the hard aperture condition, but no illusion is generated in this condition. The present experiments tested whether this motion-induced shift in position assignment with a Gabor patch can influence saccade targeting.

This simple stimulus is well-suited to examining the effects of motion-induced position shifts on saccade landing location for several reasons. First, unlike many other motion-induced position illusions (Whitney, 2002), the position shift resulting from drifting Gabors is continuously present. As a result, saccade programming can occur while the stimulus is still visible. Second, unlike stimuli used in previous studies (Zimmermann et al., 2012), the illusory position shift of the saccade target is a direct consequence of its own motion, rather than the background. Most importantly, this stimulus allows us to dissociate the target's motion from the target's location. We can therefore examine whether previous results showing a shift in either pointing responses (Yamagishi, Anderson, & Ashida, 2001) or in saccade landing location (Kerzel & Gegenfurtner, 2005) to drifting Gabors might be explained by the presence of motion energy or by a shift in the programmed location of the Gabor.

Experiment 1A

Introduction

Our first experiment examined whether motion influences position assignments for the saccade system. Simply put, is the illusory displacement of the Gabor reflected in saccade landing location? We would expect one of two outcomes – either the saccade would land at the physical location of the Gabor patch, regardless of the carrier motion direction, or saccades would be shifted in the direction of the carrier motion, consistent with the perceptual

mislocalization of the Gabor reported by subjects in previous studies (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990).

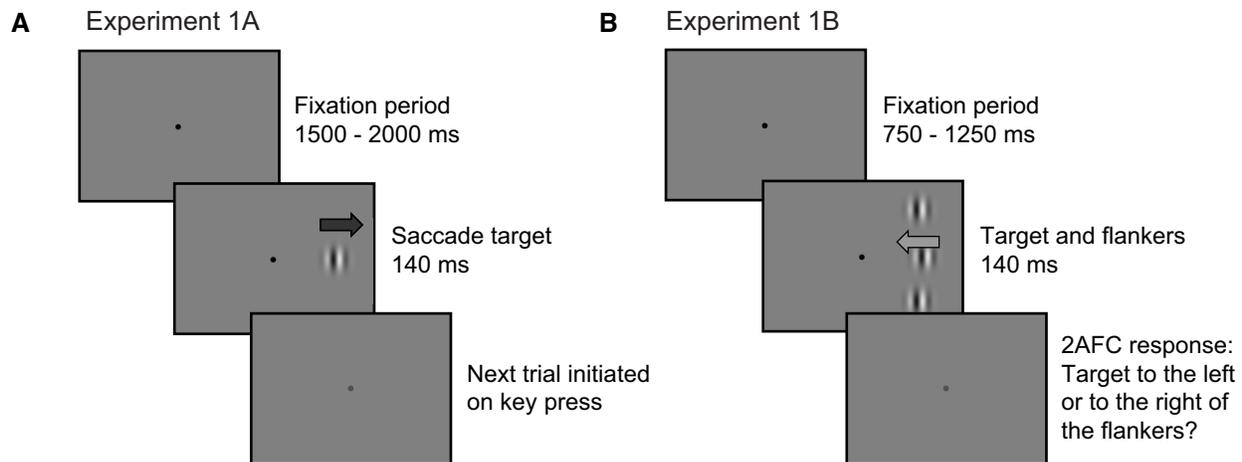


Figure 3.2. Trial Sequence for Experiments 1A (left panel) and 1B (right panel). In Experiment 1A, subjects fixated for a random interval and were instructed to saccade to the center of a target (either a Gabor, shown here, or a sinusoidal grating within a hard aperture) in the left or right visual field as quickly as possible. Subjects then initiated the next trial by pressing a key. The trial sequence in Experiment 1B was similar, with the addition of two static flankers, one above and one below the target. Subjects were instructed to maintain fixation and to respond to the offset of the target (left or right) relative to the two flankers. Arrows represent the direction of Gabor drift and were not presented to subjects.

In the first part of this experiment (Figure 3.2A), we presented subjects with two types of saccade targets—(1) drifting Gabor patches and (2) sinusoidal gratings within hard circular apertures. We measured the landing locations of the initial saccade to each of these stimuli. The inclusion of hard aperture stimuli allowed us to present the same stimulus motion with a reduced shift in perceived position (Arnold, Thompson, & Johnston, 2007; Whitney, Goltz, et al., 2003; Zhang et al., 1993). This allowed us to control for stimulus motion while only generating a shift in perceived location in the soft aperture condition. In Experiment 1B, we measured the perceptual magnitude of the illusory motion-induced position shift and compared those measurements with the illusion's effect on saccade landing position observed in Experiment 1A.

Method

Subjects. Six subjects (4 females), including the author (AK) and one experimenter (BW), participated in the experiment (mean age: 24.2, $SD = 2.5$). All observers reported normal or corrected-to-normal vision and all except the author were naïve to the purpose of the experiment.

Eye tracking. Eye movements were recorded with an EyeLink 1000 desktop mounted infrared eye tracker (SR Research Ltd., Mississauga, Ontario, Canada) used in conjunction with the EyeLink Toolbox scripts for Matlab (Cornelissen, Peters, & Palmer, 2002). Only the right eye was recorded for each subject. Subjects were calibrated with a standard 9-point calibration procedure before completing each block of trials (average error $< 0.5^\circ$). The first time point at which the velocity exceeded $30^\circ/s$ and the acceleration exceeded $8000^\circ/s^2$ was parsed as the beginning of a saccade. In addition, a motion threshold was used to delay the start of each

saccade until the eye had moved at least 0.15° . Time points at which the velocity and acceleration fell below their respective thresholds were used to determine the end of each saccade.

Stimuli and Procedure. Stimuli were presented on gamma-corrected Samsung SyncMaster 997DF monitor controlled by a Mac Mini (Apple, Inc.). The program was written in MATLAB (The MathWorks, Inc.) using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Display resolution was set to 1024×768 and the refresh rate to 100 Hz. Subjects viewed the stimulus binocularly and head position was stabilized with a chinrest at a viewing distance of 57 cm. At this distance, 30 pixels subtended approximately 1° of visual angle.

Stimuli were presented on a gray background (72.2 cd/m^2). Gabors had a spatial frequency of 0.75 cpd and had a peak contrast of 85%. The standard deviation of the contrast envelope was 0.65° . On half the trials, a sinusoidal grating with a circular hard aperture (1.4° radius, uniform contrast envelope) was presented instead of a Gabor. These gratings had a peak contrast and spatial frequency identical to the Gabors (Figures 3.1A and 3.1B).

Subjects began each trial by fixating on a dark gray circle (7.4 cd/m^2 ; 0.17° radius) at the center of the screen and initiating the trial by pressing the spacebar (Figure 3.2A). The fixation point then changed to black, and following a delay interval (selected at random between 1500 and 2000 ms on each trial), subjects were presented with a saccade target in either the left or right visual field. On half the trials, the target was a Gabor, and on the other half of the trials, the target was a sinusoidal grating within a hard circular aperture. The central position of the saccade target was jittered around a point 10° to the left or right of fixation. The range of possible jittered positions spanned 3° horizontally and 3° vertically (maximum deviation of 1.5° in any direction). The position was selected randomly on each trial to avoid stereotyped saccades (see Results section and Figure A3 in Appendix A). The bars of the sinusoid inside the aperture drifted either left or right with a temporal frequency of 4 Hz ($5.33^\circ/\text{s}$). The initial phase of the grating was randomly selected on each trial from a set of 25 possible phases.

The saccade target was presented for 140 ms, and subjects were instructed to saccade to the center of the target as soon as it appeared. The fixation dot changed back to gray 240 ms following the offset of the Gabor to signal the end of the trial. Following the completion of the saccade, subjects were instructed to move their eyes back to the fixation point and initiate the next trial manually by pressing the spacebar. Subjects each completed a single block of 400 trials. Subjects did not know in advance on any trial whether the saccade target would be in the left or the right visual field, its motion direction, or whether the target would have a soft aperture (Gabor) or a hard circular aperture. Visual field location (left or right), aperture type (soft or hard), and motion direction (left or right) were counterbalanced across trials.

Data Analysis. The data were drift-corrected offline and the x- and y- coordinates of the eye position at the end of the first large saccade on each trial were used to determine saccade landing location. Trials on which subjects made a saccade too early (in the 1000 ms prior to stimulus onset), blinked immediately prior to the saccade, or failed to make a saccade were excluded from the analysis. In addition, we excluded trials on which saccade landing locations deviated by more than 2.5° horizontally or vertically from the center of the saccade target. Together, this resulted in the removal of an average of 12.1% of trials per subject from the analysis. We repeated our analyses, excluding trials on which landing locations deviated by more than 4.5° from the center of the saccade target. This analysis resulted in the removal of 4.6% of the trials and yielded similar results (for a complete analysis at several window sizes, see Figures A1 and A2).

The data were then normalized individually for each subject to correct for any possible saccadic undershoot (Becker & Fuchs, 1969; Carpenter, 1988). Saccadic undershoot resulted in saccades to the right visual field landing slightly to the left of the saccade target and saccades to the left visual field landing slightly to the right of the target. In order to correct for this commonly reported and systematic bias, we first separately calculated the mean x-coordinates of the landing locations for the left and right motion directions within each aperture and hemifield condition for each subject. Then, the mean landing location within each condition was subtracted from the landing location on each trial for that condition. This was repeated for each possible combination of hemifield and aperture condition. The resulting normalized landing locations were pooled together across the left and right hemifields and then averaged to obtain an estimate of the mean shift in landing location resulting from the carrier motion. This analysis was repeated for each of the six subjects. The distance of each landing location from the mean of the set of normalized landing locations corresponds to the saccade error, in degrees, produced by one direction of motion. Here, positive values represent saccade landing locations consistent with direction of motion and negative values indicate saccade landing locations away from the direction of motion (regardless of whether the motion was leftward or rightward on any given trial).

Results

As expected, the trial-to-trial variations in the central position of the saccade target influenced subjects' saccade landing positions. Each subject showed a strong positive correlation between the jittered horizontal location of the saccade target and saccade amplitude, indicating that subjects did not simply saccade to the same location on every trial. The within-subject correlations ranged from 0.57 to 0.77 with a mean correlation of 0.68 (all p values < 0.001). These correlations were similar for both short and long latency saccades (see Figure A3). The mean saccade latency across subjects was 229 ms ($SD = 53.5$ ms).

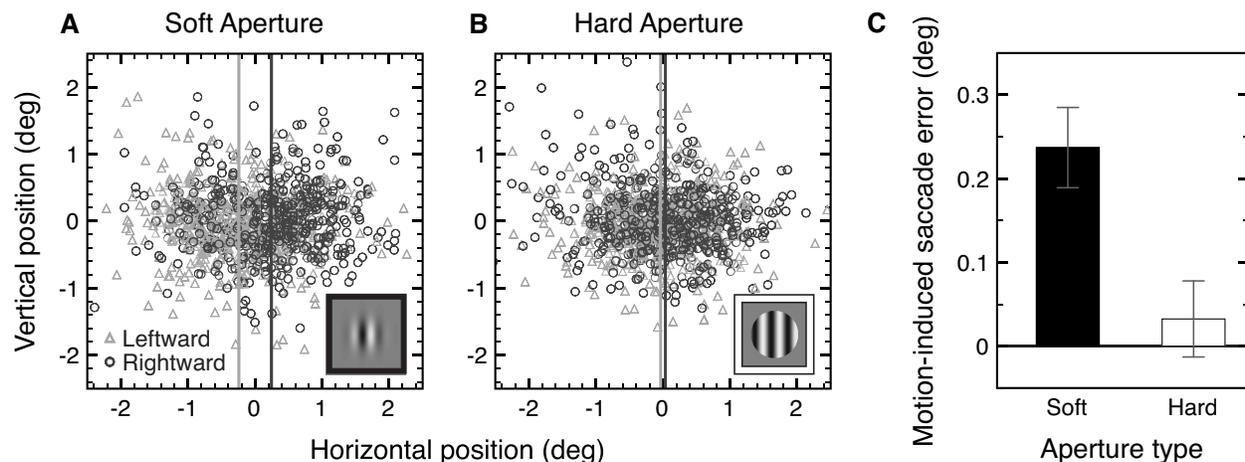


Figure 3.3. (A) Normalized horizontal and vertical saccade landing locations for the soft aperture condition for both the leftward (triangle) and rightward (circle) motion conditions for all subjects. The two vertical lines represent the mean saccade landing locations for each motion conditions (B) Normalized saccade landing locations and means for the hard aperture condition. (C) Mean saccade error (resulting from one direction of motion) across subjects within the soft and hard aperture conditions. Error bars represent bootstrapped 95% confidence intervals.

Figures 3.3A and B show the set of normalized saccade landing positions across all subjects for the soft and the hard aperture conditions. Based on the normalized landing positions, we calculated the saccade error produced by the carrier motion. As shown in Figure 3.3C, the mean saccade error was 0.24° for the soft aperture condition and 0.03° for the hard aperture condition. Saccade precision, discounting the effect of stimulus motion, was similar between the soft and hard aperture conditions (see Figure A4).

To compare the effect of motion direction for the soft aperture and hard aperture conditions separately, we performed nonparametric bootstrap tests (Efron & Tibshirani, 1993). The mean saccade error was bootstrapped by resampling each subject's data 1000 times with replacement. The bootstrapped estimates of saccade error were then averaged across the six subjects. The saccade error resulting from the stimulus motion was significantly greater than zero for the soft aperture condition ($p < 0.001$), but not for the hard aperture condition, $p = 0.16$ (two-tailed). The difference in the effect of motion between the two aperture conditions was significant, $p < .001$.

Finally, we tested whether the effect of motion on saccade landing position depended on subjects' saccade latencies. In the soft aperture condition, mean saccade error was negatively correlated with mean saccade latency across the six subjects (Spearman's rho: $r_s = -0.89$, $p = 0.03$). In other words, subjects with shorter-latency saccades had larger saccade errors in the direction of the target's motion. This correlation was not significant in the hard aperture condition ($r_s = 0.03$, $p = 1$).

To test the relationship between saccade latency and the effect of motion on landing position on a trial-by-trial basis, we combined the single-trial data from the six subjects. For both the soft aperture and the hard aperture trials, saccade error was negatively correlated with saccade latency across trials (soft aperture: $r = -.15$, $p < .001$; hard aperture: $r = -.09$, $p = .002$). Shorter-latency saccades were associated with larger saccade errors in the direction of the target's motion.

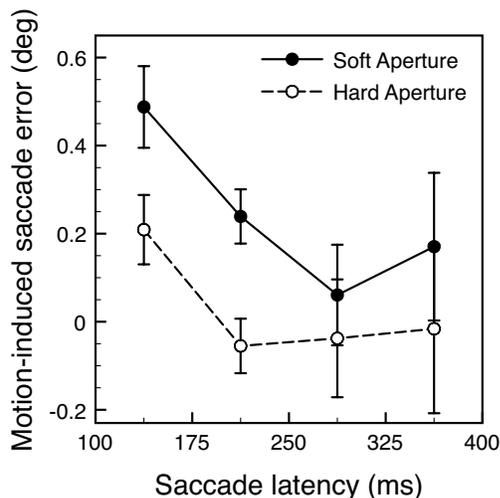


Figure 3.4. Saccade error, represented as the shift in saccade landing location resulting from one direction of motion as a function of saccade latency for both the soft (filled circles) and hard (open circles) aperture conditions. Single-trial data were pooled across subjects, then sorted into one of four latency bins. Numbers with tick marks on the x-axis represent the latency bin edges

and values are plotted at the bin centers. Error bars represent bootstrapped 95% confidence intervals.

In addition, we binned the data according to saccade latency into four evenly spaced bins between 100 and 400 ms and calculated the average saccade error by averaging the single-trial saccade errors within each bin. Figure 3.4 shows the saccade errors at each latency bin for the soft and hard aperture conditions separately. Consistent with the correlation analyses, shorter saccade latencies were associated with larger saccade errors. The majority of saccade latencies exceeded the 140 ms duration of the drifting Gabor stimulus, which prevented postsaccadic foveation of the stimulus on most trials.

Discussion

In the soft aperture condition, we found that the direction of the carrier motion biased subjects' saccade landing locations. When the Gabor drifted leftward, subjects' saccades landed more leftward, on average; when it drifted rightward, subjects' saccades landed more rightward (Figures 3.3A and 3.3C). This is consistent with the direction of the illusory displacement in perceived location reported in previous studies (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990). Notably, we do not find this result in the hard aperture condition; with a hard aperture stimulus, subjects' saccades were not influenced by the direction of the grating's motion (Figures 3.3B and 3.3C). This is consistent with previous findings describing a reduction in this perceptual mislocalization with a hard aperture (Whitney et al., 2003; Zhang et al., 1993).

The lack of an effect of motion direction on saccade landing location in the hard aperture condition indicates that subjects' saccades were not directed to the individual bars of the sinusoidal grating, since the motion of the bars is identical for the soft and the hard aperture conditions. The presence of motion alone is therefore insufficient to bias saccade landing locations. Moreover, a shift in physical position is not required to bias saccade targeting, as the physical location of the aperture does not change between the leftward and rightward motion conditions. Together, these results suggest that motion can shift the represented target position for saccades.

In addition, we found that this effect depended on saccade latency. Specifically, we observed the largest effect of the motion-induced shift on saccade landing position with saccade latencies in the range of 100-175 ms. Given these saccade latencies, the distance the saccade traveled (10° of visual angle), and the duration of the drifting Gabor stimulus (140 ms), it is highly unlikely that the effect we observed on saccade targeting could be influenced by in flight correction of the saccade or postsaccadic foveation of the stimulus.

Since our results were consistent with the previously reported effects of Gabor motion on perceived position, we wanted to determine how similar the shift in saccade landing location was to the perceptual shift. In Experiment 1B, we presented the same stimuli with the addition of stationary flankers and asked subjects to report the illusory displacement relative to these stationary references.

Experiment 1B

Introduction

In Experiment 1B, we compared the effect of drifting motion on saccade landing position from Experiment 1A to comparable psychophysical measurements of drifting motion on perceived location. As shown in Figure 3.2B, on each trial, subjects were shown a target: either a drifting Gabor or a sinusoidal grating within a hard aperture along with two stationary reference

stimuli, one above and one below the drifting target. Subjects made a two-alternative forced-choice (2AFC) response, indicating whether the target was to the left or to the right of the two reference stimuli.

Method

Subjects. The same subjects from Experiment 1A participated in 1B.

Stimuli and Procedure. The eye tracking set up and procedure in Experiment 1B were identical to those in Experiment 1A and the stimulus was similar to that in Experiment 1A. Figure 3.2B shows the trial sequence for Experiment 1B. As before, there was a random delay interval (750 - 1250 ms) prior to the onset of the target (either a Gabor or a grating within a hard circular aperture drifting leftward or rightward). The target was presented simultaneously with two flankers—one above and one below the target. The flankers were stationary, but otherwise identical to the target and had a 6.5° vertical center-to-center separation from the target. The positions of the target and flankers were jittered together 1.5 degrees horizontally and vertically around a central location 10° to the left or to the right of the fixation point. The horizontal position of the central Gabor was at one of seven possible linearly spaced offsets relative to the flankers, ranging from 1.75° to the left (represented by negative values) to 1.75° to the right (positive values) of the flankers. Subjects were instructed to judge whether the central target was to the left or to the right of the two flankers by pressing the appropriate key on a keyboard. Subjects were instructed to maintain fixation on the dot at the center of the display for the duration of the trial.

Each subject completed one set of 560 trials. Across trials, motion direction (left or right) was counterbalanced with visual field location (left or right), aperture condition (soft or hard), and with the set of seven possible target positions.

Data Analysis. Trials on which subjects' eye position deviated by more than 1° horizontally or vertically from the fixation point were excluded from the analysis. This resulted in the removal of an average of 6.2% of trials per subject from the analysis. The remaining trials were fit to a set of logistic functions using a least squares procedure. Trials from the left and right visual field locations were analyzed together, resulting in a pair of logistic functions (one each motion direction) for each type of aperture (soft or hard). The size of the illusory position shift produced by the grating's motion was calculated as half the difference between the points of subjective equality (PSEs) of the two fitted functions.

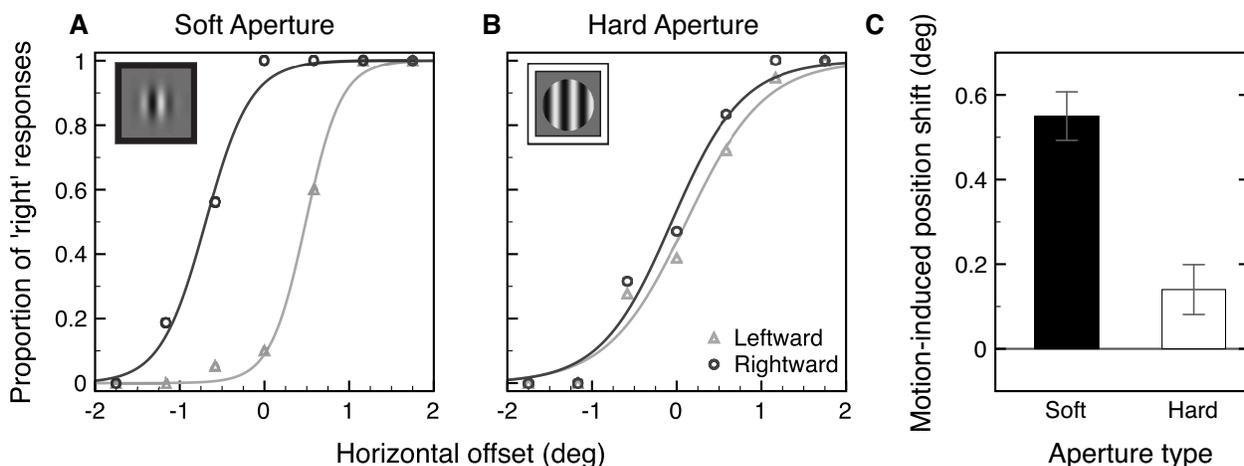


Figure 3.5. Example pair of psychometric functions from one subject for the soft aperture condition (A) and the hard aperture condition (B). The x-axis shows the horizontal offset of the

central target relative to the two flankers (- left, + right). The y-axis shows the proportion of responses that the target was to the right of the two flankers (triangles: leftward motion, circles: rightward motion). PSEs were calculated individually for each subject and then averaged across all observers for each motion and aperture condition. The motion-induced position shift (C) was calculated as half the difference between the PSEs of the two psychometric functions. Error bars represent bootstrapped 95% confidence intervals.

Results

Figure 3.5 shows example pairs of logistic functions (one for each motion direction) for a single observer in the soft aperture condition (4A) and the hard aperture condition (4B). Observers' responses on each trial for the leftward and rightward conditions were bootstrapped separately by resampling each observer's responses with 1000 samples and fitting each set of resampled data to a logistic function. The resulting bootstrapped PSEs were then averaged across the six subjects.

Figure 3.5C shows the size of the motion-induced position shift (measured as half the distance between the two PSEs) for each aperture condition. The size of the perceived shift in position was 0.55° in the soft aperture condition and 0.14° in the hard aperture condition. The size of the motion-induced position shift was greater than zero in both the soft aperture condition ($p < .001$) and the hard aperture condition ($p < .001$). The interaction between motion condition and aperture condition was significant ($p < .001$) demonstrating a significantly larger motion-induced shift in perceived position in the soft aperture condition than in the hard aperture condition.

Discussion

Experiment 1B confirmed previously reported results that there is a larger shift in perceived position resulting from stimulus motion when the motion is within a Gaussian aperture compared to a hard circular aperture (Whitney et al., 2003; Zhang et al., 1993). Although our results show that the shift in perceived location is reduced in the hard aperture condition, it is not completely eliminated. It is possible that the large stimulus eccentricity (10 degrees on average) resulted in peripheral blurring of the stimulus edges. Nevertheless, our findings are consistent with the findings in Experiment 1A; we observe a shift in perceived position where there is also a shift in saccade landing location. In other words, shifts in perceived position from motion are associated with corresponding shifts in saccade landing location. If we test subjects with a hard aperture, in which there are motion signals, but a significantly smaller illusory position shift associated with that motion, we also see no difference in saccade landing positions between the leftward and rightward motion conditions. These results support our hypothesis that motion signals, *per se*, are insufficient to strongly bias saccade landing position. Instead, motion biases the represented location of the target for the saccade system, and that this information is used to guide saccade targeting. In a follow-up experiment, we sought to further examine any potential correlation between the perceptual and saccadic errors by testing whether the pattern of saccade error was similar to the pattern of illusory displacement at different stimulus durations.

Experiment 2A

Given our finding in Experiment 1, that motion can shift the represented locations of saccade targets, we next examined how much motion information is required to shift saccade landing locations in the direction of the Gabor's motion. Previous work has shown that an illusory shift in perceived location is present with durations as brief as 30 ms and reaches its

maximum level with a durations of approximately 100 ms or more (Arnold et al., 2007; Chung, Patel, Bedell, & Yilmaz, 2007). Given the results of Experiment 1, we wanted to test whether similarly brief motion durations are sufficient to demonstrate an effect of motion on saccade landing location. To do so, we used the exact same procedure as in Experiment 1, varying only Gabor duration.

Method

Subjects. Three subjects (all female), including the author (AK), participated in Experiment 2A (mean age: 27.3). Two of the participants from Experiments 1A & B participated in Experiments 2A & B.

Stimuli and Procedure. The stimuli and procedure were identical to those in Experiment 1A, with the addition of a duration manipulation. The saccade target was presented randomly for 20, 40, 60, 80, or 100 ms on each trial. Only soft aperture stimuli (Gabor) were presented. Subjects were instructed to fixate the center of the display at the start of each trial and saccade to the target as soon as it appeared. Across trials, stimulus duration was counterbalanced with visual field location (left or right) and with motion direction (left or right). Each subject completed 4 blocks of 260 trials each. Trials on which subjects made a saccade too early, failed to make a saccade, or landed more than 2.5° from the saccade target (11.4% of the trials) were removed from the analysis. The data were then analyzed using the procedure outlined in Experiment 1A.

Results

The average saccade latency across subjects was 213 ms, comparable to that reported in Experiment 1A (229 ms). As before, we calculated the relative saccade error as the distance of each landing location on each trial from the mean of the set of normalized landing locations where positive values represent saccade landing locations consistent with direction of motion and negative values indicate saccade landing locations away from the direction of motion. We then pooled the single-trial data from the three subjects. As in Experiment 1A, there was a negative correlation between the magnitude of the saccade error and saccade latency, $r = -0.18$, $p < 0.001$. When calculated individually for each of the five duration conditions, there was a negative correlation between saccade error and latency at all but the 20 ms condition; these were significant at a Bonferroni adjusted alpha level (α_B) of 0.01 (all r values < -0.15 , all p values < 0.001 ; for the 20 ms condition: $r = 0.003$, $p = 0.94$).

Given the observed latency effect, we calculated the effect of the target's motion on saccade landing position separately for three latency bins: 100-170 ms, 170-240 ms, and 240-380 ms. This resulted in an approximately similar number of trials within each bin. Figure 3.6A shows the mean saccade landing locations at each duration for all three latency bins. In the shortest latency bin (100-170 ms), there was a significant effect of the Gabor's motion on saccade landing position at all durations of 40 ms or longer ($\alpha_B = .003$; all p values $< .001$). There was no significant effect at any duration in either the 170-240 ms latency bin or the 240-380 ms bin.

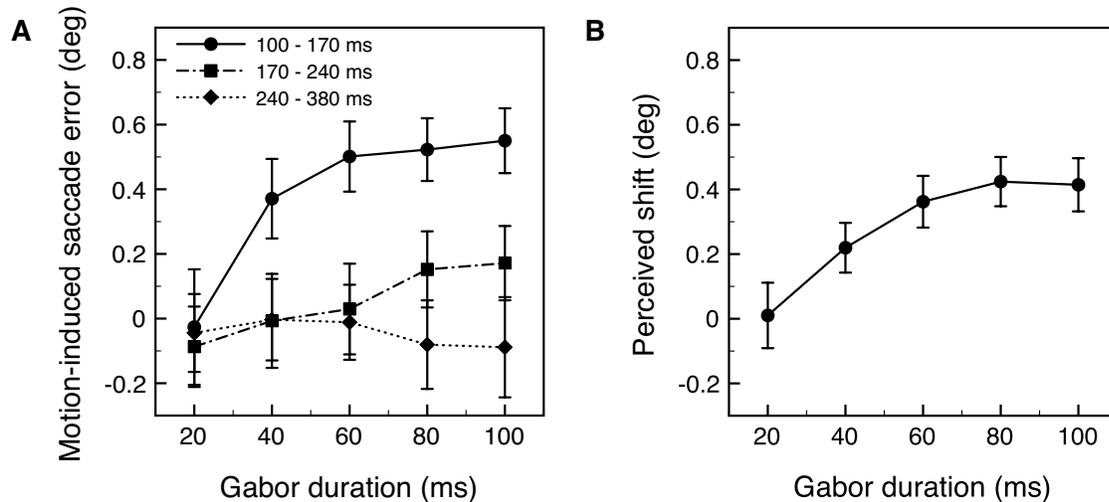


Figure 3.6. (A) Saccade error—the shift in saccade landing location resulting from one direction of motion—as a function of Gabor duration (only the soft aperture was used in Experiments 2A and 2B). Single-trial data were pooled across subjects and then sorted into one of three latency bins, represented by the separate lines. (B) Perceived shift resulting from one direction of motion for the same subjects as in (A), calculated as half the difference between PSEs for each pair of psychometric functions (similar to 4A). Error bars represent bootstrapped 95% confidence intervals.

Discussion

We found a significant effect of Gabor motion on saccade landing location, and this effect depended on the duration of the motion. The motion-dependent saccadic mislocalization increased until approximately 60 ms before leveling off (Figure 3.6A). Consistent with the findings in Experiment 1A, there was a smaller effect of the Gabor's motion on saccade landing position when the saccades were longer in latency.

The pattern of saccade error as a function of stimulus duration is similar to previously reported behavioral measurements of the shift in perceived position with drifting Gabors. Arnold et al (2007) show that the illusory shift has an initial increase, followed by a leveling off around 180 ms. Similarly, Chung et al. (2007) report that the position shift reaches an asymptotic value around 100 ms at high speeds ($16^\circ/\text{s}$). While the shift in saccade landing location as a function of stimulus duration is broadly consistent with previously reported psychophysical results, our stimuli differed in speed, contrast and eccentricity from the previous studies. Therefore, we obtained measurements of the perceived shift within the same set of observers in Experiment 2B to compare the magnitude of saccade error with the perceptual mislocalization at different durations.

Experiment 2B

Introduction

In order to measure the motion-induced position shift at different stimulus durations, we used a paradigm in Experiment 2B similar to that in Experiment 1B. Subjects were asked to report the position (left or right) of a central drifting Gabor relative to two stationary references. In this experiment, we varied stimulus duration using the same set of durations used in Experiment 2A.

Method

Subjects. The same subjects from Experiment 2A participated in Experiment 2B

Stimuli and Procedure. The stimuli and procedure, including eye tracking, were identical to those in Experiment 1B, with the addition of the same duration manipulation from Experiment 2A. Subjects performed the same vernier discrimination task on a central target flanked by two stationary references, one above and one below the target. Only the soft aperture stimuli were presented, and as before, subjects were instructed to maintain fixation at the center of the display. Each subject completed two blocks of 700 trials each, in which stimulus duration, motion direction, visual field location, and the position of the target were counterbalanced across trials. An average of 3.5% of trials were excluded from the analysis due to a failure to maintain fixation.

Results and Discussion

Figure 3.6B shows the motion-induced perceptual shift in the Gabor's location as a function of its duration. The motion-induced illusory shift was calculated as half the difference between the PSEs of the pair of psychometric functions (similar to those shown in Figure 3.5A) for each duration condition. The data were bootstrapped as described in Experiment 1B. There was no significant effect of the Gabor's motion on position judgments with a 20 ms stimulus presentation ($p = .86$), but the effect of the Gabor's motion was significant at all other durations at a Bonferroni adjusted alpha level (α_B) of .01 (all p values $< .001$). Similar to the pattern observed with saccade error, the motion-induced shift in perceived position initially increased with stimulus duration and then reached an asymptotic level with a duration of about 60-80 ms. These findings replicate the pattern of results reported by Arnold et al. (2007) and Chung et al. (2007), demonstrating a shift in perceived location that is present at very brief durations.

General Discussion

The experiments here tested whether the saccade system can use motion-induced position shifts to update the represented locations of objects. In Experiment 1, we show that saccades to a drifting Gabor were shifted in the direction of the carrier motion, exhibiting the same mislocalization effect that has been reported in the psychophysical literature (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990). Importantly, when a hard circular aperture is used, the effect of the carrier motion on perceived location is greatly reduced, and its effect on saccade landing location is eliminated. In Experiments 2A and 2B, we also demonstrated that the pattern of perceptual mislocalization at different durations mirrors that of saccade error at the same set of durations. Specifically, in Experiment 2A we showed that very brief motion (as little as 40 ms) is sufficient to shift the represented position for saccade targeting, consistent with the minimum motion duration required to produce a perceptual shift (Experiment 2B; see also Arnold et al., 2007 and Chung et al., 2007). In addition, the mislocalization effect reaches its maximum with durations of approximately 60-80 ms for both saccades and for perception.

There are several sources of information that the saccade system might use to predict the future locations of moving targets, including changes in the position of a target, or its motion. Although previous work has established that physical changes in object location over time can be used to guide saccade targeting (e.g., Becker & Jürgens, 1979; Deubel, Wolf, & Hauske, 1982; Robinson, 1973; Ron et al., 1989), our results demonstrate that they are not necessary. Experiment 1A showed that object motion alone is insufficient to strongly bias saccade landing locations and that the combination of motion and a soft aperture was required. In the hard aperture condition, where the shift in perceived position was greatly reduced, there was no bias in saccade landing locations even though the same motion was present. Our results are consistent with the idea that motion can bias the represented position of the target, which, in turn, biases

saccade targeting. Although previous work using motion-induced position illusions has suggested that position shifts from motion may guide saccade targeting (de'Sperati & Baud-Bovy, 2008; Kerzel & Gegenfurtner, 2005; Zimmermann et al., 2012), it is possible that these effects were simply due to the presence of stimulus motion in the display. In contrast, our study included a control condition with identical stimulus motion, but a shift in perceived position occurring in only one condition. Therefore, we can conclude that it is the position shift produced by the stimulus motion, rather than simply the presence of motion in the display, that accounts for the saccade error observed in these experiments. On the whole, it is likely that the saccade system uses multiple sources of information together to predict the future locations of saccade targets as they move and as observers move in their environment.

Across both sets of our experiments, there are similarities between the pattern of errors in saccade landing location and those in perceived location. However, there are many studies in the dual visual systems literature that suggest object localization for action is dissociated from perceptual localization (for reviews, see Goodale & Westwood, 2004; Goodale & Milner, 1992). Some of the evidence to support this idea comes from work demonstrating that under certain circumstances, saccadic localization may resist illusions of position that the perceptual system is susceptible to. For example, Wong & Mack (1981) induced an illusory displacement in the location of a target dot by shifting the location of a frame that surrounded it. Subjects were instructed to saccade to the target either immediately or following a delay period after its offset. Their results indicated that the target's saccade landing location reflects its perceived location, but only when the saccades were memory-guided. In contrast, saccades directed immediately to the target were not affected by the illusion, suggesting that it is just physical (egocentric) location that determines saccade localization, at least for immediate saccades. This supports a possible dissociation between perception and action.

More recent work has examined the effects of motion-induced position illusions on saccade landing location, and has shown errors in saccade targeting consistent with the perceptual mislocalization of objects. For example, the flash-drag effect (FDE), in which the position of a stationary object is shifted in the direction of motion of a different object (Whitney & Cavanagh, 2000), has been shown to influence saccade targeting (de'Sperati & Baud-Bovy, 2008; Zimmermann et al., 2012). Consistent with the results of Wong and Mack (1981), the effect of the visual motion on saccadic localization increased with longer delays, albeit on a shorter timescale; saccade errors were larger with long-latency saccades, on the order of 250 - 600ms (de'Sperati & Baud-Bovy, 2008; Zimmermann et al., 2012). In addition, memory-guided saccades to a flash-lag stimulus, in which a stationary flash appears to lag behind an adjacent moving object (Nijhawan, 1994) are consistent with the illusion; landing locations are accurate when subjects saccade the flashed object, but are shifted in the direction of the motion when saccades are directed to the location of the moving object (Becker, Ansorge, & Turatto, 2009).

The delay dependence of saccadic mislocalizations leaves open the possibility that immediate saccades are based on physical object position and not the perceived object location. If there is any effect of a perceptual illusion, it might only appear with a delay of a few hundred milliseconds. De'Sperati & Baud-Bovy (2008) suggest that such latency effects are due to the longer time required for processing the position shift. This implies that the veridical location is represented first, which is then updated to reflect additional perceptual processing that produces the illusory shift. This is broadly consistent with studies suggesting that the effects of an illusion on saccade targeting are larger with voluntary saccades (McCarley, Kramer, & DiGirolamo, 2003), which are typically longer in latency (Hallett, 1978). In contrast, our results demonstrate

that position updating for the saccade system happens rapidly, as we observe large shifts in saccade targeting consistent with the Gabor's motion when the saccades are reflexive and short in latency.

In summary, we found that the well-established psychophysical effect described by De Valois and De Valois (1991) was also reflected in saccade landing location, and that this effect built rapidly, requiring as little as 40 ms of motion to influence saccade landing position. This supports the idea that the visual system uses motion to change the represented position of an object at early stages of visual processing (Fukiage & Murakami, 2013; Kosovicheva et al., 2012; Whitney et al., 2003), with saccade targeting shifted accordingly. Future work should examine the circumstances under which motion-induced position shifts influence action – and how quickly position information can be updated for perception and action. Our results raise the possibility that the visuomotor system employs motion-induced position shifts to predict the locations of moving objects, thus improving the accuracy of saccadic targeting in dynamic scenes and helping to explain how the visual system allows us to respond to a dynamic world.

Chapter 4: Position representations for action lead perception: Evidence from saccades to drifting Gabor targets

In order for us to interact with our environment, our visual system must be able to rapidly and precisely update the represented positions of objects so that we can know where objects are in the world and act accordingly. This is particularly important in the case of moving objects, as the time necessary to process information from the retina could result in a mismatch between an object's position in the world and its represented location. The brain's ability to compensate for such delays is critical to our ability to interact with the world in our daily lives. For example, without this ability, we would be unable to hit a baseball accurately or avoid an oncoming car when crossing the street. While updating perceived position on a rapid time scale is important, arguably it is more important for motor systems to have access to this information so that we can reach and saccade to objects. Whether or not we consciously perceive that the car has moved, we need to be able to get out of its way. The question, then, is whether the time needed to update target location information differs between perception and action. Here we explored the possibility that changes in stimulus position may be reflected in saccade landing location before we can even register a shift in perceived location.

Much of the literature examining the relationship between conscious perception and action has focused on whether reaching movements and saccades are susceptible to visual illusions (for reviews, see Bruno, 2001; Franz, 2001; Goodale & Milner, 1992; Goodale & Westwood, 2004). However, comparatively little work has been devoted to the crucial question of whether there is any difference in the speed at which information is updated for the perceptual and motor systems. Several early studies have examined possible temporal dissociations between perception and action, particularly with reaching movements. For example, Castiello and colleagues describe a series of experiments in which subjects reached for a target that was displaced at the moment that they began reaching for it (Castiello & Jeannerod, 1991; Castiello, Paulignan, & Jeannerod, 1991). Subjects corrected their reaching movements and were asked to verbalize when they perceived the target to have shifted position. Castiello and colleagues found that verbal responses lagged the subjects' manual reaching correction to the displacement by approximately 300 ms. However, the inherent delays in producing a verbal response versus correcting a motor response render these results difficult to interpret: does this lag reflect actual differences in processing for action versus perception, or is it an artifact of the verbal response process? Another study by Paulignan, MacKenzie, Marteniuk, and Jeannerod (1990) used a similar paradigm in which the target subjects were reaching for was shifted once the hand was in motion. Their subjects only reported noticing the shift when the movement was nearly complete, suggesting that the movement adjustment was made before subjects were even aware of it. However, the use of a verbal response in this study again precludes a complete answer to our question of whether perceptual awareness lags behind motor actions, as it is difficult to dissociate the delay in perceptual updating from the delay imposed by generation of a verbal response.

In addition to these studies on reaching movements, previous work on saccadic eye movements has offered some insight into differences in temporal delays between action and perceptual awareness. One possibility is that saccade targeting can occur before the target's perceived (future) location has been assigned. Previous work by de'Sperati and Baud-Bovy (2008) as well as Zimmermann et al. (2012) has shown that saccades to flashes near a moving object were shifted in the direction of motion and that this saccadic mislocalization effect was

positively correlated with the latency of the saccade. In other words, longer latency saccades were associated with a larger saccade error. De'Sperati & Baud-Bovy (2008) suggest that these latency effects are due to the longer time required for processing the position shift; in their view, the demands of acting on an object quickly mean that the saccade system does not always have time to wait for the perceptual processing to complete before initiating the saccade. While this is one possibility, a positive correlation between mislocalization and saccade latency does not necessarily indicate relatively sluggish perceptual processing.

To directly test whether position assignment for saccade targeting precedes assignment for perception, we measured how quickly position information is updated for saccades and for perception. This question has been previously examined in the saccade literature by determining the delay between the time of a physical change and when a saccade reflects this change. Specifically, previous work has shown that there is a “dead time” for saccades - an 80-100 ms window prior to the onset of a saccade in which no new information can be used to influence the programmed saccade location (Aslin & Shea, 1987; W. Becker & Jürgens, 1979; Findlay & Harris, 1984). Similarly, we can ask a related question in regard to perceptual updating: what is the delay between the time that an event occurs and when we are able to perceive a change in the world? By using a novel stimulus and approach, the experiments below directly compare the delay associated with updating perceived location and saccadic dead time within the same trials. This will address whether we can act on changes in the world before we can perceive them.

Experiment 1

Introduction

In order to compare the time course of updating of position information between perception and action, we used a stimulus that allowed us to separate physical position from perceived position. That way, any changes in saccade targeting or judgments of perceived location are independent of the retinal location of the target. To achieve this, we used drifting Gabors as targets for both saccades and for perceptual judgments (see Experiment 2). Previous work has shown that the motion of a sinusoidal grating within a static Gaussian contrast envelope (blurred aperture) results in an illusory shift of the entire stimulus in the direction of motion while the aperture itself remains stationary (see Figure 4.1; De Valois & De Valois, 1991; Ramachandran & Anstis, 1990; see Whitney, 2002 for a review). Additionally, previous results (Kerzel & Gegenfurtner, 2005; Kosovicheva, Wolfe & Whitney, 2014) have shown errors in saccade targeting that are consistent with this motion-induced position shift. Specifically, leftward and rightward motion produces saccade errors consistent with the motion direction when a soft aperture is presented, but when the motion is presented within a hard aperture, the influence of the motion is reduced (Whitney, Goltz, et al., 2003; Zhang et al., 1993). Given that this stimulus allows us to dissociate physical position from perceived position, and that motion direction (independent of physical location) has a large and consistent effect on saccade landing location, we used drifting Gabors with a soft aperture to measure the temporal relationship between perception and action in updating represented position.

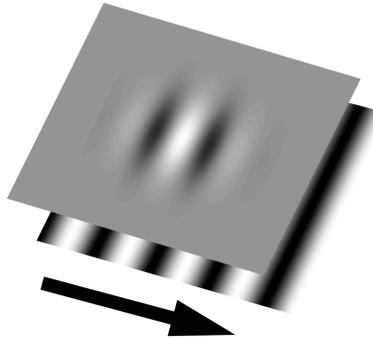


Figure 4.1. Saccade targets consisted of a moving sinusoidal grating (carrier) within a static Gaussian contrast envelope. Previous work has shown that the perceived location of a drifting Gabor is shifted in the direction of the carrier motion (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990).

It is important, however, to first confirm that drifting Gabors as saccade targets produce saccadic “dead time” estimates similar to those reported in previous studies. Previous work has estimated saccadic “dead time” (the interval prior to saccade onset at which visual information cannot be used to influence the saccade) to be approximately 80-100 ms for shifts in physical position (Aslin & Shea, 1987; W. Becker & Jürgens, 1979; Findlay & Harris, 1984). This estimate is based on measuring saccade landing location to physically displaced stimuli, rather than the illusory displacement that occurs for the drifting Gabors we have previously used. Therefore, we wanted to validate these findings when position assignment was based on motion within the stimulus, rather than physical displacement. In Experiment 1, we tested whether there is a similar “saccade dead time” when there is no shift in physical position. To do this, we presented subjects with a drifting Gabor that reversed motion direction, and we presented a cue around the time of the motion reversal that instructed subjects to saccade. By obtaining a distribution of saccade latencies around the time of the motion reversal, we were able to estimate the shortest saccade latency following the motion reversal at which landing location is influenced by the new motion direction.

Method

Subjects. Three subjects—the author (AK), one experimenter (BW) and one naïve observer—participated in the experiment (2 female; mean age: 23.3). Subjects reported normal or corrected-to-normal vision and gave informed consent prior to participation.

Eye tracking. Eye movements were recorded with an EyeLink 1000 desktop mounted infrared eye tracker (SR Research Ltd., Mississauga, Ontario, Canada) used in conjunction with the EyeLink Toolbox for Matlab (Cornelissen et al., 2002). Only the right eye was recorded for each subject. Subjects were calibrated with a standard 9-point calibration procedure before completing each block of trials (mean error < 0.5°). Gaze information was parsed into saccades and fixations, with the first time point at which the velocity exceeded 30°/s and the acceleration exceeded 8000°/s² indicating the beginning of a saccade. Time points at which the velocity and acceleration fell below their respective thresholds defined the end of each saccade. In addition, the onset of a saccade required a minimum eye motion of 0.15°; eye movements with amplitudes below the motion threshold were treated as fixations.

Stimuli and Procedure. The stimuli and procedure for Experiments 1 and 2 were adapted from those used by Kosovicheva, Wolfe and Whitney (2014). Stimuli were presented on a 19" gamma-corrected Samsung SyncMaster 997DF monitor. The program was written in MATLAB (The MathWorks, Inc, Natick, MA) using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and run on a Mac Mini (Apple, Inc., Cupertino, CA). Stimuli were presented with a resolution of 1024×768 and a refresh rate of 75 Hz. Subjects viewed the stimulus binocularly at a distance of 57 cm, and head motion was limited with a chinrest. At this distance and screen resolution, 30 pixels correspond to approximately 1° of visual angle.

Stimuli were presented on a gray background (72.2 cd/m^2). Gabors had a spatial frequency of 0.75 cpd and had a peak contrast of 85%. The standard deviation of the contrast envelope was 0.65° . As shown in Figure 4.1, the Gabors drifted either left or right with a temporal frequency of 4.17 Hz ($5.56^\circ/\text{s}$) while the contrast envelope remained stationary. On each trial, the initial phase of the grating was randomly from a set of 18 possible phases.

As shown in Figure 4.2, subjects began each trial by fixating on a black circle (2.5 cd/m^2 ; 0.34° diameter) at the center of the screen and initiating the trial by pressing the spacebar. Following a delay interval (selected at random between 1500 and 2000 ms on each trial), subjects were presented with a leftward or rightward drifting Gabor in either the right or the left visual field. The central position of the Gabor was jittered around a point 10° to the left or right of fixation. The range of possible jittered positions spanned 3° horizontally and 3° vertically (maximum deviation of 1.5° in any direction). The position was selected randomly on each trial to avoid stereotyped saccades. The Gabor's motion direction reversed (from left to right or vice versa) after 1440 ms and continued to drift for another 1440 ms after the reversal.

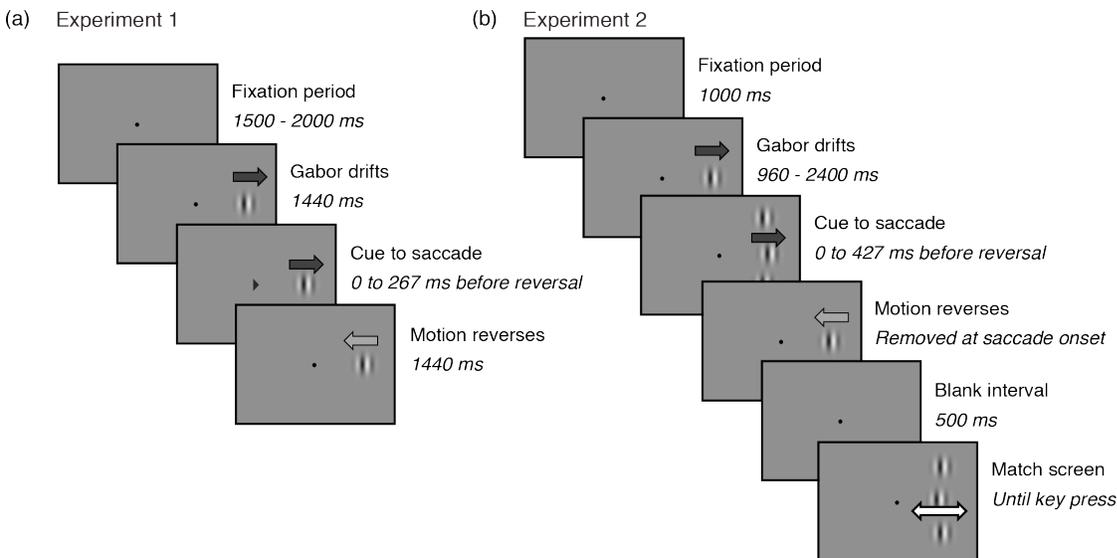


Figure 4.2. Trial sequence for Experiments 1 and 2. (A) In Experiment 1, subjects were presented with a single drifting Gabor (left or right motion direction) in either hemifield. The Gabor drifted at a constant rate for 1440 ms before reversing direction and drifting for another 1440 ms in the opposite direction. Subjects were presented with a cue to saccade (central arrow at fixation) at one of five times between 0 and 267 ms prior to the moment of the reversal. (B) In Experiment 2, the saccade target drifted for one of four durations between 960 and 2400 ms before reversing direction and then drifting in the opposite direction until the subject initiated the saccade. Subjects were presented with two stationary flankers, one above and one below the

target, that served as a cue to saccade. At the end of the trial, subjects made a saccade back to the fixation point and adjusted a stationary Gabor to its perceived location at the time that the flankers appeared.

Subjects were instructed to saccade to the center of the Gabor following presentation of a central arrow cue that replaced the fixation point. The central arrow was a black triangle (0.27° wide and 0.51° high) pointing to the visual field (left or right) in which the Gabor was presented. The cue was presented at one of five randomly selected linearly spaced times between 0 and 267 ms before the reversal. Subjects were instructed to withhold their saccade until the appearance of the arrow cue. Trials in which the subject began a saccade before the onset of the cue, as measured by a deviation larger than 1° horizontally or vertically from the fixation point, were aborted and excluded from data analysis. In addition, trials in which the saccade onset was within the first 67 ms (five frames) following the cue's appearance were also aborted (as a saccade in response to cue onset within that window was unlikely). Subjects were given feedback in the form of a beep whenever a trial was aborted. Following the saccade, subjects were instructed to saccade back to the fixation point and initiate the next trial by pressing the spacebar. Subjects completed three blocks of 320 trials, and eye position was re-calibrated after each block. Within each block, there were an equal number of trials for each unique combination of visual field location (left/right), initial motion direction (left/right), and cue time, and the trials were presented in a random order.

Data Analysis. The data were drift-corrected offline, and the horizontal and vertical eye positions at the end of the first large saccade on each trial were used to determine saccade landing location. We excluded trials in which saccade landing locations deviated by more than 3.5° horizontally or vertically from the center of the Gabor, as well as trials in which subjects made a saccade prior to the cue onset, blinked immediately prior to the saccade, or failed to make a saccade. Altogether, this resulted in the removal of 7.8% of trials from the analysis.

The data were then individually normalized for each subject to correct for any possible saccadic undershoot (Becker & Fuchs, 1969; Carpenter, 1988). Specifically, saccades to the right visual field on average landed 0.24° more leftward (relative to the target center) than saccades to the left visual field, $p < 0.001$. In order to correct for this systematic bias, we first separately calculated the mean x-coordinates of the landing locations within each hemifield condition for each subject (see also Kosovicheva, Wolfe, & Whitney, 2014). Then, the mean landing location within each hemifield condition was subtracted from the landing location on each trial for that condition. The resulting normalized landing locations were pooled together across the left and right hemifields and then averaged to obtain an estimate of the mean shift in landing location resulting from the initial carrier motion direction. This analysis was repeated for each subject. The distance of each landing location from the mean of the set of normalized landing locations corresponds to the saccade error, in degrees, produced by one direction of motion. Here, positive values represent saccade landing locations consistent with the initial direction of motion and negative values indicate saccade landing locations consistent with the final direction of motion (regardless of whether the motion was leftward or rightward on any given trial).

Unless otherwise specified in the text, confidence intervals for parameter estimates for fitted functions (see Results) were generated using a nonparametric bootstrap procedure (Efron & Tibshirani, 1993). Individual trials from each subject were resampled with replacement and then fit to a logistic function using a least-squares procedure. This procedure was repeated 1000 times to obtain an estimate of a 95% confidence interval.

Results

Consistent with previous studies, the trial-to-trial jitter of the physical position of the saccade target influenced subjects' saccade landing positions (Kosovicheva, Wolfe, & Whitney, 2014). Each subject showed a strong positive correlation between the jittered horizontal location of the saccade target and saccade amplitude, indicating that subjects did not simply saccade to the same stereotyped location on every trial. The within-subject correlations ranged from 0.70 to 0.77 with a mean correlation of 0.74 (all p values < 0.001). Across all trials, the median saccade onset latency relative to cue onset was 242 ms.

We recalculated saccade latency relative to the time of the reversal of the Gabor's motion (Fig. 4.3). The variable cue timing relative to the time of the Gabor's reversal was effective in producing a range of saccade latencies from shortly before the time of the reversal to several hundred milliseconds after to the reversal: 95% of the saccade latencies fell between -47 ms and 429 ms relative to the moment of the reversal, with a median of 144 ms.

Figure 4.3A plots saccade error as a function of saccade onset latency relative to the moment of the Gabor's reversal for an example subject, where negative latencies represent time prior to the moment of the reversal, and positive latencies are after the moment of the reversal. Here, a positive saccade error is consistent with the Gabor's initial motion direction, and a negative error is consistent with the Gabor's final motion direction. At early saccade onset latencies, saccades are generally consistent with the direction of motion prior to the reversal. However, as saccade onset latency increases, saccade error changes to be consistent with the direction of motion following the reversal.

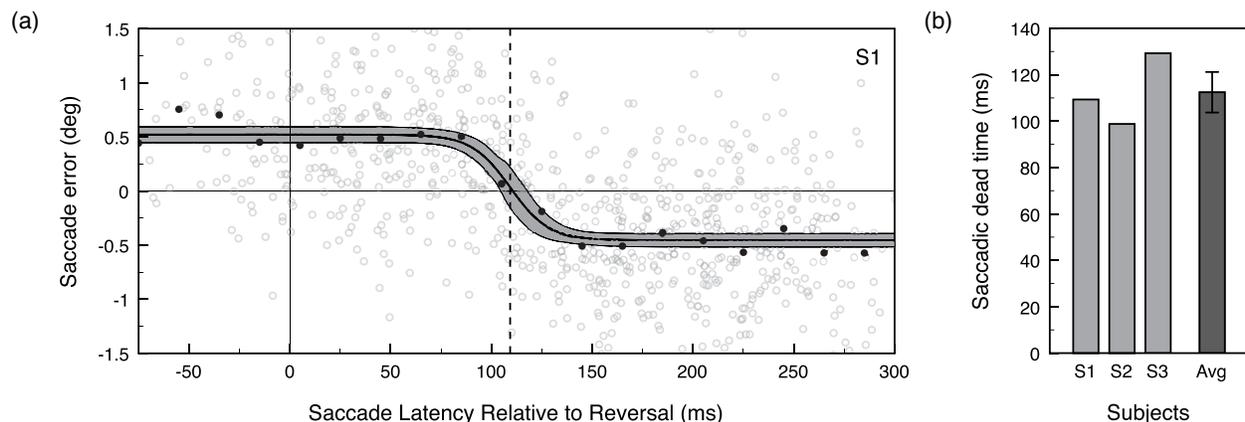


Figure 4.3. (a) Saccade error plotted as a function of saccade latency relative to the moment of the reversal for an example subject. Positive errors indicate saccades in the direction of the motion prior to the reversal, and negative errors indicate saccades in the direction of motion following the reversal. Gray dots represent single trial saccade errors, and black dots represent average errors in 20-ms bins. The line at 0 ms represents the moment of the Gabor motion reversal. The inflection point of the logistic function (dashed line) served as our estimate of saccadic dead time. (b) Estimates of saccadic dead time for each subject and group average. Error bars represent bootstrapped 95% confidence intervals.

To calculate the moment at which saccade landing locations change from being in the initial direction of the Gabor's motion to the direction following the Gabor's reversal, we fit the trial-by-trial saccade error with a logistic function and used the inflection point of the logistic fit as an estimate of saccade dead time. Figure 4.3A shows an example curve fit to the set of saccade errors as a function of saccade onset latency. As shown in Figure 4.3B, the mean

inflection point of the logistic function across the three subjects was 112 ms, (95% confidence interval: 104-121 ms). This time point marks the midpoint of the transition between saccades that were primarily in the direction of motion prior to the reversal and saccades that were primarily in the direction of motion following the reversal. In other words, saccades with an onset latency of around 112 ms were influenced by motion prior to the reversal as much as they were by motion after the reversal.

Discussion

Our results in Experiment 1 replicate and extend previous findings of saccadic dead time. By cuing subjects to saccade to a drifting Gabor at a range of times before and after it reversed motion direction, we were able to measure the delay with which saccade targeting is updated following changes in the represented position of a target, independent of its physical location. Previous work has shown that when the physical position of a saccade target changes around the beginning of a saccade, saccade programming is not updated instantaneously, and that there is a “dead time” interval during which physical shifts in target location prior to a saccade do not influence saccade targeting (Aslin & Shea, 1987; W. Becker & Jürgens, 1979; Findlay & Harris, 1984). These studies have shown that it takes approximately 100 ms for the new target location to be reflected in an observer’s saccade landing locations. In Experiment 1, the motion following the reversal starts to influence subjects’ saccade landing points when the saccades begin approximately 100 ms after the motion reversal. Therefore, when there is no shift in physical position (and only a perceptual shift), saccade dead time is comparable to when there is a shift in physical position.

Experiment 2

Introduction

In Experiment 1, we showed that as saccade onset latency relative to the motion reversal increases, saccade errors change from being consistent with the direction of motion prior to the reversal to being consistent with the direction of motion following the reversal, and that this shift lags the actual change in motion direction by approximately 100 ms. In other words, it takes the saccade system approximately 100 ms to update position shifts from changes in motion. The next step is then to test which process is faster, updating representations for perception or for saccade planning – does action follow perception, or vice versa?

To answer this question, we must determine how long it takes for perceived position to be updated. Is there a lag in updating perceived position that is distinct from saccadic dead time? In other words, how soon following a change in visual input does the visual system register a change in perceived location? To test this, along with the saccade dead time, we used a similar paradigm to that used in Experiment 1, with the addition of a perceptual judgment of the Gabor’s position after the saccade was completed. During the trial, subjects were presented with two brief (40 ms) stationary flankers simultaneously with the drifting Gabor target, at or before the moment of the motion reversal. These brief static flankers served as the subjects’ cue to saccade. At the moment that the saccade was initiated, the drifting Gabor target was removed from the screen (whether or not it had reversed direction), preventing subjects from fixating it. Finally, at the end of each trial, subjects made a saccade back to fixation and were presented with a match display. Here, subjects adjusted a stationary response Gabor to where they perceived the drifting Gabor target to have been at the moment the static flanking cues appeared. Critically, removing the stimulus at the moment the saccade was initiated provided the perceptual and oculomotor systems access to the same information about the stimulus. By comparing the saccade errors and

perceptual errors on a trial-by-trial basis, we were able to determine how closely the two are correlated, and whether this correlation increases or decreases when a temporal lag is applied to the saccade onset latencies.

Method

Subjects. Four subjects—the author (AK), one experimenter (BW), and two naïve observers—participated in the experiment (2 female; mean age: 25.5). Subjects reported normal or corrected-to-normal vision and gave informed consent prior to participation.

Stimuli and Procedure. The experimental setup and eye tracking procedure was identical to that in Experiment 1, with the inclusion of static flankers presented near the moment of the target Gabor's reversal in the test display. In addition, a second display (a match display) was added in which subjects performed an adjustment task, indicating the perceived location of the drifting Gabor target relative to the static flanking cues at the moment that they appeared (see Fig 2b).

To minimize the possibility that subjects could anticipate the moment of the Gabor target's reversal, the Gabor reversed direction after being presented drifting in one direction for either 960, 1440, 1920, or 2400 ms. In addition, the onset of the static flanking cues was randomly selected from one of five linearly spaced times between 0 and 427 ms prior the reversal of the Gabor target's motion. As before, the position of the Gabor was jittered; the range of possible locations spanned 3° horizontally and 3° vertically (maximum deviation of 1.5° in any direction).

The flanking cues were horizontally aligned with each other and had a vertical center-to-center separation of 6.5° from the target in each direction. The drifting Gabor target had one of 5 horizontal offsets relative to the two flanking cues: -0.75° , -0.375° , 0° , 0.375° , and 0.75° (where negative is leftward and positive is rightward). The flanking cues were stationary (each with a randomly selected phase) and presented for 40 ms. Unlike Experiment 1, in which the Gabor target continued to drift for 1440 ms following the motion reversal, here the target was removed from the screen once the subject initiated the saccade, as measured by a deviation greater than 1° horizontally or vertically from the fixation point. In this experiment, any motion information that influenced saccade landing position must have been acquired prior to saccade initiation, as the drifting Gabor target was removed from the screen at the moment of saccade onset. This eliminates any potential influence of the stimulus after saccade initiation. As before, any trials in which the eye deviated by more than 1° from the fixation point, either prior to the cue onset, or within the first 67 ms of the cue onset, were aborted and removed from the analysis. Subjects were instructed to saccade back to the fixation point following completion of the saccade.

After the test display, subjects were then presented with a match display in which they were instructed to adjust the position of a peripheral Gabor to match the perceived location of the drifting Gabor target relative to the static flanking cues. In the match display, the two stationary flankers reappeared after a 500 ms blank interval, with a third, stationary adjustment Gabor in between them. The flankers were presented in the same location that they occupied during the test display, while the central (adjustment) Gabor was set to a randomly selected position on each trial between 2.5° to the left of the flankers and 2.5° to the right of the flankers. The subject then adjusted the horizontal position of the central stationary Gabor until it was in the relative location that subjects perceived the drifting Gabor target at the moment that the static flanking cues appeared. Subjects were instructed to maintain fixation at a screen-centered fixation point (to match the presaccadic fixation location) while adjusting the central Gabor position to the left and right with the arrow keys. Subjects were instructed to press the spacebar when they had matched

the target Gabor location. The next test display then appeared following an intertrial interval (ITI) of 1000 ms. Subjects completed four blocks of 200 trials each, and eye position was recalibrated after each block. Visual field location (left/right), initial motion direction (left/right), initial Gabor drift duration (i.e., time prior to the reversal), and cue time were counterbalanced across trials. The order of the trials was randomized within each block.

Data Analysis. The same normalization procedure described in Experiment 1 was applied to the data in Experiment 2. The same trial exclusion criteria resulted in the removal of 13.6% of trials from the analysis.

Results

As in Experiment 1, each subject showed a strong positive correlation between the jittered horizontal location of the saccade target and saccade amplitude. The within-subject correlations ranged from 0.50 to 0.80 with a mean correlation of 0.69 (all p values < 0.001). Across trials, the median saccade latency relative to cue onset was 262 ms. Continuing with the analysis procedure from Experiment 1, we recalculated saccade latency relative to the time of the reversal of the Gabor target's motion. The larger range of cue times resulted in a larger range of saccade onset latencies relative to the Gabor target reversal compared to Experiment 1; 95% of the saccade latencies fell between -212 ms and 421 ms relative to the moment of the reversal, with a median of 79 ms. As before, saccades to the left visual field landed more rightward (relative to the target) than saccades to the right visual field, (mean difference of 1.39° , $p < 0.001$). As described in Experiment 1, saccade errors were re-centered based on the mean landing position within each visual field. Saccade error as a function of saccade onset latency relative to the reversal was fit to a logistic function, and the inflection point of the logistic fit across the four observers was 93.6 ms (95% CI: 73.1-114.2 ms).

Perceptual mislocalization was measured in the adjustment task (from the match screen) by subtracting the physical position of the drifting Gabor target from the adjusted position of the response Gabor relative to the two static flankers. There was a bias to localize both left and right visual field stimuli further from fixation; averaged across the two motion directions, right visual field stimuli had a 0.17° rightward error and left visual field stimuli had a 0.42° leftward error, both significantly greater than 0° , $p < 0.001$. To correct for these systematic biases, we performed the same normalization procedure on the perceptual data as we did the saccade data; the mean error within each hemifield was subtracted from the error on each trial. Just as with saccade error, positive values indicate errors consistent with the direction of motion prior to the reversal, and negative values indicate errors consistent with the motion direction after the reversal.

Perceptual error followed a similar pattern to saccade error; earlier saccades (and therefore earlier stimulus offsets) were associated with a localization error consistent with the motion direction prior to the reversal, and later saccades/stimulus offsets were associated with perceptual error consistent with the motion direction after the reversal. To estimate the time course of the motion-induced shift in perceived location relative to the time of the reversal, we fit the perceptual error as a function of saccade onset latency (stimulus offset) to a logistic curve. Similar to the estimate of saccadic dead time, the inflection point of the logistic served as an estimate of the temporal delay for updating perceived location following the motion reversal. Across subjects, the mean inflection point of the logistic function for perceptual error was 140 ms (95% CI: [121 159]). The inflection point of the curve fitted to the perceptual error data (140 ms) was significantly greater than that fitted to the saccade data (94 ms), (mean difference: 46

ms, $p = 0.016$). Figure 4.4 shows the difference between the inflection point of the logistic function fitted to the saccade errors and that fitted to the perceptual errors for each subject.

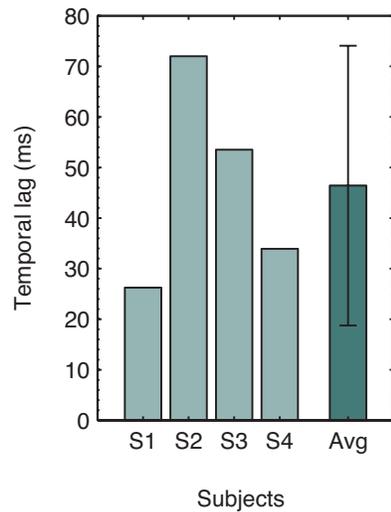


Figure 4.4. The temporal lag in updating perceived position compared to saccade landing location following the drifting Gabor target's reversal. The values represent the difference between the inflection point of the logistic function fitted to the saccade errors (shown in Figure 4.3) and the analogous function fitted to the perceptual errors from the match (i.e., adjustment) screen. Positive values indicate a later inflection point for perceptual errors compared to saccade errors, and negative values indicate a later inflection point for saccade errors compared to perceptual errors. Error bar represents the bootstrapped 95% confidence interval.

The difference in the inflection points between the two logistic functions gave us an estimate of the relative lags with which location is updated for perception and saccadic targeting. The perceptual judgments in Experiment 2 also allowed a more fine-grained comparison between saccade error and perceptual error. Specifically, we found a significant correlation between perceptual error and saccade error on a trial-by-trial basis (mean across subjects: $r = 0.22$, $p < 0.001$; see Figure B1 in Appendix B). In other words, trials in which saccade errors were in the direction of motion following the reversal also tended to have perceptual errors in the direction of motion following the reversal. Although this correlation points to a similarity between representations for perception and for action, the difference in the inflection point of the logistic functions for saccade error and perceptual error suggests that the relationship between saccade error and perceptual error might be stronger if a temporal lag is applied to the saccade data. For example, while the perceptual error on a given trial correlates with the saccade error on that same trial, the error might be even *more* similar to saccade errors on different trials with longer latencies (approximately 40 ms longer). That is, there may be a higher correlation between than within trials.

To test the hypothesis that saccade error is more strongly correlated with perceptual error when a temporal delay is applied to the saccade error, we calculated the cross-correlation between saccade error and perceptual error as a function of temporal delay (Fig. 4.5). Since saccade onset latencies relative to the reversal are not linearly spaced, we first averaged saccade errors associated with identical saccade latencies (in 1-ms bins, corresponding to the maximum temporal resolution of the eye tracker). Latency values for which there was no saccade were

estimated by linearly interpolating the neighboring points. The two lines in Figure 4.5A represent the average saccade error and average perceptual error within each bin. In addition, each line was re-centered on zero by subtracting the mean saccade error and mean perceptual error from each point in their respective functions. To calculate the cross-correlation function, the discrete Fourier transform (DFT) of the mean-subtracted perceptual errors was multiplied by the complex conjugate of the DFT of the mean-subtracted saccade errors. The resulting values were inverse Fourier transformed and then normalized such that the autocorrelations at a temporal lag of zero were equal to 1.

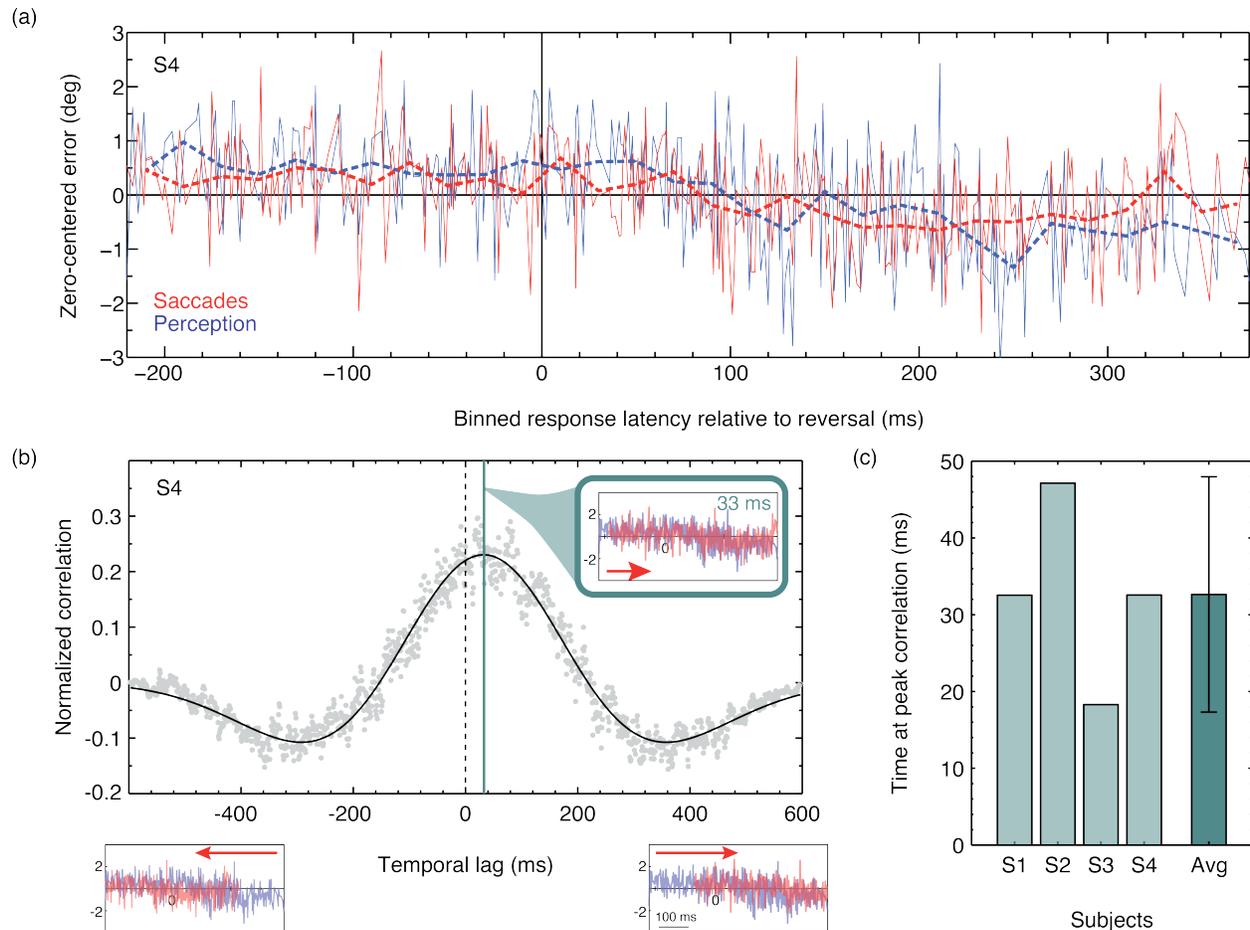


Figure 4.5. (a) Saccade error (red) and perceptual error from the match screen (blue) plotted as a function of onset latency relative to the drifting Gabor target's reversal for one subject, with saccade latencies sorted into 1-ms bins (the maximum temporal resolution of the eye tracker). Data points at which there was no saccade for a given latency were linearly interpolated based on neighboring points. Both saccade error and perceptual error are shown re-centered on zero (with their respective means subtracted from each trial). Dashed red and blue lines show averages in 20-ms bins for illustrative purposes. (b) Cross-correlation function of the two error plots shown in (a). Positive lags on the x-axis represent temporal offsets between the two functions at which saccade errors are shifted later in time relative to perceptual errors, negative lags represent offsets at which saccade errors are shifted earlier in time relative to perceptual errors, and zero represents no temporal offset. The data were fitted by a difference of Gaussians (DOG), and the

solid vertical line shows the temporal lag at the peak correlation. (c) Temporal lag at peak correlation in milliseconds, based on the DOG fit for each subject and the group average. Error bar represents the bootstrapped 95% confidence interval.

Figure 4.5B shows the normalized cross-correlation function for one subject, where positive lags represent a shift of the saccade error function later relative to perceptual error, and negative lags represent a shift of the saccade error earlier relative to perceptual error. If there were no difference in the time course of updating position information for saccades and perceptual judgments, the correlation would be strongest with a lag of 0 ms. This would indicate that the saccade error on each trial is best correlated with the perceptual error on that particular trial. However, if position information for saccades is updated more quickly than for perception, we would expect to find a positive lag, indicating that the saccade errors are better correlated with perceptual errors on trials with longer saccade latencies. The cross-correlation function was well fit by a difference of Gaussians (mean $R^2 = 0.94$), and the peak of the fitted curve was used to estimate the maximum point of the function. As shown in Figure 4.5C, across subjects, the mean peak of the fitted cross-correlation function was 33 ms (95% confidence interval: 17 - 48 ms). The peak of the function was significantly greater than zero, $p < .001$. We obtained similar estimates of the temporal lag between saccade error and perceptual error by repeating this analysis with 20-ms bins (Figure B2) and by calculating Pearson's r at different temporal lags instead of cross-correlations (Figures B3 and B4).

Discussion

In Experiment 2, we employed a position judgment task to directly compare errors in saccade landing location to errors in position judgments within the same trials. Our results showed a positive correlation between the two measures, demonstrating similar patterns of error for position perception and for saccade targeting. Logistic fits to perceptual error as a function of saccade onset latency (identical to stimulus offset) had an average inflection point of 140 ms, compared to 94 ms for saccade error (the estimated dead time for saccades). Surprisingly, our results also indicated that saccade error correlates more strongly with perceptual error when a 30-40 ms temporal lag is applied to the saccade data than when there is no lag applied (i.e., when they are temporally matched). In other words, the correlation between perceptual error and saccade error is highest when they are correlated *across* different sets of trials rather than *within* the same set of trials. This indicates that saccade error must be shifted later relative to perceptual error and therefore that the assignment of perceived position lags behind position assignment for the saccade system.

General Discussion

The experiments described here demonstrate that the represented locations of saccade targets are updated more quickly than they are perceived. Our results point to a temporal dissociation between perception and action that could reflect strategic differences in the use of information over time by the visual and motor systems (Castiello et al., 1991; Goodale & Milner, 1992; Westwood & Goodale, 2011; Whitney, Westwood, et al., 2003). In Experiment 1, by measuring saccades to a drifting Gabor target around the time that it reversed direction, we demonstrated that it takes the saccade system approximately 100 ms to update position information from motion-induced position shifts. In Experiment 2, we directly compared perceptual error and saccade error in localizing drifting Gabor targets at different saccade onset latencies relative to the time of the reversal. At the start of each saccade, the stimulus was

removed from the screen, eliminating any additional retinal input from the drifting Gabor target. Therefore, once the saccade began on each trial, there was no further input that could be used to update position assignment for perception. Our results showed that perceived location and saccade landing location correlate most strongly, not within the same set of trials, but across different trials—when a 30-40 ms temporal lag is applied to saccade error. In other words, we find that it takes less time for position information to be updated for saccades than for perceived position.

However, one possible explanation for our findings is that the perceptual position representation might be susceptible to decay in memory while observers perform the adjustment task. The loss of information over time might contribute noise and uncertainty in observers' responses, which could bias observers towards reporting the perceived position of the drifting Gabor target at an earlier time point in the trial. If this were the case, we might expect that for trials where responses occurred later after the offset of the target, a larger temporal lag would be required to match perceptual errors with saccade errors. However, we found that reaction times in the adjustment task were not correlated with the absolute magnitude of the perceptual errors (mean Pearson's r across subjects = -0.004; $p = 0.764$), or with the signed magnitude of the motion-induced shift in perceived position (mean Pearson's $r = 0.01$; $p = 0.65$; see Figure B5), indicating that subjects were just as accurate when they took longer to make their response. In addition, for each subject, we separately computed the lag (analysis from Figure 4.5) for the trials with the fastest half of reaction times and the slowest half of reaction times. The temporal lag corresponding to the peak of the cross-correlation function was similar between the fast and slow response trials (37 vs 27 ms, respectively, $p = 0.616$; see Figure B6), indicating that any decay in the fidelity of the represented position of the target cannot account for the temporal lag observed between perception and action.

Finally, we confirmed that the lag in updating position information for perception is attributable to variation in the size of the motion-induced position shift over time, rather than resulting from noise in our data. To do this, we analyzed the foveal bias – a component of our data that exhibited no systematic variation over time (see Figure B7). Both the saccade and perceptual data were transformed to reflect the degree of undershoot relative to the target, where positive values represent a bias towards localizing targets toward the fovea and negative values represent a bias to localize targets away from the fovea. We then performed the same cross-correlation analysis depicted in Figure 4.5 and computed the temporal lag that resulted in the highest correlation between perceptual error and saccade error. The peak of the cross-correlation function was not significantly different from zero ($p = 0.278$; see Figure B7), indicating that the amount of foveal bias correlated most strongly within the same trials than across trials shifted temporally relative to one another. This also demonstrates that biases in localization for perception and saccades are organized around the motion reversal, and that the motion reversal produces differential delays in position updating.

Together, our experiments suggest that the visuomotor system updates position information based on stimulus properties faster than perceived position can be updated. A large portion of the literature examining the relationship between perception and action has focused particularly on whether motor systems are susceptible to the same illusions (e.g., illusions of stimulus position) that the visual system is subject to, and there is considerable debate regarding the extent of these similarities between perception and action and under what circumstances they occur (Aglioti, DeSouza, & Goodale, 1995; Franz, 2001; Goodale & Milner, 1992; Goodale & Westwood, 2004). While our results provide some evidence for similar patterns of error between

perception and action, they introduce a critical dissociation—even when perception and action exhibit similar errors on the same trials, updating of perceived position lags behind motor updating, and perceptual position information cannot determine motor responses. It is possible that previous experiments reporting similar errors between perception and action (e.g., Franz, Gegenfurtner, Bulthoff, & Fahle, 2000; Pavani, Boscagli, Benvenuti, Rabuffetti, & Farnè, 1999) may instead have underlying differences in the time course at which information is updated. A dissociation in these time courses would be consistent with parallel streams of processing for perception and action, consistent with the dual-systems hypothesis (Goodale & Milner, 1992; Milner & Goodale, 1995).

The duality in the temporal processing of information for perception and action reveals a strategic optimization. Because the world will not wait for our perceptual processing to catch up, it is critical that we are able to respond as quickly as possible to changes in the world (for example, stepping on the brake as soon as it is necessary) regardless of whether or not we have yet consciously perceived those changes.

Chapter 5: Conclusion

As we have discussed, position representations in the human visual system are exceptionally flexible and can be influenced by spatiotemporal context (e.g., Cai et al., 1997; Roelofs, 1935; Ross et al., 1997; Whitaker et al., 1997) as well as cognitive factors (e.g., Sheth & Shimojo, 2001; Suzuki & Cavanagh, 1997). Visual motion, in particular, has large and wide-ranging effects on the represented locations of objects in the visual field (De Valois & De Valois, 1991; Nijhawan, 1994; Ramachandran & Anstis, 1990; Whitney & Cavanagh, 2000). In this set of experiments, we have gained a more complete understanding of both where in the visual system this process occurs, and how it affects motor responses.

By showing that a motion-induced position shift can bias the spatial tuning of a low-level aftereffect, Chapter 2 provided evidence that motion can shift position representations in early visual areas. This early influence of motion on visual processing is also seen in motor responses—as discussed in Chapter 3, the same motion-induced position shifts in perceived location are also seen in saccade landing locations. However, changes in perceived location do not appear to drive changes in saccade landing location. Instead, in Chapter 4, we demonstrated an important dissociation between perception and action: motion-based position assignment for saccade targeting precedes position assignment for perception. This may be part of an adaptive mechanism by which the visual system prioritizes our need to avoid or engage with moving objects in the world by rapidly updating representations for action.

To return to the example from the first chapter, our visual system accounts for the motion of an oncoming car from the earliest stages of visual processing, and even more usefully facilitates our action to avoid the car before we perceive a change in its position. The necessity of motion as a factor in object representation in the human visual system cannot be understated – motion is a fact of our visual world, and the human visual system is elegantly equipped to account for it quickly and accurately.

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Appendix A: Supplemental Figures for Chapter 3

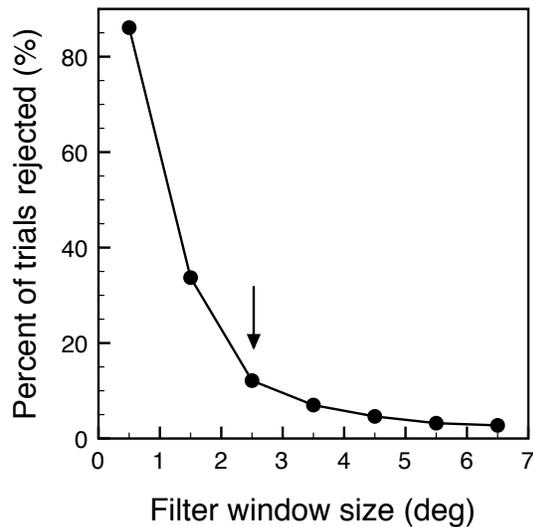


Figure A1. Proportion of trials excluded from the analysis in Experiment 1A as a function of filter window size. Filter window size is the maximum deviation (in degrees) allowed in any direction from the center of the saccade target for inclusion in the analysis. The filter window size for the manuscript was 2.5 degrees (indicated by arrow). The lower asymptote of function is 2.75% (due to eye blinks or no saccades detected).

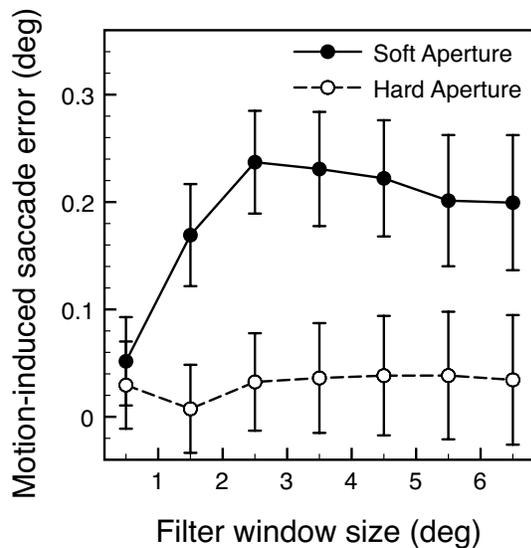


Figure A2. Mean saccade error produced by one direction of motion as a function of filter window size (see Figure A1). Saccade error represents the shift in saccade landing location produced by one direction of motion (see Figure 3.2C). Error bars represent bootstrapped 95% confidence intervals. The difference between the soft aperture and the hard aperture conditions was significant at all filters except at 0.5 degrees ($p = .43$, for all other filters $p < .001$). The lack of difference at small filter window sizes is a necessary consequence of excluding saccades that

have a motion-dependent bias. In other words, at small filter window sizes (such as 0.5 deg), there is a selection bias that reduces the motion-induced shift in saccade landing location.

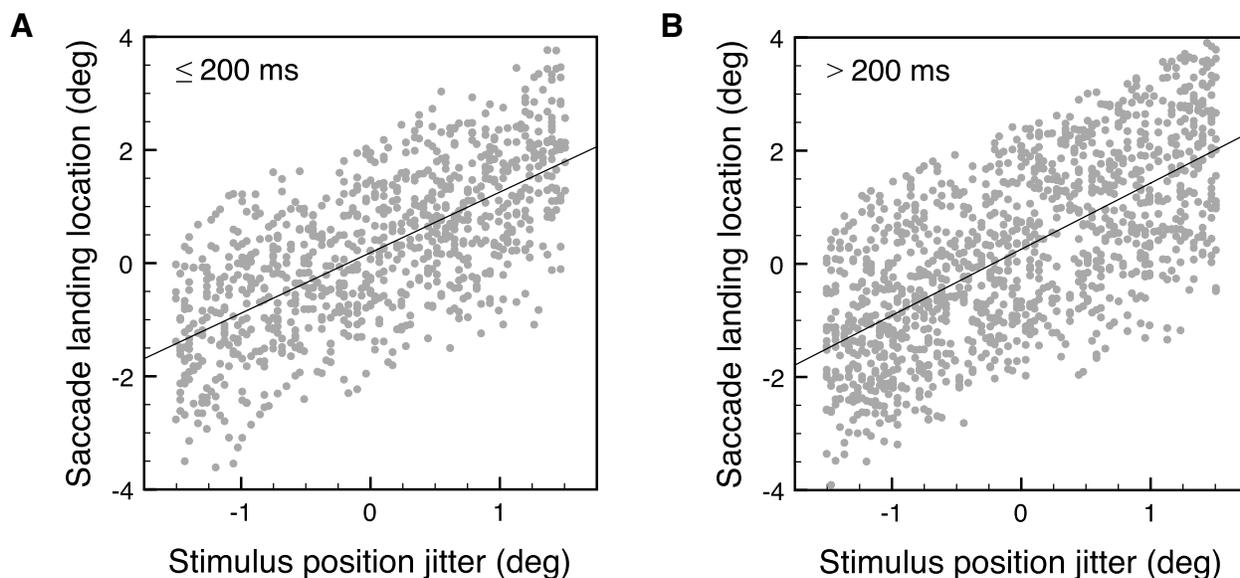


Figure A3. Horizontal saccade landing location versus horizontal stimulus position jitter for both (A) short latency saccades and (B) long latency saccades for all six subjects in Experiment 1A. Each point represents a single trial and positions are shown relative to the average location of the Gabor across trials. Saccade landing position correlated with stimulus position jitter at both short (≤ 200 ms) and long (> 200 ms) saccade latencies ($r = .67$ and $r = .66$, respectively).

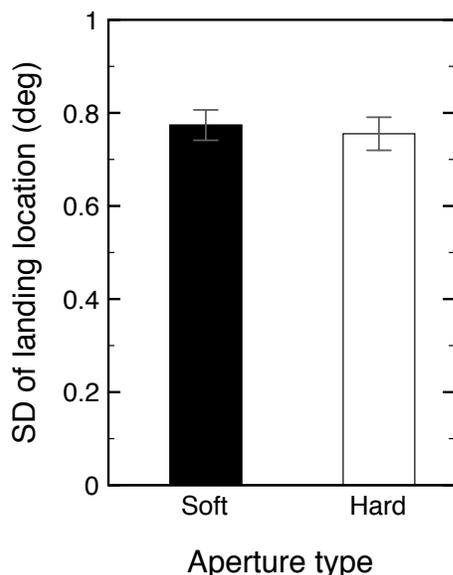


Figure A4. Precision of saccade landing location is similar in both the soft and hard aperture conditions. Values on the y-axis represent the horizontal standard deviation of saccade landing location after subtracting the mean landing location for each motion direction. The bars represent the average of 6 subjects, and the difference between the soft and hard aperture conditions (0.77 vs 0.76) is not significant, $p = 0.48$. Error bars represent bootstrapped 95% confidence intervals.

Appendix B: Supplemental Figures for Chapter 4

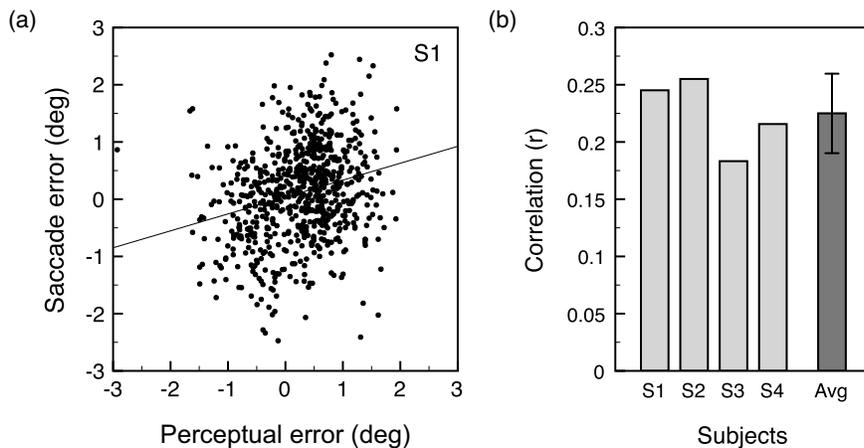


Figure B1. Trial-by-trial correlation between saccade error and perceptual error (from the adjustment task), for an example subject (panel A) and for all subjects (panel B). As in Figure 4.3, positive errors are consistent with the motion direction prior the reversal, and negative errors are consistent with the motion following the reversal. Correlation values are Pearson's r . Error bar represents bootstrapped 95% confidence interval.

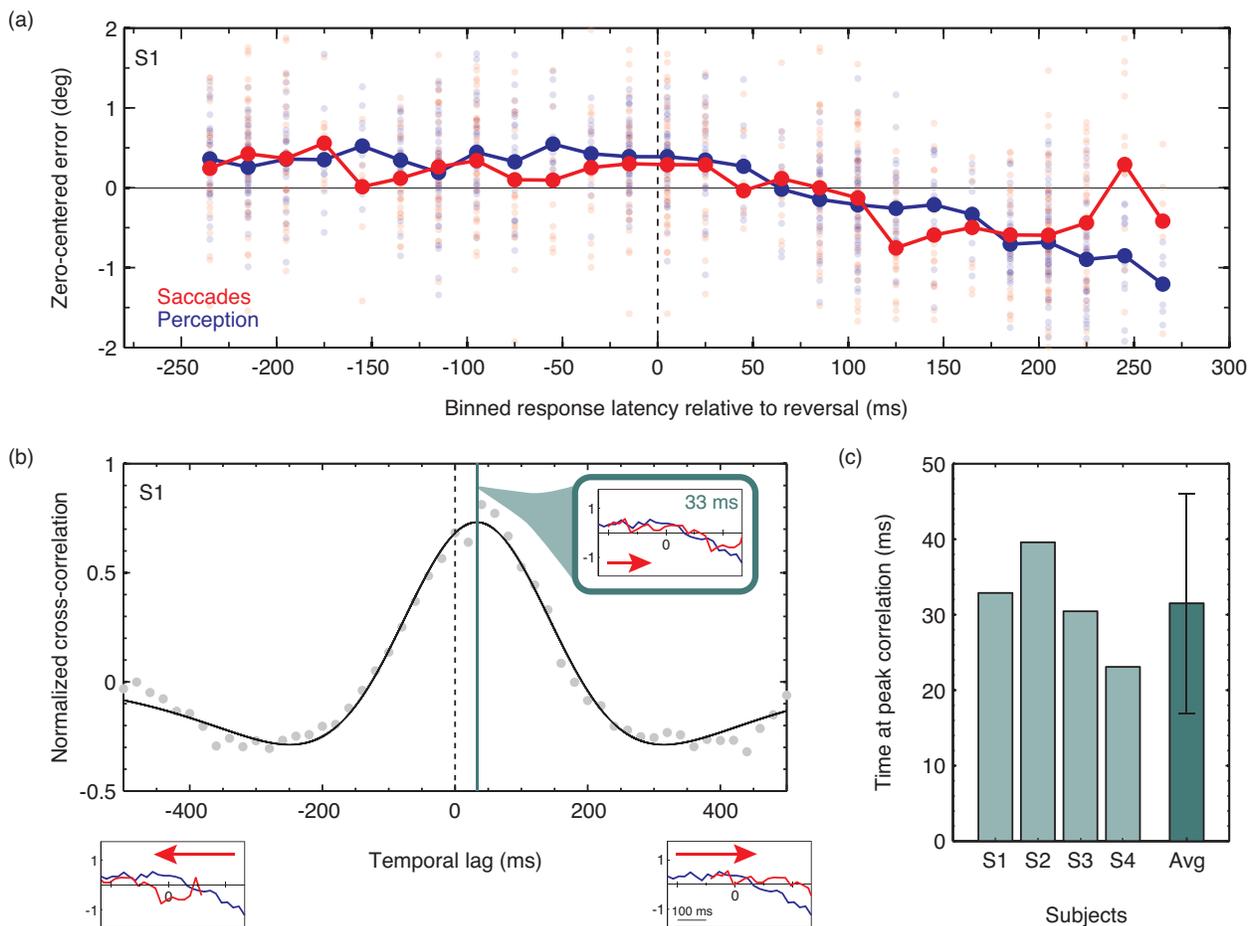


Figure B2. The same analysis shown in Figure 4.5 and described in the Results section of Experiment 2, with 20-ms bins (the smallest bin size that does not require interpolation). In this analysis, saccade error and perceptual error were separately averaged in 20-ms latency bins to obtain a linearly-spaced distribution of latencies, shown in (a). Values are plotted at the bin center. The same procedure was repeated for perceptual errors. The cross-correlation function, shown in (b), was fit by a difference of Gaussians ($R^2 = 0.98$). As shown in (c), the mean peak of the fitted cross-correlation function was 32 ms (95% confidence interval: 17 – 46 ms) and was also significantly greater than zero, $p < 0.001$.

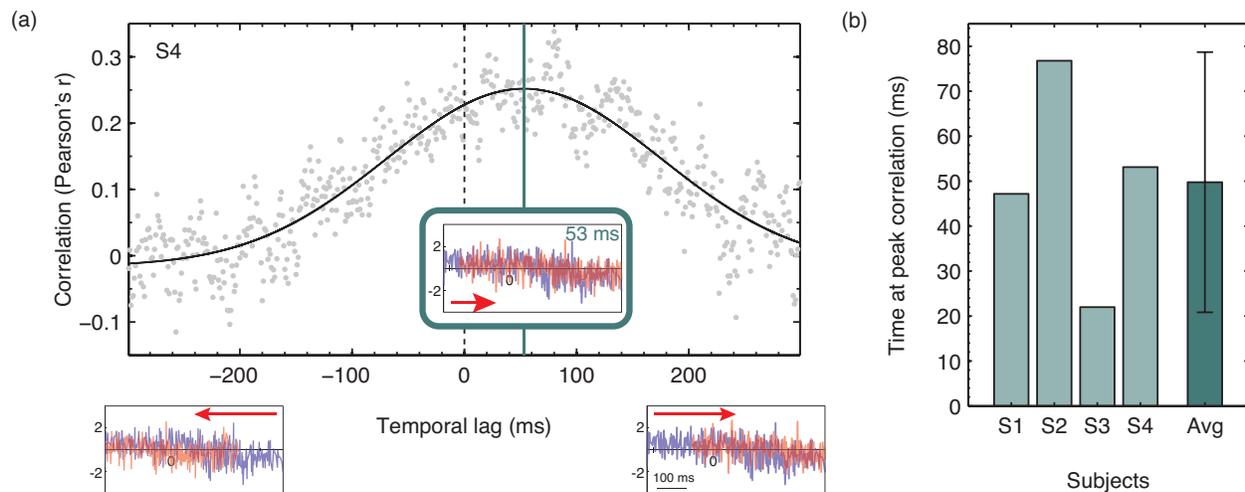


Figure B3. The same analysis shown in Figure 4.5b and c (with 1-ms bins) using a correlation coefficient (Pearson's r) instead of computing the cross-correlation function. The correlation at each temporal lag was fit to a Gaussian function, ($R^2 = 0.76$), and the peak of the fitted function was used to estimate the temporal lag that maximized Pearson's r . This peak (50 ms) was significantly greater than zero, $p < 0.001$.

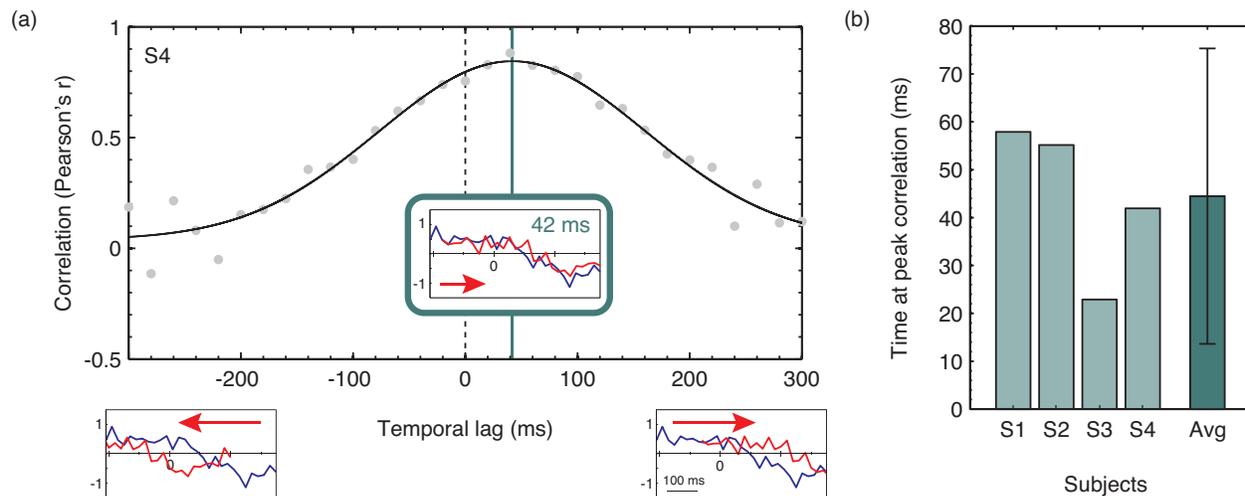


Figure B4. Same as B3, using 20-ms interpolated bins instead of 1-ms bins. The correlation at each temporal lag was fit to a Gaussian function ($R^2 = 0.94$), and the mean peak of the function (45 ms) was significantly greater than zero, $p = 0.008$.

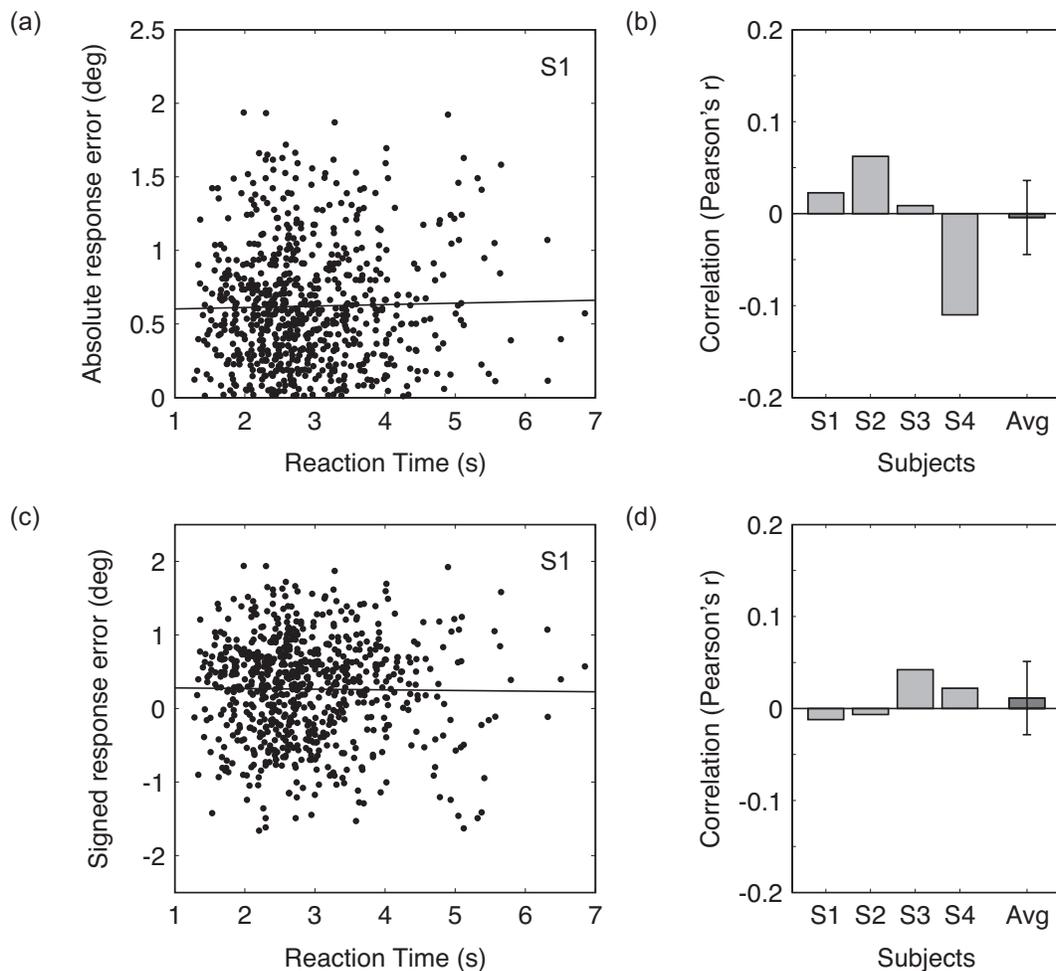


Figure B5. Perceptual errors in the adjustment task as a function of reaction time. (a) Data from an example subject plotting reaction time in the adjustment task versus the absolute magnitude of the perceptual error on each trial. (b) Group data showing that reaction times in the adjustment task were not correlated with the size of the perceptual errors (mean Pearson's $r = -0.004$; $p = 0.764$), (c) Same as (a), plotting the signed magnitude of the motion-induced shift in perceived position, where positive values indicate responses in the direction of motion prior to the reversal, and negative values indicate responses in the direction of motion following the reversal. (d) Group analyses also showed no correlation between reaction times and signed errors at the group level (mean Pearson's $r = 0.01$; $p = 0.65$).

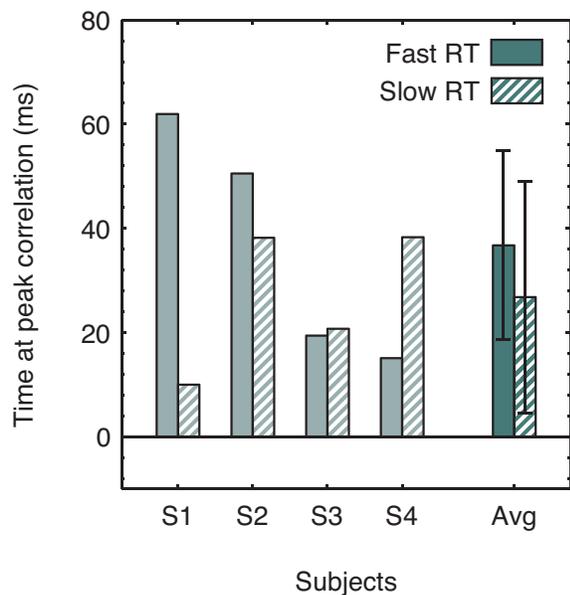


Figure B6. Time at peak correlation based on data averaged in 1-ms bins and DOG fit (similar analysis to Figure 4.5c) split in half based on reaction time. The time at peak correlation was computed separately for trials with values below the median (filled bars) and for values above the median (striped bars). There was no significant difference between time at peak correlation for trials with short reaction times and trials with long reaction times (37 vs 27 ms, $p = 0.616$).

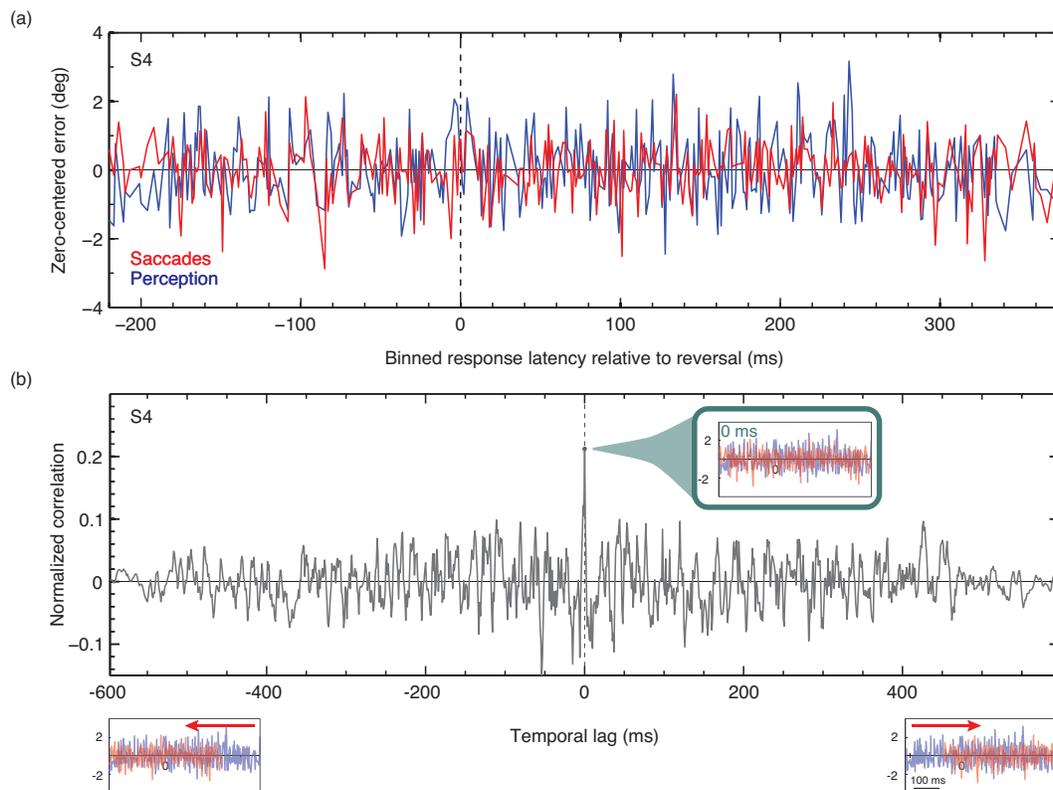


Figure B7. Cross-correlation analysis computed on the magnitude of foveal bias. (a) Similar to Figure 4.5a, except the ordinate shows the magnitude of the zero-centered foveal bias for saccade

error and perceptual error. Positive values represent more foveal responses and negative values represent more eccentric responses. (b) Cross-correlation function, similar to Figure 4.5b, calculated on the magnitude of the foveal bias. For each subject, we measured the temporal lag that produced the highest correlation value. Across subjects, the mean temporal lag producing the highest correlation was 0 ms (95% confidence interval: -53 to 41 ms) and was not significantly different from zero, $p = 0.278$). These data confirm that perceptual and motor localization biases are strongly correlated on a within-trial basis. They also suggest that the differential delay for perception and action (Fig. 4.5) is because of the motion reversal.

Appendix C: Ancillary comments

What did visual area 1 say to visual area 2?

'LO2!

Why couldn't the vision scientists map an area?

Because it was MT!

Why did the psychophysicist stop his experiment?

He got Ga-bored with it.

Why did the psychophysicist change the frame rate for his experiment?

He said it Hertz his eyes.

Why did the vision scientist get kicked out of the conference?

He was too eccentric.

Why didn't the vision scientist stay for very long at the party?

He RSVP'd.

Why did the vision scientist go to the harbor?

He wanted to learn about Bayes.

Why did the chicken cross the road?

He didn't, we just briefly flashed the road while the chicken was moving toward it.

Why did the psychophysicist go to the gym?

He wanted an impossible figure.

Why are psychophysicists so flexible?

They like to adapt.

Why was the psychophysicist missing a lot of line breaks in his manuscript?

He had inhibition of return.

What happened to the pirate who wanted to do high-field imaging?

He was cursed to sail the 7Ts!

Why do vision scientists make for strict teachers?

Because they track their pupils.

What does Patrick Cavanagh's lab do to old testing equipment?

Descartes it away!

What do you call a psychophysicist who psychoanalyzes his data?

Sigmoid Freud.

What did the vision scientist order at the steakhouse?
d' rib.

When do psychophysicists take the elevator?
They don't. They prefer staircases.

Where do photons go when they've been bad?
They go to prism.

What do you call a wimpy neuroscientist that goes away for 4 years and comes back a body builder?
A fast Fourier transform.

Why did the neuron sit through all the TV commercials?
He wanted to stay tuned.

Why did the vision scientist use a coupon when buying light bulbs?
He wanted to discount the illuminant.