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

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Motion can bias the perceived location of a stationary stimulus (Whitney & Cavanagh, 2000), but whether this occurs at a high level of representation or at early, retinotopic stages of visual processing remains an open question. As coding of orientation emerges early in visual processing, we tested whether motion could influence the spatial location at which orientation adaptation is seen. Specifically, we examined whether the tilt aftereffect (TAE) depends on the perceived or the retinal location of the adapting stimulus, or both. We used the flash-drag effect (FDE) to produce a shift in the perceived position of the adaptor away from its retinal location. Subjects viewed a patterned disk that oscillated clockwise and counterclockwise while adapting to a small disk containing a tilted linear grating that was flashed briefly at the moment of the rotation reversals. The FDE biased the perceived location of the grating in the direction of the disk's motion immediately following the flash, allowing dissociation between the retinal and perceived location of the adaptor. Brief test gratings were subsequently presented at one of three locations—the retinal location of the adaptor, its perceived location, or an equidistant control location (antiperceived location). Measurements of the TAE at each location demonstrated that the TAE was strongest at the retinal location, and was larger at the perceived compared to the antiperceived location. This indicates a skew in the spatial tuning of the TAE consistent with the FDE. Together, our findings suggest that motion can bias the location of low-level adaptation.

Keywords: motion processing, flash-drag effect, tilt-aftereffect, orientation adaptation

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Introduction

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., De Valois & De Valois, 1991; Ramachandran & Anstis, 1990; 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

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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, but see Liu, Ashida, Smith, & Wandell, 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, Öğmen, & 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 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: (a) the adaptor's physical (i.e., retinal) location, (b) its perceived location, based on measurements obtained in the first part of the experiment, and (c) an equidistant control location in the opposite direction (its *antiperceived* location).

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

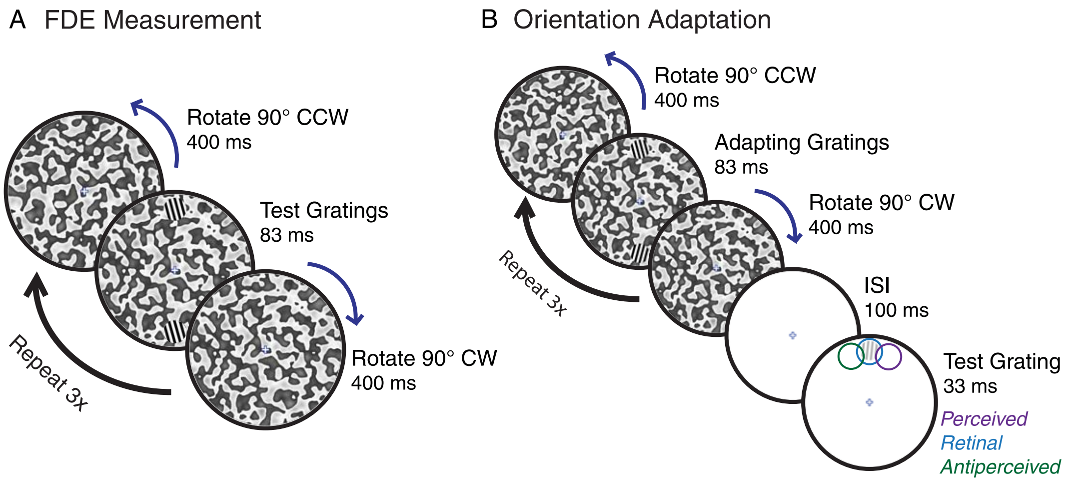

Figure 1. Stimulus presentation sequence for the flash-drag measurement (A) and the orientation adaption (B) portions of Experiment 1.

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 (four female), including one author (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° 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 × 768 and a refresh rate of 60 Hz.

On each trial, observers viewed a patterned disk (10° radius) shown in Figure 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 intertrial interval (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 1A shows the stimulus presentation sequence used to measure the flash-drag effect. Using a two-alternative forced choice

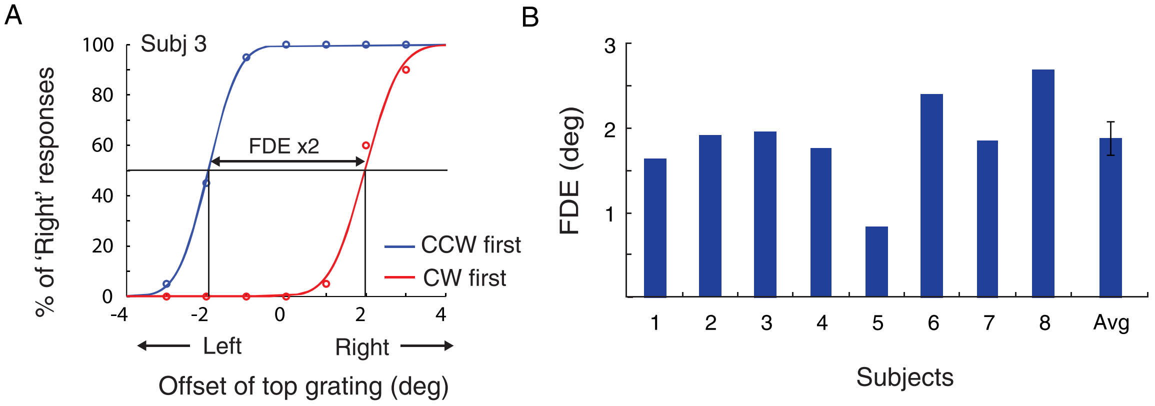

Figure 2. (A) Example flash-drag measurement data from one subject. The FDE was measured as half the difference between the PSEs in the two rotation directions. (B) FDE sizes for all subjects in Experiment 1. Error bar represents ±1 *SE*.

(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 seven locations relative to the vertical midline of the display shown in Figure 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 three times, for a total adaptation duration of 250 ms on each trial.

As shown in Figure 1B, following an interstimulus interval (ISI) 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: (a) one adapting grating (focused attention condition), with the test grating at its retinal, perceived, or antiperceived location or (b) 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 2A, the size of the flash-drag effect is equal to half the difference between the points of subjective equality (PSEs) in the two rotation direction conditions. Figure 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 direction with 1,000 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, $p < 0.001$. Figure 2B shows the size of the FDE for all

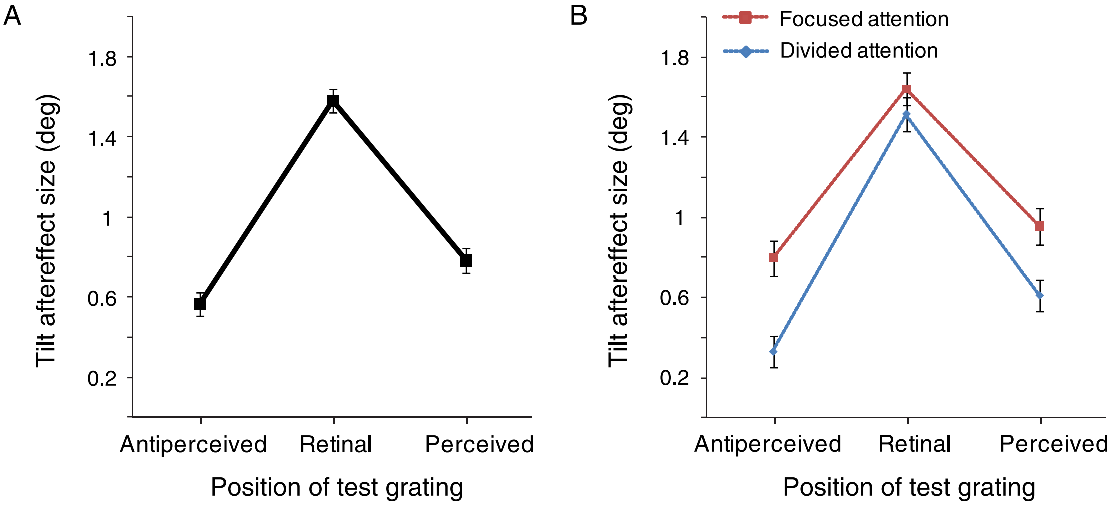

Figure 3. (A) Results from Experiment 1 showing the size of the TAE at each of the three test locations. (B) TAE size divided by attention condition. Error bars represent bootstrapped ±1 *SD*.

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.

Tilt aftereffect measurement

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

$$TAE = \frac{PSE_{adapt\,right} - PSE_{adapt\,left}}{2} \tag{1}$$

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 3A shows the size of the TAE at each location collapsed across attention conditions, and 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 1,000 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 eight observers. Averaged across the two attention conditions, the TAE was greater at the retinal compared to the perceived location, $p <$ 0.001 and greater at the retinal compared to the antiperceived location, $p < 0.001$. A comparison between the nonretinal locations showed that the TAE was larger at the perceived compared to the antiperceived location, $p = 0.007$. Thus, while the TAE was greatest at the retinal location, it was larger at the perceived compared to the antiperceived location.

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 & Spirn, 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 ($p = 0.006$) and antiperceived locations ($p < 0.001$), but no difference at the retinal location, $p = 0.19$. 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, $p = 0.26$.

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 eight subjects between (a) the size of the FDE and (b) 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, $r = 0.73$, $p =$ 0.04. 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

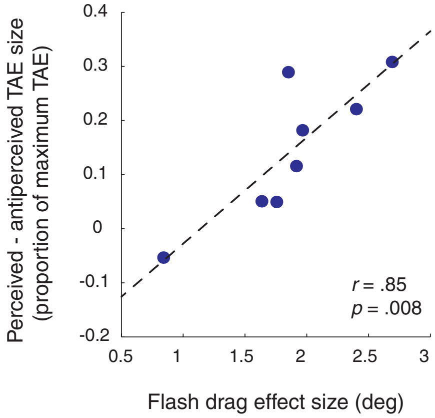

Figure 4. Correlation between the size of the FDE (shown in Figure 2B) and the difference in TAE size between the perceived and antiperceived locations in Experiment 1. Differences in TAE size are based on values normalized to the maximum TAE for each observer and each point represents one subject.

correlation using normalized TAE estimates, calculated as a proportion of each observer's maximum TAE. This correlation, shown in Figure 4, was also significant, $r = 0.85$, $p = 0.008$. In addition, we calculated Spearman's rank correlation coefficient as a nonparametric measure of the relationship between FDE size and the difference in TAE size, which yielded a similar result, $r_s = 0.83$, $p = 0.02$.

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 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 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

$$y = -b{*}|x - s| + m \tag{2}$$

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

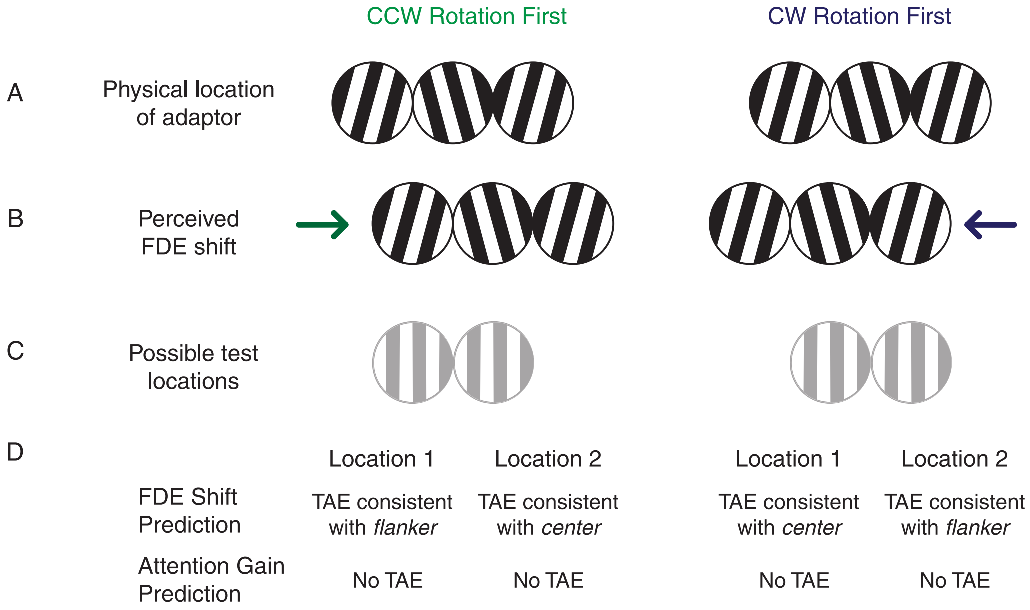

Figure 5. Predictions for Experiment 2. Subjects were presented with three adapting gratings, shown in A. The central grating always had the opposite orientation of the two flanking gratings. The two possible test locations (halfway between the central and each flanking grating), shown in C, were identical 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 CCW and CW 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.

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 (Figure 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 (Figure 5C), halfway between the central grating and one of the two flanking gratings.

Figure 5D outlines the two possible sets of results: (a) the expected results if the effect in Experiment 1 is due to a shift in the retinotopically adapted location and (b) 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 (three female), including one author (AK) participated in the experiment. The mean age of the participants was 25 with a range from 23 to 30.

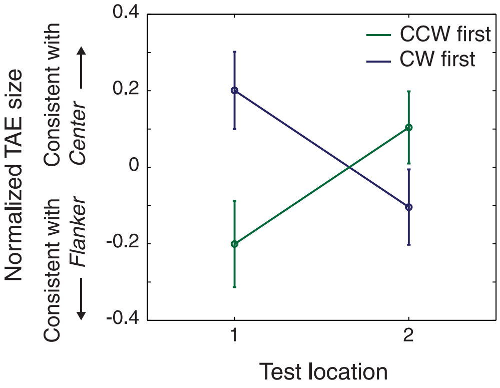

Figure 6. Size of the TAE as a function of test location in Experiment 2. Test location 1 corresponds to the perceived location of a flanker with initial CCW rotation and to the location of the central grating with initial CW rotation. Test location 2 corresponds to the perceived location of the central 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*.

Stimuli

The stimulus was the same as in Experiment 1, with the addition of two flanking gratings, as shown in Figure 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: (a) left, right, left or (b) right, left, right (Figure 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 Figure 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 (Figure 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 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 clockwise (CW) and counterclockwise (CCW) rotation.

As shown in Figure 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 1,000 samples. At Location 1, the TAE was greater in the CW-first rotation condition compared the CCW-first rotation, $p = 0.008$. There was a trend toward the reverse pattern at Location 2, $p = 0.13$. The difference in the TAE between the initial CW and CCW conditions was significantly different across the two test locations, $p = 0.004$. This significant interaction demonstrates a reversal in the TAE across rotation conditions between the two test locations.

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

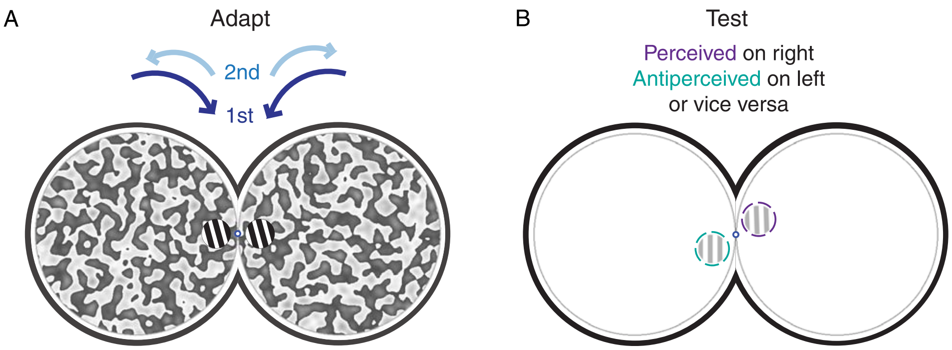

Figure 7. Adaptation (A) and test (B) stimuli in Experiment 3. Initial inward, followed by outward rotation (A) produces a flash-drag effect that shifts the perceived location of the adaptor above fixation. In the test display (B), a grating was presented at the perceived location on one side of the 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.

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 Figure 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 7, we presented two disks rotating in opposite directions to eliminate any net motion, making cyclotorsional eye movements unlikely.

Method

Participants

Three observers (one female), including two authors (AK and 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°. Subjects fixated on an outlined circle 0.25° in diameter (blue outline on either side was 0.1°) while the two disks, centered 7° to the left and right of fixation, rotated in opposite directions. At every other rotation reversal, two square wave gratings, 1° in radius, 1.5 cpd, were presented, centered 1.5° to the left and right of fixation. The gratings were each 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 seven 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.

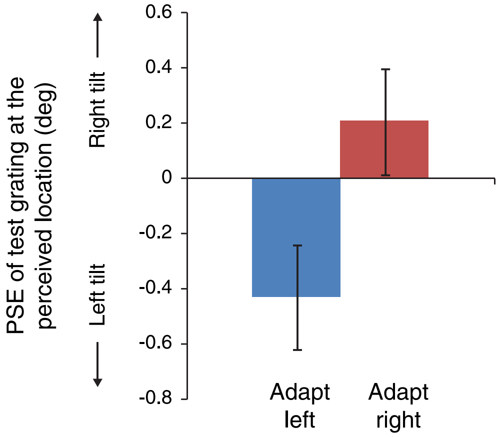

Figure 8. Results from Experiment 3. The PSEs (the tilt of the test grating at the perceived location that produces a vertical percept) in the adapt left and adapt right conditions were consistent with the TAE. For instance, adaptation to a left-tilted grating produces a percept of a rightward-tilted 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*.

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° while the tilt of the test grating at the perceived location was varied between −6 and +6° 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 0.6° of visual angle ($SD = 0.11°$), and was significantly above zero, $p < 0.001$.

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 8, was bootstrapped for each subject with 1,000 samples. Each bootstrapped sample was then averaged across subjects. The difference between the two adaptation directions was significant, $p = 0.02$.

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 (a) the positions of two black dots presented above and below fixation, *off the rotating disk*, and (b) 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 (one female), including one 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 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.

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 seven 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 seven 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.

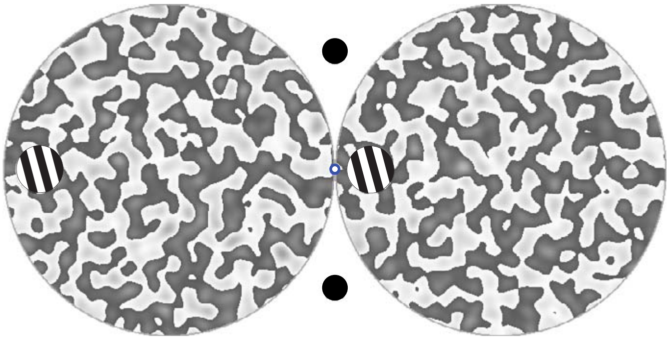

Figure 9. Stimulus used in Experiment 4. As in Experiment 3, the disks oscillated inward and outward. At every other rotation reversal, subjects were presented with two square wave gratings on the rotating disks—one close to fixation and one on the opposite end of the adjacent disk. In addition, subjects 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 (a) whether the top dot was positioned to the right or left of the bottom dot or (b) whether the outer grating was above or below the inner grating.

Results

Dot position judgments

We compared position judgments of two dots presented above and below fixation between the two disk rotation directions. Figure 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 ($SD = 0.04°$) in the inward-first rotation condition, and .008° ($SD = 0.03$) in the outward-first rotation condition.

The difference between the two psychometric functions was bootstrapped for each subject with 1,000 samples. Each bootstrapped sample was then averaged across subjects. The difference between the two motion directions was not significant, $p = 0.32$.

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 10B shows the psychometric function for all subjects across grating positions. The mean FDE was 1.62 degrees of visual

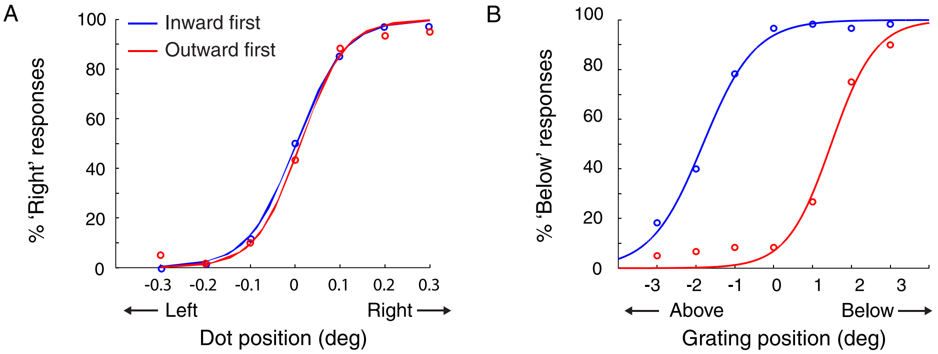

Figure 10. (A) Dot position judgment data from Experiment 4. Subjects were asked to judge the positions of two dots above and below fixation. Each curve plots the percent of responses that subjects judged the top dot to the right of the bottom dot for each of the two rotation directions. (B) Grating 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.

angle ($SD = 0.38°$) and was significantly greater than zero, $p < 0.001$. 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 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 9, initial inward (i.e., CW rotation of the left disk) produces both (a) a downward shift in the perceived position of the more eccentric grating and (b) 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 (Ölveczky, 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.

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