



The Drifting Edge Illusion: A stationary edge abutting an oriented drifting grating appears to move because of the ‘other aperture problem’

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ABSTRACT

We describe the Drifting Edge Illusion (DEI), in which a stationary edge appears to move when it abuts a drifting grating. Although a single edge is sufficient to perceive DEI, a particularly compelling version of DEI occurs when a drifting grating is viewed through an oriented and stationary aperture. The magnitude of the illusion depends crucially on the orientations of the grating and aperture. Using psychophysics, we describe the relationship between the magnitude of DEI and the relative angle between the grating and aperture. Results are discussed in the context of the roles of occlusion, component-motion, and contour relationships in the interpretation of motion information. In particular, we suggest that the visual system is posed with solving an ambiguity other than the traditionally acknowledged aperture problem of determining the direction of motion of the drifting grating. In this ‘second aperture problem’ or ‘edge problem’, a motion signal may belong to either the occluded or occluding contour. That is, the motion along the contour can arise either because the grating is drifting or because the edge is drifting over a stationary grating. DEI appears to result from a misattribution of motion information generated by the drifting grating to the stationary contours of the aperture, as if the edges are interpreted to travel over the grating, although they are in fact stationary.

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1. Introduction

The motion of a translating line viewed through a stationary circular aperture is ill-defined as long as the terminators of the moving line are not visible through the aperture (Wallach, 1935). Despite the fact that the line could in fact be traveling along an infinite number of trajectories that all lie on a single ‘constraint line’ in velocity space (Adelson & Movshon, 1982), the perceived direction of motion viewed through the aperture is always perpendicular to the line’s orientation. This ‘aperture problem’ is believed to arise because of the limited spatial extent of the receptive fields of motion-detecting neurons found early in the visual pathway. The response of these detectors to a moving contour is one-dimensional (1D), and therefore ambiguous, because they can only respond to the motion component perpendicular to the contour (Marr & Ullman, 1981). Because of the close link to the physiology of the early visual system, understanding how motion is perceived when moving gratings are viewed through apertures remains a central focus in vision research.

Interestingly, under certain circumstances, motion viewed through a stationary aperture can cause the position of the aperture to appear laterally displaced from its true position. Ramachandran and Anstis (1990) showed that when a rigid, coherently drifting

random-dot pattern was viewed through a stationary window cut out of another static (or twinkling) noise field, such that the successive portions of the drifting random-dot pattern revealed themselves as the dots passed “behind” the stationary window, the window, which was formed by the boundaries of coherent motion, appeared displaced in its spatial position. This positional displacement was in the same direction as the direction of dot motion.

De Valois and De Valois (1991) showed a similar effect using a stationary drifting Gabor stimulus, in which a moving sinusoidal luminance-defined grating was windowed (and therefore limited in its extent) by a two-dimensional Gaussian envelope that was stationary at all times. In these stimuli, the drifting of the grating produces a pronounced (but static) shift in the perceived location of the patch. Again, the perceived displacement was parallel to the perceived direction of motion.

Building on these findings, Zhang, Yeh, and De Valois (1993) found that an illusory motion of a stationary aperture could be induced that depended upon the direction of grating drift. They found that a ‘hard’ (i.e. sharp edge) aperture presented in the fovea appeared to move in the direction opposite the grating movement, which they called ‘simultaneous motion contrast’. In contrast, a ‘soft’ (fuzzy edge) aperture presented in the periphery appeared to move in the same direction as the drifting grating, demonstrating what they called ‘motion integration’. These results were discussed in the context of interactions between short-range and long-range motion mechanisms and with respect to the

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significance of boundaries in determining the figure–ground relationship of motion signals.

Tse and Hsieh (2006) extended this work by translating the ‘drifting Gabor’ patch perpendicularly to the direction of the drifting grating. When viewed in the periphery, the patch appeared to continually drift away from fixation although in fact it was just moving vertically. This demonstrated that not just the speed but also the direction in which the patch was perceived to move could be influenced by the local motion of the drifting Gabor. In each of these cases, the perceived motion of the Gabor patch was reasonably predicted by a weighted, approximately linear integration of the motion within the patch and the motion of the patch itself.

These examples demonstrate an important link between the detection of local motion and the determination of an object’s position or trajectory in space. In the case of a stationary object, local motion can influence its perceived position in space. In the case of a moving object, this influence is continuously exerted along the object’s path, leading to biases in the object’s perceived speed and direction.

Here, we characterize a novel stimulus in which motion viewed through a stationary aperture makes the aperture itself appear to continuously move. Specifically, when a drifting grating is viewed through a stationary oriented aperture, like the parallelogram configuration shown in Fig. 1A and Demonstration Video 1, the aperture itself appears to translate continuously up and down as the grating drifts back and forth, even though the aperture is in fact stationary. In fact, it is not necessary to have an aperture at all. It is sufficient to have a stationary edge abut an oriented drifting grating. Under certain circumstances, such a stationary edge will itself appear to drift as shown in Demonstration Video 2. As such, we refer to the illusory motion as the Drifting Edge Illusion (DEI). However, in this paper, we will examine stimuli that are barber-pole stimuli that can be thought of as drifting gratings viewed through apertures. In the vertical configuration shown in Demonstration Video 3, the aperture is perceived to translate back and forth from left to right. Unlike the static displacement of the stationary aperture reported by De Valois and De Valois (1991), which was in a direction consistent with that of the drifting grating, the aperture here is perceived to move continuously in a direction that is inconsistent with that of either grating drift or terminator motion. Because the perceived direction of the illusory motion is not parallel with the local component or the terminator motion along the elongated edge of the aperture, the speed and direction of the global aperture motion is not easily predicted by an integration (such as a weighted vector summation) of local and object-motion sources (unlike the stimuli used by Zhang et al. (1993) or Tse and Hsieh (2006)). As can be observed in Demonstration Video 1, the illusory motion is predominantly vertical, which is inconsistent with the local component motion and local terminator motion along the elongated edges of the aperture, both of which are obliquely oriented.

Importantly, and perhaps surprisingly, not all configurations of this stimulus produce illusory motion of the static aperture. For example, if the orientation of the drifting grating is perpendicular to the orientation of the aperture, as shown in Fig. 1B and Demonstration Video 4, illusory motion is not perceived. This indicates that the local terminator motion along the short edges of the aperture, which are vertical in both the configurations shown in Fig. 1A and B, is not the determining factor underlying the DEI. The existence and speed of illusory motion seems to depend upon both the direction of local motion and the shape and orientation of the aperture. Again, a true aperture is not required. It is sufficient to have a grating that drifts along a single edge (see Demonstration Video 2), as if partially occluded by that edge. Under the right conditions, a single edge will appear to drift in a direction very different from the motion of any local moving terminators or normal

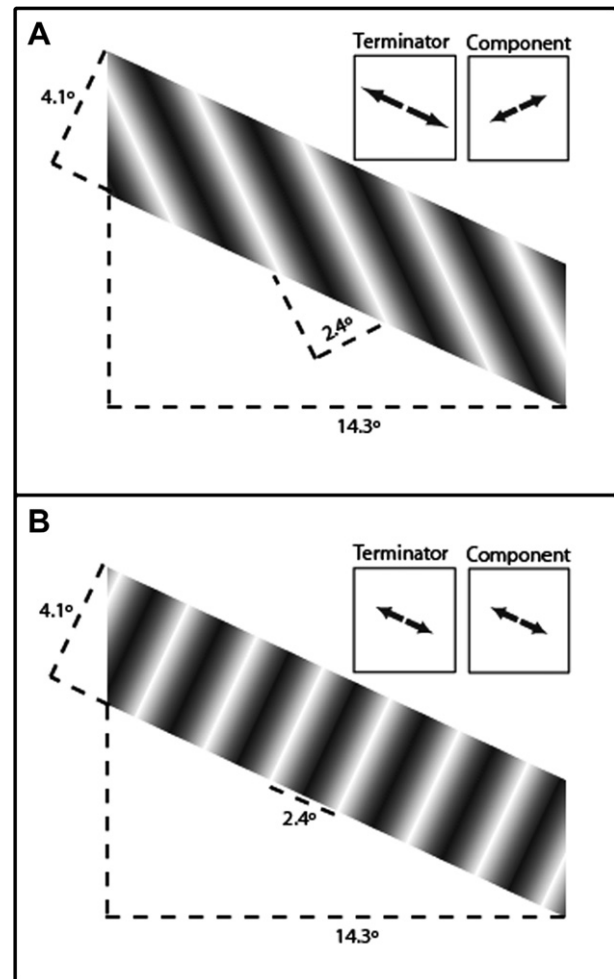


Fig. 1. The Drifting Edge Illusion (DEI) stimulus configurations. When an obliquely oriented grating is drifted behind an obliquely oriented aperture, as shown in (A), an illusion of the entire grating drifting vertically may be perceived. However, not all configurations of this stimulus will lead to the illusory motion percept. The configuration shown in (B), in which the orientations of the aperture and grating are perpendicular to each other, does not produce the illusory motion. In configurations such as these, there are two distinct sources of motion information: the component motion perpendicular to the orientation of the grating and the terminator motion parallel to the orientation of the aperture. The relative magnitudes and directions of these motion sources are shown for each of these two stimulus configurations; note that the DEI is not observed when these two sources are identical to each other. These two stimulus configurations, as well as others, were examined in Experiment 1, and the sizes shown here reflect the sizes of the stimuli used in that experiment.

motion components of the grating itself. In this paper, we explore the DEI using a parallelogram aperture, but could just as well have explored the effect using drifting gratings moving against a single edge. The examples given above illustrate the importance of the relative angle between the edge and drifting grating in determining whether or not the DEI will be perceived. We systematically explore this relationship, examining under what conditions the DEI is perceived. Here we examine configurations with apertures that are roughly horizontal like that shown in Demonstration Video 1.

2. Stimulus presentation

The visual stimulator was a 2-GHz Dell workstation running Windows 2000. The stimuli were presented on a 20-in. Mitsubishi flat-screen CRT monitor with a 1600 × 1200-pixel resolution and an 85-Hz frame rate. Luminance values were measured using a PHOTO RESEARCH® PR®-1980A Pritchard® Photometer (Photo Research, Chatsworth, CA, USA) at a distance of 7'. Observers viewed

the stimuli on a black background (0.04 cd/m^2) from a distance of 53 cm with their chin in a chin rest. Participants were required to maintain central fixation. Fixation was ensured using a head-mounted eyetracker (Eyelink2, SR Research, Ontario, Canada; Tse, Sheinberg, & Logothetis, 2002). Any time the subject's monitored left eye was outside a fixation window of 1.5° radius while the stimulus was present, the trial was automatically aborted, and restarted when the subject regained fixation. The eyetracker was recalibrated whenever the subject's monitored eye remained for whatever reason outside the fixation window while the subject reported maintaining fixation. Once calibration was completed, the experiment resumed with the last aborted trial.

3. Experiments 1a and 1b

In this first pair of experiments we characterized the relationship between the orientation of the aperture and the orientation of the drifting grating, in terms of the strength of the DEI. First, we systematically varied the relative angle between the aperture and the grating and determined, on a trial-by-trial basis, how frequently the illusory motion was perceived. Second, we used a motion-nulling technique to measure the speed of the illusory motion under different relative-angle configurations.

3.1. Observers

Prior to each of the experiments presented in this paper, potential participants were shown a configuration similar to that shown in [Demonstration Video 1](#) played continuously in an uncontrolled environment, and the illusory motion was described. Each of the five participants included here indicated that they could see the illusory percept. A small number of potential participants were excluded from participation due to the fact that they could not perceive the illusion. Prior to the experiments, all participants included in this study gave written, informed consent according to the guidelines of the Department of Psychological and Brain Sciences, and the internal review board of Dartmouth College. Five participants with normal or corrected-to-normal vision carried out Experiments 1a and 1b (three of whom participated in both).

3.2. Experiment 1a

3.2.1. Methods

3.2.1.1. Procedure. In each trial, participants were presented with an oriented, sinuswave grating (white: 73.6 cd/m^2 ; black: 0.04 cd/m^2 ; $C_m = 0.99$) of limited spatial extent, giving it the shape of a parallelogram, as shown in [Fig. 1](#). The period of the sinuswave grating was 2.4° (0.417 cpd) of visual angle. The limited spatial extent of the grating is functionally equivalent to an aperture through which a larger grating is being viewed. The aperture had a horizontal width of 14.3° of visual angle, and a perpendicular height of 4.1° of visual angle.

In half the trials, the orientation of the grating was fixed at 115° from horizontal, while the aperture was pseudo-randomly chosen from seven angles: -25° , -15° , -10° , -5° , 0° , 10° , or 25° from horizontal. In the other half of the trials, the aperture was fixed at -25° from horizontal, while the orientation of the grating was pseudo-randomly chosen from seven angles: 65° , 80° , 90° , 95° , 100° , 105° , or 115° from horizontal. The grating drifted back and forth (perpendicular to its orientation angle) once at a speed of 11.5° visual angle/s for 1.5 s (0.75 s in each direction) and then disappeared. The initial drift direction was randomly determined for each trial. After each trial, participants were required to indicate, by pressing one of two buttons (yes/no), whether they perceived the DEI in that trial or not. Once they indicated their response,

the next trial began. Each combination of grating and aperture angles was shown 15 times, for a total of 195 trials.

3.2.2. Results Experiment 1a

For each participant, the percentage of trials for which the DEI was perceived was computed for each stimulus condition. The data were sorted into and plotted as two specific groups: the first group examined the percentage of trials in which the DEI was perceived when the orientation of the grating was 115° away from horizontal, plotted as a function of the orientation of the aperture away from horizontal. The second group examined the percentage of trials in which the DEI was perceived when the orientation of the aperture was fixed at -25° away from horizontal, plotted as a function of the orientation of the grating. These values were then averaged across the five participants, and the standard error of the mean for each condition was computed. The group data, shown in [Fig. 2](#), illustrate that for a fixed grating angle of 115° there was a systematic relationship between the frequency with which the DEI was observed and the orientation of the aperture. Across all conditions, the DEI was perceived most often during trials in which the aperture was oriented at -25° from horizontal ([Fig. 2A](#)). Similarly, the data also show that when the aperture angle was fixed at -25° from horizontal ([Fig. 2B](#)), there was a systematic relationship between the frequency with which the DEI was observed and the orientation of the grating. Plotting the data as a function of the relative angle between the aperture and grating as shown in [Fig. 2C](#), where logit functions have been fit to the group data, makes it clear that the DEI is more likely to be perceived the farther from perpendicular the orientations of the aperture and grating become, seemingly independent of the absolute angles of either the aperture or grating.

3.3. Experiment 1b

In Experiment 1a we found that the DEI was more likely to be observed when the relative angle between the aperture and grating deviated from 90° . In this experiment, we sought to quantify the magnitude of the DEI in terms of the perceived speed of illusory motion. Using a motion-nulling paradigm, we applied the method of constant stimuli to determine the speed at which the aperture, in three different stimulus configurations, needed to be translated in order to cancel the perception of the DEI. Based on the subjective observation of the DEI as shown in [Demonstration Video 1](#), it is assumed that as the grating drifts, if the terminator motion has an upward component, then the predicted motion of the DEI would be upward. On the other hand, if the terminator motion has a downward component, then the predicted motion of the DEI would be downward. For the stimuli tested here, it would be equivalent to assume that if the orthogonal component motion of the drifting grating had an upward component, then the predicted motion of the DEI would be downward and visa-versa. This model makes it difficult to anticipate the predicted direction of the DEI using a configuration in which both the component and terminator motion had the same vertical direction. However, the results of Experiment 1a indicate that the DEI is not observed with such configurations.

3.3.1. Methods

3.3.1.1. Procedure. The stimuli presented were the same size, shape, and luminance as in Experiment 1a, with the exception that in all trials, the aperture was oriented at an angle of 25° from horizontal, and the grating was randomly chosen from either 65° , 80° , or 115° from horizontal. Thus, in any given trial there was one of three possible relative angles between the orientations of the aperture and grating: 40° , 55° , or 90° . The grating drifted perpendicularly to its orientation angle in one direction or the other (chosen randomly)

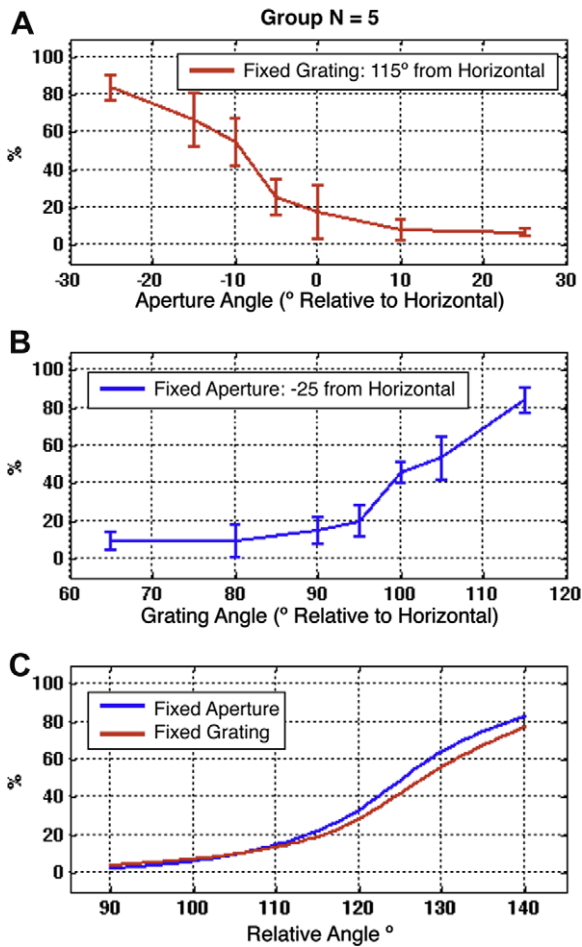


Fig. 2. Results of Experiment 1. On a trial-by-trial basis, observers viewed stimulus configurations similar to those shown in Fig. 1. After each trial, observers reported whether the DEI was perceived or not. For each aperture and grating angle combination presented, the percentage of trials in which the DEI was observed was computed. Data from each subject were then averaged together and standard errors of the mean for each condition were computed. These data were sorted into two groups: (A) trials in which the orientation of the grating was 115° from horizontal, and (B) trials in which the orientation of the aperture was -25° from horizontal. A systematic relationship between the orientations of the grating and aperture and the magnitude of the DEI is observed. This relationship is summarized in (C) where logit functions that have been fit to the data shown in (A) and (B) are plotted as a function of the relative angle between the aperture and grating. Specifically, the DEI is not perceived when the orientations of the aperture and grating are perpendicular to each other, and is systematically perceived more often as the relative angle deviates from 90°.

at a speed of 11.5° visual angle/s for 1 s and then disappeared. While the grating drifted, the whole stimulus (aperture and grating) was translated vertically either up or down on the screen. This vertical translation could either be congruent (i.e. in the same direction, up or down) or incongruent (i.e. in the opposite direction, up or down) with the anticipated direction of the DEI. On each trial the speed of the translation was chosen from one of seven speeds: -8, -6, -5, -4, -2, 0, or 3, multiplied by 0.19° visual angle/s. A positive value indicates that the movement was in the same direction as (i.e. congruent with) the illusory motion; a negative value indicates that the movement was in the opposite direction as (i.e. incongruent with) the illusory motion. After each trial, participants were required to indicate, by pressing one of two buttons (2AFC), whether the aperture was moving up or down. Once they indicated their response, the next trial began. Each pairing of grating angle and speed was shown 15 times in a pseudorandom order, for a total of 315 trials.

3.3.2. Results

For each grating angle and actual translational velocity, we computed the percentage of trials in which the reported direction of translation was congruent with the direction of the DEI. The data from each subject were then fit with logit functions, and the 50% point corresponding to the speed of translation necessary to null the illusory motion of the DEI was computed. The data shown in Fig. 3 illustrate that in both the 65° and 80° conditions, a global translation in the direction opposite to the direction of the DEI was necessary for the grating to be perceived as stationary (one-sample t -test 65°: $t(4) = 3.58$, $p < 0.03$; 80°: $t(4) = 3.95$, $p < 0.02$). In the 115° condition, however, no translation was necessary ($t(4) = 1.26$, $p > 0.27$), reflecting the fact that the DEI was not perceived in this condition. A repeated measures ANOVA with a linear contrast applied to the three groups indicates a statistically significant linear relationship between relative angle and the magnitude of the DEI ($F(1,4) = 9.98$, $p < 0.04$). Thus there is a significant linear relationship between the perceived speed of the illusory motion and the relative angle between the grating and aperture.

4. Experiment 2

The results of Experiments 1a and 1b indicate that the relative angle between the aperture and the grating is critical in determining whether or not and how strongly the DEI will be perceived. However, the motion-nulling technique used in Experiment 1b was based on an assumption that the perceived direction of the DEI is along the vertical axis. While this assumption conforms to the subjective impression of the illusory motion (see [Demonstration Video 1](#)), in

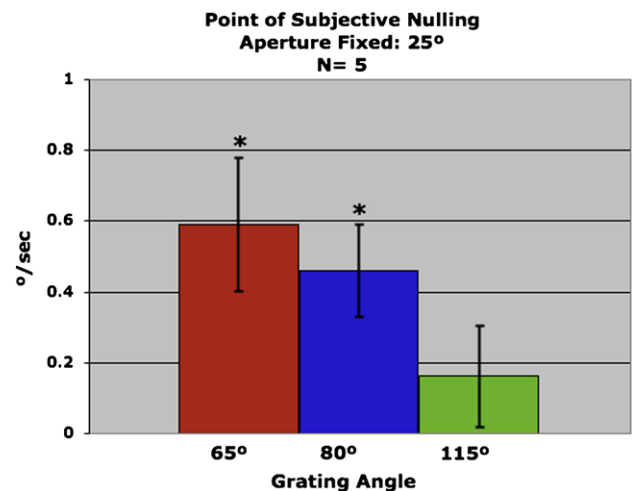


Fig. 3. Results of Experiment 1b. In Experiment 1b, observers were presented with three of the stimulus configurations, corresponding to a relative angle between the aperture and grating of 40°, 55°, and 90°, that were used in Experiment 1a. On each trial, not only did the grating drift behind the aperture, but the entire grating was translated at one of seven different speeds along the vertical axis. On some trials, this translation was in the same direction as the DEI and in others it was in the opposite direction as the DEI. After each trial, observers were asked to report the direction of this translational motion. For each of the three stimulus configurations and each of the seven translational speeds, the percentage of trials that the reported direction was congruent with the DEI was computed. For each subject, these data were fit with a logit function from which the 50% point, corresponding to the speed of translational motion required to null the DEI was interpolated. The values from each subject were then averaged together. The data shown here indicate that a statistically significant amount of motion in the direction opposite that of the DEI was required to cancel the illusory motion in the two configurations (red and blue) where the aperture and grating were not perpendicular to each other. This indicates that the DEI was perceived in the two conditions in which the relative angle between aperture and gratings was less than 90° and not in the 90° configuration. Error bars indicate the standard error of the mean across subject. * $p < 0.05$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this paper.)

this experiment we explicitly measured the perceived direction of the DEI to verify whether or not this assumption is valid.

4.1. Methods

4.1.1. Observers

Five participants (four of whom participated in either Experiments 1a or 1b) with normal or corrected-to-normal vision carried out the experiment.

4.1.2. Procedure

Observers were presented with one of five possible stimulus configurations consisting of a drifting grating and an aperture. The gratings had a period of 1.6° (0.625 cpd) of visual angle with the luminance and contrast of the gratings used in Experiments 1a and 1b. For each stimulus configuration, the aperture had a horizontal length of 8.6° of visual angle and a perpendicular height of 2.6° of visual angle. In half the trials, the orientation of the grating was fixed at 115° from horizontal, while the aperture was pseudo-randomly chosen from one of three angles: -25° , -15° , or -10° from horizontal. In the other half of the trials, the aperture was fixed at -25° from horizontal, while the orientation of the grating was pseudo-randomly chosen from one of three angles: 100° , 105° , or 115° from horizontal. The grating drifted back and forth (perpendicular to its orientation angle) at a speed of 7.9° visual angle/s for three seconds (changing direction every 0.75 s) and then disappeared. A randomly oriented red line then appeared on the display. If participants did

not perceive an illusion on a particular trial, they disregarded the red line and pressed a button to begin the next trial. If they did perceive an illusion, they used the left and right arrow keys of a standard keyboard to rotate the line until its orientation matched the perceived direction of the illusion, a separate button was then pressed recording the line's orientation and the next trial began. Each combination of grating and aperture angles was shown 20 times, for a total of 100 trials.

4.2. Results

As was the case in Experiment 1a, observers were more likely to perceive the DEI the farther the relative angle between aperture and grating was from 90° . Fig. 4A shows the percentage of trials in which the DEI was perceived for each condition. Again, the likelihood of perceiving the DEI was the same for the pairs of configurations that led to the same relative angles (130° and 125°). For the trials in which the DEI was perceived, the perceived direction of motion was binned into groups of 10° (relative to vertical). The histograms shown in Fig. 4B illustrate that for each condition, the modal response is along the vertical axis. There were a number of trials in which the perceived direction of motion was non-vertical; this may reflect the possibility that multiple factors may influence the perceived direction of the illusion. However, the fact that the modal response was vertical in each configuration tested suggests that the assumption of verticality underlying the motion-nulling technique used in Experiment 1b and in subsequent experiments is not unreasonable.

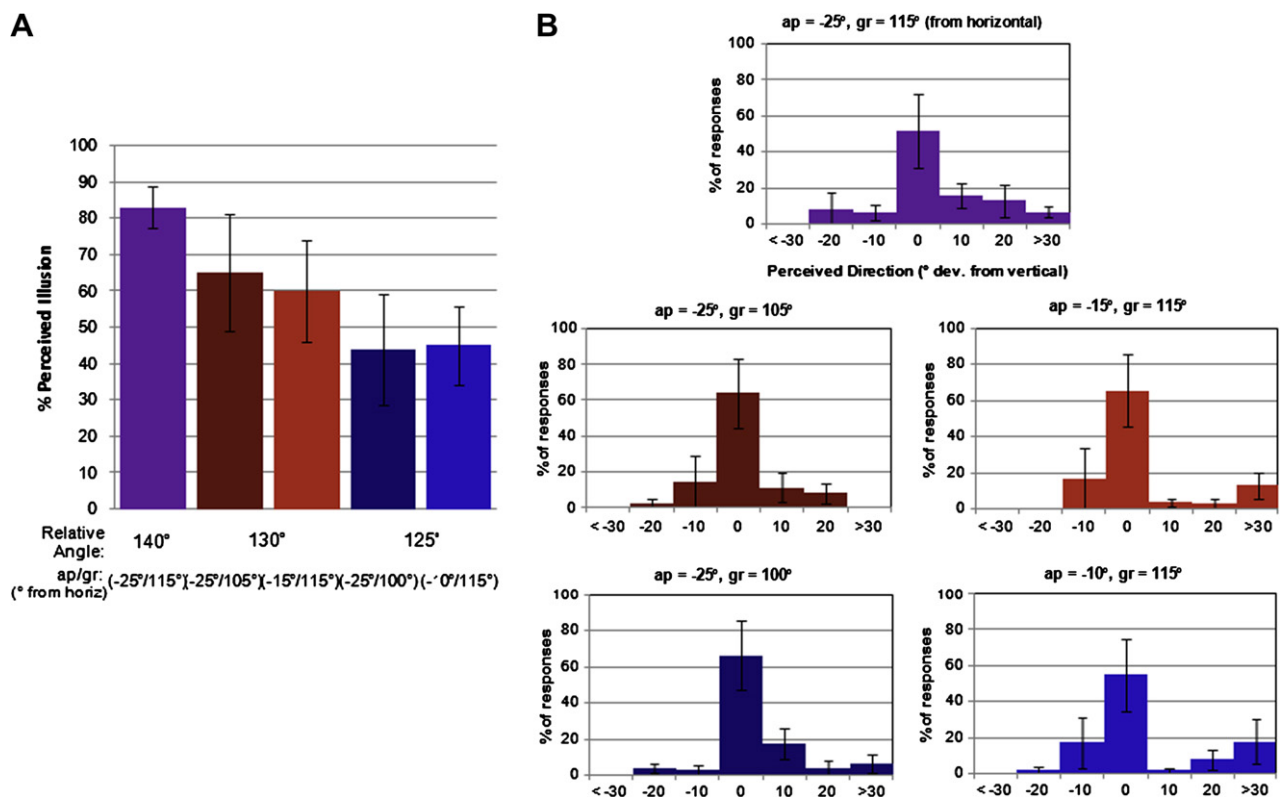


Fig. 4. Results of Experiment 2. In Experiment 2, observers were asked to quantify the perceived direction of the DEI under five of the stimulus configurations used in Experiment 1a. Three relative angles, 140° , 130° , and 125° , were tested by varying either the orientation of the aperture or the angle of the grating. (A) Prior to indicating the perceived direction of the DEI, observers had to report whether or not the illusory motion was perceived. The percentage of trials in which the DEI was perceived is presented as a function of relative angle. As in Experiment 1a, the DEI was more likely to be perceived the farther from 90° the relative angle between aperture and grating was, independent of the absolute angle or either the aperture or grating. (B) On those trials in which the DEI was perceived, observers were asked to indicate the direction of the perceived motion. Here, we present, for each stimulus configuration, the percentage of trials in which the direction (binned) of the DEI was perceived. For each configuration, the modal response was along the vertical axis.

5. Experiment 3

The results of Experiments 1 and 2 indicate that the critical variable in determining whether or not the DEI will be perceived is the relative angle between the aperture and the grating. While the data certainly support this conclusion, one wonders why the DEI has not been previously reported in the literature. Even as early as Wallach's (1935) account, barberpole stimuli have been investigated using a relative angle between aperture and grating of greater than 120°, which, according to Experiments 1 and 2, should produce percepts of the DEI if relative angle alone is sufficient to drive the illusory percept. In the configurations examined in Experiments 1 and 2 that led to the strongest percepts of the DEI, both the aperture and grating were obliquely oriented. Interestingly, most if not all studies investigating the barberpole illusion have been conducted using either vertically or horizontally oriented apertures and/or gratings. This leads to the hypothesis that the DEI depends upon both the aperture and the grating being obliquely oriented. If the aperture and/or grating is vertically or horizontally oriented, it is possible that the DEI may be weak or even not present at all. In the third experiment, we explicitly test this hypothesis by fixing the relative angle between the aperture and grating, while changing the absolute angles of both the aperture and drifting grating by a fixed amount, so as to allow either the aperture or the grating to be either horizontally or vertically oriented.

5.1. Methods

5.1.1. Observers

Five participants (four of whom participated in one or more of the previous experiments) with normal or corrected-to-normal vision carried out the experiment.

5.1.2. Procedure

Participants were presented with one of three possible stimulus groups consisting of a drifting grating and an aperture (as shown in Fig. 5). The gratings had a period of 1.6° (0.625 cpd) of visual angle, the luminance and contrast of the gratings were the same as those used in Experiments 1 and 2. In the first stimulus (Fig. 5A), the aperture was oriented at an angle of 50° from horizontal, with a horizontal length of 8.6° of visual angle and a perpendicular height of 2.6° of visual angle, and a grating oriented vertically at an angle of 90° relative to horizontal. The second stimulus (Fig. 5B) consisted of a horizontally oriented aperture subtending the same horizontal distance as the first aperture and the same perpendicular height. In this stimulus, the grating was oriented at -40° from horizontal, thus preserving the same 40° relative angle between the two. The third stimulus (Fig. 5C) was similar to a configuration tested in Experiments 1 and 2, with an aperture oriented at 25° from horizontal and the grating oriented at 65° from horizontal. Thus in each of the three conditions the relative angle between the aperture and grating was the same.

In each trial the grating moved perpendicularly to its angle of orientation in one direction or the other (chosen randomly) at a speed of 6.9° visual angle/s for 1 s and then disappeared. As in Experiment 2, while the grating drifted, the whole stimulus (aperture and grating) translated vertically on the screen either congruently or incongruently with the predicted direction of the DEI. The speed of translation was chosen to be one of the following: -6, -2, -1, 0, 1, 2, or 6, multiplied by 0.19° visual angle/s (a positive value indicates the translation was congruent with the illusory motion, a negative value indicates the translation was incongruent with the illusory motion). After each trial, participants were required to indicate whether the aperture was moving

up or down by pressing one of two buttons (2AFC). Once they indicated their response, the next trial began. Each pairing of stimulus and speed was shown 15 times, for a total of 315 trials. The stimuli were presented in a pseudorandom order and the direction in which the grating drifted was randomly determined from trial to trial.

5.2. Results

As in Experiment 1b, for each of the three stimulus configurations and actual translational velocities, we computed the percentage of trials in which the reported direction of translation was consistent with the direction of the DEI. The data from each subject were then fit with logit functions from which the 50% point, corresponding to the speed of translation necessary to null the illusory motion of the DEI, was computed. The data, shown in the insets of Fig. 5, illustrate that the DEI is not perceived when either the grating is vertically oriented (two-tailed, one-sample t -test: $t(4) = 0.18$, $p > 0.86$) or when the aperture is horizontally oriented ($t(4) = 2.40$, $p > 0.07$). As was the case in Experiments 1 and 2, the DEI was perceived ($t(4) = 3.88$, $p < 0.02$) when both the aperture and grating are obliquely oriented. A repeated measures ANOVA ($F(2,8) = 10.45$, $p < 0.007$) indicates a significant main effect of absolute angle on the DEI. We note however, that when the aperture was horizontally oriented, there appears to be a small (albeit not significant at the $\alpha = 0.05$ level) effect of the DEI. [Demonstration Video 5](#) illustrates an example of a horizontally oriented aperture configuration similar to the one tested here. Although much weaker than observed in [Demonstration Video 1](#), an observer may notice a small amount of the DEI (particularly when viewed peripherally) when the aperture is horizontally oriented. Taken together, these results support the hypothesis that the DEI may not be readily observed in many of the classical configurations used to study the barberpole illusion.

6. Experiment 4

The motion of a grating viewed through an aperture is ill-defined, giving rise to the familiar 'aperture problem'. In the case of a rectangular aperture, the dominantly perceived direction of motion is parallel to the orientation of the aperture (Wallach, 1935), presumably because a processing stage of figure-ground segmentation has determined that the terminators are intrinsic to the moving grating and are not artifacts arising from occlusion (Nakayama & Silverman, 1988a; Nakayama & Silverman, 1998b). However, this stage of figure-ground segmentation is itself subject to ambiguity. Although the perceptual outcome is most often one in which the terminators are deemed intrinsic (i.e. 'owned' by the drifting grating), this need not be the case in the physical world. For example, the same terminator motions could arise along an edge if the edge were moving and the grating were stationary, or vice-versa. By manipulating the stimuli, we can eliminate the ambiguity of figure-ground segmentation, thereby classifying the terminators as intrinsic both at the stage of stimulus input and at the stage of perceptual output. In this fourth experiment, we seek to determine whether or not the DEI is perceived under conditions in which the terminators are explicitly made to be intrinsic.

6.1. Methods

6.1.1. Observers

Five participants (all five of whom participated in one or more of the previous experiments) with normal or corrected-to-normal vision carried out the experiment.

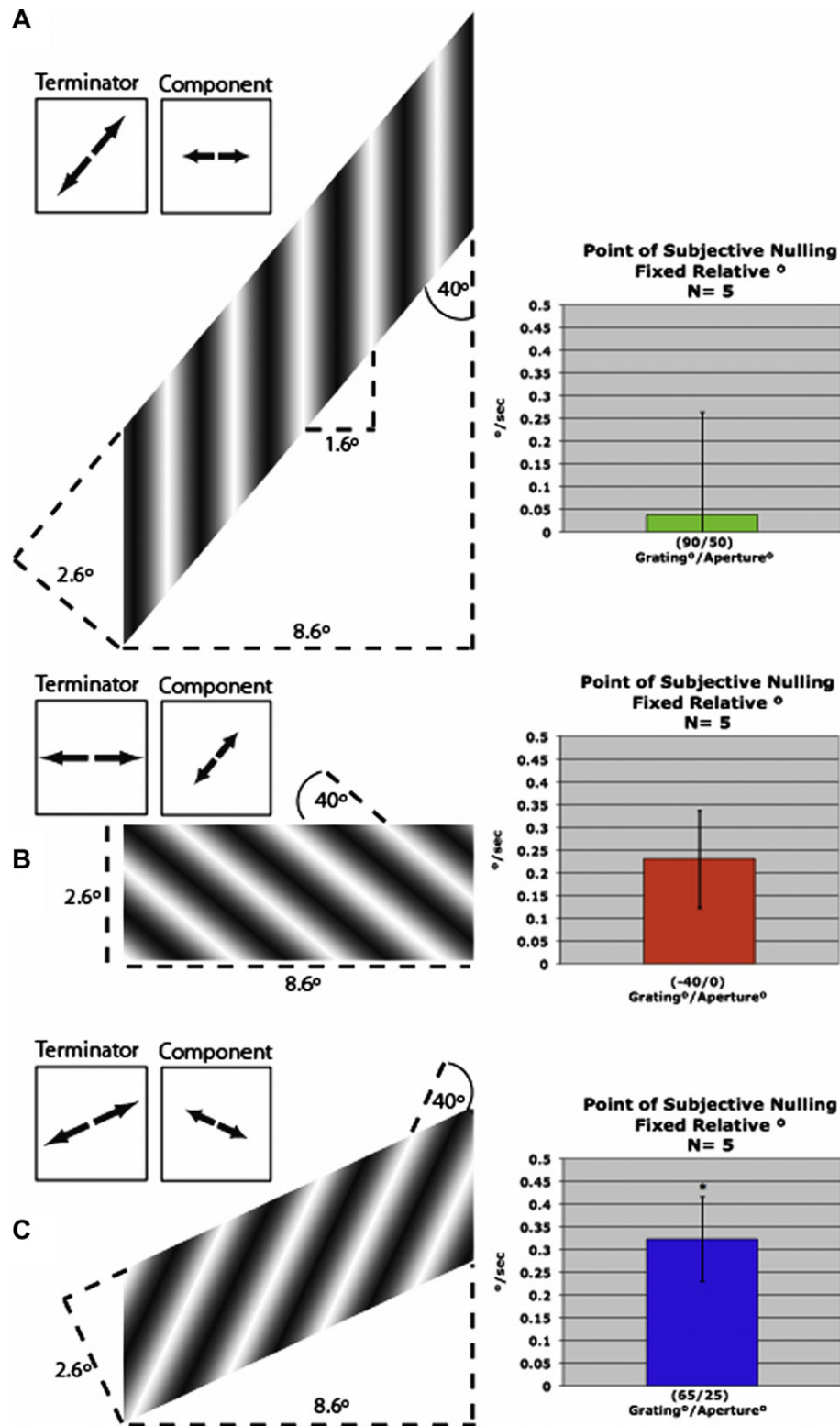


Fig. 5. Non-oblique orientations of Experiment 3. Experiment 3 used three configurations each having a relative angle between aperture and grating of 40° . In Experiments 1 and 2, this relative angle was shown to produce the DEI. Although the relative angle was fixed at 40° , the absolute angles of the aperture and grating were chosen so that in (A) the orientation of the grating was vertical, in (B) the orientation of the aperture was horizontal, and in (C) both the aperture and grating were obliquely oriented. As in Experiment 2, the mean point of subjective nulling, or the speed at which the grating needed to be translated along the vertical axis in order to cancel the DEI, was interpolated for each of the three configurations. The results indicate that only in the condition where both the aperture and grating were obliquely oriented was a significant ($p < 0.05$) amount of motion in the direction opposite the DEI required to null the illusory percept (although there appears to be a small effect of the DEI in the horizontal aperture condition). This indicates that the DEI was weaker in the two conditions in which either the aperture or grating was not obliquely oriented. Error bars indicate the standard error of the mean across subject. $p < 0.05$.

6.1.2. Procedure

Observers were presented with one of three possible stimulus configurations as shown in Fig. 6. Each display consisted of two vertically oriented gray occluders (8.19 cd/m^2) positioned in front of a black background (0.04 cd/m^2), so as to create a parallelogram aperture 8.1° in width and 2.2° in height, oriented at 25° from horizontal. In each of the three stimuli, a series of gray bars oriented at 65° from horizontal drifted through the obliquely oriented aperture formed by the two occluders.

The first stimulus, the 'solid' condition (shown in Fig. 6A), consisted of bars that were solid gray (30.4 cd/m^2) each with a width of 0.4° visual angle separated by 0.25° visual angle (0.04 cd/m^2) creating a square-wave grating with a duty cycle of $\sim 62\%$. In this configuration the dominant perceived direction of motion is parallel to the aperture; however, because the bars could in fact be extending out behind the occluders, at the level of the image there is ambiguity in the figure-ground segmentation. In the second stimulus, the 'gap' condition, the size of the aperture was increased by shifting the upper and lower occluders 0.25° visual angle up and down, respectively. As shown in Fig. 6B, this had the effect of placing a 0.25° gap between the top and bottoms of the bars and the respective occluders. In this configuration the terminators are explicitly intrinsic in the sense that there is no possibility that the bars could be extending out behind the occluders. In the third configuration, the 'outline' condition, a different approach was taken to disambiguate the figure-ground segmentation. As shown in Fig. 6C, the bars were defined by contour outlines only, rather than solid fields, thereby explicitly defining the terminators as intrinsic.

On each trial, the light gray bars moved along the orientation of the aperture through the gap in the gray occluders in one direction or the other (chosen randomly) at a speed of 4.6° visual angle/s for 1 s and then disappeared. As in Experiments 1b and 3, while the gray bars drifted, the whole stimulus (occluders and bars) translated vertically. The translation speed on a given trial were chosen in a pseudorandom fashion from one of seven speeds: $-8/3$, -2 , $-5/3$, $-4/3$, $-2/3$, 0 , or 1 , multiplied by 0.19° visual angle/s (a positive value indicates the movement was congruent with the illusory motion, a negative value indicates the movement was incongruent with the predicted direction of the DEI). After each trial, observers were required to indicate by pressing one of two buttons (2AFC) whether the stimulus was translating up or down. Once they indicated their response, the next trial began. Each pairing of stimulus and speed was shown 15 times, for a total of 315 trials.

6.2. Results

As in Experiments 1b and 3, for each of the three stimulus configurations and actual translational velocities, we computed the percentage of trials in which the reported direction of translation was consistent with the direction of the DEI. The data from each subject were then fit with logit functions from which the 50% point corresponding to the speed of translation necessary to null the illusory motion of the DEI was computed. The data, shown in Fig. 7, illustrate that the DEI is perceived in each of the three conditions (two-tailed, one-sample *t*-test: Solid: $t(4) = 5.47$, $p < 0.006$; Gap: $t(4) = 3.28$, $p < 0.031$; Outline: $t(4) = 5.03$, $p < 0.008$). However, the magnitude of the DEI was not equivalent across the three stimulus conditions (Repeated Measures ANOVA: $F(2,8) = 13.599$, $p < 0.004$); the magnitude of the DEI observed in the gap condition is smaller than that of the other two.

One hypothesis for why the DEI is weaker in the gap condition is that the motion of the DEI is generated along the edge of the aperture, not the edge of the gap, and is thus limited to the space that defines the gap. As can be observed in Demonstration Video 6, the gray occluders are generally not perceived to move, whereas the motion of the aperture is limited to the space within the gap. This provides a limiting factor in the gap condition that is not present in the other two: presumably, if a larger gap were provided, the full magnitude of the DEI would be observed. In the Solid condition, where there is no gap, the motion of the DEI is generated along the edge of the gray occluder which defines the aperture. As can be seen in Demonstration Video 7, the gray occluders themselves can at times be perceived to move along with the grating. At other times it will appear as though the grating is in the foreground in front of a gray background. In neither of these conditions do the gray occluders seem to provide a limiting factor on the magnitude of the DEI.

7. Discussion

7.1. Summary of results

We have introduced a novel stimulus configuration that leads an oriented, static aperture containing a drifting grating to appear as though it is globally translating, when in fact it is stationary. Similarly, a static edge can appear to move if it abuts a moving grating. The purpose of the experiments reported in this paper was to characterize this illusory percept in terms of the stimulus

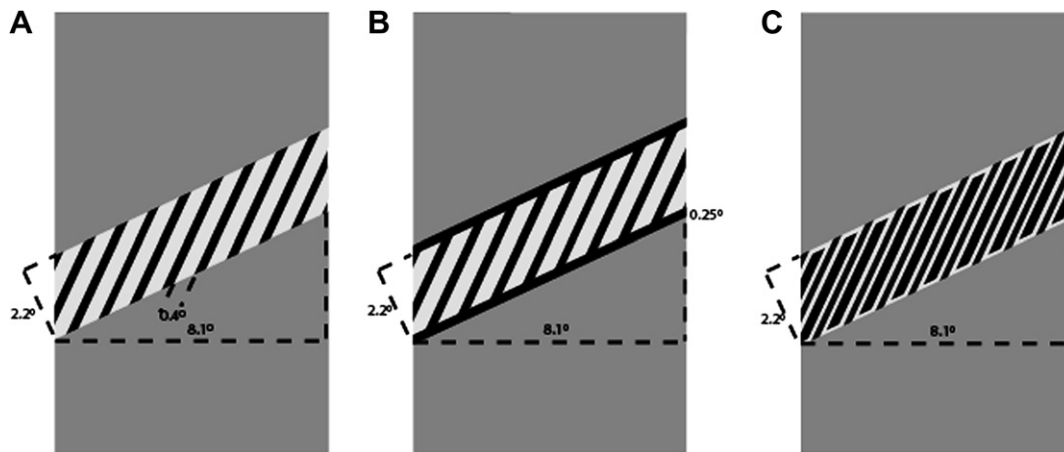


Fig. 6. Explicitly defined 'intrinsic' terminators. Experiment 4 used three configurations each with a relative angle between aperture and grating of 40° and each having the same absolute angles. Unlike the previous experiments, square-wave rather than sinewave gratings were used. Although the generally perceived direction of the drifting gratings in all three configurations is parallel to the aperture, in (A) the terminators of the gratings are ambiguous in the sense that they could in fact be extending behind the gray occluders. In (B) where a gap has been introduced and (C) where the bars of the grating are defined by outlines, the terminators are explicitly defined to be intrinsic to the bars.

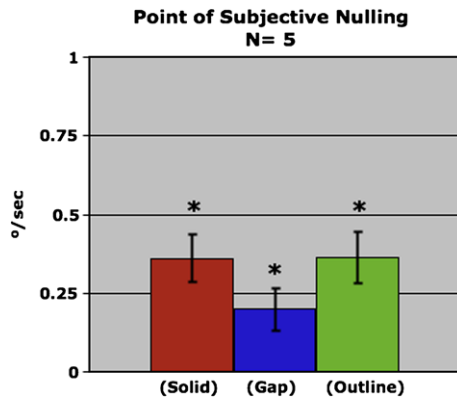


Fig. 7. Results of Experiment 4. Shown are the mean points of subjective nulling for each of the three configurations used in Experiment 4. The results, which indicate a significant amount of motion along the vertical axis was needed to cancel the DEI, show that the DEI was perceived in each of the three configurations. Interestingly, the amount of motion necessary to cancel the DEI in the 'gap' condition was less than either of the other two. Error bars indicate the standard error of the mean across subject. * $p < 0.05$.

configurations that influence whether or not and how strongly the illusory motion is perceived.

The results of these experiments can be distilled into three main findings:

1. The results of Experiments 1a and 1b demonstrate that the relative angle between the aperture or edge and the drifting grating is critical in determining whether or not and how strongly the DEI will be perceived. Specifically, if the orientation of the grating is perpendicular to that of the long edges of the aperture, the DEI will not be perceived. As the relative angle between the aperture and grating deviates from perpendicular, the strength of the DEI increases, as measured by its perceived speed, approximately linearly, at least in the domain of the relative angles tested.

2. The results of Experiment 3 demonstrate that relative angle between the drifting grating and the oriented edge against which it drifts is not the only factor that determines whether or not the DEI will be perceived. Specifically, the DEI is much weaker when a relative angle that produced a strong percept of the DEI in Experiments 1a, 1b, and 2 was tested using absolute angles where the aperture was oriented horizontally, or the grating was oriented vertically. Thus the DEI is strongest when both the aperture and drifting grating are oriented obliquely.

3. The results of Experiment 4 demonstrate that the DEI may be perceived even under stimulus configurations in which the line-ends or terminators of the drifting grating are explicitly made to be 'intrinsic' (Nakayama & Silverman, 1988a; Nakayama & Silverman, 1998b) to the grating and cannot have arisen due to occlusion.

Furthermore, [Demonstration Video 2](#) reveals that all that is necessary to achieve the effect is a drifting grating against a single edge. An aperture works as well, but is not necessary.

7.2. The role of relative angle

The motion of a translating line viewed through a circular aperture is ill-defined (Wallach, 1935). Despite the fact the line could in fact be traveling along an infinite number of trajectories that all lie on a 'constraint line' in velocity space (Adelson & Movshon, 1982), the perceived direction is always perpendicular to the line's orientation. This is believed to arise because of the limited spatial extent of motion-detecting neurons found early in the visual pathway. The response of these detectors to a moving contour is 1D, and therefore ambiguous, because they can only respond to the motion component perpendicular to the contour (Marr & Ullman, 1981).

It has long been known that if a drifting line is viewed through a rectangular, rather than circular, aperture, the direction of motion is commonly perceived to be parallel with the orientation of the aperture rather than perpendicular to the line's orientation (Wallach 1935). This so-called 'barberpole illusion' illustrates the importance of line-ends, or terminators, in determining the perceived direction of motion.

The orientations of the aperture and grating define the directions of terminator and component motion, respectively. The motion of the terminators is parallel to the orientation of the aperture and the component motion is perpendicular to the orientation of the grating. As [Fig. 1B](#) illustrates, when the aperture and grating are perpendicular to each other, the motion signals from the terminators and components are identical. However, as the relative angle between the aperture and grating deviates from the perpendicular, the directions of the motion signals from these two sources also deviate from each other.

The results of Experiment 1b indicate that as the relative angle between terminator and component sources increases, so does the magnitude of the DEI. Of note is the fact that as the relative angle increases, so does the speed of the terminator motion relative to that of the component motion. Specifically, the speed of the terminators is equal to the ratio of the component speed and the cosine of the angle between the terminators and the gratings. It is possible that the discrepancy in both the direction and speed between these sources of motion information underlies the DEI, and that the magnitude of the DEI is modulated by the relative speeds of these two motion sources. This is consistent with the observation that the DEI is not perceived when these sources of motion are identical to each other.

This hypothesis predicts that the magnitude of the DEI should vary with the cosine of the angle between the terminator and component-motion sources. While the results of Experiment 1b demonstrate a linear relationship between relative angle and magnitude of the DEI, additional data will be required to determine if such a non-linear relationship indeed exists.

However, the above hypothesis is not supported by the results of Experiment 3, which indicate that the DEI is much weaker if either the grating is oriented vertically or the aperture is oriented horizontally. The results of Experiment 3 suggest that in addition to the relative angle between the aperture and grating, the absolute angles of each are also important. In particular, the data suggest that the DEI is stronger when oblique angles of both the aperture and grating are used as compared to when one or the other is not obliquely oriented. The effect of absolute angle can also be observed by tilting your head while viewing [Demonstration Video 1](#); the illusory motion that is ordinarily perceived will be reduced when the head is tilted so as to align the grating vertically or the aperture horizontally. This also demonstrates that the DEI is maximized for oblique grating and aperture orientations in retinal rather than world coordinates, suggesting that the effect derives from relatively early motion representations, before the computation of motion trajectories in world coordinates.

There is a rich physiological and psychophysical literature that suggests a functional segregation between the processing of oblique orientations and those that are vertical or horizontal. A phenomenon termed the 'oblique effect' (Appelle, 1972), for example, demonstrates that visual acuity, estimation and discrimination of lines, gratings and angles is better for vertical and horizontal orientations than for oblique ones (Appelle, 1972; Berkley, Kitterle, & Watkins, 1975; Bouma & Andriessen, 1968; Campbell, Kulikowsky, & Levinson, 1966; Jastrow, 1892; Mach, 1861). Similar findings of preferential processing for non-oblique orientations have recently been reported in behavioral studies examining eye movements (Krukowski & Stone, 2005) and pointing (Smyrnis, Mantas, & Evdokimidis, 2007). Interestingly, the oblique effect

has also been observed in non-human primates (Bauer, Owens, Thomas, & Held, 1979; Boltz, Harwerth, & Smith, 1979), cats (Parriss, 1964) and even octopi (Sutherland, 1957). Based on psychophysical (McMahon & MacLeod, 2003) and electrophysiological studies in non-human primates (De Valois, Yund, & Helper, 1982), cats (Bauer & Jordan, 1993; Li, Peterson, & Freeman, 2003), and ferrets (Coppola & White, 2004) as well as neuroimaging studies in humans using fMRI (Furmanski & Engel, 2000) and ERP (Blakemore & Campbell, 1969; Maffei & Campbell, 1970) it is believed that the oblique effect arises from processing in visual cortex and not from the initial geniculate-cortical projection. It could be, for example, that non-oblique orientations are processed by dedicated detectors whereas other orientations depend on the relative responses of a population of obliquely oriented filters. The oblique effect has also been shown in a motion context. For example, motion discrimination is better along cardinal directions than oblique ones (Ball & Sekuler, 1980; Greenwood & Edwards, 2007; Gros, Blake, & Hiris, 1998; Matthews & Welch, 1997), and an illusory “direction repulsion” between two moving planes of dots was minimized at cardinal directions (Gros et al., 1998). For plaids, a coherent percept is more likely to be perceived when the global direction is cardinal than when it is oblique (Hupé & Rubin, 2004). Dakin, Mareschael, and Bex (2005) showed that the oblique effect for motion, as is the case for stationary stimuli, is likely mediated by local motion detectors found early in the visual system. One hypothesis is that the non-preferential processing of oblique orientations leads to unstable or inaccurate spatial localization information triggering the DEI. Conversely, an alternative hypothesis is that the preferential processing of non-oblique orientations somehow overrides the processes underlying the DEI or prevents them from producing the illusory percept. There exist other motion illusions that arise when the ability to spatially localize the position of the object is non-optimal, as is the case of the motion capture of low-contrast or chromatic stimuli (Ramachandran, 1987).

The fact that the DEI is significantly influenced by the relative angle between the aperture and grating raises the possibility that it is related to a class of stationary illusions of perceived orientation called tilt-illusions (Dakin et al. 1999; Fraser, 1908; Gibson & Radner, 1937; Oyama, 1975; Tanaka, 1982; Zöllner, 1860; for review see: Kitaoka, 2007). In these stationary illusions, the perceived orientation of a line or grating can be significantly influenced by the orientations of surrounding (e.g., Asch & Witkin, 1948a; Asch & Witkin, 1948b; Gibson & Radner, 1937) or intersecting lines (e.g., Zöllner & F, 1860). Like the DEI, the relative angle between the target and inducing lines plays a key role in determining the strength of the illusory tilt, with acute angles producing strong effects and more perpendicular angles producing little or no effect (Maheux, Townsend, & Gresock, 1960; Morinaga, 1933; Oyama, 1975; Wallace & Crampin, 1969). The most commonly reported effect is that of acute-angle expansion in which the acute angle between the target and inducers is overestimated, leading to the perceived orientation of the target being tilted away from the orientation of the inducers. The opposite effect, or acute-angle contraction, has also been reported in the form of the Fraser Illusion (Fraser, 1908) and the ‘indirect effect’ (Gibson & Radner, 1937). Unlike the DEI, stationary tilt-illusions tend to persist even if one of the components is not obliquely oriented; however, it has been reported that both the Zöllner illusion and the Poggendorf illusion are stronger if the target lines are oriented at 45° rather than either vertically or horizontally (see Green & Hoyle, 1964; Leibowitz & Toffey, 1966; Oyama, 1960). Since acute angles exist along the upper and lower edges of the aperture in the DEI configurations, it is unclear whether acute-angle contraction or acute-angle expansion alone could account for the DEI. Rather, it would seem as though one of these would have to be operating along one edge

of the aperture and another operating along the other edge. As such, although both the DEI and stationary tilt-illusions share some common features, we do not believe the DEI arises due to the same inhibitory processes operating between orientation-tuned neurons that are hypothesized to underlie these stationary tilt-illusions (Bekesey, 1967; Blakemore, Carpenter, & Georgeson, 1970; Tyler & Nakayama, 1984).

7.3. The assignment of motion to contours

In real-world situations, there can be multiple and even adjacent or overlapping sources of motion in the visual scene. In order to be able to distinguish the motion of one object from that of another adjacent or overlapping object, there are at least two problems that must be solved by visual processing: the determination of what the object is, and the determination of the speed and direction in which that object is moving. In the case of a complex real-world scene, it is likely that due to occlusion, portions of more than one object and thus potentially more than one source of motion can occupy a local area of the visual image. In such a scenario, the motion signals present at that location in the image must be attributed to the various contours present at that location. In order for an accurate representation of the visual scene to be constructed, the motion signals must be correctly attributed to the moving contours that produced them. In certain instances, the spatio-temporal dynamics of the retinal image generated by a moving object are consistent with more than one possible combination of motion-contour attribution. For example, we have previously reported a multi-stable stimulus called the bar-cross-ellipse illusion (Caplovitz & Tse, 2006) in which a single dynamic stimulus configuration can lead to dramatically different form and motion percepts. Each of the percepts of the bar-cross-ellipse illusion corresponds to a unique combination of contour-motion attribution that corresponds to a different segmentation of occluding and occluded surfaces.

Under certain circumstances, there is ambiguity in the interpretation of motion signals that are generated along the edge of an aperture. Specifically, as the anorthoscopic percepts of the bar-cross-ellipse illusion illustrate, these motion signals may belong to either the occluded or occluding contour. In causal terms, the motion of terminators along a contour can occur either because the edge is stationary and the grating is drifting, or because the edge is drifting over a stationary grating, or both could be moving. At the level of image information along an edge, this problem cannot be unambiguously solved. Its solution requires constraints from non-local motions not arising from the edge, and requires prior assumptions on the likelihood of edge motion or lack thereof. This ambiguity creates a new form of aperture problem such that whenever there is a field of motion viewed through an aperture, or against an edge, this ambiguity must be resolved. The stimuli used in producing the DEI extend the study of this ‘other aperture problem’ from the circular apertures previously studied (e.g., Zhang et al., 1993) to the oriented apertures examined here.

Here, we raise the hypothesis that the DEI arises from a failure to accurately resolve this new form of aperture problem leading to a misattribution of motion information to a contour that itself is not moving. In the case of the DEI, the motion information generated by the drifting grating gets misattributed to the stationary contours of the oriented aperture. The data suggest that the relative angle between aperture and grating must span the horizontal (as tested here) meridian in order for the DEI to be perceived. In such configurations, the vertical component of the terminator and component motions will have opposite signs in that if the terminators are moving upwards, then the component motion will be oriented downwards and visa versa. Perhaps the conflict in the

sign of motion in the vertical axis between these two sources of motion information contributes to the illusory motion being generated.

It is interesting to note the result of the gap condition in Experiment 4, which showed a reduced magnitude of the DEI. Although there were explicit contours of the gray occluders defining the gap, the illusory motion seems to be attributed only to the implied contour defining the aperture. This is precisely what one would expect given the above hypothesis, since only the contour of the aperture and not that of the gray occluder has a motion signal present along its edge.

While the precise neural mechanism underlying this hypothesis is unknown, it is important to note that the response of a neuron tuned to both orientation and motion is inherently ambiguous. A given neuron could fire identically to an optimal orientation with suboptimal motion for the receptive field, or to an optimal motion with suboptimal orientation. A cell 'listening' to this neuron in isolation would not be able to determine whether the signal it received was due to orientation or motion. In the absence of dedicated detectors for each orientation/motion combination (which may in fact exist for only the special case of vertical and horizontal orientations), the 'true' orientation and motion of the stimulus could only emerge from a population code. It could be errors in such population coding that lead to the misattribution of the motion of a moving contour to a stationary one.

As we have previously noted, there are two sources of motion information that are generated by the moving grating: the component motion of the grating itself and the terminator motion along the edge. In the DEI displays, the perceived direction of the grating generally follows that of the terminators that move parallel to the orientation of the aperture. This demonstrates that the terminator motion is being attributed to the contours belonging to the grating rather than those belonging to the aperture. In contrast, the component motion that is generated perpendicular to the linear portions of the grating's contours is seemingly discarded with respect to the grating's perceived motion. This observation suggests that it is information associated with the discarded component motion, perhaps in the form of relative motion that is misattributed to the contours of the aperture. This view is consistent with the fact that the direction of the DEI is not parallel to the orientation of the aperture, which one would expect from a relative motion or motion capture signal generated by the terminator-driven perceived direction of the grating. It is further consistent with the fact that the DEI is not perceived in configurations in which the component motion is parallel to the orientation of the aperture. In the outline condition of Experiment 4 the terminators were explicitly defined. In this configuration, all component motion is discarded with respect to the perceived direction of the grating, and is thus available to be misattributed to the contour of the aperture leading to a strong percept of the DEI.

While the evidence supports the notion that the DEI is driven by component-motion sources, it remains unclear why the direction of the illusory motion is predominantly along the vertical axis rather than either parallel to the component motion, or perpendicular to the orientation of the aperture. Although the modal response as shown in Experiment 2 was along the vertical axis for all of the stimulus configurations we tested, a number of responses for each configuration were not along the vertical axis. Although the perceived direction of the DEI is predominantly vertical, particularly when observed for the first time, we have noticed that when viewing the DEI configurations over extended periods of time, the direction of illusory motion may not always be vertical, and can at times appear to have a horizontal component as well. It seems clear that the oblique orientations of the motion sources trigger a misattribution of motion information to the stationary edges of

the aperture, however the perceived direction of the motion is likely to be influenced by multiple factors including the orientations of the aperture and grating as well as global shape characteristics (like the intrinsic verticality of the short edges) of the aperture itself.

8. Conclusions

Here, we have introduced a novel stimulus in which a drifting grating viewed through a stationary aperture or against a single stationary edge can lead to an illusory motion percept, where the stationary aperture or edge appears to move. We have demonstrated that both the relative and absolute angles of the aperture and grating play a key role in determining the magnitude of the DEI. The illusion appears to be strongest when both the aperture and grating are obliquely oriented. We argue that motion viewed through an aperture may be subject to an additional form of aperture problem in which motion information along the edge of the aperture may arise from either motion within the aperture or edge and/or motion of the aperture or edge itself. We raise the hypothesis that the DEI arises when the seemingly discarded component-motion signals (or at least the vertical components of these) get misattributed as relative motion to the stationary contours of the aperture. This hypothesis raises an interesting possibility that motion perception can be influenced by relative motion signals generated not by a perceived source of motion information but rather by a source of motion information, the component motion, which has been seemingly discarded from the percept of the moving contour that produced it.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.visres.2008.07.014](https://doi.org/10.1016/j.visres.2008.07.014).

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