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Wakes and spokes: New motion-induced brightness illusions

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Abstract. Under certain conditions, high-contrast moving figures induce adjacent illusory regions, 'wakes' and 'spokes', which have contrast polarity opposite the inducing figures. In this paper we document properties of these novel phenomena. When the illusions are induced by a moving bar, spokes appear on the side of the bar closer to fixation and connect the bar to the fixation point, regardless of the momentary position of the bar or whether it is moving to the left or to the right. Although spokes often extend up to the fixation point, they never extend beyond it. This is not due to blocking of the spoke's spread by the fixation point, because in another experiment spokes extend directly through an intervening figure. Whereas spokes emanate from the end of a horizontally moving bar closest to fixation, wakes emanate from the end farthest from fixation. In contrast to spokes, wakes do not show a towards-fixation bias. Instead, the wake's end trails the position of the bar, like a ship's wake. The higher the bar velocity, the more the end of the wake appears to trail it, suggesting that wakes are caused by a process which spreads from the edge of moving figures. Wakes and spokes, as distinct illusions, should provide significant constraints on theories of human motion and brightness perception processes.

1 Introduction

The spokes and wakes illusions are schematized in figure 1: when three white discs revolve around a fixated point against a dark background, observers perceive regions slightly darker than the background connecting the fixation point with each of the discs. We call these regions 'spokes'. Similar regions or 'wakes' emanate from the more eccentric side of the discs, roughly as shown in figure 1 (Tse 1997; Holcombe et al 1998; visit www.wjh.harvard.edu/~holcombe for a demonstration; also found at www.perceptionweb.com/perc1099/holcombe.html, and archived on the annual CD-ROM sent with the December 1999 issue). In informal experiments, dozens of observers have reported that they perceive these illusions both in displays created on a computer monitor and in displays created by physically rotating a picture of the stimulus. The use of discs is not necessary: all luminance-defined high-contrast figures that we have tried induce the illusions when set in motion around a fixation point. In addition, the illusions often can be perceived when figures translate along a straight path rather than revolve around the fixation point. We will provide evidence that spokes, which appear on the side of a figure closer to fixation, and wakes, which appear on the side of a figure farther from fixation, result from distinct underlying processes.

In a one-sentence description, Mayzner (1975) described an illusion "like the blades of a fan" (page 43) which may be the same as the spokes illusion, but we have found no systematic descriptions of spokes or wakes, even though these illusions may have important implications for motion processing, brightness perception, and possibly patterns of cortical lateral inhibition. Here, we explore the illusions and document two intriguing properties of the spatial configuration of the illusory regions. First, when a bar translates along a horizontal path below a fixated point, the spokes extend up to but not beyond

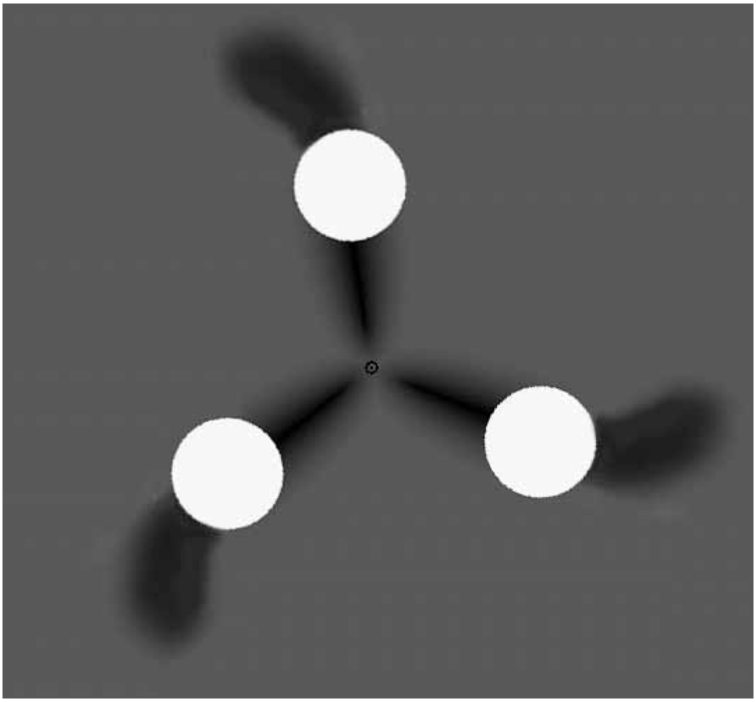

Figure 1. An approximate illustration of observer AH's percept when three white discs rotate clockwise around a central fixation point against a dark-grey background. In general, observers perceived faint black regions or 'spokes' connecting the fixation point and each disc. In addition, observers perceive similarly colored regions emanating from the more eccentric side of each disc, the ends of which seem to lag the position of the discs. Because this phenomenon may be generated by a different process from that which generates the spokes on the central side of the discs, we refer to it by a distinct name: 'wakes'.

the fixated point, regardless of whether the bar is to the left or right of fixation or whether it is moving to the left or right. The second property is an aspect of wakes, and we document it when a horizontally moving bar sweeps directly across the fixation point. The higher the bar velocity, the more the wake slants toward the direction opposite the bar's motion, just as a fast ship's wake slants more than a slow ship's.

2 Experiment 1

In experiment 1 we documented the spatial configuration of the spoke induced by a horizontally moving bar located $\frac{1}{2}$ deg below a fixated point. We show that this spoke extends to the fixation point regardless of whether the moving bar is below and to the left of, directly below, or below and to the right of the fixation point, and regardless of whether the bar is moving leftward or rightward.

2.1 *Method*

2.1.1 *Observers.* Each of the four observers had normal or corrected-to-normal vision. All were experienced psychophysical observers, and one was the first author.

2.1.2 *Stimuli and procedures.* Observers fixated on a dot of approximately 2 min of arc diameter (1 pixel and $\sim$6.4 cd m^{-2}) from a distance of approximately 63 cm. The display was on a 13-inch Apple monitor with a 66-Hz refresh rate. Approximately 27 min of arc below the fixation point, a white bar ($\sim$85.5 cd m^{-2}), height $\sim$110 min of arc, width $\sim$43 min of arc moved horizontally against a black background ($\sim$0.1 cd m^{-2}). The bar appeared at a point 3.4 deg to the left of fixation and moved at a speed of 2.79 deg s^{-1}

until it was 3.4 deg to the right of fixation. Subsequently it disappeared and immediately reappeared 3.4 deg to the left of fixation and continued moving to the right. Each observer was asked whether he perceived a faint shape darker than the background above the bar. After each reported that he did, the observer was told to draw the shape perceived (the spoke) when the moving bar was aligned with a probe outline rectangle drawn 8 min of arc below the path of the bar. The observers, who were experienced users of Canvas™ drawing software (www.deneba.com), were given unlimited time to view the stimulus on one screen and make their drawings in Canvas™ over a static duplication of the stimulus display on an adjacent screen. The probe outline rectangle was first drawn below the bar's path 41 min of arc to the left of fixation and the observer drew the spoke perceived when the moving bar was aligned with the probe. The probe was subsequently drawn below the bar's path directly below fixation and then below the bar's path 41 min of arc to the right of fixation and the observers drew the spoke perceived in each case. Observers were told to simply draw the shape of the spoke and not attempt to duplicate the blurriness of the spoke's edges (one observer's more precise portrayal of spokes is shown in figure 1).

After they made their drawings, the observers participated in a series of trials in which they were asked to click with the mouse on the tip of the spoke (the point farthest from the bar to which the spoke extended). The trials consisted of 12 stimulus conditions presented in pseudorandom order. These conditions consisted of all combinations of direction of motion of the bar (leftward or rightward) with vertical position of the bar (centered on fixation or 27 min of arc below it) and horizontal position of the probe rectangle (aligned with fixation, centered 41 min of arc to the left of fixation, or centered 41 min of arc to the right of fixation). Observers AH, LS, and MA participated in 180 trials, and MW participated in 108. Each stimulus was presented until the observer either indicated that he did not see a spoke when the bar was aligned with the probe, or until he clicked the mouse on the tip of the spoke. At the end of each trial, the screen rapidly flickered between black and white to prevent persistence of the wake across trials and to maintain a roughly constant level of light adaptation.

2.2 *Results and discussion*

Figure 2 shows in grey the observers' initial drawings of the spokes for the conditions in which the moving bar was below and to the left, directly below, or below and to the right of the fixation point. The centers of the black circles and ellipses correspond to the mean position of the spoke tip in each condition. The ellipses themselves represent the standard errors of these means. The differences between observers' responses when the bar was moving leftward and when the bar was moving rightward were miniscule and statistically insignificant, so the data are collapsed across direction of motion. The first number below each bar is the number of trials in which the observer perceived a spoke in that condition, the second number is the total number of trials of that condition. The observers' responses indicate that they perceived each spoke to extend from the top of the moving bar approximately to the fixation point, regardless of whether the bar was moving leftward or rightward, or whether it was below and to the left of, directly below, or below and to the right of fixation. This result suggests that the spokes are generated by a process which has a strong towards-the-central-fovea or 'centripetal' bias.

When the moving bar was not below fixation but rather passed directly over the fixation point, each of the observers indicated on each trial that he did not perceive a spoke or wake. Apparently motion towards or away from fixation is not as effective a stimulus for spokes as motion in other directions; this issue is discussed further in the discussion of experiment 2.

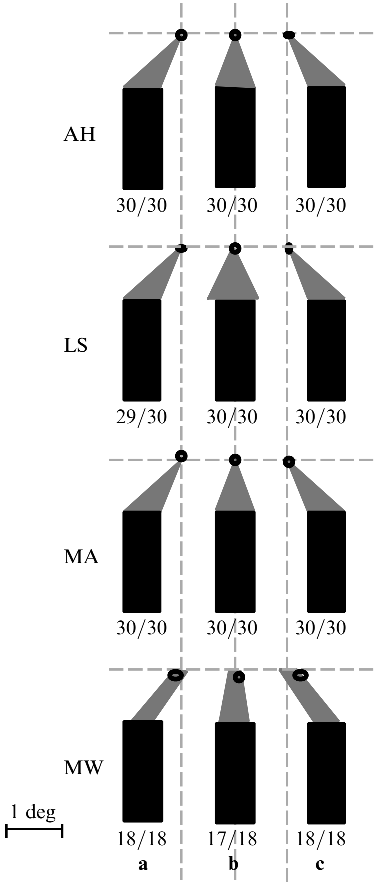

Figure 2. In experiment 1, four observers watched a white bar move from left to right below a fixation point. In separate trials, observers were asked to draw the spoke perceived when the bar was below and to the left of fixation (panel a), directly below fixation (panel b), or below and to the right of fixation (panel c). For each position and each observer, the moving bar is schematized in black and the relative position of the fixation point is indicated by the intersections of the dotted lines. After the observers made their initial drawings, shown in grey, on subsequent trials they simply indicated the position of the spoke's tip. The differences between the observers' responses when the bar was moving to the left and when it was moving to the right were miniscule and insignificant; the overall means lie at the centers of the black ellipses. The ellipses themselves represent the standard errors about each mean. The first number below each bar is the number of trials in which the observer perceived a spoke in that condition, the second number is the total number of trials of that condition.

If the spoke-generating process were not biased towards the central fovea, spokes might still appear preferentially between the bar and the fixation point by virtue of the visual system being more sensitive closer to the central fovea. However, this account would not predict that the spoke would extend to the fixation point but not significantly beyond, nor that the spokes would head straight for fixation rather than in a curved path. The best explanation of the results of experiment 1 appears to be that the spokes-generating process has a centripetal bias.

3 Experiment 2

The results of experiment 1 suggested that spokes reflect a strong centripetal process, which causes the spokes to extend towards fixation. In addition, a strong centripetal bias would also explain why the spokes did not extend beyond the fixation point: once the spokes reach fixation, spreading any further would mean spreading in a non-centripetal direction. There are, however, other possible explanations why the spokes did not extend beyond the fixation point.

One is that the fixation point itself may have blocked the spread of the spoke. Experiment 2 was designed to test whether an intervening figure prevents the appearance of a spoke on the other side.

Another possibility is that the appearance of the spoke up to but not beyond the fixation point was a coincidence of the particular stimuli we used. Under this scenario, if we had used stimuli which induced stronger spokes, the spokes would have extended past the fixation point. Experiment 2 explores this possibility as well, by varying the distance of the stimulus from the fixation point.

3.1 *Method*
3.1.1 *Subjects.* The four observers were the same as in experiment 1.

3.1.2 *Stimuli and procedures.* The procedure of this experiment was very similar to that in experiment 1, but the stimuli were quite different. The background of the screen was $\sim$0.9 cd m^{-2}. From approximately 63 cm away, observers fixated on the center pixel ($\sim$14 cd m^{-2}) of one of two vertical line segments ($\sim$6 cd m^{-2}, length 51 min of arc, width 2 min of arc, separated by 46 min of arc). A bar ($\sim$85 cd m^{-2}, 43 min of arc wide, 102 min of arc long) revolved clockwise around the center pixel of one of the vertical line segments. The bar's end always pointed toward this center point. In figures 3 and 4, the vertical line segments are shown in dark grey, the moving bar is light grey, the spoke perceived is shown in dark grey, and the black lines represent data.

To create the different conditions of the experiment, the nonfixated vertical line was positioned $\sim$46 min of arc to either the right or the left of the fixated line, and the bar's center of orbit was either the fixation pixel or the center pixel of the non-fixated vertical line. These two factors were combined with a third, position of a probe line. The probe line appeared $\sim$10 min of arc outside the path of the bar's rotation, either directly above the center of the bar's rotation (0°) or at one of 7 other positions evenly spaced along the circle of the bar's path.

At the beginning of the experiment, the probe line was in the position directly to the left of the stimulus and observers were shown each stimulus condition and asked to attend to their percept when the bar was aligned with the probe line. Observers were asked to draw any region between the fixation point and the bar which was darker than the background (ie they were asked to draw the spoke). The observers were also told that they could instead indicate that they did not see such a region. Occasionally observers reported seeing similar regions (ie wakes) beyond the more eccentric end of the bar, but they were told to ignore these percepts. As in experiment 1, the observers were given unlimited time to view the stimulus on one monitor and make their drawings, over a static duplication of the stimulus display, on an adjacent monitor, using Canvas™. Also as in experiment 1, during the trials following this drawing phase, each observer was asked to attend to his percept when the bar was aligned with the probe line and to either indicate that no spoke was perceived or to click with the mouse on the spoke tip (the point farthest from the moving bar to which the spoke extended). For each of the four display conditions, the probe bar was presented seven times in each of the eight different positions. The observers took a short break approximately halfway through the 224 trials, which were presented in pseudorandom order.

3.2 *Results and discussion*
Each graph in figures 3 and 4 shows, for a specific display condition and observer, the mean endpoints of the spokes for each position of the bar. Figure 3 shows the data for the conditions in which the observer fixated on the center pixel of the vertical line at the center of the bar's orbit, and figure 4 shows the data for the conditions in which the observer fixated on the center pixel of the vertical line to the left or the right of the center of the bar's orbit. For each condition, each observer's drawing of the spoke when the bar was directly to the left of fixation is also shown. The data suggest the following:
(i) *Spokes have a bias to extend towards the fixated region.* In the conditions of experiment 2 shown in figure 4, the observer fixated a point which was not the center of the bar's orbit and was not in the direction that the bar was pointing. Despite the fact that the fixated point had no consistent relationship to the bar or its motion, when the spoke was perceived it extended from the moving bar in the direction of the fixation point, for all the observers except MW. MW perceived the spoke to extend towards the center

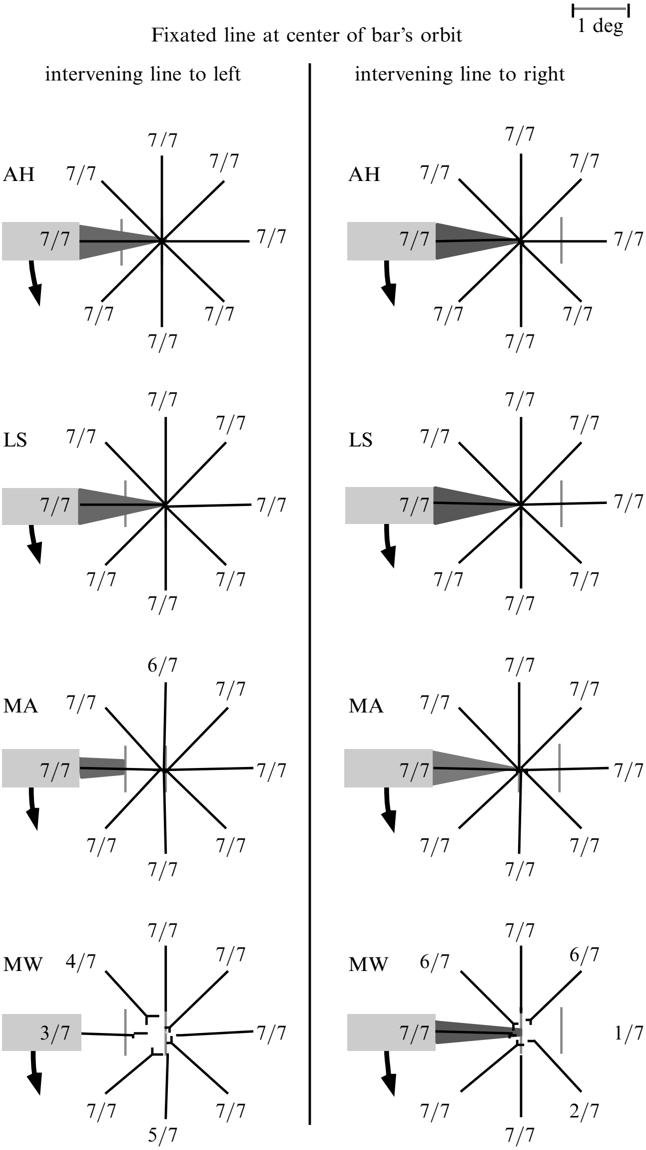

Figure 3. The data for each observer and condition in which the observers fixated on the dot at the center of the bar's orbit. The two vertical lines with fixation dots in their centers are drawn in grey. (The central vertical line is obscured in most cases by the black data lines.) The moving bar is shown as it appeared when directly to the left of fixation, and in dark-grey is the observer's corresponding drawing of the spoke. For each position of the bar at which the observer was asked to indicate the position of the spoke's tip, a dark line connects the position of the bar with the mean spoke tip indicated. The number indicates the number of observations that this point is based on, for example 6/7 means that the observer indicated the perceived endpoint of the spoke in 6 out of 7 of the trials; on the 7th he indicated that he did not see a spoke. The figure shows that all of the observers except MW almost always perceived the spoke to extend to the fixation point, even when the spoke had to extend through the intervening line to do so. Observer MW saw the spoke much less often than the other observers, and he perceived the spoke to extend towards, but not all the way to, the fixation point. The mean endpoint of his responses in a condition is only shown when he perceived the spoke on more than 1 of the 7 trials. MW's standard errors were larger than the other observers'. The x and y components of his standard errors are indicated by line segments extending from the mean perceived spoke endpoint; the standard errors of the other observers were smaller than one pixel in every condition.

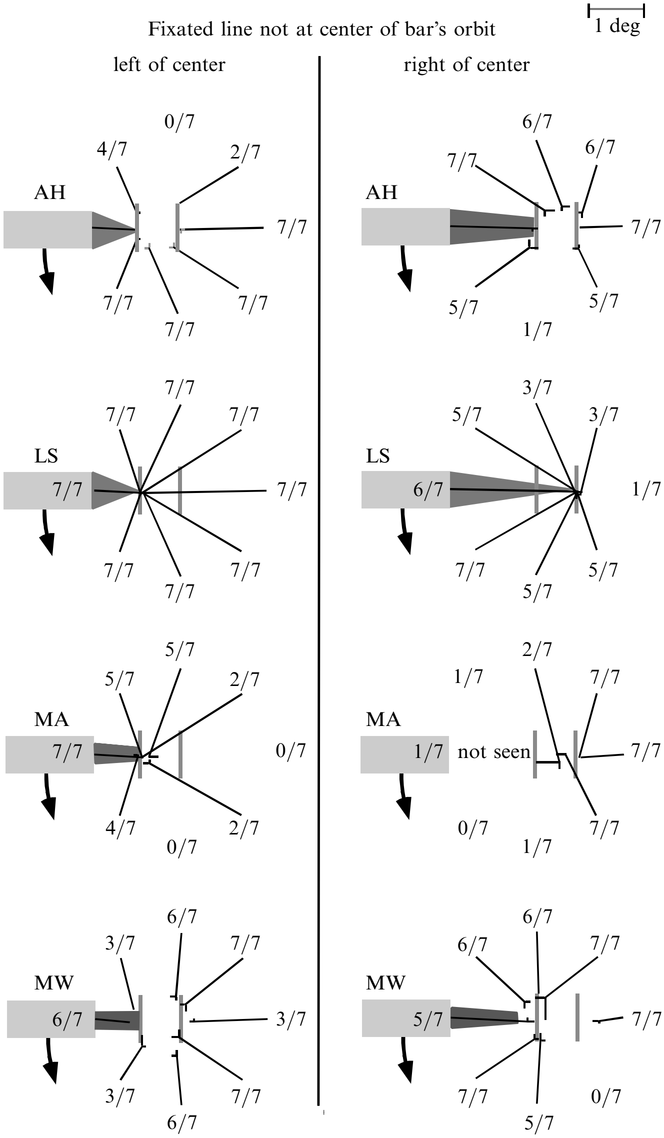

Figure 4. The data for the conditions of experiment 2 in which the observer did not fixate on the point at the center of the bar's orbit, but rather fixated at the midpoint of the vertical line to the left or the right of the center, are shown in this figure in the same manner as in figure 3. When both the x and y components of the standard errors were less than one pixel, error bars are not shown. The mean endpoint of the wake is only plotted in those cases in which it was seen on more than 1 of the 7 trials. The figure shows that, for each observer except MW, when the spoke was visible it extended toward the fixated point rather than toward the center of the bar's revolution. For MW, the spokes extended towards the center of the bar's revolution or towards a point between the fixated point and the center of the bar's revolution.

of the bar's orbit or towards a point between the fixated point and the center of the bar's orbit. However, in experiment 1 even MW perceived the spoke to extend to the fixation point rather than in the direction perpendicular to the bar's trajectory or in the direction the bar was pointing. We conclude that the spokes have a centripetal bias. We discuss possible reasons for MW's pattern of results after point (ii).

(ii) *Spokes do not extend past the fixated region.* Especially revealing are the conditions when the bar was very close to fixation, in which the spokes would have extended significantly past the fixation point if they had been as long as when the bar was in other positions. That the spokes did not extend past the fixation point even in these conditions shows that it was not just a coincidence of the stimuli of experiment 1 that caused the spokes to not extend past the fixation point. Another possible reason, however, that the spokes did not extend past the fixation point in experiments 1 and 2 is that an intervening figure such as the fixation point blocks the spokes. But the results of experiment 2 show that spokes can extend through intervening figures: all observers except MW perceived the spoke to extend directly through the nonfixated vertical line when it was positioned between the moving bar and the fixation point. Therefore it is unlikely that blocking by the fixation point could be responsible for the fact that the spokes never extended past fixation in both experiments 1 and 2. Observations by the authors indicate that when there is no fixation point in the conditions of experiments 1 and 2, but rather an empty region is fixated, the spokes still do not extend past the fixated region.

Other effects are manifest in the results of experiment 2. Although the spokes clearly had a centripetal bias, for MW they did not always extend exactly toward the fixation point. Instead, the spokes sometimes extended more in the direction tangential to the bar's motion. The spokes may be formed by a process which generally spreads tangential to the bar's motion but manifests the centripetal bias owing to stronger neural connections in the centripetal direction. Thus, as in MW's data in figure 4, the spokes sometimes extend in directions intermediate between these two directions. The spokes may be strongest when these two directions coincide (when the bar orbits the fixation point), and weaker when they do not, which would explain why the spokes often were not perceived when the figure did not orbit the fixation point (all subjects in figure 4). This would also explain the absence of the spoke percept in experiment 1 when the bar was vertically centered with the fixation point, because in that case the motion of the bar was directly towards or away from the fixation point rather than orbiting it. Another reason for the frequent absence of the spoke in some conditions of figure 4 may be the greater eccentricity of the bar in these conditions, as the spokes may weaken with increasing eccentricity.

Finally, there is some sign, particularly in the data of figure 4, that intervening figures can block the spread of the spokes, even though in other cases the spokes spread right through the intervening vertical line. It may be that intervening figures can block spokes, but only when the spokes are weak, as when the bar was far from fixation in the conditions of figure 4.

4 Experiment 3

In experiments 1 and 2, observers made judgments about 'spokes': the illusory regions emanating from the end of the moving bar closer to fixation. However, with certain displays a region of similar appearance is also perceived to emanate from the end of a moving figure farther from fixation, as illustrated in figure 5. In contrast to the spokes, which show the large centripetal bias measured in experiments 1 and 2, in informal explorations of wakes we perceived no comparable effects on the orientation of wakes. There was, however, an effect of the velocity of a horizontally moving bar on the orientation of its wake: the faster the bar moved, the more the top of the wake seemed to trail it, as occurs with a ship and its wake. In experiment 3 we documented and measured this effect.

4.1 *Method*

4.1.1 *Subjects.* Eight experienced psychophysical observers with normal or corrected-to-normal vision participated.

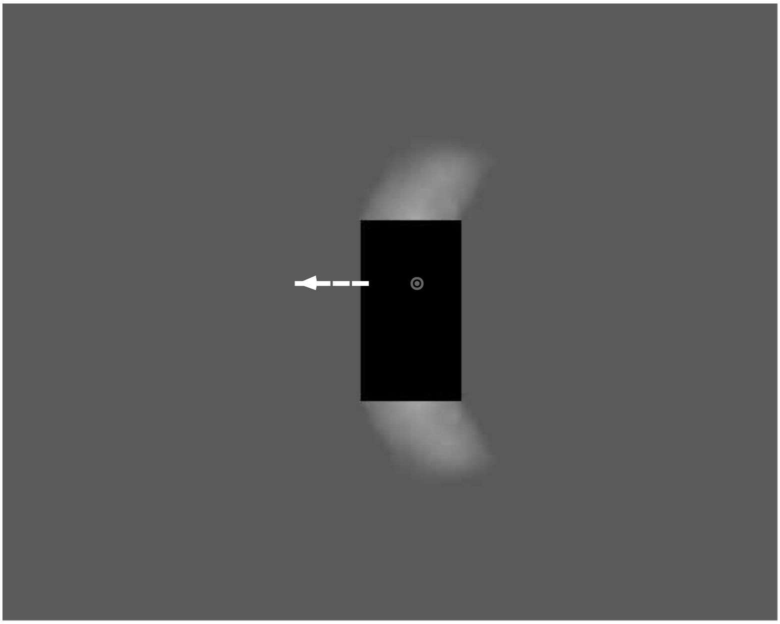

Figure 5. Observer AH's illustration of the percept when a horizontally moving bar passes directly over the fixation point, as in experiment 4. If the bar is darker than the background, regions lighter than the background are perceived immediately above and below the moving bar. The ends of these regions or 'wakes' appear to lag the position of the bar, like the wakes created by a ship.

4.1.2 *Stimuli and procedures.* Each observer sat approximately 57 cm from a 13-inch 66-Hz Apple monitor in a dark room. A black bar (width 27 pixels or $\sim\frac{1}{2}$ deg, height 52 pixels or ~ 1 deg, approximately 95 cd m^{-2}) moved back and forth over a grey fixation point against a white background, from one edge of the screen to the other and back again. Each observer participated in five trials for each of 12 bar speeds. Four observers were told to judge the orientation and width of the wake on the top side of the bar and four were told to judge the wake on the lower side of the bar. Two of the observers in each of these groups were told to judge the wake as the bar passed over the fixation point from right to left, and the remaining four observers were told to judge the wake as the bar passed over the fixation point from left to right.

The observers indicated the orientation and width of the wake by using a mouse to adjust the orientation and width of a rectangle located at the bottom of the screen until it matched the orientation and width of the wake. Observers judged the width and orientation of the wake on the basis of the point where it joined the bar. In doing so, observers could freely switch between fixating the adjustment rectangle and fixating the fixation point, in order to adjust the rectangle's angle and width until their estimates were as precise as possible.

4.2 *Results and discussion*

Despite the large range of bar speeds used, bar speed did not have a significant effect on the mean width of the wakes (as a regressor in a general linear model, $F_{1,7} = 3.5$, $p = 0.10$). The mean width of the wake, 23 pixels, was a bit narrower than the width of the bar, 27 pixels ($t_{11} = 8.954$, $p < 0.0001$).

The mean angle of the wake, relative to vertical, is plotted for each bar speed in figure 6. A regression revealed that the effect of bar speed is significant, $F_{1,7} = 35.3$, $p < 0.001$. The linear pattern ($r^2 = 0.96$ for a regression of the means shown in figure 6) is consistent with the possibility that the wake in all cases is caused by neural inhibition

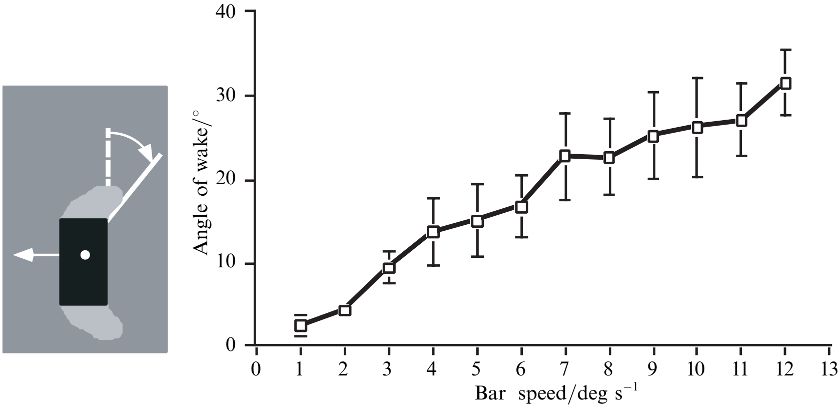

Figure 6. The mean angle of the wake, relative to vertical, and the standard error for this mean plotted for each bar speed. The faster the bar, the greater the angle.

which spreads perpendicular to the motion of the bar at a constant speed. Such a model would predict that as the bar moves on, the wake would form an angle with the bar which linearly increases with bar speed.

Although there is clearly a large effect of bar speed on the angle of the wakes, the speed of the inducing figure does not appear to affect the orientation of spokes. In informal investigations we varied the speed of the inducer in a variety of spoke displays and the spokes always extended towards the fixation point.

Experiment 1 also featured a bar which translated horizontally across the fixation point, but in the conditions of experiment 1 the observers did not perceive a wake. There are a number of differences between the display conditions of experiment 1 and experiment 3 that may have resulted in this discrepancy. In particular, in experiment 3 a black bar appeared against a white background, whereas in experiment 1 a white bar appeared against a black background, and informal experiments suggest that black against white is a more effective inducer of wakes than white against black, even when the amount of contrast is equated.

5 General discussion

The preceding experiments document properties of illusory, motion-induced brightness phenomena which, if previously reported, apparently have been mentioned only in passing (Mayzner 1975). With a moving high-contrast figure, on the side closer to fixation observers perceive a spoke with contrast polarity opposite that of the inducing figure. Experiments 1 and 2 show that spokes are strongly biased to extend towards but not beyond the foveated region. On the opposite (farther from fixation) side of a moving high-contrast figure, observers often perceive wakes, which are very similar in appearance to spokes. Experiment 3 showed that the angle that these wakes make with the moving figure increases with inducer speed, such that the end of a wake lags the moving figure more at higher speeds. In informal investigations, spokes did not show this property, as they invariably extended towards the foveated region.

Human brightness processing also yields the phenomena of brightness spreading (eg Cornsweet 1970; Paradiso and Nakayama 1991), phantoms (Tynan and Sekuler 1974), and grating induction (McCourt 1982). What is the relationship of wakes and spokes to these other phenomena? The results of experiment 2 show that spokes can extend directly through intervening contours, which suggests that spokes are not caused by the brightness-spreading process thought to propagate brightness signals from contours up to other bounding contours (eg Burr 1987; Paradiso and Nakayama 1991). Spokes and wakes seem quite dissimilar to phantoms, as phantoms are visible without stimulus motion

(Gyoba 1983) and rapidly decline in strength with increasing stimulus luminance (Gyoba 1994), whereas our informal experiments suggest that neither is true of spokes and wakes. Finally, the induced grating illusion also seems to arise from a process different from those that generate wakes and spokes. When observers view a grating with an occluder covering the middle of the grating, they perceive an illusory grating of opposite phase filling the occluded region. Although the brightness relations of this illusion are similar to that of wakes and spokes, induced gratings remain strong with stationary inducers, whereas wakes and spokes disappear when the inducers stop moving. In addition, induced gratings are clearly visible with equiluminous chromatic inducers (Zaidi 1989), whereas spokes are not (Holcombe et al 1999).

We suggest that a motion-triggered lateral inhibition process may underlie wakes. The increase in angle of the wakes as the speed of a moving bar increases is consistent with the idea that wakes are caused by a wave of lateral inhibition emanating from the bar's edge. Such a wave forms an angle with a moving inducer because the wave continues traveling as the inducer moves on.

The type of wave of lateral inhibition which may explain wakes is, however, inconsistent with the properties of spokes. The spokes have a strong centripetal bias not evident in the wakes. The theory of a wave of lateral inhibition might be adapted for the spokes by postulating, in part, that the wave of the spokes travels by connections which are centripetally biased. However, such a theory would predict that the spokes would appear curved rather than extending straight to fixation. This is a consequence of the older part of the wave, which originated at an old position of the inducer, still traveling towards the fovea while a new wave is generated at the inducer in its new position. Not only should the arms be curved, but if the wave speed does not increase in proportion to the inducer's speed, this curvature should become larger with increasing inducer speed, just as the angle of the wakes increased with inducer speed. However, in informal investigations we varied the inducer speed widely but never observed significant deviations of the spokes from a straight-to-fixation path, even though the same speeds resulted in conspicuous angles in the case of the wakes (figure 6). We conclude that spokes and wakes are generated by distinct, although possibly related, processes.

The strong centripetal bias of the spokes (especially evident in figure 2) seems to dissociate them from all other illusory brightness phenomena. The centripetal bias may stem from a motion-processing mechanism underlying the spokes, as centripetal biases have been documented in the perception of motion. Edwards and Badcock (1994), using large multidirectional random-dot kinematograms, found greater sensitivity to centripetal than centrifugal motion. Raymond (1994), however, measured motion sensitivity in different parts of the visual field by using much smaller displays, and found a centripetal bias only for eccentricities larger than 5 deg, which is more peripheral than the displays used in the present experiments. Yet in a study of neurons in the posterior parietal lobe of macaques, the cells which preferred centripetal motion outnumbered those which preferred centrifugal motion by three to one (Motter et al 1987). In addition, in smooth-pursuit responses, initial eye acceleration to a centripetally moving target is greater than to a centrifugally moving target (Tychsen and Lisberger 1986).

On the other hand, other measures indicate a centrifugal rather than a centripetal bias in motion processing. Albright (1989) found that, of cells in MT with receptive fields in the periphery, more preferred centrifugal motion than centripetal motion. Most cells in area MST also seem to prefer centrifugal motion (Saito et al 1986; Tanaka and Saito 1989). Takeuchi (1997) found that visual search for expanding motion among contracting distractors was more efficient than search for a contracting target among expanding distractors, suggesting that expanding or centrifugal motion is more salient than centripetal motion.

It is unclear which of these experiments reflect processes that could account for the centripetal bias we have discovered in the spokes. The coexistence of these opposite biases within the visual system provides leverage, however, to work out the processes which underlie and are associated with the spokes illusion. We believe that this type of work will eventually lead to the discovery of the role of the wakes-generating and spokes-generating processes in normal, veridical brightness and motion perception.

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