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The directional tuning of the barber-pole illusion

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Abstract. In order to study the integration of local motion signals in the human visual system, we measured directional tuning curves for the barber-pole illusion by varying two crucial aspects of the stimulus layout independently across a wide a range in the same experiment. These were the orientation of the grating presented behind the rectangular aperture and the aspect ratio of the aperture, which in combination determine the relative contributions of local motion signals perpendicular to the gratings and parallel to the aperture borders, respectively. The strength of the illusion, ie the tendency to perceive motion along the major axis of the aperture, obviously depends on the spatial layout of the aperture, but also on grating orientation. Subjects were asked which direction they perceived and how compelling their motion percept was, revealing different strategies of the visual system to deal with the barber-pole stimulus. Some individuals respond strongly to the unambiguous motion information at the boundaries, leading to multistable percepts and multimodal distributions of responses. Others tend to report intermediate directions, apparently being less influenced by the actual boundaries. The general pattern of deviations from the motion direction perpendicular to grating orientation—a decrease with aspect ratio approaching unity (ie square-shaped apertures) and with gratings approaching parallel orientation to the shorter aperture boundary—is discussed in the context of simple phenomenological models of motion integration. The best fit between model predictions and experimental data is found for an interaction between two stimulus parameters: (i) cycle ratio, which is the sine-wave gratings equivalent of the terminator ratio for line gratings, describing the effects from the aperture boundaries, and (ii) the grating orientation, responsible for perpendicular motion components, which describes the influence of motion signals from inside the aperture. This suggests that the most simple cycle (terminator) ratio explanation cannot fully account for the quantitative properties of the barber-pole illusion.

1 Introduction

The perceived direction of motion of lines moving behind apertures has been studied extensively since the early 20th century, the most thorough treatment being Wallach's classic paper (Wallach 1935). The motion direction of a line can be broken down into two orthogonal components: one *perpendicular* to the line and one *parallel* to it. If the line is perfectly straight and has no texture, the parallel component can only be perceived at its ends, whereas the sections of the line that are distant from the endings cannot be determined unambiguously because there is no shift of any brightness discontinuity along the line. The motion direction of a featureless line that extends far out into the periphery of the visual field or a line that is restricted by an aperture is therefore inherently ambiguous because the parallel component cannot be determined, which is usually referred to as the 'aperture problem' (Marr and Ullman 1981; Adelson and Movshon 1982; Hildreth and Koch 1987). A prominent case of such ill-defined motion direction is observed when a set of oblique lines or a grating is moving behind an elongated rectangular aperture, a slit, leading to the impression of a movement along the major axis of the aperture: the so-called 'barber-pole illusion'. These stimuli can help us to understand the way the perceptual system combines the local motion

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signals into a single *global* perception of motion (Braddick 1993, 1997; Smith et al 1994). A line or a grating moving behind a slit provides two types of local motion signals. On one hand, the local motion signals in the regions distant from the slit boundaries are ambiguous because the local spatio-temporal intensity changes of the pattern could be the result of an infinite number of possible displacements, as a consequence of the aperture problem. On the other hand, the intersections of the moving contours with the slit boundaries, which are often labelled 'terminators', provide unambiguous (but potentially nonveridical) local motion signals along the boundary, because there is no visible displacement of the contour across the boundary. This disambiguation can be interpreted as the unique matching of distinct features provided by the terminators (Ullman 1983; Shiffrar et al 1995; Del Viva and Morrone 1998), or as motion energy that is picked up by orthogonal pairs of simple luminance-based motion detectors only along the boundary but not orthogonal to it (Reichardt 1961, 1987; Adelson and Bergen 1985). Wallach (1935) demonstrated in an extensive series of experiments that in such cases of inconclusive information the entire object is perceived to be moving in a single direction which is determined by the unambiguous signals from the aperture boundaries. In the barber-pole illusion, the motion of a grating behind a slit aperture is thus perceived to be along the long axis of the slit.

There are two obvious ways of manipulating the stimulus configuration to study the integration of ambiguous and unambiguous local motion signals. First, the unambiguous motion signals are affected by the local angle of aperture boundaries. Indeed, when the edges of the aperture are indented at 45° in order to exclude local motion signals in the direction of the aperture boundary, the illusion becomes progressively weaker as the size of the indentations increases relative to the grating period (Kooi 1993). This disappearance of the illusion in the absence of vertical terminator motion clearly suggests that the overall shape of the aperture in itself is not important and, more specifically, supports the view that the illusion results from some form of integration of the unambiguous and ambiguous motion signals. In a similar way, the exclusion of conflicting unambiguous information—by tilting the shorter boundaries of the aperture such that they are parallel to the grating—leads to stronger barber-pole illusion (Castet and Zanker 1999).

Second, unambiguous local motion components could be added to the ambiguous motion stimulus suffering from the aperture problem. For instance, when moving lines are cut into little segments (Power and Moulden 1992), the line endings do provide unambiguous direction information, which may conflict with the orthogonal direction component attached to the continuous line sections. The perceived direction of motion in such stimuli depends on stimulus parameters such as contrast, the number of line gaps (terminators), and the length of stimulus presentation (Lorenceau et al 1993). Detection of the veridical motion direction is better with short line segments (more terminators) and high contrast. With few gaps in the lines, and at low contrast, the two directions may dissociate, creating a transparency effect with the lines moving behind a grid that induces the gaps. Support for the view that line terminators that are part of a gap in a line can be processed independently of the line terminators at the end of the line, comes from the observation that a single gap will typically appear to 'slide along' the line if it is moving in a different direction to the line ends (Castet and Wuerger 1997). Similarly, when random dots are superimposed on a grating moving horizontally behind a narrow vertical slit (Shiffrar et al 1995), the dots have little effect on the perceived motion of the grating which appears to move vertically whereas the dots appear to move horizontally, creating an impression of transparency. Only as the aspect ratio of the aperture approaches 1 : 1 do the dots start to influence the perceived movement of the grating, and subjects predominantly report horizontal motion. These experiments demonstrate that unambiguous motion signals are integrated with ambiguous motion signals to some extent in a process resembling that of motion capture (Ramachandran and Cavanagh 1987), thus creating a coherent motion percept. On the other hand, larger discrepancies in the distribution of local motion signals lead to the percept of multiple surfaces, which could best be described as motion transparency (Braddick and Qian 2001).

A third way to manipulate the relationship between ambiguous motion components perpendicular to the gratings of a barber-pole stimulus and the unambiguous, but conflicting, terminator components is to change grating orientation. The orientation of a periodic pattern moving behind a rectangular, upright aperture affects the number of terminators, or pattern cycles in the case of a sine-wave grating, which are moving horizontally and vertically, respectively. This effect can be traded against the variation of the ratio of horizontal and vertical motion components that can be generated by changing the aspect ratio of the aperture, in order to test the validity of the unambiguous signal ratio as predictor of perceived direction. Whereas it is a standard procedure to change the aspect ratio in order to vary the strength of the barber-pole illusion (eg Power and Moulden 1992), only little is known about the effects of changing grating orientation [however, small variations were used by Castet et al (1999)]. A preliminary report on the effect of changing the angle of the grating relative to the aperture (Kirita 1988) demonstrates some influence on the strength of the illusion. Subjects were shown a square-wave grating generated on a cathode ray tube behind a cardboard aperture that could be rotated, and were asked to report the duration of perceiving the barber-pole illusion by holding down a response button. The illusion weakened with decreasing angle between the grating and the major axis of the aperture. With a small range of angles tested at a single aspect ratio of the aperture, and only the strength of the illusion estimated, this study, however, falls short of providing a data set that can be pitched against quantitative predictions. Furthermore, the cardboard aperture may have introduced brightness, colour, or depth cues that accentuate the boundary, which are known to alter the strength of the barber-pole illusion (Shimojo et al 1989; Castet et al 1999). Finally, in Kirita's experiments the subjects were allowed to track the grating with their eyes, which might have caused a sensation of movement along the aperture which would not necessarily be seen if the experiment were repeated with a fixation point. Therefore the currently available literature data do not provide sufficient evidence about the interaction of aspect ratio and grating orientation, which is crucial for the understanding of the spatial integration of local motion signals in the barber-pole illusion.

We wanted to overcome these experimental limitations by obtaining a comprehensive data set on how grating orientation and aperture shape together affect perceived direction, which lends itself to quantitative comparison with models of motion integration. To this end, we measured directional tuning curves for the barber-pole illusion, keeping the following aspects in mind:

- avoid pre-empting the subjects' responses by not asking them to 'look for' the illusion (ie for horizontal or vertical motion),
- record, instead, the actually perceived direction of motion and strength of the motion stimulus (ie how compelling their percept was),
- provide a fixation point to avoid tracking eye movements,
- mask the grating in the screen image to exclude any binocular depth cues,
- vary grating orientation and aspect ratio of the aperture independently.

Our major aim was to vary the relative contributions of the different local motion signals (ie the two unambiguous directions from the aperture boundaries and the ambiguous motion direction from the central aperture region) over a wide range, and independently from each other, in order to test quantitative predictions from simple integration mechanisms (see section 5). The most important methodological advancement in the present experiment is that our observers were subjected to many short trials and were allowed to indicate the actual direction they perceived (instead of a binary decision whether they see the illusion or not) together with the strength and consistency of their percept. This procedure resembles that of Castet et al (1999) in allowing for the full range of possible directions, but differs in that there are only a few subjects who perform many trials. In following this experimental strategy, we have the opportunity to study individual strategies, rather than being restricted to pool responses from a large number of subjects.

2 Materials and method

2.1 *Stimuli*

Stimuli were generated with a Cambridge VSG 2/3 graphics board hosted by a standard PC. The experimental program was a custom-made application written in C. Stimuli were displayed on a digital monitor (Eizo Flexscan T662-T, 19 inch) with a pitch of 75 pixels per inch and a frame rate of 67 Hz. The viewing distance was 200 cm. Each stimulus trial consisted of 100 frames (duration ~ 1.5 s), which were generated by the graphics board instantaneously by scrolling a black-and-white grating in the video memory and plotting it to the screen only within the aperture, while keeping the rest of the screen at an average grey level. The grating was determined by a sine-wave function with a period of 20 pixels which corresponds to 0.2 deg when viewed from 200 cm. The speed of the apparent motion of the grating along the major (longer) axis of the aperture was kept constant in all trials at 1 pixel per frame (0.7 deg s^{-1}). The grating moved up in half of the trials and down in the other half (for the horizontally oriented apertures this made the grating appear to move to the right or left). The five different grating motion directions α (15°, 30°, 45°, 60°, and 75°) that were used in our experiments are defined as angles of the perpendicular motion component, in order to allow for immediate comparison with the behavioural responses. Seven different aperture shapes were used: a perfect square, three horizontally oriented, and three vertically oriented rectangular apertures with identical area and different aspect ratios, A, of $1:2$ (corresponding to $1.37° \times 2.75°$), $1:4$ ($0.97° \times 3.8°$) and $1:8$ ($0.69° \times 5.5°$). Some of these stimuli are illustrated in figure 1.

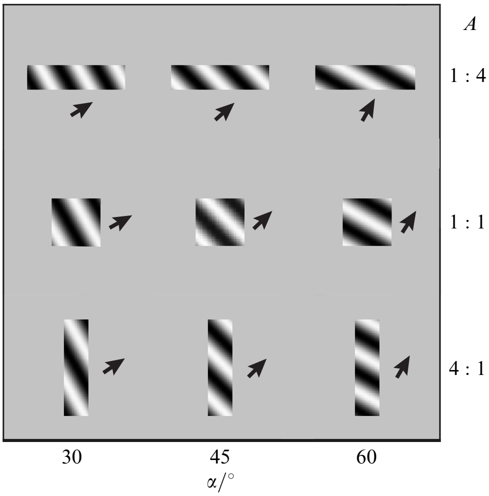

Figure 1. Sketches of barber-pole stimuli with a grating motion direction α of 30° (left column), 45° (middle column), and 60° (right column). The apertures in this example have an aspect ratio A, of 1 : 4 (top row), 1 : 1 (middle row), and 4 : 1 (bottom row), respectively. The direction of sine-wave grating motion is indicated by the small black arrows.

2.2 *Subjects*

Four naïve subjects were recruited from friends and relatives of the authors to volunteer for the experiment. These subjects were generally unfamiliar with the purpose of the study and had little or no knowledge of perceptual psychology. One can assume that anyone has seen the barber-pole illusion at some stage, so these subjects were certainly not naïve to the basic effect, but they were clearly unaware of the specific properties of the stimulus set tested and of any perceptual ambiguity that may emerge from such stimulus conditions. Three other subjects, including one of the authors and one lab member, both experienced psychophysical observers, were informed about the general purpose of the experiment. These subjects had no particular expectation about their response patterns and could not relate consciously any stimuli to any specific reported direction. So it was not surprising that these two different groups of subjects showed no different patterns of results (Fisher 1999). The age of the subjects ranged between 30 and 63 years. The individual patterns of results could not be related to age or familiarity with the experiment. All subjects had normal or corrected-to-normal eyesight.

2.3 *Procedures*

At the start of each experiment the subjects were read out instructions explaining the procedures in detail. They were seated comfortably in front of the screen and asked to fixate a red spot at the centre of the screen. Because the provision of a fixation target does not guarantee reliable fixation, we observed our subjects from time to time to make sure they actually followed the instructions and asked them after the experiment whether they had any difficulty maintaining fixation. Our subjects did not report any problem with keeping stable gaze, and we did not observe any major instabilities, and in particular no relation of any eye excursions to the stimulus parameters. We refrained from using an eye-tracker for continuous recordings of eye movements, in order to avoid discomfort for our subjects and keep the experimental time as short as possible.

The stimulus appeared on the screen, as initiated by pressing a mouse button. A short time after each stimulus presentation, a white circle with a line originating in its centre appeared, which was oriented in a random direction. The subjects were asked to use the computer mouse to draw this line to the perceived direction of motion, β (the last perceived direction in the case of unstable percepts), and to indicate by the length of the line whether this percept appeared strong and consistent to them, or weak and unreliable. The mouse settings were then entered by pressing one mouse button, to be recorded by the computer program and written to a data file for later processing. It was explicitly pointed out to the observers that the line length should not be related to perceived speed. The reason for using this combined task lies in the multistable percepts that the barber-pole stimulus can elicit in some observers, which can switch between the two directions along the aperture boundaries and the oblique direction from the centre of the stimulus. We did not want to bias our observers by asking them whether they saw any particular direction, but left them the opportunity to report any intermediate position as they perceived them. Whereas most observers were rather confident about what direction they were actually seeing, some of them were puzzled by the ambiguity. We therefore invited our subjects to report their dominating perceived direction together with some indication about how compelling this percept was, in other words the 'strength of the motion percept'. Data from all trials were weighted with perceived strength, leading to averages that gave us a measure of perceived direction which took the reliability of the individual responses into account. A posteriori analysis of the data revealed, however, that there was no pattern of differences between the data weighted with this kind of confidence rating and the unweighted data.

Subjects were allowed to ask questions about the instructions if there was anything they were unsure about, but not about the purpose of the experiments. They were invited to practise observing and responding to the stimuli until they felt confident that they understood what was required of them, and generally had 10 – 20 practice trials before asking to start the experiment. After completion of all experiments, subjects were given a brief description of the purpose of the experiment and the key concepts behind it, and could discuss the experiments and make comments on them. The experiment consisted of 10 blocks of trials in total for each subject. Each block consisted of 70 trials making in total 700 trials for each subject for this experiment. All subjects but one completed this experiment which was combined with another test (not reported here) in two sessions, performing 5 blocks of the experiment in each of the two sessions.

2.4 *Data analysis*

The first stage of data analysis was to create an amalgamated data file for each subject for all 700 trials, and to normalise the data with respect to the up/down direction of grating motion. To this end, the response direction β and grating angle α for the trials where the stimuli moved down (and to the left) were rotated by 180°, so that the expected barber-pole illusion direction was always 90° for the vertically oriented aperture and 0° for the horizontally oriented aperture. All responses greater than 105° or less than $-15°$ were then excluded as outliers, after all subjects reported making occasional mistakes. For the four naïve subjects there were not more than 3 outliers in a total of 2800 individual trials. Perceived directions were plotted as a function of grating angle and aperture shape for each subject to study individual response strategies (see figures 2 and 3 for two examples). The data from all observers were averaged to generate the final directional tuning curves (see figure 4).

3 Results

The distribution of the observers' responses showed some variation between individuals, particularly in the degree to which subjects showed a bistable response to the stimulus, with the perceived direction of motion alternating between the two main axes, or a more continuous transition with the majority of responses at intermediate directions. The responses of two typical subjects following different strategies, EF and RG, are shown in the form of a scatter plot in figures 2a and 2b, respectively. The abscissa of each graph shows the five values of the grating motion direction, α, used in the experiment. The ordinate gives the angle, β, at which subjects reported the grating to move. Each data point represents the direction of motion reported for a single stimulus presentation. The reported strength of the percept is not shown in this figure.

If, for a first analysis, the reported strength of the motion stimulus is ignored, it is obvious from figure 2 that subject EF, predominately reporting the cardinal directions (0° and 90°) with few intermediary directions, has a different response pattern than subject RG, who reports a large number of intermediate directions producing a smooth transition in the tuning curves between the two cardinal directions. In the extreme case of a square-shaped aperture ($A = 1:1$) and grating motion direction of 45°, when the stimulus should induce no vertical or horizontal preference, RG reports consistently a direction around 45°, whereas EF has a multistable percept with response clusters around 0°, 45°, and 90°. When the grating motion angle separates from the major axis of an elongated aperture (see data points for $A = 1:8$), for EF the illusion (ie reliable percepts close to the major axis) begins to break down by some of the responses changing to the other cardinal direction. This overall pattern of results suggests that EF is more susceptible to the barber-pole illusion, her bimodal distribution of responses mainly reflecting the orientation of the longer boundary of the aperture, than RG, whose broader distribution of responses shows a stronger influence from the grating orientation. Because involuntary eye movements (that might be elicited by the barber-pole stimulus despite the provision of a fixation target) naturally would

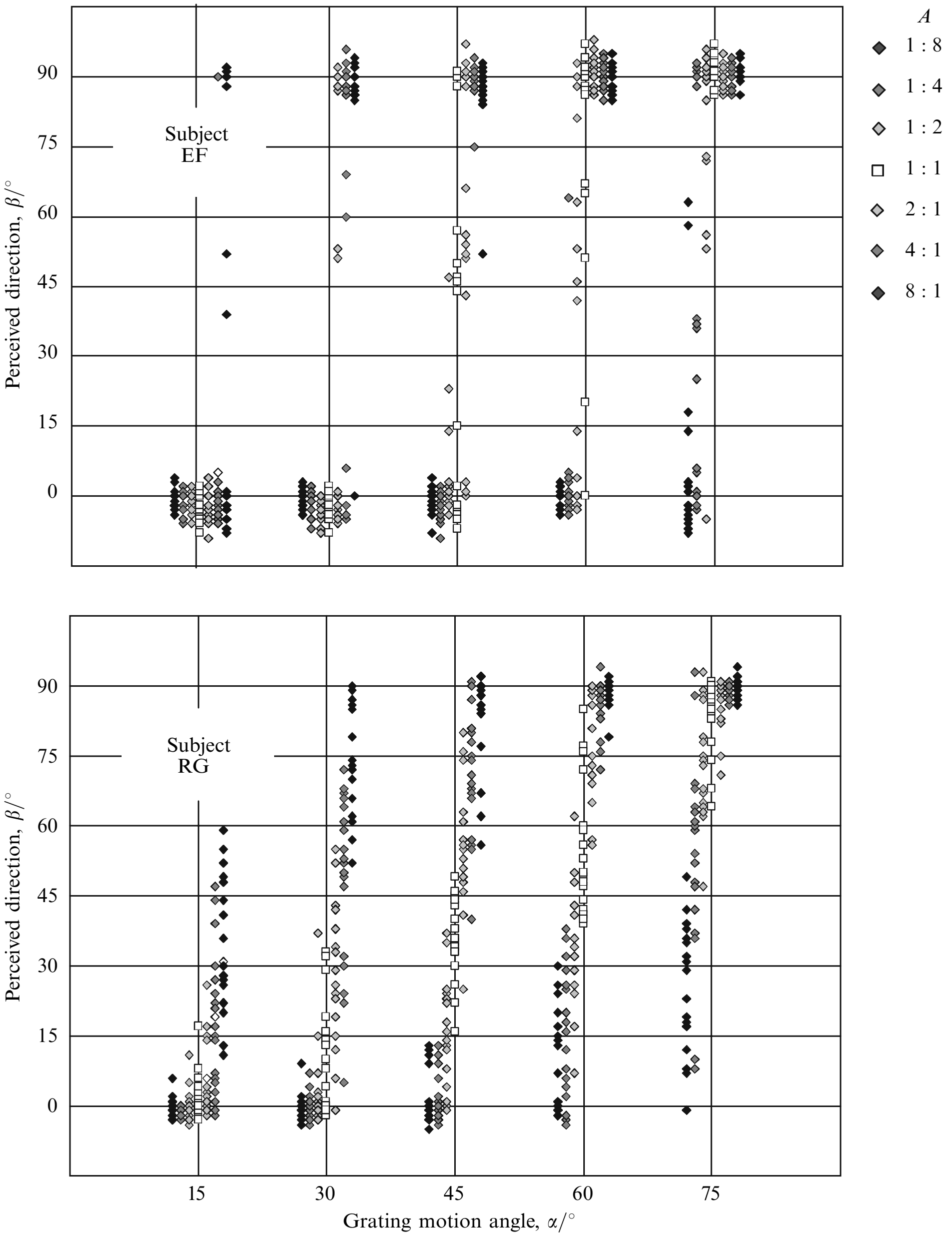

Figure 2. Example scatter plots of individual responses from two subjects. Perceived direction of grating motion β is plotted against grating motion angle α. The subcolumns for each grating motion angle are the seven aspect ratios (see legend box). (a) Subject EF shows a bistable response, with the majority of reported directions being along one of the aperture boundaries. (b) Subject RG shows a continuous transition of responses from one major axis to the other one.

affect the retinal image motion, it could be speculated whether different reliability in maintaining stable fixation (and a peculiar relation between stimulus layout and such eye movements) could account for different response patterns in the two subjects. From our simple method of observing the subjects and asking them about any problem with maintaining fixation we have no indication whatsoever that this would be the case. To exclude this possibility reliably and objectively, however, continuous eye-movement recordings would be required.

The first impression about individual variations in response strategies is confirmed by the directional tuning curves using the weighted averages of the single responses. For this purpose, the direction reported in each trial is multiplied by the reported strength, and the sum of these values for all trials of a given stimulus configuration is divided by the sum of all corresponding strength values. These weighted averages are plotted in figure 3 for the same two subjects as a function of grating motion angle α, with the aspect ratio A of the aperture used as parameter. In addition, the grey-scale

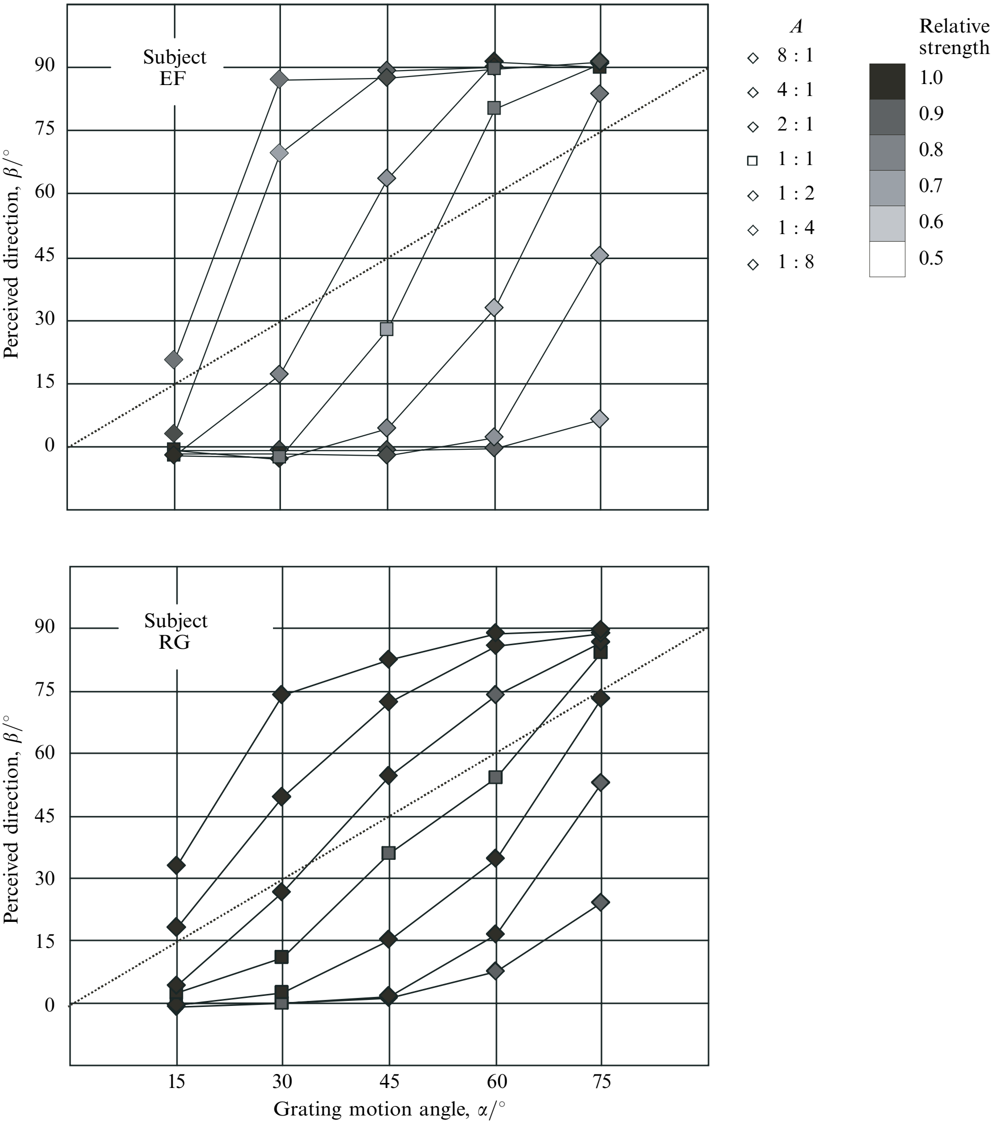

Figure 3. Weighted average of perceived direction of motion β as a function of grating angle α for different aspect ratios of the aperture (ordered from top to bottom as indicated in the upper legend) and the same subjects whose individual responses are shown in figure 2. The intensity of shading of the data symbols indicates the average strength of the motion percept reported by the subject for each trial (see lower legend). The diagonal illustrates the perpendicular motion direction, which would be perceived in the absence of aperture borders. The barber-pole illusion is reflected by the deviation from this diagonal. (a) Subject EF perceives a strong illusion with sharp transitions between the cardinal directions of perceived motion. (b) Subject RG shows a smoother transition between the two extreme directions with more intermediate percepts.

of the data symbols indicates the average strength reported for a given stimulus configuration. The deviation of the perceived direction β from the diagonal demonstrates the influence of the aperture boundaries, pulling the responses closer to horizontal and vertical directions (cf Castet et al 1999). Both subjects show a clear tendency to prefer motion directions closer to the horizontal, as indicated by a pattern of larger reductions than increases of β relative to α. Interestingly, the bimodal response distribution reflecting the dominating influence of the aperture boundaries, and thus the susceptibility to the barber-pole illusion, is connected to a reduction in observer's average confidence. In general, EF rated the strength of the motion stimulus much lower than RG, and in particular gave low ratings whenever the aperture orientation and grating orientation were in conflict or did not provide unambiguous information. This does not mean, however, that RG did not see the illusion—with 45° gratings, for instance, the reported direction is far from 'veridical' and is strongly influenced by the orientation and shape of the aperture.

The examples presented in figures 2 and 3 are the extremes of a continuum of response patterns shown by our observers. After the data from all subjects had been processed in the same way, the final directional tuning curve was derived by averaging the weighted perceived directions from all seven subjects for each stimulus configuration. The result, which is shown in figure 4a, resembles those in figure 3, with the overall tuning curves being somewhere intermediate between those of the two individuals. It confirms the general pattern of this illusion, that vertical/horizontal apertures draw the motion percept closer to vertical/horizontal direction, and the specific observation that this illusion decreases when apertures approach the shape of a square and when grating gets closer to vertical/horizontal orientation (α approaching 0°/90°). In order to assess the strength of the illusion, we shaded a region in figure 4a which indicates the range of perceived directions that are closer to the perpendicular motion component (diagonal in figure 4a) than to the direction expected as a consequence of barber-pole illusion (β values of 0° and 90°, respectively). On assuming a simple interaction between the motion signals from the grating contours and those from the boundaries, it appears that the illusion effect is stronger than the perpendicular motion components for strongly elongated apertures across an approximately 60° range of α, and for moderately elongated apertures across an approximately 45° range of α. It is also clear from this figure that there are deviations from the perpendicular motion direction even in the square-shaped aperture (white square symbols in figure 4a are not sitting on the diagonal)—which cannot immediately be interpreted in terms of a conventional barber-pole illusion.

4 General discussion

The aim of this study was to find out how the local motion signals from the three different regions in the barber-pole stimulus, namely from the two orthogonal boundary regions and the central region that may be not influenced by the boundaries, are integrated to generate a coherent motion percept. The relative contributions from these three regions were modified experimentally by systematic variation of the stimulus variables aspect ratio and grating orientation. Our results are presented in such a way that the diagonal in our data plots (figures 2–4) indicates that perceived direction is perpendicular to the grating orientation. The deviation pattern of perceived motion directions from this diagonal clearly demonstrates that the orientation and length of the aperture boundaries, as well as grating orientation do influence the perceived direction of motion. Our results confirm the cursory observation that the barber-pole illusion is weakened as the angle between the perpendicular component of the grating motion and the major axis of the aperture is increased (Kirita 1988). They also confirm that this effect cannot be completely attributed to the increase in the apparent speed

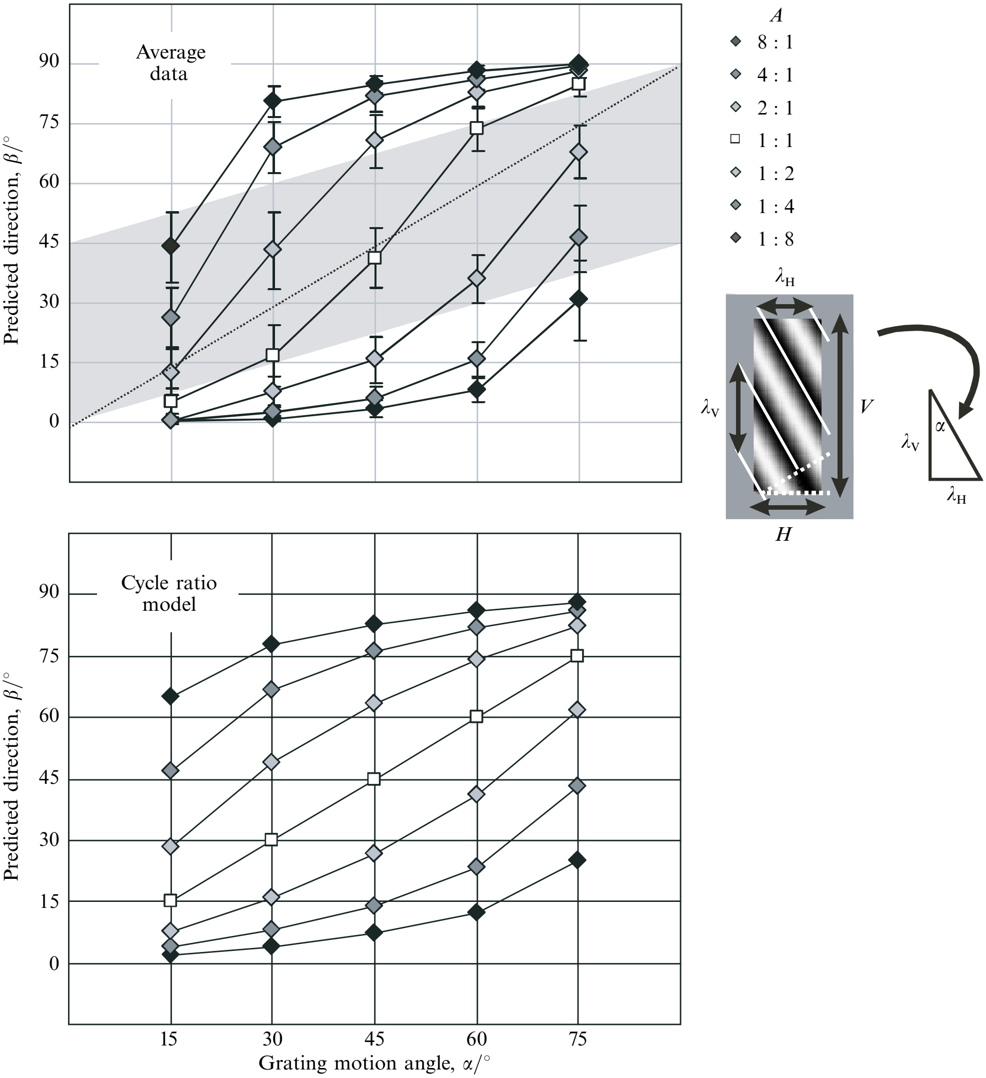

Figure 4. Directional tuning curves of the barber-pole illusion for different aperture shapes (see symbols arranged in the same sequence from top to bottom as in the legend). (a) Average experimental results from seven subjects are plotted with their standard errors of the means (error bars). The shaded region indicates a range of perceived directions with a larger contribution from the perpendicular motion components (diagonal in the diagram) than from the components emerging from the orthogonal boundaries (0° and 90°). Values outside this region indicate a dominating influence of the aperture borders. (b) Directional tuning curves predicted by the simplest version of a cycle ratio model (geometry sketched in the inset). For details see text.

of the grating along the major axis, because this was kept constant. A similar result was found when grating orientation was varied together with the aspect ratio of the aperture such as to keep the terminator ratio constant (Castet et al 1999). In further accordance with that study, we observed a stronger illusion with a horizontal than with a vertical aperture. Through the independent variation of grating orientation and aperture aspect ratio we went beyond these earlier studies by changing the stimulus parameters that are critical for the interaction between (i) the ambiguous motion signals along the grating contours and (ii) the two sets of disambiguating motion signals from the aperture boundaries. This allows a quantitative comparison of our comprehensive data set with models that might account for the pattern of perceived motion direction. In the following, we consider variants of a simple phenomenological model that will be shown to closely approximate the average experimental data. It should be noted that this model is not a computational model (like that of Bülthoff et al 1989, or Zanker et al 1997, for instance), which considers the spatial response distributions of actual motion detectors, but more a quantitative assessment of the integrated stimulus effects. We also have to keep in mind that such models need additions when it comes to account for individual decision strategies. For instance, an intermediate direction of perceived motion may be generated by the visual system by averaging two particular components or by switching between two alternatives with appropriate probability.

Attempts to account for the barber-pole illusion are usually governed implicitly or explicitly by the idea that the unambiguous information can be retrieved only from the aperture boundaries (for instance, Lorenceau and Shiffrar 1992). One model that is often used suggests that the perceived direction is determined by the ratio of line terminators travelling along the long and short sides of the aperture, the so-called 'terminator ratio'. This focus on signals from the motion boundaries resembles the general 'solution' of the aperture problem by integrating motion signals along the boundary which is regarded as a segmentation cue (eg Ullman and Hildreth 1983; Nagel and Enkelmann 1986; Nakayama and Silverman 1988). Because sine-wave gratings have no localised contours that terminate at a particular point of the aperture boundary, explicit terminators could only be identified after some pre-processing (such as extracting zero-crossings of luminance profiles). To avoid making assumptions about specific mechanisms of pre-processing, we use an equivalent measure that applies directly to sine-wave gratings (and is identical to the terminator ratio in the case of rectangular gratings). The cycle ratio, $C = n_\mathrm{V}/n_\mathrm{H}$, is the ratio between the number of grating cycles travelling along the vertical, n_V, and along the horizontal boundary, n_H, respectively. The number of stimulus cycles of a given period, λ, can be regarded as a meaningful measure of the amount of motion information available to a motion detection mechanism, irrespective whether we think about a feature-matching (Ullman 1983) or some luminance-based mechanism extracting motion energy (Reichardt 1961; Adelson and Bergen 1985).

The number of vertical (horizontal) stimulus cycles can be calculated by dividing the length of the vertical (horizontal) aperture side by the vertical (horizontal) projection of the grating period: $n_\mathrm{V} = V/\lambda_\mathrm{V} (n_\mathrm{H} = H/\lambda_\mathrm{H})$. This leads to a simple geometrical equation to predict the perceived direction β_C from the cycle ratio (see inset of figure 4b):

$$\beta_C = \arctan C = \arctan \frac{V/\lambda_\mathrm{V}}{V/\lambda_\mathrm{H}} = \arctan\left(\frac{V}{H}\tan\alpha\right) . \tag{1}$$

The predictions of this simple cycle ratio 'model' for our stimulus configurations are plotted in figure 4b for direct comparison with the average experimental results shown in figure 4a. The patterns of predicted and observed responses resemble each other, but the strength of the illusion seems to be underestimated when the perpendicular direction is oblique or gets close to parallel to the major (longer) aperture axis, and overestimated when the perpendicular direction gets close to parallel to the minor (shorter) axis. This discrepancy between model and data is particularly obvious in the failure of the model to account for the sigmoid deformation of the measured tuning curve for a square-shaped aperture.

There is no *a priori reason* to assume that the tangent of the perceived angle should depend linearly on the cycle ratio, as expressed in equation (1). A more general form of the cycle ratio model is derived by introducing an exponent k, which allows us to vary the shapes of the tuning curves. This transforms equation (1) into:

$$\beta_C = \arctan^k C = \arctan\left[\left(\frac{V}{H}\right)^k \tan^k\alpha\right] . \tag{2}$$

The match between predictions and data for an exponent $k = 2$ is shown in figure 5a as a scatter diagram where each data point represents the measured (ordinate) and predicted (abscissa) direction for one of the 35 stimuli used in our study. The tuning curve is sketched in addition, as inset in figure 5a, demonstrating that the sigmoid deformation for square-shaped apertures is now predicted adequately. A closer inspection of this figure suggests, however, that this simple-model version still tends to overestimate the strength of the illusion when the perpendicular motion component deviates from the major aperture axis. This result holds for other exponents as well, the main problem being that this model tends to ignore the strong influence of grating direction α when the grating gets close to parallel to the longer aperture boundary.

A small, but significant, variation of the model can improve the model fit drastically. So far, we have used the most parsimonious assumption that the cycle ratio completely determines perceived motion direction. If we assume an additional influence from the grating motion direction α itself, which acts independently of the cycle ratio, equation (2) is transformed into:

$$\beta_C = \arctan\left(C^k \tan^l \alpha\right) = \arctan\left[\left(\frac{V}{H}\right)^k \tan^{k+l} \alpha\right]. \qquad (3)$$

In the simplest case both exponents are set to 1, suggesting that perceived direction is affected by two inputs with equal strength, which are the cycle ratio and the grating motion direction. This minimal assumption leads to a dependence of $\tan \beta$ on A^1 and $\tan^2 \alpha$. The predictions of this model are shown in figure 5b, indicating an immediate reduction of the discrepancies between model and data. However, now the overall strength of the illusion seems to be underestimated, as demonstrated by the largely reduced deviations of the tuning curves from the diagonal (cf insets of figure 5b with 5a). An intermediate set of tuning curves can be generated by reducing the second exponent, l, to 0.5, thus assuming a stronger influence on perceived direction from aperture shape than from grating orientation. An impressive resemblance between model and data resulting from this assumption can be seen in figure 5c. It should be noted that this approach of balancing the relative inputs from the different regions of the gratings (ie trading boundary effects against responses from the contour sections distant from the boundaries) exhibits formal equivalence with the model put forward by Castet et al (1993) to account for speed estimation of moving lines by integrating veridical speed estimates from the line endings with ambiguous speed estimates from the middle section of the line. Despite the fact that the actual stimulus under investigation is not exactly the same (lines of variable length versus gratings in apertures of various shapes), the computational problem is very similar, and the models arrive at very similar conclusions. Both models are specifically looking at the interactions between motion signals from contour endings and from the central regions of the contour. Because one model is accounting for the speed and the other for the direction component of the velocity vector, they obviously converge on a coherent picture of the underlying processes.

This approach could be further developed by carefully adjusting the exponents in a systematic search of an optimal fit of the average data, but the emphasis here is on the overall quality of the fit and not on the interpretation of specific values of model parameters. Furthermore, all of these model versions have ignored the horizontal bias in the observed results. Again, this property could easily be incorporated, by giving slightly stronger weights to the horizontal input. The scatter plot in figure 5c, however, demonstrates that the fit of our unsophisticated model variant is remarkable (correlation coefficient of 0.987), capturing all crucial aspects, so we made no attempt to search for further improvements. The impressive accuracy with which the model considerations presented so far predict the actual responses does not necessarily mean

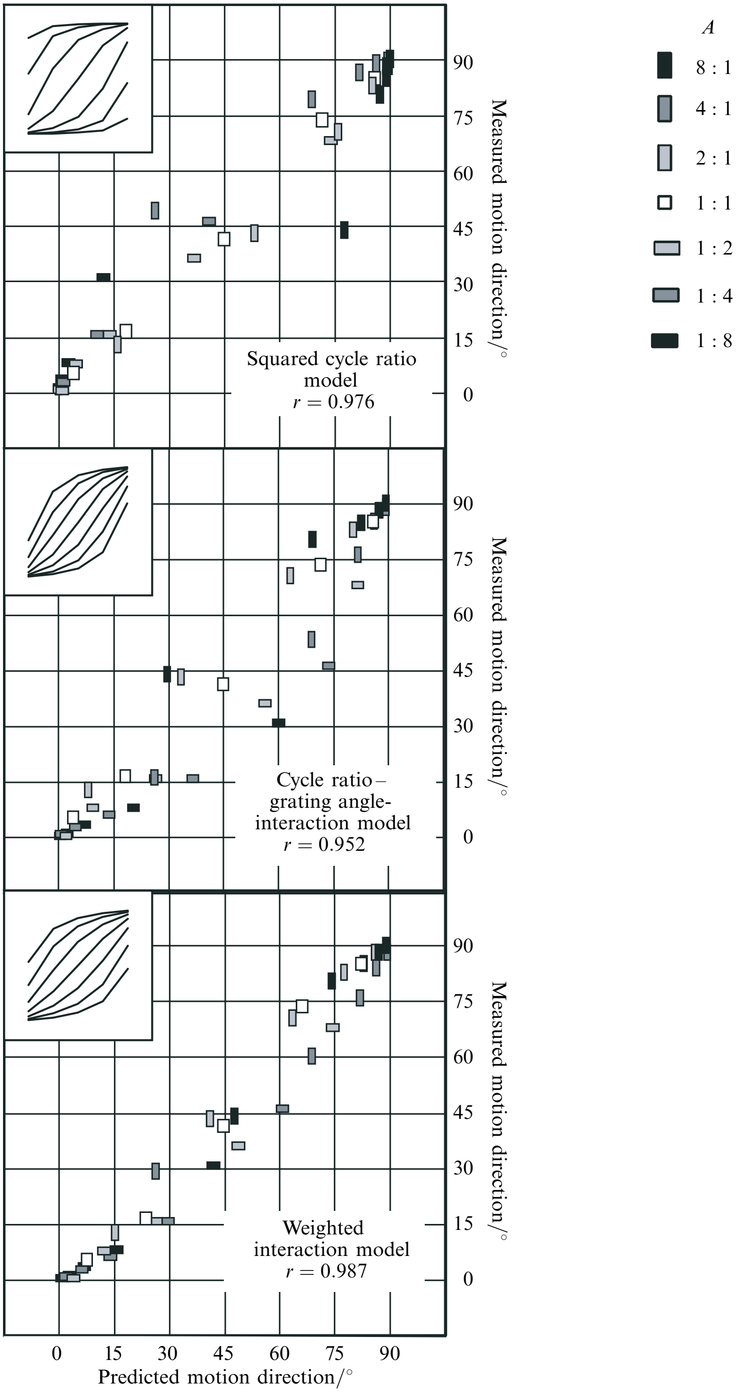

Figure 5. Scatter plots of perceived directions versus predicted responses from several versions of a simple phenomenological model as described in the text. Different symbols refer to different aspect ratios, as shown in the legend. The correlation coefficient between model and data is indicated by r; the actual model tuning curves are sketched in the insets. (a) Squared cycle ratio model, as given by equation (2). (b) Interaction of cycle ratio and grating orientation with equal weight, as given by equation (3) (with $k = l = 1$). (c) Interaction model with different weights for cycle ratio and grating orientation contributions [$k = 1$ and $l = 0.5$ in equation (3)].

that they describe uniquely the actual integration strategies of the visual system. An alternative approach, for instance, could be to segment the stimulus aperture in regions of ambiguous and unambiguous information and rate the directions from these areas relative to the areas they cover, which leads to a data fit of similar quality (Fisher 1999). Finally, one should keep in mind that so far we have only dealt with the average tuning curves, which conceal multistable percepts and interindividual variations, some of which have been discussed in the context of figures 1 and 2. Comparison of the shapes of the tuning curves in figures 2a and 2b with those in the insets of figure 5 indicates that specific patterns of deviation from the perpendicular motion direction can be generated by adjusting the exponents k and l in the cycle ratio model. In other words, allowance for individual variations of these model parameters (which have a direct meaning) can easily account for the results of individual observers. Correspondingly, dynamic parameter variation could be used as a basis to speculate about the mechanisms underlying multistability.

It is obvious from these considerations that we are dealing at this point with phenomenological models that capture the influence of critical stimulus parameters but we do not yet address the neural machinery that is responsible for the barber-pole illusion. One important aspect of this approach, however, is the observation that extracting the perpendicular motion components emerging from the grating contours is somehow necessary to produce the observed pattern of results, indicating that early interpretations of the illusion as being completely governed by 'terminators' (Wallach 1935) may be insufficient in a quantitative manner. If the perpendicular motion components were overruled by the visual system or simply ignored, the integration mechanism would exclusively deal with unambiguous—but not necessarily veridical—motion signals. Instead, our data suggest that the brain does seem to trade off the two types of information, but does not provide clues to possible mechanisms how this might be achieved. We know from a number of experiments that in a variety of aperture configurations integration mechanisms act across multiple apertures and over rather long distances (Shiffrar and Pavel 1991; Rubin and Hochstein 1993; Castet and Zanker 1999) and that the integration is governed by a number of low-level and high-level stimulus properties (He and Nakayama 1994a; Braddick 1993). There are suggestions how the areas inside the aperture might be filled in from the boundaries (Bülthoff et al 1989; Francis and Grossberg 1996), which could count as candidates for underlying mechanisms. As our data suggest, such models would need to incorporate the possibility that perpendicular components within the aperture are not completely suppressed. An interesting aspect in this context is, however, that if the same amount of 'unambiguous' information is given in a spatially incoherent manner, such as by dots superimposed to extended moving gratings (Fisher 1999), the display can lead to a segmentation in two separate motion directions, similar to transparency observed under other experimental conditions (Shiffrar et al 1995). The recovery of the perpendicular signal components in the absence of a contiguous boundary emphasises the importance of the spatial configuration between local motion signals in generating a coherent motion percept. Moving ahead from a phenomenological model to the neural mechanisms will be critical to understanding the basic strategies of motion signal integration (Liden and Pack 1999), and such an attempt needs to include computational descriptions of object boundaries and moving surfaces (He and Nakayama 1994b). Studies of the barber-pole illusion can provide crucial experimental data to such an approach.

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