

Motion-Based Mechanisms of Illusory Contour Synthesis

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Summary

Neurophysiological studies and computational models of illusory contour formation have focused on contour orientation as the underlying determinant of illusory contour shape in both static and moving displays. Here, we report a class of motion-induced illusory contours that demonstrate the existence of novel mechanisms of illusory contour synthesis. In a series of experiments, we show that the velocity of contour terminations and the direction of motion of a partially occluded figure regulate the perceived shape and apparent movement of illusory contours formed from moving image sequences. These results demonstrate the existence of neural mechanisms that reconstruct occlusion relationships from both real and inferred image velocities, in contrast to the static geometric mechanisms that have been the focus of studies to date.

Introduction

One of the most challenging problems confronting the human visual system is the recovery of occlusion relationships. The computational difficulty stems from the fact that there is no simple relationship between luminance discontinuities (“edges”) on our retinas and the presence or absence of occluding contours in the scene. Luminance discontinuities can be generated by reflectance changes, shadows, object boundaries, or abrupt changes in surface orientation, so there is no unique relationship between image contours and their environmental cause. An even more severe problem arises when portions of the occluding contour are camouflaged against a similarly colored background. In such contexts, there is no local contrast to identify the existence of a contour, yet if the visual system is to correctly segment the scene, it must be able to infer the presence of the contour from fragmentary image data. It is now well known that the visual system contains mechanisms that compensate for missing contour segments through the construction of “illusory” contours between inducing contour segments (Schumann, 1900; Kanisza, 1979). Since illusory contours do not have a counterpart in the stimulus, they reflect the activity of internal mechanisms, providing a unique window onto the neural processes underlying the computation of occlusion.

Early theories of illusory contour synthesis suggested that such contours were cognitive in origin (Gregory,

1972; Rock and Anson, 1979). However, subsequent physiological evidence has indicated that the illusory contour sensitivity may originate as early as area V2 in macaque monkeys (von der Heydt et al., 1984; Redies et al., 1986; Grosf et al., 1993), providing evidence that illusory contours arise from neural interactions early in the visual processing stream. To provide insight into the mechanisms responsible for illusory contour synthesis, a number of studies have been performed to determine the stimulus properties that constrain the perceived clarity and shape of illusory surfaces. It is now known that image properties such as inducer extent and proximity (Dumais and Bradley, 1976; Siegel and Petry, 1991; Shipley and Kellman, 1992a; Leshner and Mingolla, 1993), alignment (Rock and Anson, 1979; Bross and Michaelangeli, 1988; Shipley and Kellman, 1992b), and contrast (Dumais and Bradley, 1976; Brussel et al., 1977; Spillman et al., 1984) all contribute to the clarity of illusory contours in static images. These results have inspired neural models which invoke contour completion mechanisms that generate contours parallel to their orientation, and/or mechanisms that generate contours approximately orthogonal to the inducing contour’s orientation. Here, we report a class of illusory contours elicited by moving patterns which suggest that a distinct class of mechanisms are involved in synthesizing illusory contours from moving images.

Results

We constructed a display in which a thin diamond outline figure oscillated horizontally at a constant speed, passing behind a vertically oriented rectangular occluder (Figure 1a). The occluder was the same color as the background (black), and was therefore visible only at the points of intersection with the diamond. At the point of maximal occlusion, slightly more than half of the diamond figure remained visible. Since the same pattern of occlusion and disocclusion could have been caused by an infinite family of surfaces, the shape of the occluding surface was ambiguous. The perceived shape of the occluder may therefore reveal properties of the mechanisms underlying the recovery of occlusion geometry when it is not uniquely determined by the stimulus. In our display, a clear illusory contour appeared to delineate the edge of the occluding surface, forming a convex curve that seemed to move in a direction opposite to the occluded figure and to change shape during the occlusion event. To determine the nature of the transformation defining the perceived shape change, we measured the evolution of the illusory contour’s shape for a number of discrete time slices of the occlusion event (see Experimental Procedures). According to extant theories of illusory contour formation, the illusory contours should be biased to form roughly orthogonal to the inducing line ends (see Figure 1b), and the interpolated contour should be a smooth curve between these inductions (Grossberg and Mingolla, 1985; Finkel and Edelman, 1989; Finkel and Sajda, 1992; Heitger and von der

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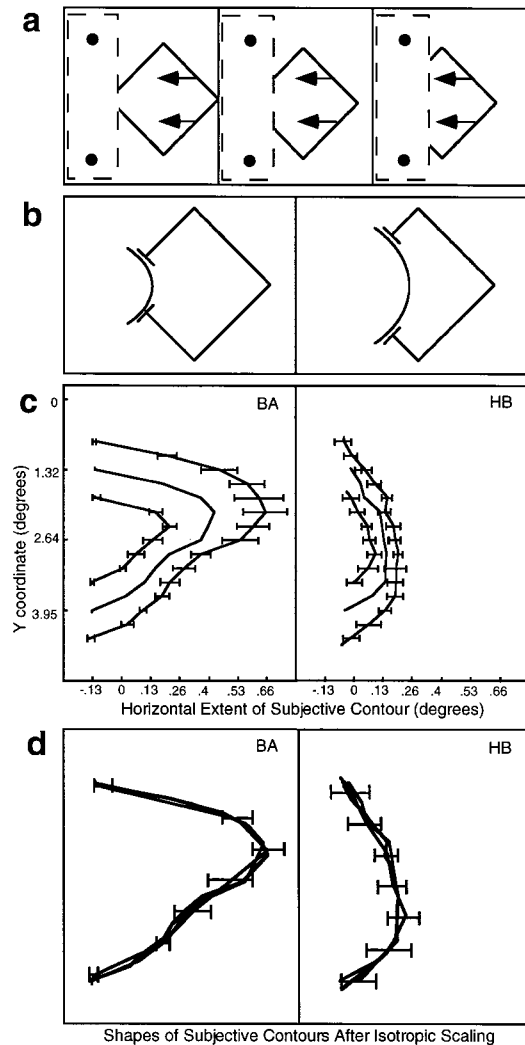


Figure 1. Stimulus Array for Experiment 1 and Time Series Data Displaying the Illusory Contour Shapes Perceived by Two Subjects (a) Schematic view of the display. A diamond-shaped outline figure was translated at a constant speed behind a vertically oriented occluder. The color of the occluder was the same color as the background, so the only information about its shape was at the points in which it intersected the outline of the diamond. (b) Qualitative predictions of illusory contour shape based on orthogonal induction mechanisms. The perpendicular to the diamond at the contour terminators always had the same orientation during the occlusion event. If the interpolation process is assumed to depend only on the angle generated at the contour terminators, the illusory contours should be the same shape, differing only in scale. (c) The perceived shape of the illusory contour generated by different amounts of occlusion. Each data point represents the averaged response of observers' adjustments of a small dot to the perceived location of the illusory contour. The horizontal positions of the dot were controlled by the observer, sampled at a number of fixed vertical positions. Contour data are shown for three different points in the diamond's motion sequence. Error bars represent 95% confidence intervals for the smallest and largest extent of occlusion; the middle curve's confidence intervals are of intermediate size. Distances in the figures are all expressed in degrees. (d) The data in (b) were scaled isotropically so that the distances between the diamond's contour terminators were equalized. Although there are individual differences in the perceived shape of the illusory contours, the change in shape of the illusory contour during the occlusion event may be characterized as a simple scaling transformation for both observers.

Heydt, 1993). Since the orientation of the inducing edges was constant during the motion sequence, there are no local changes in the geometry of the inducing contour (the diamond's edges) that would lead to a change in the local orientation of the illusory contour. However, as the diamond becomes progressively occluded, the distance between contour terminators increases. If the shape of the illusory surface depends on the distance between the contour discontinuities, then the angle formed between the illusory surface and the inducing contour would be expected to change during the occlusion event. Alternatively, if the distance between contour terminators is *not* playing a role in the perceived shape of the illusory surface, then the angles formed between the illusory contour and the inducing contours of the diamond should be invariant during the occlusion event. This suggests that the illusory contours that form at different points in time should be relatable by a transformation that preserves angle, namely, a scaling transformation. Figure 1c presents the raw data showing perceived changes in the shape of the illusory contour. In Figure 1d, the data have been normalized to equate the distances between contour terminators for each observer. The plots clearly show that the shapes of the contours are essentially identical under a uniform scaling transformation.

The discovery that the illusory contours in the time series of Experiment 1 are relatable by a scaling transformation implies that the distance between contour terminators does not change the orientation of the occluding surface formed at the contour terminators (since scaling transformations preserve angles). This suggests the possibility that the scale invariance observed in Experiment 1 is due to purely local inductions generated at the contour terminators by the inducing contours of the diamond. To assess the importance of the geometric properties of the inducing figure in determining the perceived shape of the illusory contour, we repeated this experiment using a thin circular outline figure (Figure 2a). As in Experiment 1, the circle oscillated horizontally at a constant speed behind a vertically oriented invisible rectangular occluder, and slightly more than half of the circular figure remained visible at the point of maximal occlusion. Note, however, that a bias for illusory contours to form orthogonal to the inducing elements implies that the illusory contour should be more convex when the circle is slightly occluded and become progressively flatter as the circle is progressively occluded (see Figure 2b). This purely local prediction follows from the fact that the perpendicular to the circle is nearest to vertical when the circle is half occluded (Figure 2b) and from the failure to observe any effects of the distance between contour terminators in Experiment 1. Surprisingly, however, we found exactly the *opposite* result: the illusory contour initially appears relatively flat and becomes increasingly convex during the occlusion event (see Figure 2c). The change in shape can be seen clearly when we normalize the distance between contour terminators in the same manner as in Experiment 1 (see Figure 2d). These curves were not predicted to be relatable by a scaling transformation since the orientations of the inducing contours changed throughout the motion sequence, so a change in shape is not surprising. Rather, the surprising quality of these data is that the

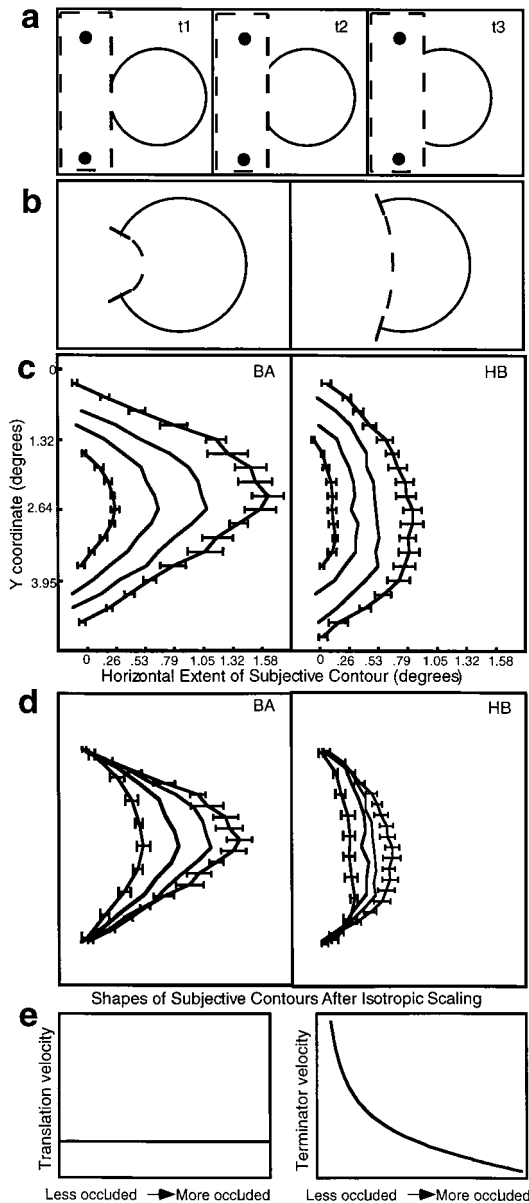


Figure 2. Stimulus Array for Experiment 2 and Time Series Data Displaying the Illusory Contour Shapes Perceived by Two Subjects (a) The motion sequence was identical to Experiment 1, except that a circle was used as the occluded figure. (b) Qualitative predictions of illusory contour shape based on orthogonal induction mechanisms. As the circle becomes more occluded, the perpendicular to the circle at its terminator becomes nearer to vertical and the predicted shape of the illusory contour flattens. (c) Observed shapes of the illusory contour formed as the circular outline figure moved behind the occluding surface. As in Figure 1, contour data are shown for different points in the circle's motion sequence, and error bars represent 95% confidence intervals. (d) The data depicted in (c) were scaled isotropically so that the distances between the contour terminators were normalized. Unlike the data depicted in Experiment 1, the changes in shape of the illusory contour during the occlusion event cannot be reduced to a simple scaling transformation. Rather, when the circle is only slightly occluded, the resulting illusory contour is relatively flat, and the illusory contour bows into a more convex shape as the circle becomes increasingly occluded. (e) The velocity profiles of the partially occluded circle (left) and the

direction of the shape change is *opposite* to that which would be predicted by the local geometry of the display.

The failure of the geometric relationships between inducing elements to predict the change in illusory contour shape observed in Experiment 2, taken together with a failure to observe any effects of distance between contour terminators in changing the local orientation of the illusory contours in Experiment 1, suggests that some other property must play a role in determining the contour shapes perceived in these displays. One natural candidate is the velocity (or some higher-order derivative of position) of the inducing contours. Indeed, pilot work revealed that the magnitude of the bowing of these illusory contours could be significantly reduced if the velocity of the display was increased. In Experiment 1, the velocity of the diamond's contour terminators was constant during the motion sequence, but this was not true for the circle used in Experiment 2: the contour terminators at the occlusion boundary had variable velocities, moving rapidly at first and slowing as the circle became increasingly occluded (Figure 2e). To assess the importance of the terminator velocity in our displays, we varied the circle's translation speed so that the velocity of the contour terminators remained constant. This required the circle to translate slowly during the initial phase of occlusion, accelerating rapidly as it passed further behind the occluding surface (Figure 3a). Remarkably, when the data were rescaled to equate the distances between the circle's terminators, the illusory contours were essentially indistinguishable (Figure 3b). This means that the transformation relating progressive members of the time series was once again a uniform scale change (see Figure 3c). Note that the same (circular) shape was used in both this and the previous experiment, demonstrating the critical role of velocity in determining the perceived illusory contour shape.

The identity of perceived shape when the data from Experiment 3 were isotropically scaled demonstrates that the instantaneous orientation of the tangent to the circle at its terminators has no identifiable effect on illusory contour shape in this display. This suggests the possibility that the scaling relationship between the illusory contours generated by the diamond figure in Experiment 1 arose from the uniform velocity of the contour terminators, rather than the orientation of the inducing contours. To test this possibility, we manipulated the aspect ratio of the diamond, and compared the perceived illusory contours across conditions that equated either terminator velocity or translation velocity of the diamonds. No reliable effects of contour orientation were observed for any of the aspect ratios examined. This suggests that the invariant velocity of the contour terminators was instrumental in generating the scaling relationship observed in the members of the time series of Experiment 1, demonstrating the need to consider the role of velocity in illusory contour shape.

contour terminators (right). The constant translation velocity of the circle generates a highly nonlinear translation velocity of the contour terminators.

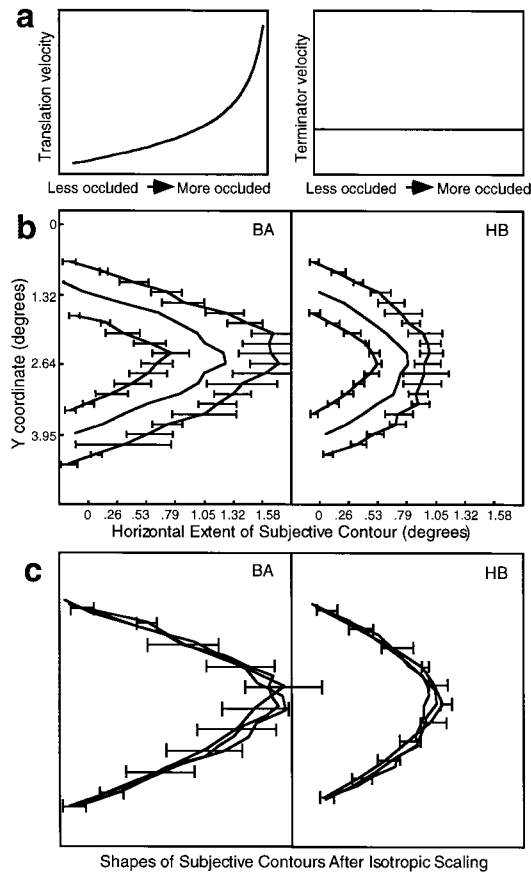


Figure 3. Stimulus Array for Experiment 3 and Time Series Data Displaying the Illusory Contour Shapes Perceived by Two Subjects (a) In this experiment, the speed at which the circle translated was varied (left) in order to hold the speed of the terminators constant (right). (b) The perceived shapes of the illusory contour for three positions in the moving sequence. The data collection method is the same as in Experiment 1, and error bars represent 95% confidence intervals. (c) The same data scaled isotropically so that the distances between the contour terminators were equalized. The changes in shape of the illusory contour during the motion sequence can now be characterized by a simple scaling transformation, even though the geometric relationships between elements of the display are identical to those in Experiment 2.

Discussion

What accounts for the apparent changes of shape and motion attributed to the occluding contour in our displays? The geometric principles used to construct contour shape from static images are incapable of explaining these data, so a new kind of model is needed. To understand our results, consider the general problem confronting the visual system with these displays. The visual system is given a pattern of motions on the retina and must recover the properties of the occluding surface from the image data. In static images, this problem reduces to inferring the shape of the occluding surface. However, in moving images, the visual system must infer both the *shape* of the occluding surface and its *state of motion* relative to other moving features in the images. If the visual system assumed that the occluding surface

was stationary, then the path traversed by the terminator would specify the shape of the occluding contour (here, a straight vertical occluder). However, if the occluding surface is *not* assumed to be stationary, then the terminator trajectory represents a combination of the occluding surface's shape and its state of motion. Indeed, observers report that the occluding contour does appear to translate in a direction opposite to the progressively occluded and disoccluded inducing contour, which means that the straight terminator trajectory could not have been generated by a straight occluder.

We have found that a simple model can explain the pattern of results observed in our data. The intuitive gist of the model is that the shape of the occluding surface is determined by a displaced version of the contour terminator's trajectory. The displacement of the occluding surface is assumed to occur in a direction opposite to the partly occluded contour's direction of motion (an "induced" motion), which means that the resultant velocity vector formed by combining the actual terminator path with this induced motion will not be oriented vertically. Consider two discrete frames in the motion sequence. In our experiments, the contour terminators always had a purely vertical trajectory. Thus, for two frames separated by a time interval Δt , the motion of the terminator was along a purely vertical path (denoted Δy in Figure 4a). The perceived orientation of the occluding surface is assumed to be determined by the vector specifying the trajectory of the terminator, displaced in a direction opposite to the inducing figure by some (unknown) amount. The model assumes that the perceived angle at the points of occlusion is proportional to the angle formed by this resultant vector. If this angle is measured relative to the vertical trajectory of the terminator over a time interval Δt , this angle can be written:

$$\phi = k \tan^{-1} (\Delta x / \Delta y) \quad (1)$$

A schematic representation of this angle is presented in Figure 4a. In the limit where the time interval Δt approaches zero, this expression becomes the ratio of two velocities:

$$\phi = k \tan^{-1} (v_x / v_y) \quad (2)$$

where v_y is the terminator velocity, v_x is the induced motion attributed to the occluder by the partially occluded surface, and k is a proportionality constant. Note that the ratio v_x / v_y is only well defined for nonzero (or near zero) terminator velocities, which restricts the velocity regimes in which one would expect to observe these phenomena (i.e., in the limit, the terminator becomes a static image feature). Note that this model specifies how the visual system computes the orientation of the illusory contour at the points of intersection with the occluded contour; no explicit theory of how the contour is interpolated between these local inductions is described. Here, we assume that changing the distance between contour terminators does not cause any change in the orientation of the illusory contour at the contour terminators, but rather simply causes a change in scale of the interpolated contour (as we observed in our data). In Equation 2, the terminator velocity v_y represents a property of our stimulus, so the remaining problem is to determine the

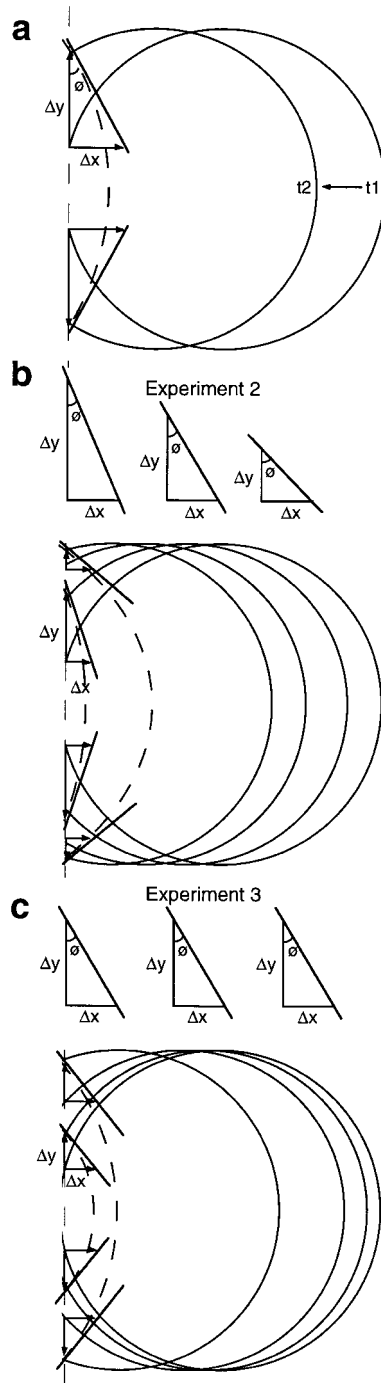


Figure 4. Schematic Views Depicting the Model in Discrete Terms
(a) The circle is shown for two discrete frames of the motion sequence. The arrow marked Δy represents the vertical position change of the illusory contour during the time interval Δt . The arrow marked Δx represents the contour's horizontal position change during Δt . The angle ϕ may be computed over the ratio of these quantities; this angle specifies the orientation of the local contour inductions, which putatively determine the shape of the interpolated illusory contour.
(b) A discrete depiction of Experiment 2 and its explanation in terms of the model. Here, the circle is shown as it moves leftward. As the circle becomes more occluded, Δy decreases; we assume that Δx remains constant through each time interval Δt (see Figure 6). The ratio of $\Delta x/\Delta y$ therefore changes such that ϕ is small for a small

functional form needed for the induced velocity profile v_x to explain the range of observed values of ϕ in our experiments.

In principle, the velocity profile of the induced motion could be a complex function that depends on a number of properties of the inducing figure (such as its size and velocity profile). However, we have found that all of our data can be successfully modeled if the speed of the occluding contour is simply assumed to be constant and independent of the velocity of the inducing target, i.e., if $v_x = c$. To see how this model explains our results, consider Figure 4b, a schematic depiction of Experiment 2. In this experiment, the position change of the terminator Δy was large as the circle was initially occluded and became smaller as the circle became more occluded. By hypothesis, the induced motion of the occluder Δx was the same per unit time during the entire occlusion sequence. Thus, when the circle was initially occluded, Δy was largest in relation to Δx , leading to a local contour induction that was near vertical. However, as the circle was increasingly occluded, Δy decreased while Δx remained constant, causing ϕ to increase as the extent of occlusion increased. To test this model quantitatively, we measured the orientation of the occluding contour as it changed throughout the motion sequence, and fit Equation 2 to our data (see Experimental Procedures). As can be seen in Figure 5, this model provides an excellent fit to the perceived orientations of the occluding surface.

The fact that the illusory contours observed in Experiments 1 and 3 were simply scaled copies of each other can also be understood with the model described above. In Experiment 3, the circle was translated in a manner that kept the vertical terminator velocity v_y constant (see Figure 5c). The induced motion attributed to the occluding surface remains constant (since the induced motion is assumed to be independent of the velocity of the circular inducer), which means that the angle ϕ must also be constant. Hence, the model predicts that the angle of the local contour induction should not change, which implies that the different members of the time series should simply be scaled copies of each other. This is indeed what we observed. A similar logic explains the results observed in Experiment 1 with the diamond figure, since the ratio v_x/v_y is also constant in this experiment.

Finally, our model can also provide an explanation for our qualitative observation that the illusory contour's perceived angle ϕ decreases as the velocity of the occluded figure is increased. Note that the terminator velocity v_y increases when the velocity of the occluded

extent of occlusion and becomes larger for increased extent of occlusion (depicted at the top). The local contour inductions are therefore predicted to be more vertically oriented at the beginning of the occlusion event, and tilt away from vertical as the circle is further occluded, which is what we observe experimentally.
(c) A discrete depiction of Experiment 3. The circle moves in such a way that Δy remains constant over each time interval Δt . Under the assumption that Δx is constant during the occlusion event, the ratio of these quantities is also constant. The angle ϕ therefore remains the same, leading to local contour inductions whose orientations do not change (depicted at the top). Thus, this model correctly predicts the scale invariance observed when terminator velocity is held constant.

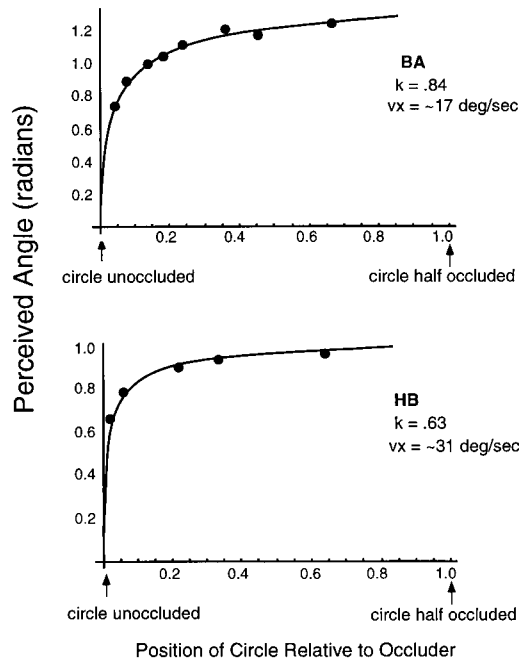


Figure 5. The Fit of Our Model to the Data of Experiment 2
The data points represent the local orientations of the illusory contours measured for two observers in Experiment 2. Time and distance have been normalized to unit length, such that the moment when the circle is first occluded is $x = t = 0$ and when the circle is half occluded is $x = t = 1$. The actual duration of this event was ~ 0.67 s, and the total distance from the beginning of the occlusion event to a half-occluded circle was $\sim 2.5^\circ$. Nonlinear parametric fits to Equation 2 were performed using a method of least squares (see Experimental Procedures).

figure is increased, whereas the induced velocity of the occluding surface is constant. As the velocity v_y increases, the ratio v_x/v_y decreases. This leads to the prediction that the angle ϕ should decrease, which is again what we have observed.

Thus, our model provides both a good quantitative and qualitative account of our data. The primary assumption of our model is that the deformations in perceived shape observed with our patterns were generated by a displacement imparted onto the illusory contour by the partially occluded figure. The two main assumptions about this induced motion are: (1) it is in a direction opposite to that of the partly occluded contour (the inducing figure), and (2) the magnitude of the induced motion is independent (or only weakly dependent) on the velocity of the inducing figure, at least for the velocity regimes considered here. We have performed control experiments to test both of these assumptions on our stimuli. To test the second assumption, we measured the magnitude of induced motion imparted onto a small dot by the circle displays used in Experiments 2 and 3. In the first experiment, the circle had the uniform horizontal translation profile used in Experiment 2, and the second experiment utilized the nonlinear translation profile used in Experiment 3. The target dot oscillated vertically with a uniform velocity in phase with the horizontal oscillation of the circle. If the velocity imparted onto the dot was a constant value, then the dot should

appear to move along a straight but tilted line (cf. Post et al., 1989). Five observers (three naive subjects and the two authors) were asked to judge the dot's apparent trajectory, and all observers reported that it appeared to move along an (approximately) straight-line path for both velocity profiles used in our experiments. The two observers (B. A. and H. B.) used in the previous studies also performed estimations of induced motion magnitude by adjusting a graphically generated line to match the perceived orientation of the dot's trajectory for the two experiments. These magnitude estimations of the induced displacement were statistically indistinguishable for the two velocity profiles but about a factor of 3 smaller than those derived for the illusory contours in our model. This difference in magnitude is not surprising, since there is no a priori reason to expect that the magnitude of motion induced onto a real and illusory target should be equal. Indeed, note that unlike the dot, the illusory contour does not have an objectively specified position, so it seems reasonable to expect that illusory contours are more susceptible to induced motion than real (i.e., contrast-defined) features.

A more striking test of our model can be derived from the assumption that the illusory occluding surface's direction of motion is opposite to that of the inducing contour. If true, this implies that it should be possible to create a display in which the occluding surface appears to originate from the opposite side of the illusory contour by inverting the direction of the inducing figure's motion. To test this prediction, we constructed a display that contained the exact same relative motion of the circle and the (straight) vertical occluder. However, rather than moving the circle leftward under a stationary vertical occluder, the circle was displaced rightward with a constant speed and the occluding surface was moved rightward at a higher constant speed. Although the *relative* motions between the occluder and occluded figure were identical in these two displays, the retinal motion of the partially occluded figure was in opposite directions when observers viewed these two displays while fixating a stationary target. Our model therefore predicts that the occluding surface should originate from opposite sides of the occluded contour in these two displays. In our circular displays, this would mean that the occluding surface would appear to originate from *inside* the circle. Note that illusory contours of this kind cannot be observed in static variants of our stimuli, so a percept of this kind falls completely outside the scope of static theories of contour synthesis. Remarkably, this is exactly what observers report. We have shown this display to 12 (naive) observers, and all have reported that the occluding surface appears to emerge from inside the circle when the retinal direction of motion is opposite to that used in our previous experiments (see Figure 6). Extant models of illusory contour synthesis would not predict this striking reversal.

One concern with the present findings is the fact that the perceived shapes of the illusory contours are quite different for the two observers. We have performed a number of control experiments to assess the cause of this difference, and have found that the most likely cause of these differences is the role of smooth pursuit eye movements. Observer B. A. reported making extensive horizontal tracking movements in the same direction

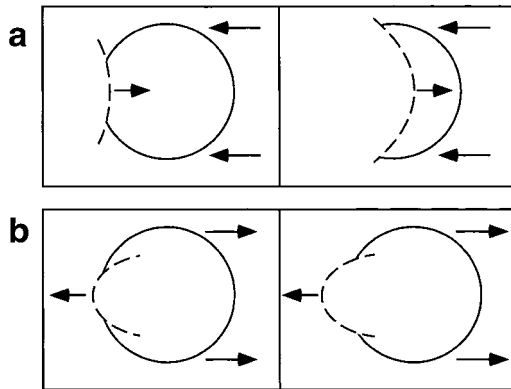


Figure 6. A Schematic of the Illusory Surface that Arose for the Two Directions of Motion of the Circle

In both displays, the relative motion between the occluding contour and circle were identical (the circle moved leftward relative to the straight vertical occluder). However, the absolute retinal motions were very different in the two cases. In (a), the circle moved leftward and the occluder was stationary. The illusory contour appeared to occlude the circle from the right. In (b), the circle moved rightward and the occluding surface moved rightward with a higher velocity. In this case, the illusory occluding surface appeared to come from *inside* the circle, moving from right to left. Note that in both cases the illusory occluding surface appeared to move in a direction opposite to the partially occluded figure, as predicted by our model (see text).

that the illusory contour appeared to move, whereas H. B. reported that she performed the task by fixating a region near the illusory contour. Although no eye movement records were made during the data collection described above, we tested the influence that such eye movements would have on the percept of the illusory contour by adding a small dot to the motion sequence that moved in the same direction as the (apparent) movement of the illusory contour. This dot was either placed in between the contour terminators or above the circle, and observers were instructed to track the dot while judging the apparent shape of the illusory contour. All five observers who viewed this display have reported that the illusory contour was strongly "stretched" in the direction of the dot's motion, which suggests that such eye movements are primarily responsible for the intersubject differences in the perceived extent of the illusory contour's motion.

Previous work has demonstrated that the human visual system is capable of constructing illusory surfaces on the basis of information present in moving displays (Wallach, 1935; Kaplan, 1969; Kellman and Cohen, 1984; Yonas et al., 1987; Andersen and Cortese, 1989; Bruno and Bertamini, 1990; Craton and Yonas, 1990; Bruno and Gerbino, 1991; Anderson and Sinha, 1997). Here, we have shown that the perceived shape of illusory contours in moving images is regulated by the relative velocities of moving contour discontinuities, and by an induced motion attributed to the occluding surface. Although it has been suggested that there may exist numerous mechanisms responsible for the host of induced motion phenomena (Duncker, 1938; Wade and Swanson, 1987; Post et al., 1989), locally generated induced

motion has been thought to reflect the operation of receptive fields that possess an antagonistic center-surround organization with respect to motion direction (Tynan and Sekuler, 1975; Anstis and Reinhardt-Rutland, 1976; Nakayama and Tyler, 1978; Reinhardt-Rutland, 1981, 1983; Nawrot and Sekuler, 1990). Indeed, one of the computational benefits of such mechanisms is that they could provide a means for determining whether retinal motion results from self-motion or from the motion of objects relative to the background (cf. Frost and Nakayama, 1983). The retinotopic dependence of the phenomena described above suggest that such low-level visual mechanisms may indeed play a critical role in the effects reported here. The antagonistic and retinotopic nature of the induced motion in the displays described herein suggests that extrastriate cortical areas MT/V5 may play a critical role in the synthesis of these illusory contours. Although motion-sensitive antagonistic interactions beyond the classical receptive field have been observed as early as V1 (Orban et al., 1987; Sillito and Jones, 1996), such antagonistic interactions are much more common and robust in MT/V5 (Allman et al., 1985; Tanaka et al., 1986; Lague et al., 1989; Born and Tootell, 1992; Raiguel et al., 1995; Xiao et al., 1997). Further research will be needed to determine the physiological locus of these mechanisms of illusory contour synthesis responsible for the contours described herein, and how these mechanisms interact with those described previously for static and moving images.

Experimental Procedures

Methods

Due to the demands of our data collection methods, participants were experienced psychophysical observers with normal or corrected to normal vision. Both subjects were authors. However, these stimuli have been shown to hundreds of naive observers, all of whom experienced the qualitative shape changes described herein.

Stimuli were presented on a Power Macintosh 9500/132 computer and viewed on an AppleVision monitor at a viewing distance of ~65 cm. Displays consisted of thin (~3 arc min) circular and diamond outline figures (~5° diameter), oscillating horizontally (at ~1.25 Hz) behind stationary rectangular occluders. The occluders were defined only by the contour terminators formed where the circle and the occluder intersected, and by two small (~0.3° diameter) anchoring dots placed on the occluding surface. These dots were present solely for the purpose of defining a static contrast in the vicinity of the occluding surface, and pilot work demonstrated that the placement of these dots had no discernible effects on perceived contour shape. The illusory contour was clearly visible when the dots were removed as well.

The display remained on the screen throughout a block of trials. To measure the position of the illusory contour, a small dot was flashed on the screen at a fixed vertical coordinate during the presentation of one of the images of the moving sequence. The observer's task was to adjust the horizontal coordinate of the dot until its position matched the perceived position of the illusory contour at that moment in time. The dot originated at a random x coordinate beginning at the top of the display, and the adjustment process was repeated at descending vertical coordinates until measurements were obtained for the entire vertical extent of the contour within the contour terminators. This process was repeated five times for each position along the contour. The illusory contour was measured during eight different frames (some of which have been omitted to prevent graphical clutter). The different experiments employed either diamond-shaped inducers (Experiments 1 and 4) or circular inducers (Experiments 2 and 3). The translation velocities of the inducing figures were identical (~4°/s) in Experiments 1 and 2 and

varied in Experiment 3 so that the terminator velocity of the partially occluded circle was held constant (also at $\sim 4^\circ/s$). In Experiment 4, a diamond with a height of ~ 6.3 arc min and a width of $\sim 5.3^\circ$ translated with a velocity of $\sim 4^\circ/s$. This was compared to a diamond of height $\sim 4.2^\circ$ and width $\sim 5.3^\circ$ translating at $\sim 6^\circ/s$, in order to keep the velocity of the diamonds' terminators constant across aspect ratios.

Modeling

Nonlinear least-squares curve fits were performed on Equation 2 using the Mathematica software package. The velocity v_y was given by the image data. There were three free parameters adjusted in this fit: v_x (the horizontal translation velocity induced in the occluding surface), a proportionality constant k , and a third parameter Δ that accounts for the temporal delay of the flashed probe dot. The phase lag was introduced to account for the effects of flashing our test probe. It has been shown that when a stimulus is flashed into a continuously moving display, the flashed target will appear shifted relative to the continuously moving display (Nijhawan, 1994, 1997; Khurana and Nijhawan, 1995). Hence, the flashed dot we used to measure the position of the illusory contour will not appear in the frame in which it was actually presented, but rather in or during some frame offset from the flash by some time lag. The effect of this lag is to introduce a shift in the origin of our coordinate space. When the circle's radius is normalized to unit length, the velocity of the contour terminator for the uniformly translating circle in Experiment 2 is:

$$v_y = (1 - [t + \Delta]) / (1 - [1 - (t + \Delta)]^2)^{1/2}$$

The fitting procedure generated values of Δ that were essentially identical for both subjects (translated into time, between ~ 85 ms and ~ 90 ms), which we used to shift the origin of our coordinate space such that the beginning of the occlusion event aligned with $t = 0$. For the other two parameters, $k = 0.63$ for H. B. and $k = 0.84$ for B. A., and $v_x = 7.65$ for H. B. and $v_x = 4.28$ for B. A. The fits are plotted in Figure 6.

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