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2-D Center–Surround Effects on 3-D Structure-From-Motion

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This study investigates how mechanisms for amplifying 2-D motion contrast influence the assignment of 3-D depth values. The authors found that the direction of movement of a random-dot conveyor belt strongly inclined observers to report that the front surface of a superimposed, transparent, rotating, random-dot sphere moved in a direction opposite to the belt. This motion-contrast effect was direction selective and demonstrated substantial spatial integration. Varying the stereo depth of the belt did not compromise the main effect, precluding a mechanical interpretation (sphere rolling on belt). Varying the speed of the surfaces of the sphere also did not greatly affect the interpretation of rotation direction. These results suggest that 2-D center–surround interactions influence 3-D depth assignment by differentially modulating the strength of response to the moving surfaces of an object (their prominence) without affecting featural specificity.

Psychophysical experiments have shown that the relative velocity of stimulus features can be used to calculate aspects of the 3-D structure of a moving stimulus (Braunstein, 1962, 1976; Johansson, 1973; Rogers & Graham, 1979; Wallach & O'Connell, 1953). The ability to compute 3-D structure from the 2-D projected velocities of stimulus features has been labeled the *kinetic depth effect* (Wallach & O'Connell, 1953) or recovery of *structure-from-motion* (Ullman, 1979). More recent studies have focused on the accuracy of perceived structure (Dosher, Landy, & Sperling, 1989; Lappin & Fuqua, 1983; Norman & Todd, 1993; Rogers & Graham, 1982); sensitivity to aspects of structure such as shape, curvature, and depth (Cornilleau-Pérès & Droulez, 1989; Norman & Lappin, 1992; Sperling, Landy, Dosher, & Perkins, 1989; van Damme, Oosterhoff, & van de Grind, 1994); sensitivity to noise (Todd, 1984); sensitivity to rigid versus nonrigid structure (Cutting, 1982; Todd, 1982, 1984); the buildup of structure over space and time (Hildreth, Grzywacz, Adelson, & Inada, 1990; Todd, Akerstrom, Reichel, & Hayes, 1988; Todd & Bressan, 1990; Treue, Husain, & Andersen, 1991); surface reconstruction or interpolation (Saidpour, Braunstein, & Hoffman, 1992; Treue et al., 1991); and cue integration (Braunstein, Andersen, Rouse, & Tittle, 1986; Dosher, Sperling, & Wurst, 1986; Johnston, Cumming, & Landy, 1994).

A variety of models have been advanced to explain these capacities (for a review, see Hildreth & Koch, 1987). Typically, visual motion analysis is thought to first involve the measurement of visual motion (i.e., the extraction of a 2-D velocity field) and, second, the use of 2-D motion to recover 3-D structure. The computation of the 2-D velocity field itself is thought to occur in stages involving the detection of local 1-D motion (Adelson & Bergen, 1985; Reichardt, 1961; van Santen & Sperling, 1985) and the resolution of the aperture problem in detecting 2-D local motion (e.g., Hildreth, 1984; M. E. Sereno, 1993). Models that compute 3-D structure-from-motion can be broadly divided into feature-correspondence models, which compute structure from corresponding image features between frames of a motion sequence (e.g., Ullman, 1979, 1984), and flow-field models, which use velocity information to compute structure (e.g., Koenderink & Van Doorn, 1986; Longuet-Higgins & Prazdny, 1980). Many of these models use a rigidity constraint—the changing 2-D image is interpreted as the projection of a rigid object in motion.

A parallel set of neurophysiological investigations in primates has uncovered several stages of motion processing at several radically different spatial scales. Initially, local velocity perpendicular to contours is detected by very small (~1°) receptive fields of neurons in layer 4B of area V1 (visual cortical area 1). Next, local pattern translation is detected (and the aperture problem solved) by some neurons in area MT (middle temporal area) with medium-sized (2°–8°) receptive fields (Movshon, Adelson, Gizzi, & Newsome, 1985). Finally, rotation, dilation, and shear are detected by neurons in MSTd (dorsal part of the medial superior temperal area) with very large (20°–100°) receptive fields (Saito et al., 1986).

At several levels in this hierarchy, there are strong opponent surrounds that have not usually been included in models of local motion detectors like those mentioned previously. For example, a random-dot surround can almost completely suppress an MT cell's center response to an optimal stimulus when the surround moves in the same

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direction (Allman, Miezin, & McGuinness, 1985a, 1985b; Tanaka et al., 1986). A number of cells in V1 and V2 have these surrounds as well (Allman, Miezin, & McGuinness, 1990; Orban, Gulyas, & Vogels, 1987). Such mechanisms seem well suited to enhance 2-D motion contrast. An unanswered question is how they might influence the calculation of 3-D depth from motion.

The goal of the present project is to understand the neural basis for determining perceived depth order in structure-from-motion stimuli. For example, dots moving in opposite directions in a single depth plane will appear to segregate into two different depth planes, one in front of the other. This stimulus is perceptually ambiguous in that either of the two directions of motion can be seen as belonging to the front surface, and the percept will spontaneously reverse over time. Explicit cues to depth applied to such a stimulus (e.g., stereo disparity, brightness, etc.) can disambiguate its perceived motion and depth order. Because unambiguous movement of a surround stimulus can powerfully influence the firing of direction-selective cells in cortex, we were interested in determining whether unambiguous surround motion could also influence perceived depth in ambiguous structure-from-motion stimuli. The nature of this influence may provide clues about the neural representation of depth order from moving stimuli.

The notion that information about the nonhuman primate brain can inform theories of the human brain is not new. Compelling evidence for the existence of specific topographic visual areas in humans similar to those found in other primates (M. I. Sereno et al., 1995; M. I. Sereno, 1998), as well as evidence for a human motion area similar to the MT–MST complex found in monkeys (Tootell, Reppas, Dale, et al., 1995; Tootell, Reppas, Kwong, et al., 1995; Zeki et al., 1991), has recently been reported. Other studies have also demonstrated comparable psychophysical performance in humans and monkeys on many visual tasks, including perceiving 3-D structure from 2-D motion (Siegel & Andersen, 1988).

The first part of the article (Experiments 1–3) demonstrates that the presence of unambiguous translational motion in a visual display can strongly influence the perceived depth of a structure-from-motion stimulus. We propose several hypotheses for this main effect. The second part of the article (Experiments 4–7) further explores the main effect and tests the proposed hypotheses. Finally, the General Discussion attempts to elucidate the underlying neural mechanisms responsible for the main effect and also relate our preferred hypothesis more generally to possible neural models (e.g., Nawrot & Blake, 1991b) and mechanisms (Bradley, Chang, & Andersen, 1998) for determining depth order from motion signals as well as to ideas about salience controls of perception.

General Method

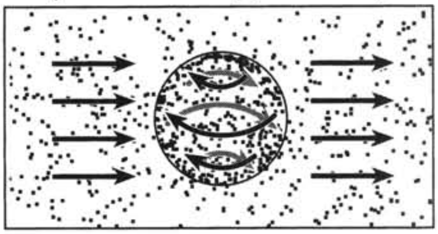
Participants

Participants were students at the University of Oregon. Twenty to 30 participants were run in each experiment. Each observer participated in only one of the seven experiments. All gave informed consent and were paid for their participation. Participants were naive about the precise aims of the experiments and, in most cases, were naive about psychophysics experiments in general. All had normal or corrected-to-normal vision.

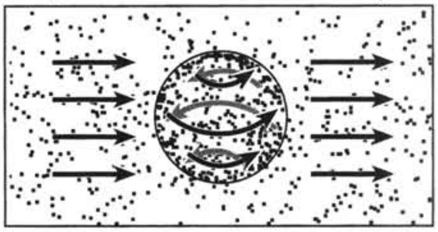
Stimuli and Apparatus

The displays used in all experiments were random-dot cinematograms consisting of a rotating object (in most cases a sphere) and a superimposed horizontal moving belt (see Figure 1). The rotating sphere was situated in the center of the display and was somewhat smaller than the vertical height of the belt. The sphere could be either transparent or opaque with respect to its own dots (i.e., appearing either as a clear sphere sprayed with colored dots against a black background or as an opaque black sphere sprayed with colored dots).

Cinematograms were produced on-line by an Iris Indigo Elan 4000 computer. A single frame consisted of approximately 1,100 single-pixel yellow dots distributed randomly on the surface of the sphere and the horizontal belt. To sprinkle dots randomly but uniformly across the sphere, an initial point on the sphere was rotated through random angles around each of the three axes. The number of dots and window size were arranged so that the computer was always capable of drawing frames in double-buffer mode at the rate of 60 new noninterlaced frames per second. We used an orthographic projection. Dots remained illuminated for the duration of the stimulus. The display subtended 14° × 14° of visual angle and appeared against a black background. The length and width of the belt subtended 14° and 7° of visual angle, respectively, whereas the diameter of the sphere subtended 4° of visual angle.



Preferred
(front surface opposite belt)



Not Preferred
(front surface same as belt)

Figure 1. Schematic diagram of the stimulus (a transparent, rotating, random-dot sphere and a superimposed horizontally moving plane of dots). The figure depicts the main effect found in Experiment 1—in many observers, there is a strong preference for the front surface of the sphere (and a variety of other transparent objects) to appear to move opposite to the direction of motion of the belt.

The dots of the moving belt appeared at one edge of the window and disappeared at the other edge.

Each dot subtended 2 × 2 min of arc. Dot density for sphere and belt surfaces was equivalent—the sphere had 200 dots sprinkled over its surface when transparent and half that amount when opaque; the belt was defined by 900 random dots. The speeds of the sphere and belt were 150 deg/s of angular velocity and 8.5 deg/s of translation, respectively.

Procedure

The monitor was viewed binocularly in a darkened room. Observers fixated a small, continuously illuminated central red dot then used the lower left control key to initiate a new stimulus. Observers were instructed to fixate the dot throughout the stimulus presentation. On each trial, the stimulus was presented for a short time (1 s), and the participant was asked to judge in which direction the front surface of the rotating sphere appeared to move. In a few of the experiments, other judgments were obtained as well, including (a) whether the sphere appeared in front of or behind the belt (Experiments 2 and 3) and (b) whether an opaque sphere appeared convex, flat, or concave (Experiment 3). Participants responded by pressing the arrow keys to indicate direction (left/right arrow keys) and depth (up/down arrow keys) and one of three keys on the keypad to indicate shape. The trial was terminated by the response keypress, and there was no feedback. Prior to the start of each experiment, observers were given 10 or more practice trials.

Part I—Experiments 1–3

In Experiments 1–3, we explored the effects of a translating surface on the perceived structure and depth of various structure-from-motion stimuli. Experiment 1 examined the perceived motion of ambiguous, transparent structure-from-motion stimuli of various shapes. Experiment 2 examined the perceived depth and the perceived motion of an ambiguous transparent sphere. Experiment 3 examined the perceived shape and depth of an unambiguous opaque sphere. We propose three possible hypotheses to explain the results.

Experiment 1: Effects of Belt Motion on an Ambiguous Structure-From-Motion Stimulus

In the first experiment, we presented a transparent object rotating about a vertical axis together with a horizontal random-dot conveyor belt passing through the object. The object consisted of one of five shapes: a sphere, cylinder, cube, volume (dots randomly positioned within a spherical boundary), or flat cylinder (two oppositely moving planes of dots). The random-dot sphere, cylinder, cube, and volume are all ambiguous stimuli that can be seen to rotate in one of two opposite directions—the direction of rotation determined by whether the observer sees the right or left moving dots in the stimulus as belonging to the front surface (or front half of the object, in the case of the volume stimulus). The flat cylinder is also ambiguous in that either plane (defined by right or left moving dots) can be seen in front of the other. Presented alone, the orthogonal projection of each object spontaneously reverses from time to time and can be intentionally reversed simply by tracking dots on one or the other of its surfaces.

We wanted to determine whether the direction of belt motion could disambiguate the perceived direction of object rotation (or, for the flat cylinder, the perceived direction of translation of the front surface). We used different shapes to see if the effect of the belt stimulus was similar for a variety of structure-from-motion stimuli (the class of stimuli consisting of at least two sets of oppositely moving features). In addition, catch trials without the belt were inserted to determine if there was a bias to perceive the ambiguous transparent object rotating (or translating) in a particular direction. Informal observations indicated the presence of a bias for one direction or the other in the condition without the belt.

Method

Participants. A total of 23 observers were run in the experiment. These observers did not take part in any of the other experiments.

Stimuli and procedure. Dots were randomly and uniformly positioned over the surfaces of the sphere, cylinder, cube, and flat cylinder or within the boundaries of the spherical volume. The diameter of the sphere, cylinder, and volume and the width of the cube and flat cylinder was 4° of visual angle. The length and width of the belt subtended 14° and 7° of visual angle.

The experiment consisted of five blocks of trials, one for each shape. The order of presentation was randomized for each observer. Each block contained 30 randomized trials—10 with left belt motion, 10 with right belt motion, and 10 with no belt present. The sphere, cylinder, cube, and volume stimuli rotated with the same (default) angular velocity (150 deg/s; 2-D dot speed 0–5.6 deg/s). The dots in the flat cylinder and the belt translated with the same (default) speed (8.5 deg/s). Responses in the belt trials were summarized in terms of the percentage of trials that the observer reported the front surface of the object moving opposite to the belt direction and, in the no-belt trials, the percentage of right (vs. left) responses.

Results

We found that the direction of movement of the conveyor belt strongly influenced most observers to report that the front surface of an ambiguous object moved in a direction opposite to the belt (Figure 1), usually overcoming a bias in the no-belt condition. For many observers, the front-surface-opposite-to-belt interpretation obtained for every stimulus presentation. These results confirmed our informal observations with an interactive version of the program, during which we noticed that reversing the direction of the belt induced instantaneous apparent shifts in rotation direction. A 1 within-factor (object shape) analysis of variance (ANOVA) performed on the percent opposite responses revealed no effect of object shape. A two-tailed t test demonstrated that the percent opposite scores differed significantly from 50%, $t(22) = 8.2, p < .001$.

Some observers, however, had percent opposite responses close to 50%. These observers showed this pattern of response because of an overriding response bias (either left or right) even with the belt present. Response bias was calculated as percent right − 50| over trials in the belt conditions. Response bias could range from 0 (no bias) to 50 (absolute bias).

We divided observers into two groups, biased and nonbiased. The biased group was defined as observers with a bias score greater than 40 in the ambiguous sphere plus belt condition—that is, participants who reported more than 90% of ambiguous stimuli as rotating in the same direction. These observers did not respond to the experimental manipulation of the belt; instead, they maintained a predominance of either *left* or *right* responses in the belt condition. All other observers were included in the nonbiased category. The nonbiased group, therefore, included observers with an intermediate level of bias as well as those with no bias (i.e., having approximately equal numbers of *left* and *right* responses in the belt conditions). Observers were divided into these two groups in this experiment in a post hoc analysis. All of the following experiments used the same criterion on an a priori basis to separate observers into biased and nonbiased groups, determined by their bias scores in the default condition of each experiment (i.e., the condition consisting of trials in which the ambiguous sphere stimulus rotates about a vertical axis with an angular velocity of 150 deg/s and is presented with the belt stimulus horizontally translating at a speed of 8.5 deg/s). The default sphere condition in all the experiments is excluded from further analysis once it has been used to classify the observers.

Our criterion for determining bias is conservative in that it excludes only very biased observers from the main group of observers. Separating biased observers allows us to remove a potential confound. When nonbiased observers show a chance percent opposite response, we can then safely attribute this result to experimental manipulation and not observer bias.

The results of Experiment 1 (after splitting observers into nonbiased and biased groups) are shown in Figure 2 (top panel), which plots the percent opposite response of nonbiased ($n = 17$) and biased ($n = 6$) observers for the five different object shapes. A 1 Between-Factor (observer type) × 1 Within-Factor (object shape) ANOVA was performed on the percent opposite responses, revealing a main effect of observer type, $F(1, 21) = 5457.3, p < .001$, but no effect of object shape and no significant interaction. In addition, two-tailed *t* tests were performed to determine whether the percent opposite scores differed from 50%. The *t* test performed on nonbiased observers was significant, $t(16) = 48.8, p < .001$; the *t* test on biased observers was not significant, $t(5) = 1.9, p < .112$.

The average bias in the belt conditions for nonbiased and biased observers was 1 and 49, respectively. These scores are clearly significantly different from each other, $t(21) = 97.7, p < .001$, suggesting that, in the belt trials, observers tended to be either strongly biased or bias free. The range and distribution of bias scores is illustrated in Figure 2 (bottom panel) for the default (sphere plus belt) condition. The other conditions have a similar distribution. In the no-belt trials, the average bias for nonbiased and biased observers was 40 and 50, respectively, indicating that most nonbiased observers do show a response bias in the object-only trials, which, however, is overridden by the motion-contrast effect (the front-surface-opposite-to-belt interpretation). Thus, although most observers show a bias in the object-only conditions, only in a minority does this bias persist in the presence of the moving belt.

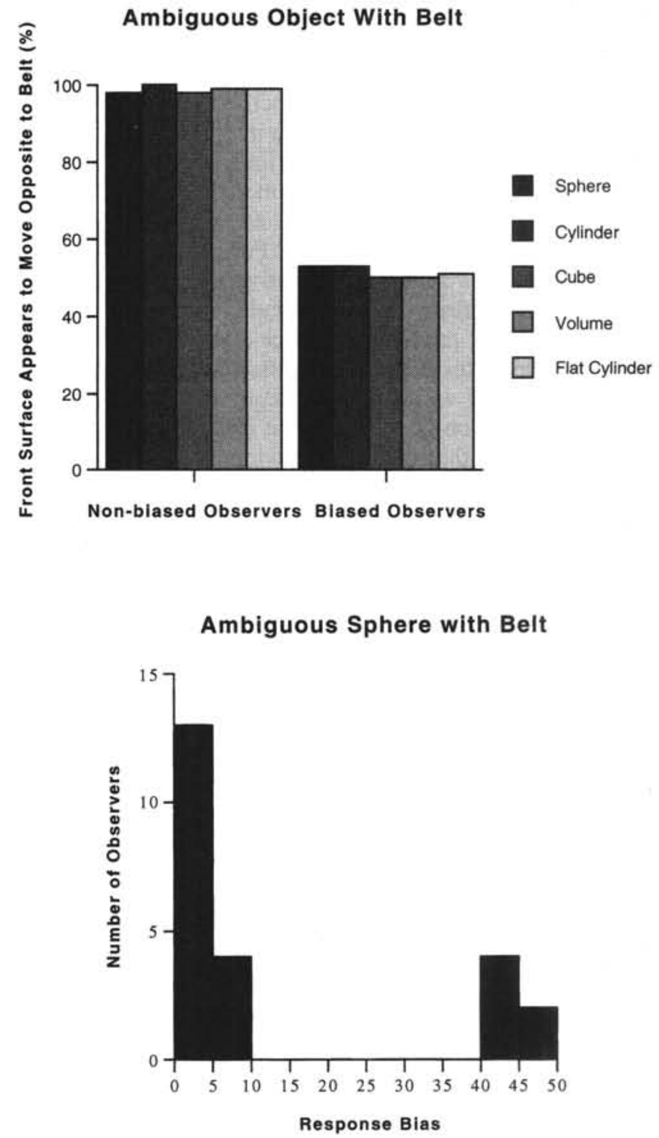


Figure 2. Appearance of an ambiguous rotating object with a moving belt—Experiment 1 results. In the top panel of the figure, the tendency to see the front surface of a transparent object (a sphere, cylinder, cube, volume, or flat cylinder) moving opposite to the belt is plotted for nonbiased and biased observers. Error bars indicate +1 *SE* over observers. (The error in this experiment was smaller than the plot symbol.) In the bottom panel of the figure, the distribution of response bias for the 23 observers in the default (sphere plus belt) condition of the experiment is shown.

Discussion

These results suggest that, for most observers, movement of a surrounding field of dots strongly affects depth assignment in an ambiguous, centered, structure-from-motion stimulus. Specifically, the direction of belt motion causes oppositely moving dots in the object stimulus to be assigned to the front (near) surface of the object.

This is interesting, in part, because it represents a situation in which a cue not directly applied to the transparent-rotating-object stimulus disambiguates its motion. Previous work has shown that an explicit depth cue applied to the stimulus itself disambiguates direction of rotation. For example, the addition of depth cues such as perspective (Braunstein, 1966; Hershberger & Urban, 1970), binocular stereopsis (Braunstein et al., 1986), relative luminance (Dosher et al., 1986), and occlusion of texture elements (Braunstein et al., 1986) disambiguates the assignment of depth and, therefore, the direction of rotation of a transparent rotating object. However, at least two other studies have demonstrated disambiguation of rotation of a transparent stimulus with a manipulation not directly applied to the stimulus itself (Eby, Loomis, & Solomon, 1989; Nawrot & Blake, 1989, 1991a).

Nawrot and Blake (1989, 1991a) found that prolonged exposure to unambiguous 3-D motion (using a transparent rotating stereo object such as a sphere) subsequently caused an ambiguous transparent rotating sphere to be seen rotating in the opposite direction. Although this effect and the one reported in Experiment 1 may be related (see General Discussion), they differ in a number of ways. In the Nawrot and Blake studies, a stereoscopic adapting stimulus was required to induce the effect. In the present experiment, the effect is induced solely from on-line relative motion and is not necessarily bound to the same retinal location (see Experiment 5).

Eby et al. (1989; see also Gillam, 1972) showed that when multiple objects (e.g., two transparent spheres) rotate in depth, they are often perceived to rotate in the same direction even when (a) the objects are spatially separated and (b) perspective information applied to each object signals counterrotation. The authors refered to this effect as *rotational linkage.* Using a similar display (five transparent rotating spheres configured like the dots on a die specifying the number five), we confirmed their results with our own informal observations—all the spheres tended to rotate in the same direction; when one sphere spontaneously reversed direction, so did the others. However, at the moment one of the spheres was made opaque (with only one direction of moving dots), the remaining spheres began rotating in the opposite direction. Opposite motion in the transparent spheres could also be induced by replacing one of the spheres with a set of translating dots (the dots appearing to move behind a square aperture). Such a stimulus resembles the sphere–belt stimulus used in this study. Thus, it seems that a motion contrast effect appears once the motion signals in a display become unbalanced (i.e., when more dots move in one direction than another).

There are several mechanisms by which the motion contrast effect of Experiment 1 (the front-surface-opposite-to-belt interpretation) might be mediated. For example, the surrounding belt could affect the apparent speed of certain parts of the object stimulus (by causing opposite-direction dots in the sphere to appear to move faster and same-direction dots slower). Depth assignment based on speed might then be disambiguated by a heuristic whereby apparent absolute fastest speed is assigned nearer the viewer. Alternatively, the belt might affect the apparent prominence of parts of the object stimulus (leaving apparent speed unchanged), followed by the application of a heuristic in which the apparently most prominent part of the stimulus is seen nearer the viewer. The neural basis of prominence may be the modulation of the firing rate of a population of neurons tuned to a particular direction, resulting in a stronger or weaker signal for that direction. Parts of the stimulus moving in the direction with the stronger (more prominent) motion signal may thus appear to be closer to the viewer. A third possibility is that the effect is due to a mechanical interpretation of a sphere rolling on the front surface of the belt. In this case, observers prefer seeing the sphere positioned in front of the belt and thus rolling with rather than grinding against the belt.

Before attempting to distinguish the three possible explanations for the main effect outlined above, we first wanted to explore other basic properties of this surround-induced effect by investigating the apparent depth relations of the sphere and belt (Experiment 2) and by substituting an opaque for a transparent sphere (Experiment 3).

Experiment 2: Effects of Belt Motion on the Perceived Depth of an Ambiguous Sphere

In Experiment 2, we investigated the perceived depth relations between sphere and belt. The depth ordering of the sphere relative to the belt is also perceptually ambiguous—the belt can be seen located in front of or behind the sphere. Experiment 1 demonstrated that the belt can influence the perceived depth order of the surfaces of an ambiguous structure-from-motion object. Will the belt also affect the perceived placement of those surfaces relative to its own perceived depth?

Method

Participants. A total of 30 observers were run in the experiment. These observers did not take part in any of the other experiments.

Stimuli and procedure. The experiment consisted of a total of 30 trials—10 with left belt motion, 10 with right belt motion, and 10 with no belt present. The sphere rotated at the (default) angular velocity (150 deg/s) and the belt translated at the (default) speed (8.5 deg/s) as in Experiment 1. Observers judged the direction of movement of the front surface of the sphere as well as the position of the sphere (front or back) relative to the belt.

Following the main experiment, observers were run through the default ambiguous sphere plus belt experiment to determine their bias classification (see Experiment 1, *Results*). Of the 30 observers run, 23 were classified as nonbiased and 7 as biased.

Results

As in Experiment 1, nonbiased observers predominantly saw the front surface of the sphere moving opposite to the belt (95% opposite responses). They also predominantly saw the sphere positioned in front of the belt (85% front responses). Biased observers had opposite (50%) and front (49%) responses very close to 50%.

Of the four possible response combinations (opposite/front, opposite/back, same/front, same/back), nonbiased observers showed a predominance of opposite/front responses (Figure 3; top panel). Two-tailed t tests demonstrated that opposite/front responses were significantly greater than 25%, $t(22) = 17.5, p < .001$. The remaining responses were significantly below 25%—opposite/back: $t(22) = -5.1$, $p < .001$; same/front: $t(22) = -54.4$, $p < .001$; same/back: $t(22) = -13.9$, $p < .001$. Biased observers showed a different pattern of results. They tended to see the sphere either in front of the belt rotating in the opposite direction (opposite/front) or behind the belt rotating in the same direction (same/back; Figure 3, top panel). Hence, the opposite/front and same/back means were significantly above 25%, $t(6) = 4.6, p < .001$, and $t(6) = 3.7, p < .011$, and the opposite/back and same/front responses were significantly below 25%, $t(6) = -3.9, p < .009$, and $t(6) = -4.3$, $p < .006$.

Further analysis of biased observers' results suggests that, when the observer's bias and the motion contrast cue are consistent (e.g., when the observer has a right front-surface bias and the belt is moving left), biased observers tend to place opposite-to-belt direction dots of the sphere in the front-most depth plane, giving rise to a high percent opposite/front response. Conversely, when the observer's bias and the motion contrast cue are conflicting, biased observers tend to place opposite-to-belt direction dots of the sphere in the back-most depth plane, giving rise to a high percent same/back response (see Figure 3, bottom panel). Two-tailed t tests show that the means in these two conditions (opposite/front responses when the motion contrast cue and observer bias are consistent and same/back responses when the motion contrast cue and observer bias are conflicting) were significantly above 12.5%, $t(6) = 8.4$, $p < .001$, and $t(6) = 7.0, p < .001$, whereas the means of all the other conditions either were not significantly different from 12.5%: opposite/back consistent, $t(6) = -0.8$, $p < .475$, and same/front conflicting, $t(6) = -0.7, p < .497$; or were significantly below 12.5%: opposite/back conflicting, $t(6) = -16.5, p < .001$ (the t statistic could not be computed for same/front consistent, same/back consistent, and opposite/front conflicting because all scores were 0). Thus, belt direction pushes the sphere either in front of or behind the belt, depending on the observer's bias.

Discussion

This experiment demonstrates that the belt not only affects the perceived depth order of surfaces within the rotating object (for nonbiased observers), it also influences the placement of these surfaces relative to itself. The experiment suggests that, for nonbiased observers, the belt causes oppositely moving dots in the sphere to be placed in the depth plane closer to the observer (hence, the predominance of opposite/front responses). In biased observers, another factor (bias) interacts with the motion contrast effect, resulting in placement of opposite-to-belt-direction dots either in the depth plane closest to the observer (when corresponding to bias direction) or in the depth plane farthest from the observer (when opposite to bias direction). Hence, there is a predominance of opposite/front and same/back responses. Interestingly, the two least reported perceptions across all observers were opposite/back and same/front. In these cases, dots in the sphere that are seen lying in the same plane as the belt are moving in a direction opposite to the belt. Clearly this is not a preferred perceptual resolution. There seems to be a perceptual bias against seeing oppositely moving surfaces occupying the same depth plane (see General Discussion).

Experiment 3: Effects of Belt Motion on the Perceived Shape and Depth of an Opaque Sphere

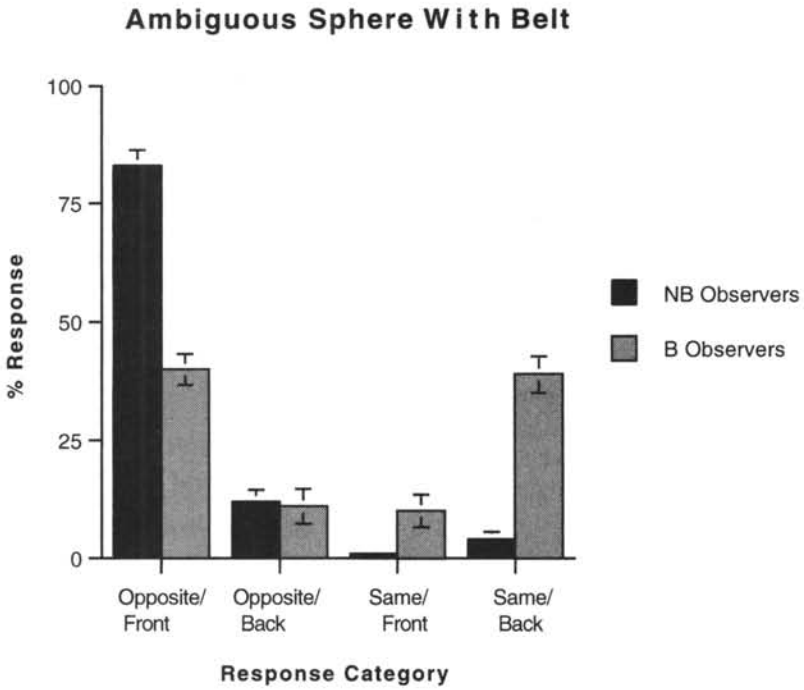
We were interested in the effect of the belt on an opaque sphere—that is, one whose front surface appears to occlude its back surface (but not the belt). It has been shown that the belt can influence the perceived depth of an ambiguous transparent sphere. Will it have a similar influence on an opaque sphere, a perceptually less ambiguous stimulus most often seen as having a convex shape? Observers judged the shape (convex, flat, concave) of the opaque-sphere stimulus, as well as the perceived depth of the stimulus with respect to the belt.

Experiments 1 and 2 demonstrated that the belt can influence the perceived depth order of the surfaces of an ambiguous rotating object as well as the depth placement of those surfaces relative to the belt. What predictions might these results generate for the present experiment? Consider two conditions of the present experiment: (a) a belt-opposite condition (the belt moves in a direction opposite to the half sphere) and (b) a belt-same condition (the belt moves in the same direction as the half sphere). With ambiguous stimuli, opposite-direction dots were most often seen by nonbiased observers as a convex surface positioned in the front-most depth plane. It is expected then that, in the belt-opposite condition, there should be a predominance of convex and front perceptions. Conversely, with ambiguous stimuli, same-direction dots are most often seen by nonbiased observers as a concave surface whose back-most dots are touching the belt. It is expected then that, in the belt-same condition, there should be more concave, flat, and, perhaps, back perceptions even though the likely overall preferred interpretation of the object stimulus is that of a rounded convex sphere.

Method

Participants. A total of 29 observers were run in the experiment. These observers did not take part in any of the other experiments.

Stimuli and procedure. In this experiment, the opaque sphere appeared either alone (20 trials) or with a belt moving in the same or opposite direction as the sphere dots (20 trials each), giving rise to a total of 60 randomized trials. The sphere and belt moved at the default speeds. Observers judged the shape of the sphere (convex,



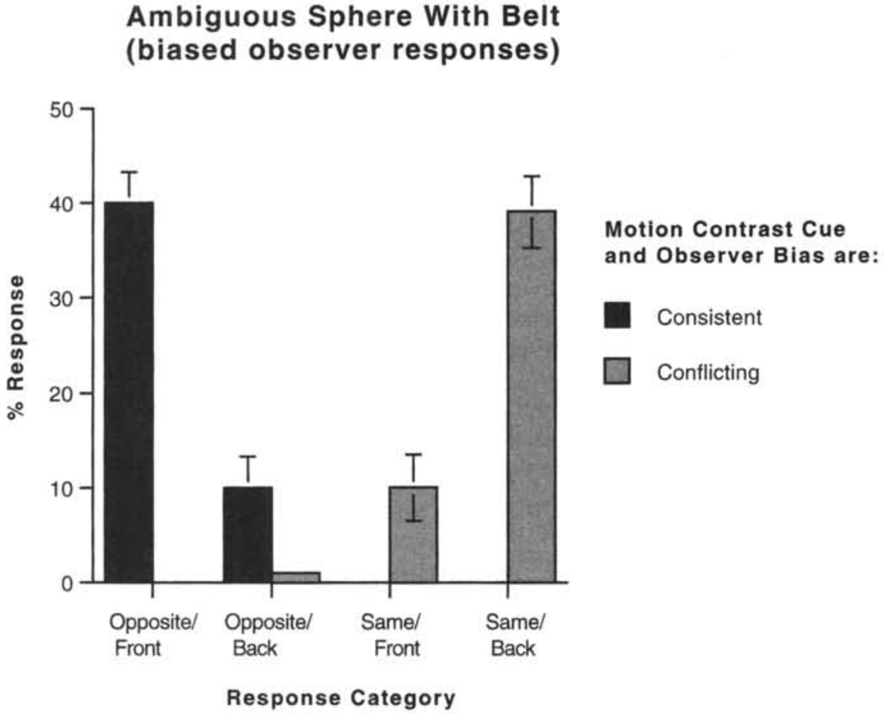


Figure 3. Appearance of an ambiguous rotating sphere with a moving belt—Experiment 2 results. In the top panel of the figure, mean percentage opposite/front, opposite/back, same/front, and same/back responses for nonbiased (NB) and biased (B) observers are plotted. In the bottom panel of the figure, biased observer responses are presented for the four response categories. In addition, a separate average is given for responses in which an observer's bias direction is (a) in agreement (i.e., consistent) with the motion-contrast cue (the front-surface-opposite-to-belt direction) or (b) in conflict with the motion-contrast cue (i.e., consistent with the front-surface-same-as-belt direction). Error bars indicate +1 *SE* over observers.

flat, concave) and whether the sphere appeared in front of or behind the belt (in trials with the belt).

Following the main experiment, observers were run through the default experiment to determine their bias, as before (see Experiment 2, *Method*). Of the 29 observers run, 22 were classified as nonbiased and 7 as biased.

Results

When presented in isolation, the stimulus was usually seen as convex (see Figure 4; top panel). The stimulus is consistent with an opaque convex rotating sphere but can also be seen as a concave rotating back-half-of-a-sphere or a flat surface with dots moving with a sinusoidal pattern of speeds. The average percent convex response was 83% (for nonbiased observers) and 93% (for biased observers) in the no-belt condition. Two-tailed *t* tests indicated that the average percent convex response was significantly greater than 33.3% for both nonbiased, $t(21) = 10.5, p < .001$, and biased observers, $t(6) = 12.6, p < .001$.

To simplify data analysis, we split observer responses into convex and nonconvex (flat and concave) responses. A 1 Between-Factor (observer type) × 1 Within-Factor (belt type) ANOVA performed on the percent convex responses demonstrated a main effect of belt type, $F(2, 54) = 22.2, p < .001$. We decided a priori that if we found a significant belt effect, we would perform follow-up contrasts comparing belt-opposite and belt-same means with the no-belt mean. There was no significant difference between the belt-opposite mean and the no-belt mean, $F(1, 54) = 1.7, p < .197$, but there was a significant difference between the no-belt and belt-same means, $F(1, 54) = 25.0, p < .001$. Thus, it appears that when the belt moves in the same direction as the sphere, there is a decrease in the number of convex responses (from 93% in the belt-opposite condition and 85% in the no-belt condition to 60% in the belt-same condition for all observers) and a concomitant increase in the number of flat and concave responses relative to the no-belt and belt-opposite conditions.

In the belt conditions, observers made front/back judgments in addition to shape judgments (Figure 4; bottom panel). A 1 Between-Factor (observer type) × 1 Within-Factor (belt type) ANOVA revealed a main effect of observer type, $F(1, 27) = 16.2, p < .001$. Mean percent front responses were higher for nonbiased observers (70%) than for biased observers (32%). There was also a main effect of belt type, $F(1, 27) = 26.5, p < .001$. Mean percent front judgments were higher in the belt-opposite condition (74%) compared with the belt-same condition (48%). Thus, the sphere stimulus appears more often to lie in front of the belt when the belt moves in the opposite direction. In addition, biased observers have a significantly greater number of back responses in both the belt-opposite and belt-same conditions compared with nonbiased observers. Two tailed *t* tests revealed that, for nonbiased observers, the mean percent front response in the belt-opposite condition was significantly greater than 50%, $t(21) = 8.5, p < .001$; the belt-same mean percent front response was not significantly greater than 50%, $t(21) = 1.0, p < .320$. For biased observers, the mean percent front response in the belt-

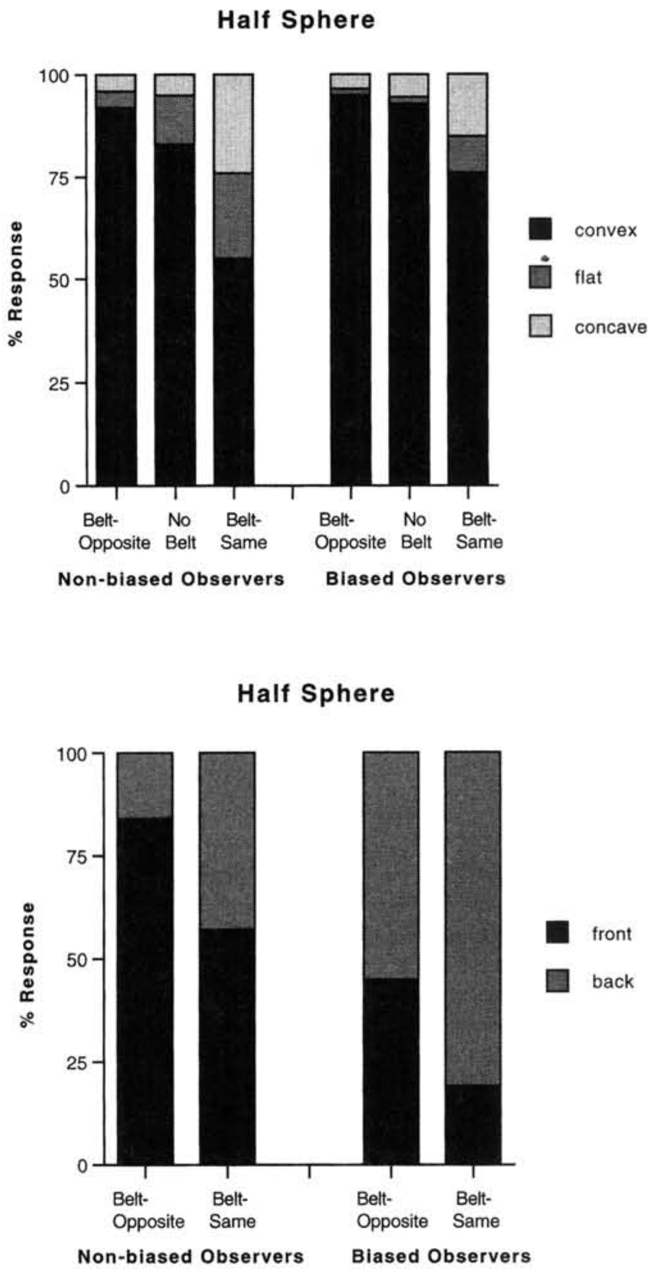


Figure 4. Appearance of an opaque (unambiguous) sphere presented by itself or with a moving belt—Experiment 3 results. In the top panel of the figure, the percentage of *convex, flat,* or *concave* responses are plotted for nonbiased (NB) and biased (B) observers for three experimental conditions—(1) when the belt was moving in a direction opposite to the sphere direction (belt-opposite), (2) when there was no belt (no belt), and (3) when the belt was moving in the same direction as the sphere direction (belt-same). In the bottom panel of the figure, the percentage of *front* and *back* responses are plotted for nonbiased and biased observers in two experimental conditions—(1) when the belt was moving in a direction opposite to the sphere direction (belt-opposite) and (2) when the belt was moving in the same direction as the sphere direction (belt-same).

opposite condition was not significantly lower than 50%, $t(6) = -0.7, p < .521$; the belt-same mean percent front response, however, was significantly lower than 50%, $t(6) = -3.6, p < .012$.

Discussion

This experiment suggests that the belt stimulus is not only capable of determining the front/back placement of surfaces of a transparent sphere stimulus (Experiments 1 and 2) but also capable of pushing a surface normally seen in front (the convex half-sphere interpretation) toward the back, even when there is no surface at the back to come to the front.

As shown in many previous experiments, this experiment demonstrates a predominance of convex responses in the no-belt condition. In biased observers, bias was overridden by the tendency to see an opaque sphere as convex. However, there were some nonconvex responses as well. This result may have come about because the binocular viewing situation provides stereoscopic information indicating that the stimulus is in fact flat. Monocular viewing may produce an even greater preponderance of convex responses.

In more detail, the experiment demonstrated that addition of a belt moving in the same direction as the sphere rotation (belt-same condition) significantly increased the number of nonconvex responses (flat and concave) compared with the no-belt and belt-opposite conditions and also the number of back responses compared with the belt-opposite condition. Addition of a belt moving in the opposite direction to the sphere (belt-opposite condition) significantly increased the number of convex responses only when compared with the belt-same condition. Although there was also an increase in convex responses when compared with the no-belt condition, this increase did not reach significance. Hence, the same-direction belt may have a stronger influence than the opposite-direction belt in changing the perceived shape of the sphere. In other terms, belt motion appears to have a greater effect on same-direction compared with opposite-direction dots in the sphere. Although this result may simply reflect a ceiling effect, it may also have a neurophysiological basis. Area MT neurons do show response facilitation to a centered preferred-direction stimulus given a surround moving in the opposite direction and also response suppression given a surround moving in the same direction. However, the suppressive effect tends to be greater than the facilitatory effect. Thus, if a center–surround mechanism underlies these psychophysical effects, the same-direction (suppressive) effect of the belt is likely to be stronger than the opposite-direction (facilitatory) effect, as the results of this experiment suggest. Future psychophysical experiments may shed light on this question.

Nawrot and Blake (1989, 1991a) were also able to induce a percept of concavity in a rotating-opaque-sphere stimulus. They showed that adapting to a transparent stereo sphere could cause an opaque sphere to appear concave when the front surface of the adapting sphere moved in the same direction as the opaque sphere motion.

Braunstein et al. (1986) have shown that binocular stereopsis can disambiguate the sign of depth in transparent rotating spheres. However, with opaque stimuli, dynamic occlusion information (texture elements disappearing as they reach the sphere's edge) often negated the binocular stereo information. It is interesting to note that the same-direction belt stimulus in this experiment was able to significantly decrease the dominant percept of convexity at least as often as a strong, explicit, stereo depth cue.

Two other issues merit further exploration: (a) the relationship between observer bias and percent front/back responses and (b) the relationship between sphere and belt speeds on shape and depth judgments. Biased observers had a significantly greater number of back responses compared with nonbiased observers. This result may be due to an interaction between their motion bias and the direction of the opaque sphere motion. Perhaps these observers pushed the sphere behind the belt when it moves contrary to their bias, leading to an overall greater number of back responses.

The relative speed of the sphere in comparison with the belt may also be an important factor in determining the structure and depth of the opaque sphere. Using an interactive version of the program, we were able to adjust the speed of the belt and a half-sphere or half-cylinder in the same-direction condition so that the impression of a cylinder or sphere was lost. This has previously been demonstrated by V. S. Ramachandran (personal communication). As the 3-D object in the center collapses, the sinusoidal variation in speed with horizontal position becomes noticeable. The cylinder or sphere percept reappears as the belt is moved much faster or slower than the average speed of the object dots.

Part II—Experiments 4–7

In Part II, we manipulated the transparent sphere and belt stimulus in various ways to test the three hypotheses proposed to account for the basic motion contrast effect (see Experiment 1, *Discussion*). Experiment 4 (tilting the axis of rotation of the sphere) and Experiment 5 (occluding portions of the belt) tested aspects of the prominence hypothesis. Experiment 6 (observing the effects of belt depth on the motion contrast effect) tested the mechanical interpretation hypothesis. Experiment 7 (manipulating the relative speeds of front and back surfaces of the sphere) tested the speed hypothesis.

Experiment 4: Effects of Tilt of the Axis of Rotation

We were interested in determining the dependence of the motion contrast effect on the angle between the axis of rotation of the sphere and the motion of the belt. Physiological data on center-surround interactions in primates predicts that the motion contrast effect strongly depends on the relative directions of dot motion in the sphere and belt. All previous experiments were run with the object axis perpendicular to the belt direction. In this experiment, we used an ambiguous sphere with its axis of rotation skewed in stages away from the perpendicular. Observers judged the direction of front surface movement using the skewed axis as a frame of reference.

Physiological studies provide evidence for maximum inhibition for a same-direction center stimulus (e.g., dots in a center stimulus moving in the same direction as surround dots) and maximum facilitation for an opposite-direction center stimulus. There is an intermediate effect for an orthogonal-direction center stimulus, although it is still somewhat inhibitory because overall, the inhibitory effect is stronger than the facilitatory effect (Allman et al., 1985a, 1985b; Tanaka et al., 1986). These results, which are the basis for the prominence explanation, predict that the belt will exert the strongest influence on the moving dots in the sphere when there is a vertical-axis ambiguous sphere and horizontally moving belt (in this case, the belt decreases the signal strength of same-direction sphere dots and increases the strength of opposite-direction dots). Likewise, a horizontally moving belt exerts the least influence on a horizontal-axis sphere (in this case, because both directions of dot motion in the sphere are orthogonal to the direction of the belt, the belt has a similar influence on the strength of both directions of dot movement and, hence, should not bias the perceived depth order one way or the other).

Method

Participants. A total of 25 observers were run in the experiment. These observers did not take part in any of the other experiments.

Stimuli and procedure. Three skew angles (14°, 42°, and 70°) of clockwise and counterclockwise rotation of the sphere axis away from the vertical were used. The belt always moved horizontally. There were 20 trials presented for each skew angle and direction of axis rotation, giving rise to a total of 120 randomized trials. For each of the three angles of skew, responses were collapsed across clockwise and counterclockwise skew, giving rise to 40 trials per skew angle. The sphere and belt moved at their default speeds.

Following the main experiment, observers were run through the default experiment to determine their bias, as before (see Experiment 2, *Method*). Of the 25 observers run, 19 were classified as nonbiased and 6 as biased.

Results

For nonbiased observers, the front-surface-opposite-to-belt interpretation of the sphere fell off as the object axis was skewed away from the perpendicular (Figure 5). When the object axis differed by 48° from the belt direction (a 42° skew), observers still saw the front surface of the sphere move opposite to the belt 78% of the time. With the object axis only 20° apart from the belt direction (a 70° skew), however, that number dropped to 61%, approaching chance (50%). The biased observers' percent opposite response was near 50% for all conditions.

A 1 Between-Factor (observer type) × 1 Within-Factor (skew) ANOVA revealed a main effect of observer type, $F(1, 23) = 50.3, p < .001$, a main effect of skew, $F(2, 46) = 26.3$, $p < .001$, and an interaction between observer type and skew, $F(2, 46) = 24.8, p < .001$. A follow-up linear contrast on the Observer Type × Skew interaction indicated that the linear trend across levels of the skew factor was different for the two types of observers, $F(1, 46) = 49.5$, $p < .001$. Therefore, as skew increases, percent opposite responses decrease in nonbiased observers but not in biased observers, whose means remain close to or at 50%.

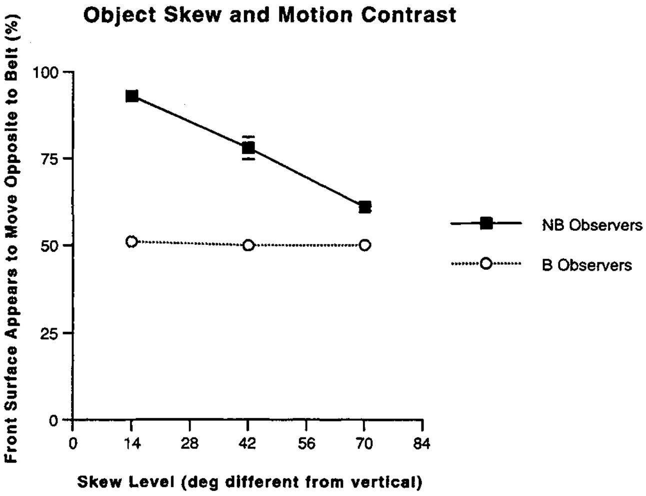


Figure 5. Object skew and motion contrast—Experiment 4 results. The percentage opposite responses for nonbiased (NB) and biased (B) observers are plotted as the object rotation axis is varied from perpendicular to the belt (as was the case in all previous conditions) to parallel to the belt. Error bars indicate +1 *SE* over observers.

Two-tailed *t* tests demonstrated that the percent opposite means in all 3 of the skew conditions for nonbiased observers were significantly different from 50%. Even the *t* test on the percent opposite scores in the condition with the largest amount of sphere skew (skew angle = 70°) in nonbiased observers was significant, $t(18) = 4.5, p < .001$.

Discussion

These results show that the belt effect is direction selective. If the effect is mediated by changes in apparent prominence because of a center–surround motion mechanism, it was predicted that the effect should drop off as object dots come to move at right angles to belt dots. As the sphere axis is skewed, inhibition of the same direction dots as well as facilitation of opposite direction dots falls off toward an intermediate point—that is, the influence of the belt on the two directions of moving dots becomes progressively similar, until it is equivalent when the sphere axis is skewed 90° from vertical. At that point, most cells in MT (but not all, see General Discussion) show little effect of a surround.

As predicted, the effect of the surround on determining perceived depth order (i.e., in producing a high percent opposite response) does, in fact, fall from 91% opposite responses (with a 14° tilt of the sphere axis away from vertical) to 61% opposite responses (with a 70° tilt away from vertical). A straight line fit to the data intersects the 50% opposite response level at 90°, suggesting that the belt indeed has no effect on the perceived depth order of the sphere when the direction of movement of the belt dots is orthogonal to the directions of movement of the dots in the sphere. This experiment, then, provides additional evidence for the prominence hypothesis.

Experiment 5: Belt Occlusion

We performed this experiment to determine whether the main effect depends on belt dots actually being superimposed on sphere dots. We tested this question by occluding portions of the belt. A requirement of superposition would support the mechanical hypothesis (the sphere seen rolling on the belt). The prominence hypothesis, however, gains support if it is shown that moving dots distant from the sphere can nevertheless influence its perceived structure.

How far out do the inhibitory surrounds of MT cells extend? The estimates are fairly consistent across studies and suggest that the surrounds extend a fair distance outside the classical receptive field border. Using a masking annulus of variable outside diameter (similar to that used in the present experiment), Allman et al. (1985a, 1985b) suggested that the surrounds are 7–10 times the diameter of the center receptive field. Tanaka et al. (1986) reported that for center receptive fields between 4° and 12° in diameter, the average strength of surround inhibition is still significant with a 20° mask, falling off by 40°. Defining the outer limit of the surround as the perimeter where surround inhibition falls to 50%, Raiguel et al. (1995) reported that this perimeter is 2–5 times the diameter of the classical receptive field. Although this estimate seems somewhat smaller than the 7–10 diameter estimate obtained by Allman et al., it is in reasonable agreement given that the Allman et al. measure was intended to find the outer limit of influence versus the 50% level of inhibition.

Method

Participants. A total of 25 observers were run in the experiment. These observers did not take part in any of the other experiments.

Stimuli and procedure. The transparent sphere (with a diameter of 4° visual angle) was placed against a larger (20° × 20° visual angle) background. In addition, a centered black circle of varying diameters (0°, 4°, 8°, 12°, 16°, and 20° visual angle) occluded the belt dots. Occluders ranged from 0° (no occlusion) to 20°, which left only the four corners of the belt unoccluded. The sphere and belt moved at their default speeds. There were 20 trials presented for each occlusion diameter, giving rise to a total of 120 randomized trials.

Following the main experiment, observers were run through the default experiment to determine their bias, as before (see Experiment 2, *Methods*). Of the 25 observers run, 17 were classified as nonbiased and 8 as biased.

Results

The percent opposite responses fell off as the diameter of the occluder increased in size (Figure 6). However, even at a diameter of 20° visual angle, there was still a significant motion-contrast effect—the percent opposite responses in nonbiased observers was 73%.

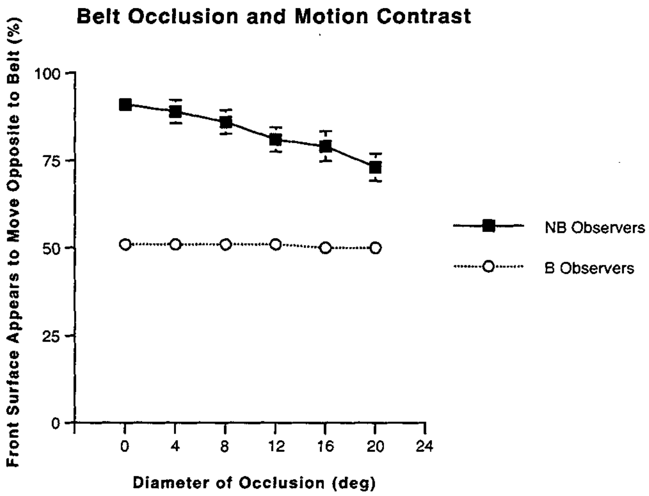


Figure 6. Belt occlusion and motion contrast—Experiment 5 results. The percentage opposite responses for nonbiased (NB) and biased (B) observers are plotted as the diameter of a circular occluder increases. Error bars indicate +1 *SE* over observers.

A 1 Between-Factor (observer type) × 1 Within-Factor (occlusion) ANOVA revealed a main effect of observer type, $F(1, 23) = 47.2, p < .001$, a main effect of occlusion, $F(5, 115) = 8.0, p < .001$, and an interaction between observer type and occlusion, $F(1, 115) = 7.4, p < .001$. A follow-up linear contrast on the Observer Type × Occlusion interaction indicated a significant difference in the slopes across observer types, $F(1, 115) = 35.2, p < .001$. Nonbiased observers showed a systematic (linear) decrease in percent opposite responses as occlusion was increased.

Two-tailed t tests demonstrated that the percent opposite means in all 6 of the occlusion conditions for nonbiased observers were significantly different from 50%. For example, the t test on the percent opposite scores even in the condition with the largest amount of belt occlusion (occlusion diameter = 20°) in nonbiased observers was significant, $t(16) = 5.8, p < .001$.

Discussion

These results suggest that the main effect involves substantial spatial integration—there is still a significant percent opposite response when the belt dots are separated from the center of the sphere by 10°. They are consistent with a prominence explanation and the idea that a center–surround motion mechanism may underlie the effect. They also disconfirm a mechanical interpretation because there is an effect even when the belt is not touching the sphere.

How similar is the falloff of the main effect with larger diameter occluders in our experiment to the falloff of surround inhibition in the physiology experiments? Given that the diameter of our sphere stimulus is 4° and assuming that the average diameter of MT cells' receptive fields in the foveal region is ~5° (for a review of receptive field size estimates, see Raiguel et al., 1995), and further assuming that the surrounds are 7–10 times the diameter of the center receptive field, we can roughly predict that surround effects will fall off somewhere within a 35° to 50° diameter mask. Our results are consistent with this prediction, considering that we still found a significant surround effect (i.e., percent opposite response significantly greater than 50%) for the largest mask diameter (20°). In addition, if a straight line is fit to nonbiased observers' data, this line intersects the 50% opposite response level at a 47° diameter mask, within the range of foveal MT surround effects in monkeys.

Future work is needed to experimentally determine the diameter at which the motion contrast effect disappears by using test stimuli positioned even further out in the periphery. Future work may also be able to determine if the falloff in mean percent opposite response is due to belt dots lying farther out in the periphery or to a decrease in the number of dots in the belt stimulus. To test this, the number of dots present in the peripheral stimulus would have to be kept constant.

Experiment 6: Effects of Belt Depth

One possible interpretation of the front-surface-opposite-to-belt effect is that observers are predisposed first to see the sphere in front of the belt and then as if it were rolling on the belt. We tested for this mechanical interpretation by varying the stereo depth of the belt so that it appeared either behind or in front of the sphere.

If observers predominantly see the front surface of the sphere move opposite to the belt when the belt is in front of the sphere, the apparent physical situation is one in which the front surface of the sphere grinds against the belt. Thus, if the mechanical hypothesis is true (that there is a preference for seeing the sphere rolling vs. grinding on the belt), an increase in *same* responses is predicted when the belt appears in front of the sphere. A *same* response is consistent with the apparent 3-D situation in which the sphere is seen rolling on the back surface of the belt.

With regard to the prominence hypothesis, we do not know from neuroscience studies whether or not the activity or tuning of direction-selective cells is affected by the depth of a moving surround. Physiology experiments have not yet been performed in which the relative stereo depths of moving center and surround stimuli are varied.

Method

Participants. A total of 21 observers were run in the experiment. These observers did not take part in any of the other experiments.

Stimuli and procedure. Four stereo belt depths were used (−0.2°, −0.07°, 0.07°, and 0.2° visual angle of disparity). There were 20 trials presented for each belt depth, giving rise to a total of 80 randomized trials in the experiment. The belt stereo was rendered in red and green dots, and the sphere (and fixation point) was rendered in yellow dots visible through both filters of the red-green glasses worn by observers. Observers judged the perceived direction of motion of the front surface of the sphere.

Following the main experiment, observers were run through the default experiment to determine their bias, as before (see Experiment 2, *Method*). Of the 21 observers run, 18 were classified as nonbiased and 3 as biased.

Results

Varying the belt disparity did not compromise the main effect. The front surface of the sphere almost always appeared to move opposite to the belt for nonbiased observers; there was no tendency to see the front surface of the sphere moving in the same direction as the belt when the belt appeared clearly to be entirely in front of the sphere (Figure 7).

A 1 Between-Factor (observer type) × 1 Within-Factor (belt depth) ANOVA revealed a main effect of observer type, $F(1, 23) = 80.3, p < .001$ (mean percent opposite response for nonbiased observers, 94%, was greater than mean percent opposite response for biased observers, 50%). There was no main effect of belt depth nor any interaction between observer type and belt depth. A two-tailed t test demonstrated that the mean percent opposite response for nonbiased observers was significantly greater than 50%, $t(17) = 43.8, p < .001$.

Discussion

The results of this experiment seem to preclude the mechanical interpretation of the main effect—there was no reduction of percent opposite responses when the belt appeared in front of the sphere. They point instead to a lower level explanation not dependent on specific knowledge of the mechanical interaction of 3-D objects.

This experiment demonstrates that a single moving plane of dots at a variety of depths can induce a front-surface-opposite-to-belt interpretation in an ambiguous sphere. Interestingly, Nawrot and Blake (1993a) showed that two planes of dots moving in opposite directions and positioned at near and far depths induce a similar perceived depth and motion configuration in an ambiguous sphere. For example,

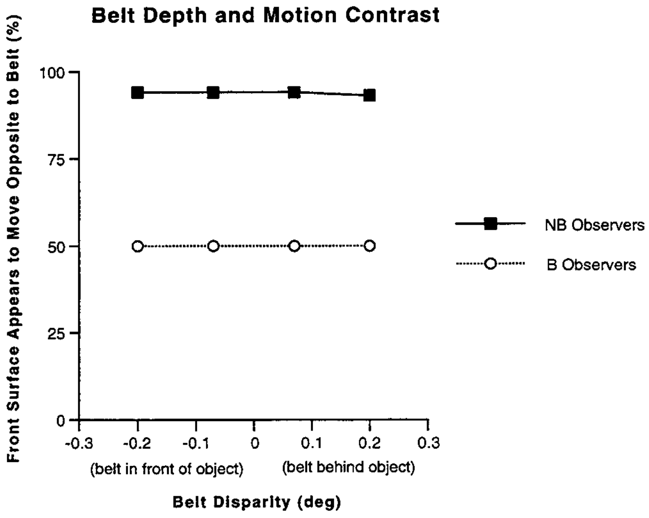


Figure 7. Belt depth and motion contrast—Experiment 6 results. Mean percentage opposite responses are plotted for non-biased (NB) and biased (B) observers as the depth of the belt relative to the sphere is varied. Error bars indicate +1 *SE* over observers.

near/right and far/left moving belts cause the front surface of an ambiguous sphere to appear to move right. Although this effect is also consistent with a mechanical interpretation (the sphere rolling between two belts), Nawrot and Blake, instead, suggested that it represents a priming effect due to the sharing of common neural substrates by dynamic stereopsis and kinetic depth (see General Discussion).

Experiment 7: Speed Depth Cue Versus Belt

Another possible explanation for the main effect with the belt is that the center–surround mechanism causes the opposite-to-belt-direction sphere surface to seemingly move faster. With the application of a heuristic that disambiguates the direction of motion by assuming that the fastest apparent absolute speed is closest, the effect is explained (see General Discussion). We wanted to directly test this hypothesis by attempting to bias the apparent direction of rotation using a sphere stimulus containing front and back surfaces rotating with different angular velocities. If the apparent speed hypothesis is correct, the faster moving surface should be seen as belonging to the front surface of the sphere.

As long as the rates of rotation of front and back surfaces do not differ greatly, the stimulus appears as a rigid unitary sphere despite the fact that individual dots appear at new x-axis locations as they pass from the front to the back of the sphere and then travel at different angular velocities. Hypothetically, a rotating sphere with its front surface moving faster than its back surface could appear as a nonrigid stimulus in which a patterned dot surface slides over an egg-shaped surface with its long axis perpendicular to the viewer and with the more pointed end nearer the viewer. No viewer reported this percept. Only when the front half was rotating more than three times as fast as the rear surface did the stimulus begin to appear nonunitary to a naive observer.

Many studies have shown that velocity gradients give rise to the perception of 3-D structure-from-motion. Braunstein and Andersen (1984), for example, showed that velocity gradients (in the horizontal and vertical dimensions) are responsible for perceived shape and depth in simulated rotating spheres. In a series of demonstrations with rotating coaxial cylinders, Ramachandran, Cobb, and Rogers-Ramachandran (1988) showed, for example, that changing the relative speed of two same-diameter cylinders could change the perceived speeds and diameters of the cylinders such that the faster rotating cylinder appeared to have greater depth (i.e., a larger diameter) and both cylinders appeared to rotate at the same speed. The authors argued that these demonstrations provide evidence that the visual system uses the heuristic of speed = depth to compute structure-from-motion. In the present experiment, we were more interested in the effects of dot speed on their front/back depth assignment rather than on changes in surface depth or sphere diameter. In displays such as ours, which present a single sphere, changing the speed of rotation does not change the perceived diameter of the sphere given its clearly delineated edges.

The speed cue was added to the sphere and was presented with and without the belt stimulus. Presenting the sphere alone allows a determination of the effectiveness of the speed cue. In the belt trials, the speed cue was placed in agreement or conflict with the motion contrast cue (i.e., the front-surface-opposite-to-belt interpretation), which allowed a determination of the nature of the relative strengths of these two cues for disambiguating depth.

Method

Participants. A total of 24 observers were run in the experiment. These observers did not take part in any of the other experiments.

Stimuli and procedure. We constructed a sphere with front and back halves rotating at different speeds. In the experiment, there were three levels of front/back relative speeds (specified as the back/front surface speed ratio): 1 (no-speed cue), 2.5, and 4 (strongest speed cue). In the no-speed cue condition, both halves of the sphere rotated at the default angular velocity (150 deg/s). In the intermediate- and strong-speed-cue conditions, the front half of the sphere rotated at 150 deg/s, and the back half rotated at 300 and 600 deg/s, respectively. Observers judged the perceived direction of the front surface of the sphere. The no-belt trials consisted of 60 total trials—20 trials each for the three levels of the speed cue. The belt trials consisted of a total of 120 trials—40 trials for each level of the speed cue. In addition, for Levels 2 and 3 of the speed cue (in the belt trials), 20 of the 40 trials were cue-agreement trials, and the remaining 20 were cue-conflict trials. Thus, the experiment consisted of a total of 180 randomized trials.

There were 17 nonbiased and 7 biased observers. Observers were divided into these two groups on the basis of response bias in the no-speed-cue belt trials. These trials are equivalent to those in the default experiment (see Experiment 2, *Method*), with the difference that they are here included in the main experiment.

Results

The relative speed of the two surfaces of the sphere showed little tendency to bias observers' perception of the direction of rotation (Figure 8; top panel). A 1 Between-Factor (observer type) × 1 Within-Factor (speed-cue strength) ANOVA revealed a main effect of observer type, $F(1, 22) = 4.28, p < .051$, no main effect of speed-cue strength, and no interaction. Two-tailed t tests demonstrated that only the means for the nonbiased observers were significantly greater than 50%: weaker speed-cue condition, $t(16) = 2.25, p < .040$; stronger speed-cue condition, $t(16) = 3.94, p < .002$.

Next, we investigated the interaction between the effects of belt motion and the effects of the speed cue on interpreting structure-from-motion (Figure 8; bottom panel). To make the between-cell variances more equivalent (some cells had a lower variance because of ceiling effects), we computed difference scores—that is, the difference between the cue-agreement and cue-conflict scores for each cue strength level and each observer type. A 1 Between-Factor (observer type) × 1 Within-Factor (speed-cue strength) ANOVA produced main effects of observer type, $F(1, 22) = 4.0, p < .055$, and cue strength, $F(1, 22) = 14.0, p < .002$, as well as a two-way interaction between observer type and cue strength, $F(1, 22) = 4.4, p < .049$. The interaction effect indicates that, as the speed ratio is increased, there is a

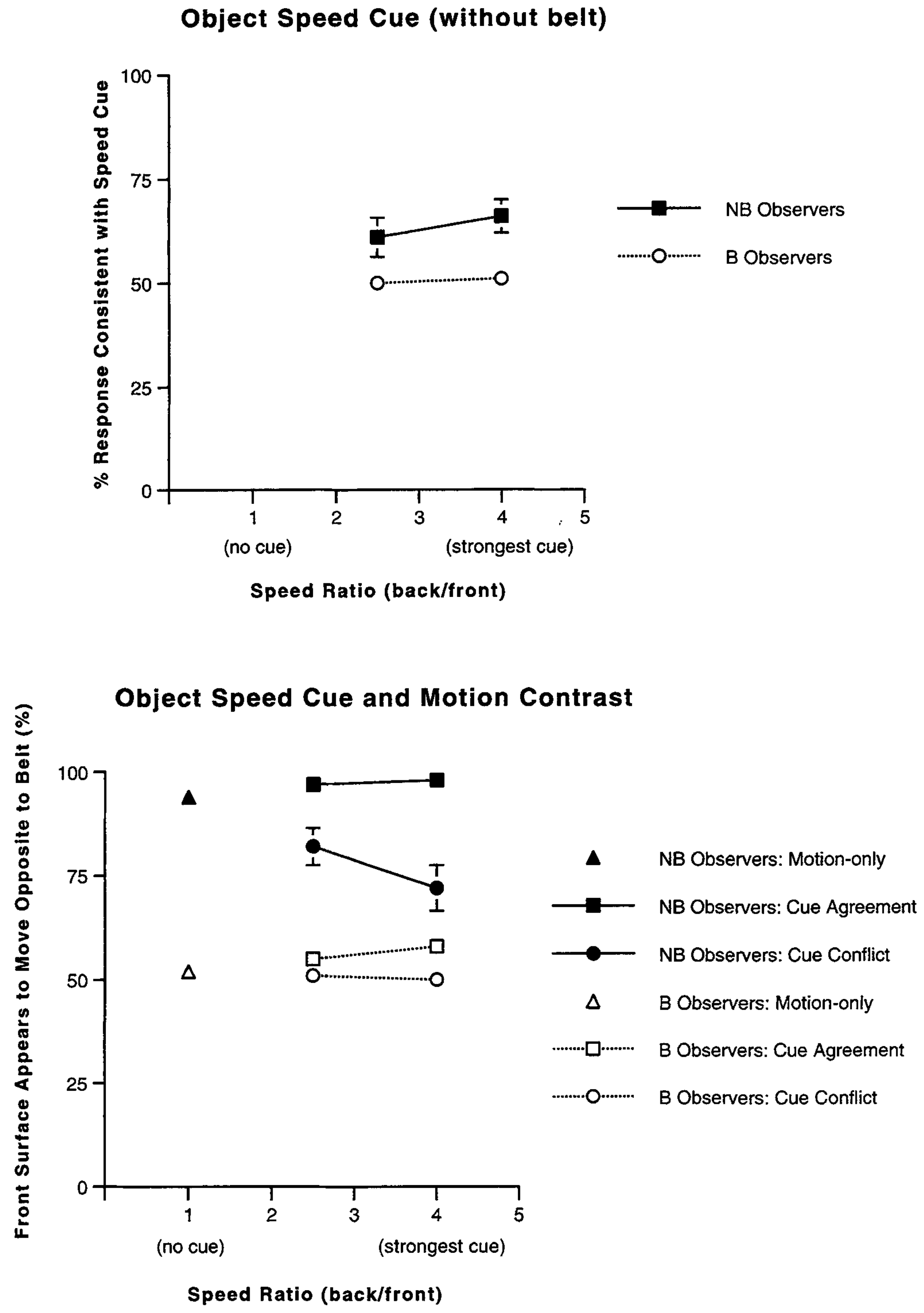


Figure 8. Object speed cue (the front/back speed ratio)—Experiment 7 results. In the top panel of the figure (no-belt conditions), the percentage response consistent with the speed cue is plotted for two strengths of the speed cue for nonbiased (NB) and biased (B) observers. In the bottom panel of the figure (belt-conditions), the percentage opposite response is plotted for two strengths of the speed cue. Cue conflict and cue agreement conditions were obtained when the speed cue was placed in conflict or agreement with the belt effect; results from nonbiased and biased observers are plotted separately. Error bars indicate +1 *SE* over observers.

greater increase in difference scores in nonbiased than in biased observers.

Discussion

Overall, nonbiased observers showed a small effect and biased observers showed no effect of the speed cue on disambiguating sphere rotation (i.e., faster moving dots were somewhat more often assigned to the front surface). When pitted against the motion-contrast cue, the motion-contrast cue dominates. For example, in the highest-speed-ratio condition, nonbiased observers' responses were consistent with the motion-contrast cue 72% of the time and the speed-ratio cue 28% of the time. The effect of the speed cue alone is similar to its effect in the belt conditions, in terms of its ability to increase or decrease the percent opposite response from the no-speed-cue baseline. It was not possible to examine the increase in percent opposite response in the nonbiased observers' cue-agreement condition because of ceiling effects.

Given that nonbiased observers were not strongly affected (either in the no-belt or belt conditions) by the speed cue and that the speed ratios used were much greater than what the surround effect might be expected to induce, it seems unlikely that the main effect can be accounted for by changes in apparent speed.

General Discussion

The relative velocity of stimulus features can be used to calculate aspects of the 3-D structure of a moving stimulus. However, relative velocities are not straightforwardly represented in the magnitude of response of direction-selective neurons in the primate visual system. At several stages of cortical motion processing, there are strong nonclassical opponent surrounds that modulate the response of neurons (Allman, Miezin, & McGuinness, 1985a, 1985b, 1990). Those results implicate 2-D center-surround mechanisms in 3-D depth assignment. The experiments reported here suggest that center–surround processing does in fact influence 3-D depth assignment. We argue that these effects work primarily by manipulating the prominence of various parts of the stimulus.

We discovered several robust effects of surround motion on the perceived structure of rotating stimuli. The primary finding was that the direction of movement of a belt (a field of random dots) disambiguated the direction of rotation of an ambiguous rotating random dot object for most observers—the direction of belt motion caused opposite-moving dots in the object to be assigned to its front (near) surface, thereby disambiguating its direction of rotation (Experiments 1 and 2). This effect was found for a variety of structure-from-motion stimuli having two sets of oppositely moving dots (Experiment 1). Most observers also tended to see an ambiguous sphere positioned in front of the belt (Experiment 2).

When the belt stimulus was presented in conjunction with an opaque rotating sphere stimulus (a stimulus with an unambiguous direction of movement), again it influenced the depth assignment of the moving dots in the sphere (Experiment 3). When the belt moved in the same direction as the sphere dots, there was a significant increase in the perception of the sphere stimulus as either flat or concave. Thus, the belt pushed the sphere dots to the back even when there was no complementary set of dots to come forward. A same-direction belt also caused the sphere to be seen more often behind the belt.

Basic Phenomenology of Center–Surround Interactions

A number of studies find that most primate MT cells are (a) inhibited by a surround moving in the same direction as the preferred center-stimulus and (b) either facilitated or unaffected by an opposite-direction surround (Allman et al., 1985a, 1985b; Tanaka et al., 1986). The strength of same-direction inhibition is uniformly distributed among neurons (Tanaka et al., 1986; Raiguel et al., 1995). The tuning properties of surround inhibition suggest that, in the majority of cells, inhibitory effects of a surround stimulus decrease steadily as the direction of the surround is shifted away from the direction of optimal center movement. Typically, inhibitory effects are significantly reduced or absent with a 90° deviation (Allman et al., 1985a, 1985b; Tanaka et al., 1986). However, the shape of the tuning curve varies from cell to cell. Allman et al. (1985a, 1985b), for example, found that nearly one third of the cells were suppressed by a surround moving in any direction, whereas one tenth were facilitated by an orthogonally moving surround. There appears to be a columnar and laminar organization of surround types in area MT: Columnar patches of cortex with a high percentage of antagonistic surround cells alternate with patches of cells without antagonistic surrounds (Born & Tootell, 1992; Raiguel et al., 1995); a significant population of neurons without antagonistic surrounds are found in the deep layers (Born & Tootell, 1992; Raiguel et al., 1995; Tanaka et al., 1986). In addition, surround inhibition is often not uniform and symmetric but, instead, is confined to restricted regions of the surround (Xiao, Raiguel, Marcar, Koenderink, & Orban, 1995). Given the large number of possible stimulus conditions, interactions between center–direction, center–speed, surround–direction, and surround–speed have not been systematically examined.

A Simple Computation of Structure-From-Motion

One simple computation for extracting structure from motion assumes that speed is approximately proportional to depth with a zero crossover point. This works well in several different contexts—for example, when an observer moves sideways across a scene or focuses on a rotating object. While moving sideways and fixating a point between the eye and infinity, the nearest and farthest objects have the fastest speeds and move in opposite directions. Distance is proportional to speed for objects nearer the eye and inversely proportional for objects beyond the fixation point (Gibson, 1966). This basic computation also accurately specifies the depth of different parts of an opaque or transparent object

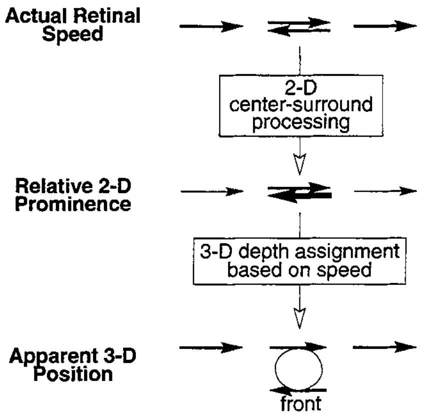


Figure 9. Canonical depth assignment from motion cues. Actual retinal speed is shown at the top. The middle shows the result of passage though the center-surround mechanism—the opposite-direction sphere surface has the maximum "prominence," and the belt has the lowest prominence through interactions with itself. The same-direction sphere surface is also reduced in prominence but not as much as the belt because of an increase in dot density (same-direction sphere dots and belt dots). Simple depth assignment based on speed (with the greatest apparent absolute value of speed assigned to the front) is shown below, explaining the main result illustrated in Figure 1.

that rotates about an axis, as in the case of our sphere stimulus.

This computation sometimes fails (e.g., when an observer moves forward, when an object or the observer's head rotates in the frontoparallel plane, or when objects move substantially away from or toward the observer). In these cases, speed increases with angular distance from the point corresponding to the direction of heading, the fixation point, or the center of object motion, and radial, circular, and spiral flow fields are generated. We return to these issues after discussing the likely origin of the main effect.

Explanation for the Main Effect

The main effect can be explained by the interplay of three factors: (a) a local–global center–surround interaction affecting prominence of different parts of the moving stimulus; (b) a tendency for the most prominent large speed to be located closest to the viewer; and (c) an assignment of depth proportional to speed. Actual retinal speed for a belt and a sphere is shown at the top of Figure 9. Focus first on the speed of the belt and the front and back surfaces of the sphere. Applying a direction-specific center–surround mechanism, the opposite-direction sphere surface acquires maximum prominence because it moves opposite to a large surround; the same-direction sphere surface is reduced in prominence by interactions with the belt; and the prominence of local pieces of the belt is reduced by interactions with other parts of the belt. Simple depth assignment can then be based on speed (with a zero crossover point). The most prominent large speed is assigned to the front as shown at the bottom of Figure 9, which explains the main result illustrated diagrammatically in Figure 1.

Figure 10 shows how the less preferred interpretation is obtained. If the most prominent and fastest left speed is instead assumed to be the farthest from the viewer, overriding our presumed heuristic, then a less preferred interpretation—yet one still dependent on depth being proportional to speed—would place the sphere entirely behind the belt. This interpretation was most often found in biased observers when the opposite-to-belt direction in the sphere differed from their bias direction (Experiment 2). In this case, bias direction proves to be stronger (more prominent) than the opposite-to-belt direction of the sphere and is consequently assigned to its front surface. The sphere is then seen behind the belt because of the preference for only one velocity at each point in depth.

Notice that both the preferred and less preferred interpretations are consistent with a mechanical interpretation of the sphere rolling on the belt. Knowledge about how mechanical objects tend to interact with each other in 3-D, however, does not seem to be a prime reason for the interpretations because manipulating the depth of the belt had no effect (Experiment 6); no reduction in the main front-surface-opposite-to-belt effect occurred, even when the belt was moved toward the viewer by stereo cues. In this condition, the sphere appears to be grinding against the belt nonmechanically instead of rolling on it. In addition, the main effect was obtained even when the sphere and belt occupied different parts of the visual field, that is, when they did not overlap in space (Experiment 5). In the absence of additional depth cues, the nonmechanical interpretations (Figure 10; the two on the left, which are labeled "rare") are rarely observed, probably because there is no systematic mapping of speed to depth (on the assumption that the speed-equals-depth heuristic allows only one velocity at each point in depth).

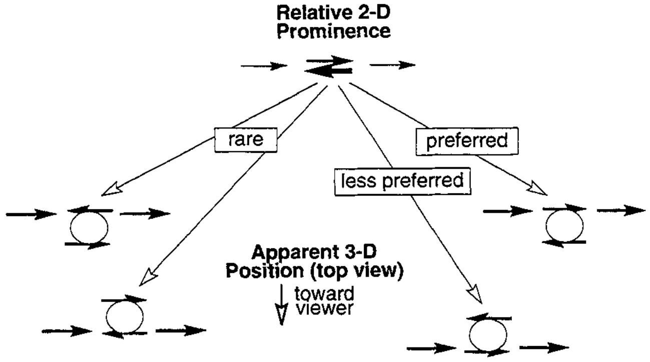


Figure 10. Alternative possibilities for depth assignment from motion cues. The preferred interpretation assigns the most prominent surface to the front while keeping depth proportional to speed (with a zero-crossover point). A less preferred interpretation overrides the most-prominent-surface-equals-front interpretation but retains depth proportional to speed. Two other "nonmechanical" interpretations do not respect depth proportional to speed (because there are opposite velocities present in the belt depth plane).

A Possible Neurophysiological Mechanism for Prominence

The prominence of a part of a stimulus may be measured within a particular cortical visual area by the vigor of the neuronal population response. The 1-D discharge rate of a particular direction-selective neuron in primate area MT conflates the levels of many different stimulus parameters—for example, speed, direction, contrast, depth, and size. Thus, a neuron tuned to a particular speed responds well to a stimulus at that speed, but its response is also affected by changes in several other parameters. For example, a reduction in the response of an MT neuron might indicate either that the speed was changed to a nonoptimal value or that the contrast of the stimulus was reduced. However, if one considers a population of neurons tuned to different speeds, it may be possible to find a peak or average response in that population that indicates the actual speed. For the sake of illustration, imagine that different speed neurons were arrayed systematically across the cortex (cf. orientation columns). As the contrast of a stimulus is reduced, the magnitude of the peak response is also reduced, but its location in our hypothetical speed map remains unchanged. The reduced response of the population can then be thought of in terms of reduced prominence. This kind of population coding of velocity, in fact, has been explicitly used in several recent models of motion analysis in MT (e.g., M. E. Sereno, 1993).

A brightness-depth cue applied to an ambiguous rotating object, such as a sphere (M. E. Sereno & M. I. Sereno, 1991) or Necker cube-like wire frame figure (Dosher et al., 1986), can disambiguate direction of rotation (observers tend to see the brighter surface in front). This cue may work by increasing the prominence of the brighter part of a stimulus (or, conversely, decreasing the dimmer part) in the sense discussed above—that is, by augmenting (or diminishing) the overall population response without changing the location of the peak response in the map of a particular parameter. For this reason, some of the effects of a brightness-depth cue may be indistinguishable from effects of the surround at several levels in the direction-selective magnocellular pathway. Thus, the firing rate of a set of velocity-selective neurons may be reduced as the brightness of a stimulus is decreased but also by addition of a same-direction surround. This conforms well to the notion of form-cue invariance discussed by Albright (1992)—in this case, prominence is the invariant cue.

Salience Controls of Perception and Prominence

We have hypothesized that prominence is associated with signal strength. Specifically, we propose that the belt cue induces, in a bottom-up manner, a more robust signal for one direction of motion compared with another in the sphere stimulus; this, in turn, strongly influences the perception of depth order from motion cues. Direct evidence for the influence of signal strength in controlling motion perception was presented in a study by Salzman and Newsome (1994) in which they demonstrated that electrical stimulation of a cluster of direction-selective neurons in area MT could shift a monkey's on-line judgment of a moving stimulus's direction of motion toward the preferred direction of the stimulated neurons. In fact, there may be a variety of ways to modulate the salience or prominence of aspects of a stimulus in a manner similar to the influence of the belt stimulus—by adjusting the relative strengths of signals.

Attention to aspects of a stimulus, for instance, may modulate activity of motion-sensitive neurons. In a functional magnetic resonance imaging study using a visual stimulus containing both stationary and moving dots, O'Craven, Rosen, Kwong, Treisman, and Savoy (1997) found that attention to moving versus stationary dots resulted in greater activation in the MT–MST motion area, indicating that voluntary attention to aspects of a stimulus can modulate neural activity in human area MT–MST. A number of other studies have also described striking effects of attention on the perception of motion (Cavanagh, 1992; Hikosaka, Miyauchi, & Shimojo, 1993a, 1993b; Lu & Sperling, 1995).

We interpret these studies to suggest that top-down attentional processes can affect low-level visual processes, such as motion perception, by modulating the salience of aspects of stimuli in a manner similar to the bottom-up processes we described—by boosting the activity of neurons selective for attended stimulus attributes, inhibiting activity of neurons selective for unattended stimulus attributes, or both. Thus, perception may be controlled by stimulus-driven bottom-up processes (as demonstrated in this article) but also by top-down attentional processes, both of which ultimately modulate signal strength to affect the salience or prominence of aspects of stimuli.

Psychophysical Evidence for Prominence Modulated by Surround Mechanisms

The skew experiment (Experiment 4) demonstrated that the motion-contrast effect is direction selective. As the axis of rotation of the transparent-sphere stimulus was tilted from the vertical to a near horizontal position, the effect faded. The belt-occlusion experiment (Experiment 5) demonstrated that the motion contrast effect could be induced by unambiguous motion located as far out as 10° in the periphery. Both of these results are explained by center–surround mechanisms modulating center response strength without changing center response specificity.

There is additional psychophysical evidence in support of this idea. Nawrot and Sekuler (1990) presented cinematograms consisting of alternating strips of dots that moved either unambiguously in one direction or in random directions. They found that when the strips were wider than ~1° of visual angle, the unambiguous strips induced a perception of opposite-direction motion in the noise strips. Murakami and Shimojo (1996) reported a similar induced motion effect. Presenting cinematograms initially configured with center dots moving in random directions and surround dots moving in a single direction (either up or down), they measured the percentage of direction signal needed in the center stimulus to offset the effect of the surround. As stimulus eccentricity increased, the largest induced contrast effect was obtained for larger stimulus diameters, suggesting that a center–surround motion mechanism that scales with eccentricity (such as that found in MT) underlies the perceptual effects.

Are There Surround-Induced Changes in Speed?

An alternate explanation for the main effect is that the surround increases the apparent speed of the opposite-direction sphere surface and reduces the apparent speed of the same-direction sphere surface. Depth assignment based on speed then follows as before, except now the apparently fastest opposite-direction speed is assigned to front, and the apparently reduced same-direction speed is assigned to back.

This explanation, however, was not supported by Experiment 7, where there was little tendency for observers to see the faster of two surfaces of an apparently rigid sphere as being closer. In addition, the surround effect still predominantly generated a front-surface-opposite-to-belt interpretation, which held true even when the retinal speed of the faster back-appearing surface was considerably greater than the speed of the surface brought to the front by the belt.

Rotating and Dilating Flow Fields

The simple mechanism of speed-proportional-to-depth fails in cases when observer or object movement produces rotating and/or dilating flow fields. One possibility is that the activation of neurons sensitive to rotation, dilation, or both somehow signals the system not to translate speed into depth. However, it is demonstrably easy to extract structure-from-motion for an object rotating about an intrinsic axis as it moves toward the observer. The explanation may therefore be that the system detecting translation in the visual field is simply insensitive to wide-field rotation and dilation. There is, in fact, evidence that neurons in primate visual area MSTd sensitive to wide-field translations ignore rotation and dilation (just as rotation- and dilation-sensitive neurons ignore wide-field translations; Duffy & Wurtz, 1991a, 1991b; Saito et al., 1986; M. I. Sereno & M. E. Sereno, 1991; Tanaka, Fukada, & Saito, 1989; Zhang, Sereno, & Sereno, 1993). It is also possible that visual field dilation and contraction simply update estimates of depth independently calculated by mechanisms sensitive only to relative translational speed.

Neural Mechanisms of Depth Order and Depth Assignment

In the model introduced above, depth order or polarity is represented implicitly by the firing of cells in MT and other directionally selective areas with polarity of depth determined by signal strength. An ambiguous sphere stimulus will cause two sets of direction-selective neurons to fire; the more strongly activated set is then taken to indicate the direction of the front surface, and the less robust, opposite-direction set represents the far depth surface. This difference in neural activity may be generated in a number of ways—for example, by suppression of the response to the surface moving in the direction of the belt, by the greater brightness of one surface, by attending to one surface, or simply by the perception that one surface lies in front in the absence of an external biasing cue.

In a similar manner, a more fine-grained representation of depth (beyond just depth order) may be implicitly represented in area MT given the speed-equals-depth heuristic with the proviso that any given speed has a near/far ambiguity such that fast speeds represent nearest or farthest depths and slow speeds represent intermediate depths. By combining this signal with prominence-based depth ordering, a structure can be unambiguously recovered from motion. It is possible that this information is interpreted and made explicit in yet another part of the brain because a fast speed sometimes means near and sometimes far. Alternatively, some researchers have suggested that MT cells with one or more restricted regions of inhibition near the center receptive field may explicitly represent changes or gradients of speed (Buracas & Albright, 1994, 1996; Xiao et al., 1995). In any case, it is clear that such information—both the relative strength of the signal as well as the direction and speed (or, perhaps, velocity difference) of local patches of the stimulus—is represented in area MT and sent further upstream.

A second model of depth order suggests that perceived depth in moving displays is tightly linked to the representation of stereo depth (Bradley et al., 1998; Nawrot & Blake, 1991a). For example, an ambiguous object perceived as rotating with its front surface moving to the right and its back surface moving to the left could be represented by near/right cells (cells tuned to near disparity and right motion) and far/left cells, even though the stimulus itself contains zero disparity. The idea is that activity is drawn from neurons in the zero-disparity channel (neurons initially highly activated by a binocularly viewed zero-disparity stimulus) to neurons representing nonzero depths. Nawrot and Blake have presented a variety of psychophysical examples in support of this proposal (Nawrot & Blake, 1989, 1991a, 1991b, 1993a, & 1993b).

Recent corroborating neurophysiological evidence has been provided by Andersen and colleagues, who have shown that approximately two thirds of the cells they studied in MT in fact preferred a particular surface order of a rotating stereoscopically defined cylinder. For example, a cell tuned to rightward movement also preferred stereoscopically defined near surfaces and, hence, responded well to a stereo cylinder whose front surface moved right. Half of these cells also showed significant perceptual effects with greater responses when the perceived surface order of an ambiguous zero-disparity cylinder (defined by the animal's response) matched the neuron's preferred surface order (defined by previous responses to a stereoscopic cylinder).

These models (Bradley et al., 1998; Nawrot & Blake, 1991b) require same-depth/cross-direction inhibition and either cross-depth/same-direction inhibition or cross-depth/cross-direction excitation. By including unit-adaptation as a feature of their model, Nawrot and Blake have successfully simulated (a) fluctuation in perception when viewing ambiguous structure-from-motion stimuli, (b) disambiguation of these stimuli with stereoscopic information, and (c) subsequent bias of perception following stereoscopic adaptation.

Can this type of model account for the main effects presented in this article? If it can be established that there are more near cells than far cells, this seems a reasonable solution. Physiological studies do in fact suggest there are perhaps twice as many near cells in area MT (Bradley et al., 1998; Maunsell & Van Essen, 1983). Given a stimulus such as an ambiguous sphere in which right-moving dots are more salient because, for example, they are brighter or a left-moving belt is present, such a stimulus will cause more overall activation in near/right cells than in far/right cells because near cells are more numerous. These near/right cells can then inhibit near/left and far/right cells, which, in turn, will disinhibit far/left cells. The end result will be enhanced activity in near/right cells followed by far/left cells. This model also accounts for the preference observers show for the two perceptual interpretations of the sphere-belt stimulus shown to the right of Figure 10. In both of these cases, only one direction of motion is represented at each depth. This model selects for these interpretations because of the cross-direction inhibition within each disparity channel.

Although the stereo-depth model of depth order extraction from structure-from-motion stimuli accounts for a number of phenomena, several open questions remain. The model has difficulty in accounting for the results of the opaque-sphere experiment in which a concave percept is sometimes generated despite the fact that there is no opposite surface to bring to the front. Second, there is a more general question of how to represent the detailed depth structure of an object. Intermediate levels of depth can of course be represented by intermediate levels of disparity. However, complex 3-D shapes can also be recovered from speed gradients in zero-disparity or monocular stimuli. As currently implemented, the stereo-depth-order models do not include speed. To include speed would require dealing with the complex mapping between speed, disparity, and depth. Determining depth from speed results in a near/far ambiguity not found with disparity. For the front or back half of a given rotating stereo object, however, speed is unambiguously related to depth, whereas the mapping between disparity and depth varies with the observer's vergence. Future work will be required to determine how these different cues are integrated to produce a unified percept.

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