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The Influence of Terminators on Motion Integration Across Space

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Individual motion measurements are inherently ambiguous since the component of motion parallel to a homogeneous translating edge cannot be measured. Numerous models have proposed that the visual system solves this ambiguity through the integration of motion measurements across disparate contours. To examine this proposal, subjects observed a translating diamond through four stationary apertures. Since the diamond's motion could not be determined from any single contour, motion integration across contours was required to determine the diamond's direction of motion. We demonstrate that observers have difficulty accurately integrating motion information across space. Performance improved when the diamond stimulus was presented at 7° eccentricity, through jagged apertures, or at low constrast. Taken together, these results imply that integration across space is more likely when the motion of contour terminators is less salient or reliable.

Aperture problem   Motion integration   Intersection of constraints   Terminators

INTRODUCTION

Both neurophysiological and psychophysical data suggest that a visual scene is analyzed at early stages of the visual system by processing local image features through parallel streams. Since humans effortlessly perform tasks requiring figure/ground segregation, extraction of structure from motion, and so forth, these local responses must be combined and integrated at some level of processing.

The integration of moving features into a coherent percept is an important and necessary step for processing images. Several studies of this issue have been conducted, either by using moving dot patterns (Lappin & Bell, 1976; Johansson, 1977; Marshak & Sekuler, 1979; Regan, 1986; Watamaniuk, Sekuler & Williams, 1989) or moving contours (Fennema & Thompson, 1979; Horn & Schunck, 1981; Adelson & Movshon, 1982; Hildreth, 1984; Nakayama & Silverman, 1988a,b; Shimojo, Silverman & Nakayama, 1989; Shiffrar & Pavel, 1992). The latter approach has received much attention because individual readings of contour velocity are inherently ambiguous.

One striking example of this measurement ambiguity, the so-called "aperture problem" (Marr, 1982), refers to the impossibility of accurately determining the direction of a straight contour (or grating) moving behind a circular aperture. The direction of the measured velocity is always normal to the contour's orientation whatever the physical velocity, since there is no directional energy available *along* the contour itself. If a rectangular aperture is used, as in the barber pole illusion, then the perceived direction of a drifting grating is colinear to the longer aperture axis, whatever the grating's orientation (Wallach, 1935). Wallach (1976) suggested that the relatively greater number of terminators moving along the longer aperture side determined the perceived direction of the grating. Hildreth (1984) proposed a slightly different explanation of the barber pole illusion in which a smoothness constraint is used to minimize the differences between locally ambiguous readings along the line and the motion of the line's terminators. The unambiguous motion of terminators would propagate toward the ambiguous center part of the contour (Hildreth & Koch, 1987; Poggio, Torre & Koch, 1989). Shimojo *et al.* (1989) refined this hypothesis by demonstrating that motion of *extrinsic* terminators, produced by accidental occlusion, do not contribute to the perceived direction of a moving grating. On the other hand, *intrinsic* terminators corresponding to real line endings would determine the perceived direction of the grating.

Shimojo *et al.* (1989) used one-dimensional drifting gratings. It has been proposed (Bonnet, 1981; Burt & Sperling, 1981; Adelson & Movshon, 1982; Watson & Ahumada, 1985) that with two-dimensional stimuli, the aperture problem can be solved by combining different component motions. Two or more local readings of velocity would be combined in order to recover the "true" velocity of moving objects. An experimental test of this hypothesis was presented by Adelson and Movshon (1982). Using superimposed moving gratings of different orientatons viewed through a circular aperture, these authors observed a coherence effect in which

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component motions fused into a global percept of a drifting plaid pattern. To account for this coherence effect, they proposed a model of motion integration involving two serial stages. According to this model, component motion is first locally analyzed by oriented detectors selective to component directions. Responses to these components are then combined at a second stage according to an intersection of constraint lines (IOC). Note that this model does not directly address the potential influence of terminator motion on perceived coherence. Psychophysical data (Lorenceau, 1987; Welch, 1989; Ferrera & Wilson, 1990) agree fairly well with the predictions of the IOC model when component motions share several characteristics. Departures from the model are observed when dissimilar plaid components are used (Lorenceau, 1987; Ferrera & Wilson, 1990; Stone, Watson & Mulligan, 1990), indicating that a refined version of the model is needed to fully account for human perceptions of coherent motion (Stone *et al.*, 1990).

One potential problem with this overlapping grating approach is that plaid patterns contain unambiguously moving local contrasts at grating intersections that can potentially influence both coherence and perceived direction (Lorenceau & Gorea, 1989; Stoner, Albright & Ramachandran, 1990). Moreover, plaid components are superimposed and hence analyzed at a single location in space. To recover object motion, the visual system must also integrate information *across* space. Thus, this type of stimulus might not be ideally suited to study all types of motion integration.

Previous research has shown that observers have difficulty integrating disparate motion measurements for both translating contours (Nakayama & Silverman, 1988b) and rotating objects (Shiffrar & Pavel, 1992). This difficulty is particularly interesting for a number of reasons. First, as previously stated, it is commonly assumed that the visual system overcomes the aperture problem precisely by combining ambiguous motion measurements from disparate regions. Secondly, while rigidity is often a very useful constraint in object interpretation (Ullman, 1979), observers seem unable to use prior knowledge of object rigidity or structure to guide their percepts of rotation (Shiffrar & Pavel, 1992). Finally, some experiments have shown that under certain conditions, observers can group motion information across disparate contours. Specifically, when stimuli are viewed through apertures containing occlusion cues, such as disparity information (Shimojo *et al.*, 1989) or T-junctions from outlining apertures (Lappin, Norman, Loken & Fukuda, 1990; Lorenceau & Shiffrar, 1990), then observers are more likely to combine motion information across apertures.

In the present paper, we examine the conditions under which human observers are able to accurately integrate motion information across disparate contours lacking occlusion cues. In particular, we investigate the role of intrinsic terminators in this integrative process. For that purpose, we used a moving diamond viewed through four invisible apertures that left the diamond's sides visible but masked its corners, as shown in Fig. 1. We found motion integration (i.e. perception of a globally coherent revolution) to be possible only under specific conditions, namely when the stimulus was viewed eccentrically or at low contrast. The results from additional experiments suggest that a reliance on the unambiguous motion of terminators may inhibit the integration of motion signals across disparate contours.

EXPERIMENT 1: MOTION INTEGRATION ACROSS SPACE

In this first experiment, we tested the ability of observers to identify the direction of a translating diamond viewed through stationary apertures. Different aperture orientations induced a sinusoidal translation of each visible contour along oblique, vertical, or horizontal axes. Depending on aperture orientation, terminator motion was (oblique apertures) or was not (vertical and horizontal apertures) compatible with an IOC solution. However, local velocity *within contours* was always compatible with a rigid motion.

Manipulating aperture visibility allowed us to examine the influence of terminator type on motion integration. When apertures are outlined, visible T-junctions indicate that terminators are extrinsic, or accidental. When apertures are invisible, terminators are intrinsic. As Shimojo *et al.* (1989) proposed, integration across apertures should be more likely with extrinsic than intrinsic terminators.

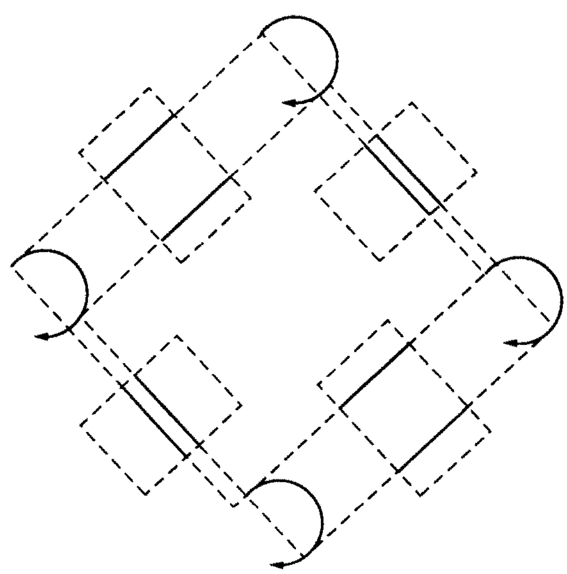

FIGURE 1. Two frames of the stimulus used in all experiments. Diamond's sides (heavy lines) are visible through four identical rectangular apertures (i.e. the visible length of diamond's sides is constant). Diamond's corners are invisible. Apertures (dashed lines) are similar to the background and thus invisible. In the outlined conditions of Experiment 1, apertures were delimited by a thin white line. A motion of translation along a circular path (i.e. a revolution) makes the determination of diamond's motion impossible from a single aperture and maintains constant contour orientations. The initial starting point of the revolution was chosen at random among eight possibilities (i.e. the initial velocity within an aperture was randomized).

Methods

Subjects. Five scientists from our laboratory volunteered to participate in this study. All were experienced psychophysical observers with normal or corrected to normal vision. While the two authors served as subjects, the remaining three subjects were unaware of the hypothesis under investigation.

Apparatus. Stimuli were displayed on a Sony RGB 19″ monitor, model number GDM-1950, with a 1023 × 1280 pixel resolution and 60 Hz refresh rate. The monitor was controlled by a Leanord Elan p.c. 386-AT. Specially designed graphics software (Lorenceau & Humbert, 1990) was used to drive an Adage PG 90/10 graphics card. Subjects used the p.c. keyboard to indicate their responses. Reaction times were also recorded. This apparatus was used in all experiments.

Stimuli. The stimulus, an outlined white diamond visible through four stationary apertures, is shown in Fig. 1. The width of the diamond's white outline subtended 1.02 min of visual angle when seen from a distance of 84 cm. The diamond had side lengths of 5.1 deg of visual angle and a luminance of 111 cd/m². Because apertures occluded the diamond's corners, only four straight 1.8° long segments were visible. Depending on the trial, the four apertures were either oblique, vertical, or horizontal relative to the observer, as shown in Fig. 2. Whatever the aperture orientation, the length of each visible contour remained constant. Aperture size was 1.8° × 1.8° (oblique), 2.6° × 1.3° (vertical), or 1.3° × 2.6° (horizontal). The separation between aperture centers was 3.4°. Apertures also differed by whether or not they were outlined. Non-outlined apertures had the same luminance and color as the background and were therefore "invisible". Outlined apertures had a white line of width 1.02° added to their circumference. A red fixation point, in the shape of a cross, was continuously visible in the center of the display. The background was gray with a luminance of 2.5 cd/m².

To maintain constant stimulus eccentricity and orientation, the diamond stimulus was designed to translate along a circular path (i.e. a revolution). On each trial, the direction of translation was either clockwise or counter-clockwise relative to the fixation point. The clockwise vs counter-clockwise discrimination could not be made from any single aperture. The diamond translated along 162° of the circular path in 300 msec. Path radius was 0.4°. The entire stimulus disappeared as soon as the diamond reached the end of its trajectory. To minimize training effects, the diamond had eight different trajectory starting positions, each separated by 45°. The direction of translation and the trajectory starting point were randomly chosen on each trial.

Procedure. Subjects sat with their eyes approx. 84 cm from the computer screen with unrestrained head position. Each trial began with the presentation of the translating diamond. Subjects were instructed to maintain fixation and to determine whether the diamond moved clockwise or counter-clockwise relative to the

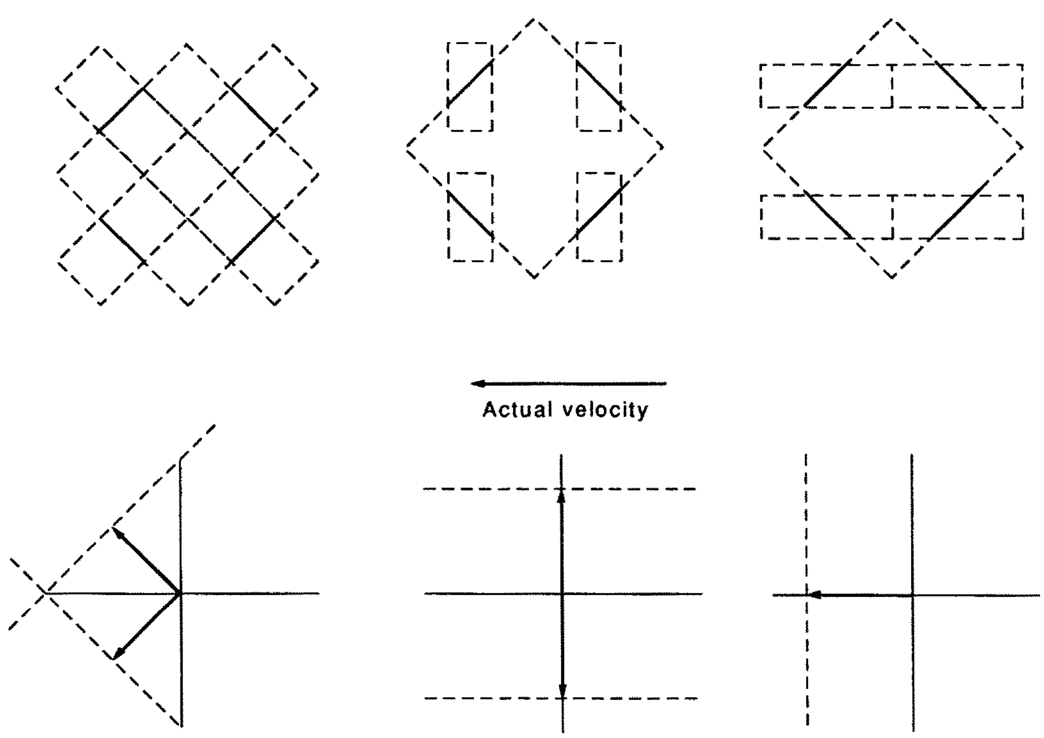

FIGURE 2. (a) The three aperture types of Experiment 1. Aperture boundaries (dashed lines) were either invisible or visible (outlined conditions). Diamond's side (solid lines) were visible. (b) Motion of terminators plotted in a velocity space for the different aperture orientation. A motion of translation is used for clarity. Note that a solution from an IOC computation exists for oblique apertures (i.e. the lines of constraint intersect at a single point), whereas no IOC can be computed from terminator motion when vertical apertures are used. For horizontal apertures, the motion of terminators is identical to the motion of the translating diamond.

fixation point. Subjects were asked to respond as rapidly as possible by pressing one of two buttons on a keyboard. The next translating diamond appeared automatically 800 msec after the button press. All subjects completed 10 practice trials with feedback before beginning the experimental trials. No feedback was given after the practice trials. Viewing was binocular. Subjects were told that the stimulus consisted of a rigid outlined diamond translating behind four windows. All subjects completed four experimental blocks containing 180 trials each (60 trials per aperture orientation). Two blocks contained outlined apertures and two contained invisible apertures. The different aperture orientations were randomly intermingled within each block.

Results

When asked to describe their perception of the four diamond contours through invisible apertures, observers reported a strong non-rigid percept of four jigging lines. This perceived non-rigidity suggests that motion integration across disconnected contours is difficult, whatever the orientation of apertures (i.e. whatever the direction of component motion). Accordingly, accuracy in the invisible aperture conditions is poor, as shown in Fig. 3(a).

However, when apertures were outlined, the translating diamond appeared more rigid. As a result, when the diamond was viewed through outlined apertures, observers were significantly more accurate in their direction discrimination performance [$F(1,4) = 46.83$, $P < 0.005$]. An analysis of the reaction times across the outlined and invisible aperture conditions clearly demonstrated that the performance difference was not the result of a speed–accuracy trade-off. Across aperture orientations, performance was somewhat better [$F(2,8) = 6.2$, $P < 0.05$] when the orientation of the invisible apertures delimited an IOC compatible motion (oblique apertures), and worse when no such IOC solution existed (vertical and horizontal apertures).

Discussion

Previous research has demonstrated a significant influence of terminator type on motion integration. More specifically, Shimojo *et al.* (1989) found increased grouping of motion information across contours when disparity information indicated that contour terminators were accidental, or extrinsic. These researchers also proposed that two-dimensional depth cues should suffice to promote cross-contour integration. The present findings strongly support their prediction since the presence of visible T-junctions in the outlined aperture condition resulted in large improvements in performance.

Since performance is consistently poor when the translating diamond was viewed through invisible apertures, the question arises as to why component motions cannot be combined across space into a rigid percept. To address this question, we reconsider the nature of the stimulus visible within each aperture. The ambiguity of a translating homogeneous contour viewed through an aperture ultimately arises from the lack of identifiable features along the contour's length. Since each point along the contour is identical to every other point, an infinite number of translations appear identical. A number of researchers have argued that the visual system

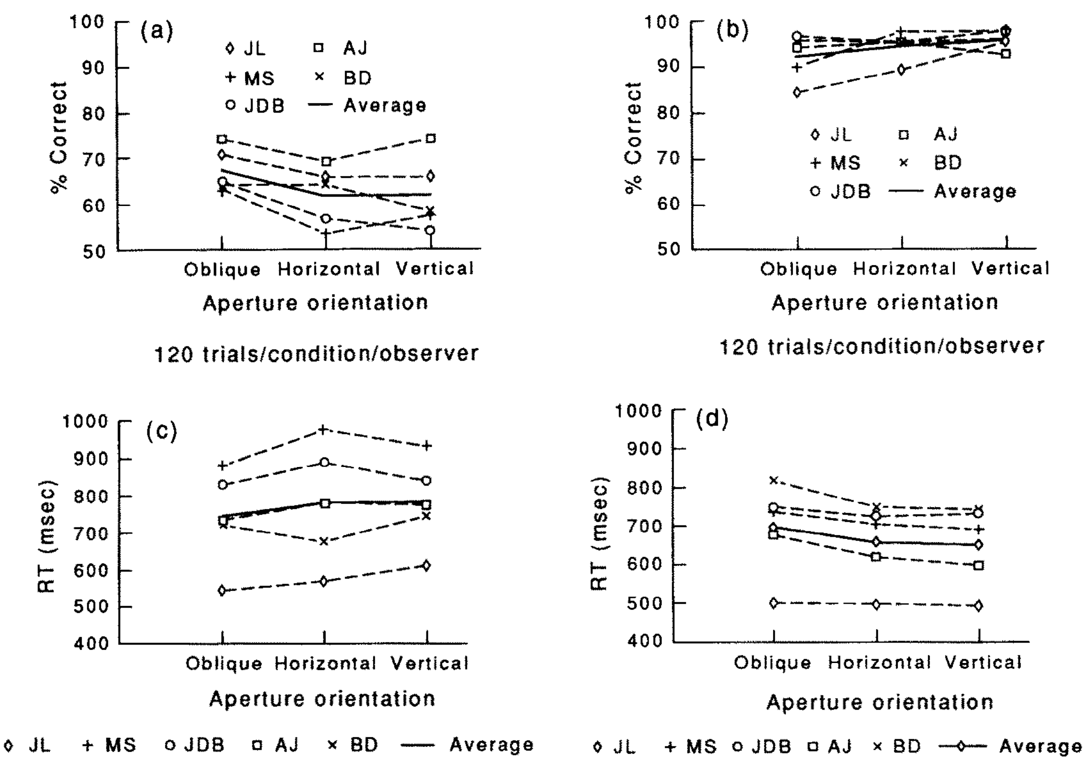

FIGURE 3. Results of Experiment 1. (a, b) Accuracy in direction of revolution judgements for five subjects as a function of aperture orientation. (a) Invisbile apertures. (b) Outlined apertures. (c, d) Reaction times of correct responses as a function of aperture orientation. (c) Invisible apertures. (d) Outlined apertures.

overcomes the inherent ambiguity of such stimuli by relying on the motion of contour terminators (Wallach, 1935, 1976; Hildreth, 1984; Nakayama & Silverman, 1988; Shimojo *et al.*, 1989; Shiffrar & Pavel, 1992). Reliance on terminator motion might bias the visual system toward local interpretations within apertures rather than more global interpretations across apertures (Shimojo *et al.*, 1989; Shiffrar & Pavel, 1992). We set out to test this hypothesis more directly by reducing the salience of terminator motion under a variety of conditions.

EXPERIMENT 2: INTEGRATION VARIES ACROSS THE VISUAL FIELD

It has often been suggested that image processing is different in central as compared to eccentric vision (Westheimer, 1982; McKee & Nakayama, 1984; Koenderink, van Doorn & van de Grind, 1985). More specifically, the ability to accurately locate positions is degraded in periphery (Westheimer, 1982; Burbeck & Yap, 1990). Thus, presenting our stimulus in periphery should introduce an uncertainty about terminator position. Such a degradation of position information might lessen the visual system's reliance on terminator motion and, as a result, facilitate integration across contours. To test this idea, we replicated the invisible aperture conditions from the previous experiment with peripherally presented stimuli.

Methods

The stimulus was identical to that used in the invisible aperture conditions of Experiment 1 except that the center of the diamond was presented at 7° eccentricity from the fixation point. Subjects were asked to identify the direction (clockwise or counter-clockwise) of the diamond's translation. The stimulus was presented either to the left or right of the fixation point, which was located in the center of the display. Presentation location and aperture orientation were randomly chosen on each trial. There was no scaling of stimulus size or contrast. Four subjects (the authors and two naïve subjects) participated in this experiment.

Results and discussion

All observers reported that when viewed eccentrically, the diamond appeared rigid and moved coherently. Although the stimulus was randomly presented to either the left or right of fixation, which rendered this task more difficult than the centrally displayed invisible aperture conditions in Experiment 1, accuracy was near ceiling for all observers, as shown in Fig. 4. Since directional judgements could not be made without information from two or more contours, this result strongly implies that observers are much more likely to integrate across contours in periphery. Accuracy does not differ significantly with aperture shape [$F(2,8) = 0.23$, $P > 0.10$], although this may result from the obvious ceiling effects. We argue that this dramatic improvement in performance reflects weakened reliance on terminator motion resulting from degraded positional accuracy in periphery.

Improved performance with peripherally presented stimuli indicates that motion integration might not be uniform across the visual field. Differences between central and eccentric processing of visual motion have often been noticed (McKee & Nakayama, 1984). These differences have generally been explained by the increase of receptive field size with increasing eccentricity (Rovamo & Virsu, 1979). Consequently, scaling for size generally results in similar performances for central and eccentric vision. One could argue that motion integration is better in periphery because detectors with larger receptive fields integrate over larger areas. We attempted to address this potential problem by greatly reducing stimulus size in central vision. Observers looking at a 3.5 times smaller diamond never report a strong rigid percept. To verify this effect, four subjects replicated the same clockwise vs counter-clockwise discrimination task with these smaller stimuli. Their results, which are very similar to the poor performances found with invisible apertures in the first experiment, are summarized in Fig. 4. This finding suggests that, within the range we examined, scaling for size does not result in a rigid percept similar to that observed in periphery. In addition, if the absence of integration in central vision were due to a lack of large receptive fields, one should

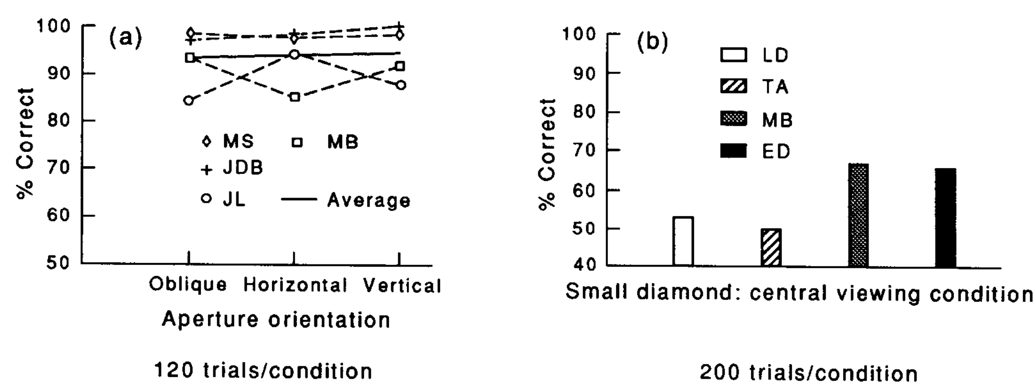

FIGURE 4. Results for Experiment 2. (a) Accuracy for four subjects as a function of aperture orientation in 7° peripheral vision. (b) Accuracy for a 3.5 times smaller diamond presented in central vision (only the oblique apertures were used). Note that reducing the size of the diamond does not enhance performance.

never be able to integrate the component motions of our stimulus in central vision. The following two experiments demonstrate that this prediction is not valid.

EXPERIMENT 3: IMPROVED INTEGRATION WITH NOISY CONTOUR LENGTHS

To lessen the visual system's potential reliance on terminator motion, we presented our diamond stimulus through apertures of varied shape. Jagged-edged apertures were used so that from one frame to the next, the lengths of the visible diamond contours varied. This manipulation was thought to disrupt the salience of terminator motion possibly by degrading the ability of terminator motion detectors to respond consistently over time. Also, while contour terminators can act as strong correspondence cues, differences in contour lengths have been shown to minimize correspondence strength between terminators (Ullman, 1979). If consistent responses to high luminance terminators disrupt cross-contour integration in central vision, then adding "noise" to terminator motion might enhance motion integration across contours.

Methods

Subjects. Five researchers served as subjects. Two of the subjects were the authors and had participated in the previous experiments. The remaining three subjects had not participated in the previous experiment and were unaware of the hypothesis under investigation.

Stimuli and procedure. As in the previous experiments, observers viewed a translating diamond through four apertures. The visible contours had a luminance identical to that used in the first experiment (111 cd/m^2). However, in this experiment, the apertures had jagged as opposed to straight edges, as shown in Fig. 5. These jagged edges were created by adding a high frequency sinewave to each aperture edge. For technical reasons, only vertical rectangular apertures were used.

Five different levels of noise, created by varying the sinewave amplitude, were chosen: 0, 10, 20, 30, and 40%. During diamond translation, the visible length of each contour varied between the maximum and minimum lengths of the chosen noise level. For example, in the 10% noise condition, contour length varied sinusoidally between 1.61° and 1.89°. Similarly, in the 40% noise condition, contour length varied between 1.44° and 2.16°. Length variations were not correlated across apertures. Within each aperture, length variations were symmetrical about the center of the visible contours. For that reason the overall direction of any single contour was not affected by the noise. As before, aperture edges were not outlined. The area inside and outside the apertures were of identical color and luminance. The procedure was identical to that of the first experiment. Subjects completed two blocks of 300 trials (60 for each of the five noise levels). Noise level was randomized within each block.

Results and discussion

The results, shown in Fig. 6, illustrate that directional performance improves with increasing terminator motion noise. While large differences were found between naïve and practiced subjects, the proportional improvement in performance was similar for all subjects. Since performance depends on accurate motion integration across disconnected contours, we conclude that increasing contour length variability increases motion integration accuracy across contours. When contour length varies, the direction of terminator translation also varies abruptly. This added variance may decrease the reliability of terminator motion. As a result, the visual system may abandon local image interpretations based

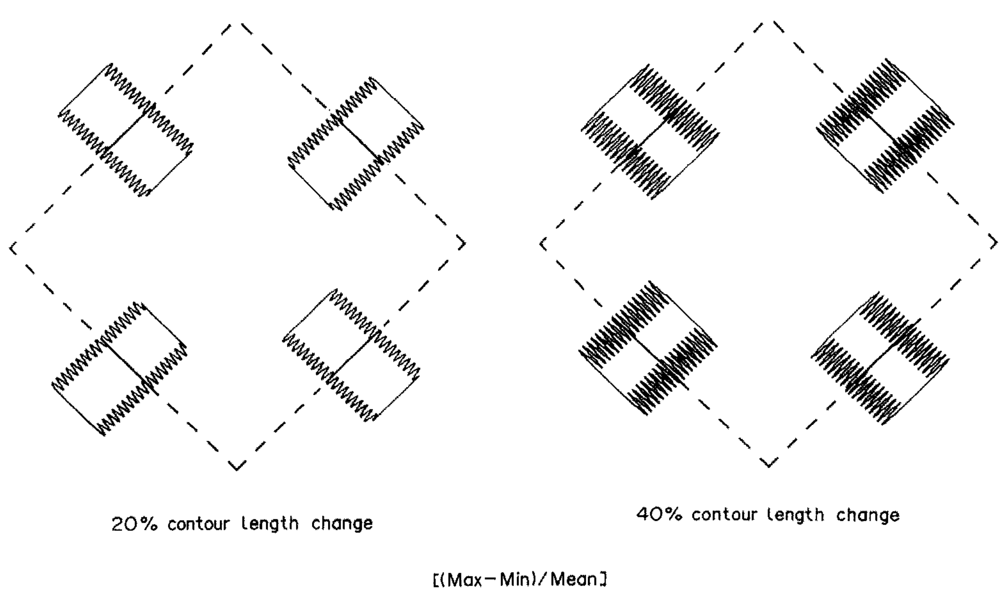

FIGURE 5. Stimulus used in Experiment 3. Variable contour lengths were produced by using invisible apertures with jagged edges. The noise between apertures was uncorrelated. The variations in the line lengths were symemtrical about the center of the lines. Thus, within each aperture, a segment was seen to translate along a straight path.

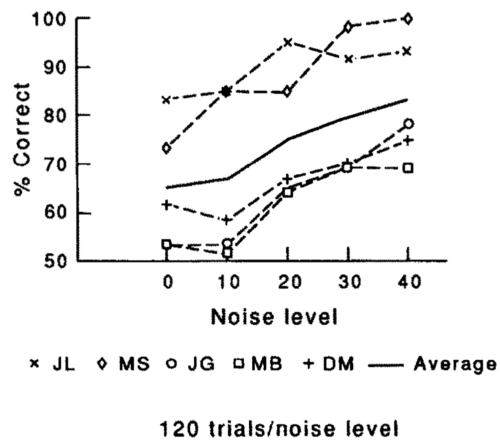

FIGURE 6. Results for Experiment 3. Direction accuracy obtained in central vision, for five levels of terminator motion noise (variable contour lengths). Performance increases as noise increases. Average of five observers is also shown (continuous line).

on terminator motion. Instead, the visual system may default to more global interpretations by combining translation signals across contours.

Unfortunately, the use of jagged-edged apertures results in some potentially important confounds. For example, as contour length changes, so does the distance between contours. To control against this and other factors, we needed to decrease terminator salience without varying contour length over time. In the final experiment, we therefore returned to the straight-edged, invisible apertures of the first experiment and added luminance filters to them.

EXPERIMENT 4(A): IMPROVED INTEGRATION WITH LOW CONTRAST TERMINATORS

To vary the salience of terminator motion, we filtered the visible contours of the translating diamond stimulus such that terminator luminance was either increased or decreased relative to the center contour luminance. With these two filter types, we were able to ask the question: Does terminator contrast influence motion integration across contours?

Subjects. Four subjects participated in this experiment. All subjects were unaware of the hypothesis under investigation.

Stimuli and procedure. The stimuli and procedure were identical to those used in the invisible aperture condition of the first experiment with the exception that contour luminance was not uniform. While background luminance remained constant at 12 cm/m^2, the diamond's contours were filtered in one of two ways. The luminance distributions of the contours resulting from the two types of filtering are shown in Fig. 7. In one condition, the contour terminators were low contrast (12 cd/m^2) while the contour centers were high contrast (up to a peak of 96 cd/m^2). The reverse was true for the second condition in which the filtered contours had high contrast terminators (96 cd/m^2) and a low contrast center (12 cd/m^2). In both conditions, luminances of the intermediate contour areas varied smoothly.

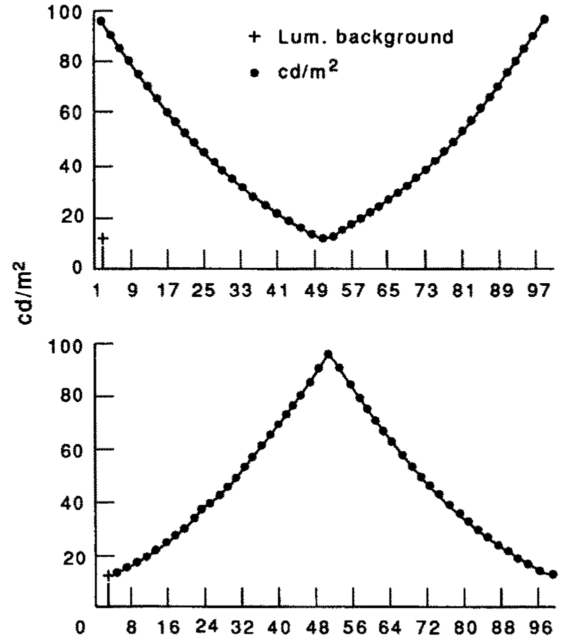

FIGURE 7. Illustration of the two types of filtering used in Experiment 4. Luminance of visible contours as a function of position within apertures. (a) Low terminator contrast and high contour contrast. (b) High terminator contrast and low contour contrast.

Results and discussion

Results are plotted for four observers in Fig. 8. As expected from the appearance of the stimulus, directional discrimination was significantly better with low contrast terminators [$F(1,3) = 14.84$, $P < 0.05$] as compared to high contrast terminators. This trend held for all subjects.

This finding adds further support to the hypothesis that a reliance on terminator motion inhibits the integration of motion information across contours. When terminators were high luminance and therefore salient, the visual system appeared to favor local motion interpretations within apertures. However, when terminators were low contrast, and therefore less salient, subjects were better able to determine the diamond's direction of translation. Because the diamond's direction of translation could only be determined by the

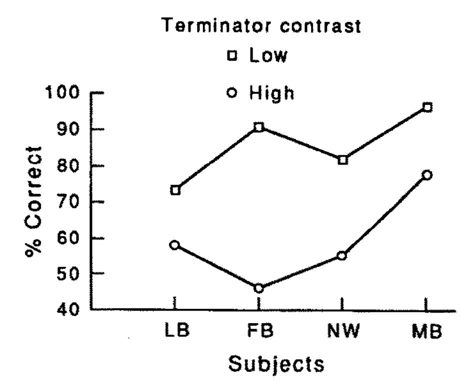

FIGURE 8. Accuracy measured for the two filtered apertures. Vertical apertures are used. Data for four observers. (a) Low terminator contrast produces high performance. (b) High terminator contrast produces low performance.

combination of translation signals across contours, the visual system appears to be more likely to make more global interpretations across apertures when terminator motion is less salient. Our stimuli actually presented a conservative test of the above hypothesis because in the low contrast terminator condition, the distance between the visible portions of the four contours was actually greater than in the high contrast terminator condition. While the distance between contours was greater in the low contrast terminator condition, subjects were more likely to combine translation signals across contours.

EXPERIMENT 4(B): IMPROVED INTEGRATION WITH LOW CONTRAST DIAMOND

Does the performance of the previous experiment reflect the variation of the relative contrast between terminators and contours or does it depend on the absolute contrast of terminators alone? To answer that question, we replicated the experiment with the diamond at five different luminance levels. Note that varying the luminance of the lines also changed the diamond/background contrast.

Methods

Subjects. Five subjects participated in this experiment. One was an author, MS, and the remaining four subjects were not familiar with the experimental situation and performed practice trials prior to the experiment.

Stimuli and procedure. The stimulus and procedure were identical to those used in the first experiment with the exception that the luminance of the lines was randomly changed on each trial from one of five possible values (0.7, 1.5, 4.0, 7.0, and 20.0 cd/m^2). The screen background was black and the room was dimly lit. Only the oblique rectangular apertures were used in this experiment. Each subject performed two blocks of trials on different days. A block consisted of 300 trials, 60 for each luminance level.

Results and discussion

Results are plotted for five observers in Fig. 9. As expected from the phenomenal appearance of the stimulus, accuracy increased as the luminance of the diamond's contours decreased. Reaction times also slightly decreased with increasing luminance.

Low contrast should result in lowered responses to both terminator and contour motion. It is worth noting that despite this modification, the percept and the performance are deeply affected by contrast manipulation: the diamond appeared rigid and performance was near ceiling for the lowest contrast used. This result is consistent with the hypothesis that two categories of detectors are processing the diamond motion. Terminator motion may be analyzed by detectors with low contrast sensitivity, whereas the contour may involve detectors with high contrast sensitivity.

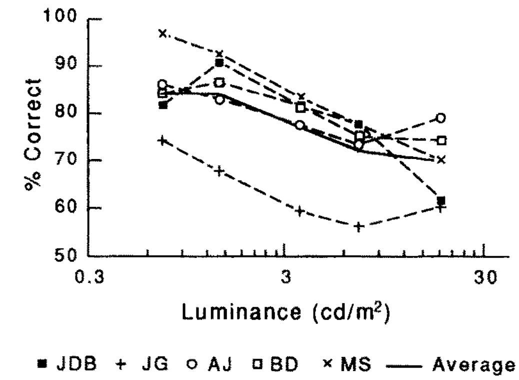

FIGURE 9. Results for Experiment 4(B). Performance for diamonds at five luminance levels plotted in semi-log coordinates. Performance decreases as luminance inceases for all five subjects. Average performance is also shown (continuous line).

GENERAL DISCUSSION

We were interested in determining how the motion of terminators contributes to the process of integrating motion signals across space. In the first experiment, we demonstrated that observers have difficulty in accurately performing a direction of translation task when this task requires the integration of motion information across disconnected contours. This difficulty occurred even though observers had prior knowledge of both object shape and rigidity. Motion integration was found to improve with outlined and jagged apertures, in 7° periphery, and at low contrast. Adelson and Movshon (1983) described similar phenomena with a moving version of the Herringbone illusion. We interpret this set of results as supporting the hypothesis that the relative responses to terminator and contour motion determine whether or not cross-contour motion integration will occur.

Motion integration and extrinsic vs intrinsic terminators

Shimojo *et al.* (1989) produced a distinction between "extrinsic" terminators produced by accidental occlusion and "intrinsic" terminators corresponding to veridical contour end points. These authors demonstrated that the perceived direction of a grating translating behind a rectangular aperture was strongly influenced by the availability of depth information. It was proposed that the visual system uses the presence of occlusion cues to classify visible end points as extrinsic and that this classification resulted in improved cross-contour integration. The presence of intrinsic terminators, in turn, resulted in poor cross-contour integration. It was further suggested that extrinsic terminators would be "subtracted" prior to the integration process, whereas intrinsic terminators would not.

In our experimental conditions, terminators should be classified as "intrinsic" since stereoscopic disparity was absent and no monocular cues were provided. Only for the outlined aperture conditions would the terminators be classified as "extrinsic" since the presence of T-junctions in this situation serves as a monocular depth cue. In agreement with what would be predicted from the influence of terminator classification on motion integration, the results of Experiment 1 show that when intrinsic terminators are clearly visible, motion integration fails. Instead, moving contours are segregated into several independent contour motions. On the other hand, when apertures are outlined, thus providing monocular occlusion cues, contour motion is easily integrated in a rigid percept (Lappin *et al.*, 1990; Lorenceau & Shiffrar, 1990).

However, when stimui are viewed eccentrically or with noisy terminator motion or at low contrast (Experiments 2, 3, and 4), motion integration is facilitated even though intrinsic terminators are present in the moving image. Hence, the distinction between intrinsic and extrinsic terminators is not sufficient to account for the conditions under which cross-contour integration may occur.

The present results suggest that when the salience of terminator motion is, by any means, weakened, integration across space of contour motion is facilitated. We now discuss this issue in more detail, for the conditions used in the different experiments.

Motion integration with intrinsic line endings

Influence of the direction of line ending motion on integration. In Experiment 1, three different aperture shapes were used. Depending on aperture orientation, terminator motion is constrained along different axes. It is worth noting that integration is poor whatever the direction of terminator motion. When oblique apertures are used, line ending motion is the same as contour motion. Thus, plotting terminator motion in a velocity space leads to a unique veridical solution through an IOC from component terminator motion. With vertical or horizontal apertures, terminator motion cannot be used to compute a unique solution since the lines of constraint do not intersect. However, this difference produced weak differences in accuracy. Although this result is not evidence that the visual system does or does not perform an IOC computation (a vector summation would lead to the similar conclusion in our conditions), it suggests that the response to terminator motion may compete with the integration process.

Eccentric viewing conditions. Experiment 2 demonstrated that viewed eccentrically, our stimulus appeared rigid and moved coherently. We have previously discussed the possibility that motion integration improves because receptive field size increases with eccentricity. As a result, multiple contours would be more likely to fall within the receptive field of a single detector. This interpretation is not satisfying. First, we presented our stimulus at 7° eccentricity, which results in a small increase in RF size either in area V1 or in area MT (Mikami, Newsome & Wurtz, 1986) but a large increase in performance. Second, reducing the size of the diamond by a factor of 3.5, thus correcting for the magnification factor, does not improve performance (see Fig. 4). Furthermore, if large RF were required for motion integration, and if no such RF did exist in central vision, then one should never be able to integrate component motion into a rigid percept in central vision. Experiments 3 and 4 demonstrated this prediction to be false.

The increase of RF size with eccentricity in V1 is equivalent to a decrease of the density of small RFs. The effect of eccentric presentation we observed could be explained by the lack of small RFs in periphery, able to signal terminator motion. The relatively stronger response to contour motion could then account for the facilitated integration in periphery.

Noisy terminator motion under central viewing conditions. This interpretation is strengthened by the results in central vision of Experiment 3. When we artificially weakened the responses to terminator motion by using apertures with jagged edges, performance improved. With such apertures the velocity (speed and direction) of terminators changes from frame to frame. We assume that this uncertainty about terminator velocity prevents the production of a reliable response to terminator motion. Since the response to contour motion is not affected by the manipulation of aperture edges, a reliable integration of contour motion can still be performed.

Influence of contrast on motion integration. The same interpretation can account for the improved accuracy observed with low contrast terminators and high contrast contours [Experiment 4(A)]. In this case, terminator velocity is not affected by contrast manipulation. Only the responses to terminators should be decreased at this low contrast. According to our hypothesis, this decrease in the response to terminator motion enhances motion integration. When terminators are high contrast and contours are low contrast, performance is poor, suggesting that the integration process is disrupted. Again, these results suggest that the relative responses to terminator and to contour motion governs the integration process.

Finally, we found that when both terminator and contour contrast is low, integration is facilitated [Experiment 4(B)]. Although low contrast should result in lowered responses to both terminator and contour motion, this change in contrast affects deeply the motion percept. This result suggests that the response to terminator motion is carried out by detectors with higher contrast thresholds than that of detectors responding to moving contours. This further suggests that different detectors respond to terminators and to contours.

This difference could be accounted for by the spatial frequency content of our stimulus. For instance, high spatial frequency selective detectors could respond to terminators, whereas detectors selective to lower spatial frequencies could respond to contour motion. One could suggest that in central vision, motion integration is not observed at high contrast because terminators would be coded by high spatial frequency selective detectors that do not feed into the integration process. However, according to this hypothesis, superimposed gratings (plaids) of high spatial frequencies should not be perceived as a coherent moving percept. Such failure to perceive coherent motion with high frequency plaids has never been reported (Adelson & Movshon, 1982; Lorenceau, 1987). In addition, we observed that removing high spatial frequencies by blurring the stimulus does not produce a coherent rigid motion percept. Thus, it does not seem that the high spatial frequency content of our stimulus is directly responsible for the phenomena described above.

With the diamond stimulus used in all experiments, one can speculate that two categories of motion detectors could be activated at early stages. The first category would involve detectors that respond to a straight line moving through their receptive field, providing ambiguous reading of velocity. The second category would concern detectors that are selectively activated by the motion of terminators. One could argue that detectors with large receptive fields could be activated simultaneously by several moving segments. This would imply that such detectors are able to code simultaneously several orientations, together with the relative motion between segments. To our knowledge, such detectors are not found at early stages of motion processing. Such detectors should be activated by responses from lower level detectors, belonging to both categories mentioned above, and thus constitute the "integrator" under investigation.

Shimojo *et al.* (1989) have suggested that the notion of terminators could be related to the activity of "end-stopped cells", commonly encountered in striate areas of the visual cortex (Hubel & Wiesel, 1965; Gilbert, 1977; Dobbins, Zucker & Cynader, 1989; Peterhans & von der Heydt, 1989; Versavel, Orban & Lagae, 1990). The density of end-stopped cells is known to decrease with eccentricity (Orban, 1984). In addition, end-stopped cells have low contrast sensitivity (Orban, personal communication). Our interpretation of the present results is compatible with such properties. On the other hand, recordings from single units in striate areas of monkeys suggest that neurons in areas V1 and V2 are selective to the direction of moving contours and behave as end-free cells. These neurons feed an extra striate area, MT (Van Essen, Maunsell & Bixby, 1981; Maunsell & Van Essen, 1983) where neurons are found to respond to pattern rather than component motion (Albright, 1984; Movshon, Adelson, Gizzi & Newsome, 1985; Rodman & Albright, 1989) suggesting that area MT has integrative properties.

If end-stopped and non-end-stopped cells are involved in the phenomena we described, one would speculate from our results that the responses of end-stopped cells to terminator motion compete with the integration process, possiby through inhibitory interactions. To our knowledge, such inhibition has not yet been described.

The current findings also suggest that poor cross-contour motion integration do not arise simply from the use of non-object-like stimuli. Previous studies of the integration of translation signals across disparate contours have relied on stimuli such as gratings (Shimojo *et al.*, 1989) or markings placed near a sinewave (Nakayama & Silverman, 1988b). The object rigidity constraint (Ullman, 1979) states that observers select image interpretations consistent with a rigid object and therefore should be more likely to integrate motion signals across contours whenever such an integration would be consistent with a rigid object. In the present expeiment, subjects were informed that the visible contours belonged to a single rigid diamond. Yet, poor performance in the invisible aperture conditions indicates that subjects were unable to accurately combine translation signals across contours, even though such an integration would have resulted in an image interpretation consistent with a simple rigid object. Thus, this experiment demonstrates that, as with rotation (Shiffrar & Pavel, 1992), prior knowledge of object shape and rigidity is insufficient to promote the accurate combination of translation signals across contours.

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