Increased Motion Linking Across Edges with Decreased Luminance Contrast, Edge Width and Duration

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Accurate interpretations of image motion require the segmentation of motion signals produced by different objects with the simultaneous integration of motion signals produced by the same object. We investigated a motion integration paradigm in which the direction of an object's motion could only be determined from an integration of motion signals across the disconnected object edges. In a series of experiments we show that observers' ability to determine object motion depends significantly upon stimulus duration, luminance contrast and edge width. These effects suggest that the visual system, after some delay, relies upon relatively thick, luminance defined contour discontinuities to segment moving images. Copyright © 1996 Elsevier Science Ltd.

Motion segmentation   Motion integration   Isoluminance   Direction discrimination   Color   Duration

INTRODUCTION

The accurate identification of physical objects from retinal images requires the integration or linking of visual information across retinal regions. This linking requirement is particularly evident in the interpretation of object motion because local motion measurements made within small receptive fields are inherently ambiguous. How motion linking occurs is the topic of much debate (Adelson & Movshon, 1982; Braddick, 1993; Hildreth, 1984; Ramachandran & Anstis, 1983; Shiffrar & Pavel, 1991; Stoner & Albright, 1993; Wilson *et al.*, 1992). Early attempts to understand how the visual system determines what parts of an image should be grouped together were made by Gestalt psychologists who developed rules, such as common fate and good continuation, that describe when visual elements are organized into coherent objects (Wertheimer, 1912). Recently, Livingstone & Hubel (1987) proposed that the magnocellular pathway of the geniculostriate system may be responsible for the application of Gestalt-like linking rules. More specifically, these researchers proposed that 'magno functions may include deciding which visual elements, such as edges and discontinuities, belong to

and define individual objects in the scene' (Livingstone & Hubel, 1988). We conducted a set of experiments to test this magno-linking hypothesis. Because of the physiological properties of cells in the magnocellular pathway, including their responsiveness to transient stimulation (Merigan & Maunsell, 1993), researchers have suggested that the magnocellular system analyses motion-related information (Livingstone & Hubel, 1988). The following studies were based on the assumption that if the magno system is responsible for linking motion signals when they define an object, then linking should decrease with decreases in magno system activity.

The situation of interest, illustrated in Fig. 1, consisted of a translating diamond figure viewed through multiple windows or apertures. The apertures were positioned so that only the diamond's straight edges were visible. The corners of the diamond figure could not be seen. When viewed through an aperture, the motion of each visible edge was ambiguous because the component of motion parallel to the edge could not be measured. As a result of this aperture problem, an infinitely large family of different motions is consistent with the motion of each visible edge (Wallach, 1935, 1976). The human visual system is thought to overcome this measurement ambiguity by linking motion signals across differently oriented edges (Adelson & Movshon, 1982; Wilson *et al.*, 1992). The multiple aperture display used in the current series of experiments mimics this need for motion linking because the diamond's direction of translation can only be determined from a linkage of motion signals across diamond edges.

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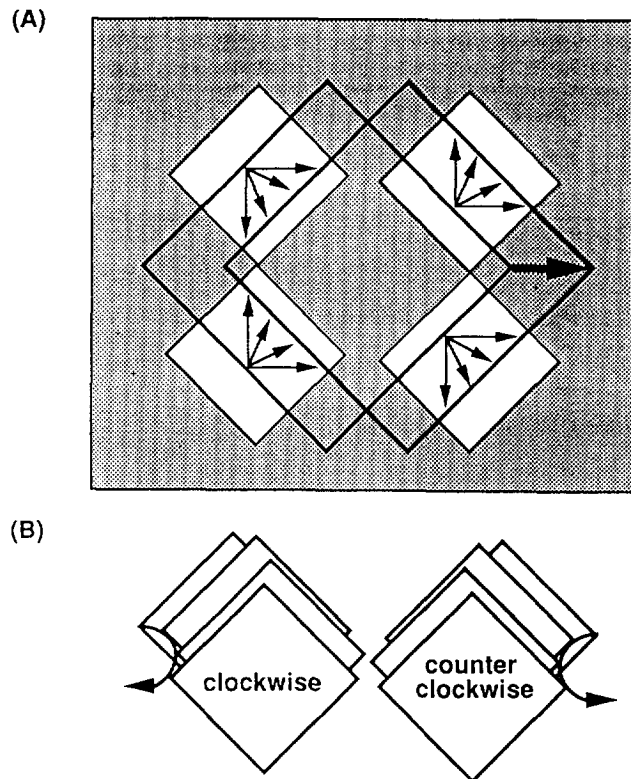
(A)

(B)

FIGURE 1. (A) Because of the aperture problem, a moving line viewed through a relatively small aperture is ambiguous. We examined the visual system's ability to link individually ambiguous motion signals when a translating diamond figure is viewed through four stationary apertures. The apertures were positioned so that the diamond's corners were never visible. As a result, the diamond's direction of translation could only be determined by linking motion signals across two or more visible edges. (B) On any trial, the diamond translated along a circular path in a clockwise or counter-clockwise direction. The diamond's orientation did not change.

EXPERIMENT 1

Linking and contrast

The first test of the magno-linking hypothesis examined the role of luminance in motion linking by manipulating the luminance contrast of a chromatic translating diamond display. Since the magno system does not respond selectively to different wavelengths of light (Derrington et al., 1984; Shapley, 1990), it is thought to be inactive (Livingstone & Hubel, 1988; Shapley, 1990) or at least less active (Merigan & Maunsell, 1993) at isoluminance. If the magno system controls the linkage of motion signals across objects, then linking should decrease as luminance contrast approaches isoluminance. The purpose of this experiment was to determine whether observers could link motion signals across the disconnected edges of the translating diamond stimulus when the luminance of the diamond edges approached the luminance of the background.

Methods

Subjects. Four observers volunteered to participate in this study. All had normal or corrected-to-normal vision.

Subjects were naive to the exact hypothesis under investigation.

Stimuli

The stimuli were displayed on a Sony 19" RGB monitor with a 1023 × 1280 pixel resolution and a 60 Hz refresh rate. A 386 Leanord personal computer was used to control stimulus generation, presentation and data collection. This apparatus was used in all of three experiments.

Before beginning the experiment, the red–green isoluminant point of each observer was measured with heterochromatic flicker fusion. Subjects observed a 17 deg × 5.4 deg checkerboard of green and red squares at a viewing distance of 114 cm. The color of each square in the checkerboard flickered from red to green or from green to red at 15 Hz. We measured equiluminance by fixing the luminance of the green squares at 4.92 cd/m^2 and asking subjects to change the luminance of the red squares, by the method of adjustment, until the flicker fused or disappeared. On six different trials, the luminance of the red squares was initially set at 1.0 or 9.0 cd/m^2 and subjects changed the luminance of the red squares with a mouse device until the flicker first disappeared. The mean and variance of the upper and lower flicker fusion limits were determined. We then selected the mean of this interval for each subject as their red–green equiluminance point. This procedure was used to determine the isoluminance point for each subject in all three experiments.

The experimental stimulus consisted of a red diamond outline translating behind four stationary, green apertures positioned so that four diamond sides were visible. Red and green were selected because neurons in the parvocellular pathway show color opponency of the red/green type and, therefore, should be responsive to this color difference across variations in their relative luminance (Derrington et al., 1984; Shapley, 1990). Moreover, motion linking is likely along this axis in color space (Krauskopf & Farell, 1990). The width of the diamond outline subtended 1.6 min of visual angle from the subjects' viewing distance of 114 cm. The diamond had side lengths of 3.67 deg of visual angle (DVA) but only 1.34 DVA of each side was visible through the square apertures. Aperture size was 1.34 by 1.34 DVA while the separation between apertures was 2.5 DVA. A small, stationary fixation point was continuously present in the center of the monitor, which was also the center of the diamond.

The green background was homogeneous and had a constant 4.92 cd/m^2 luminance. The red diamond had one of five different luminance levels. The lowest luminance was that determined by the flicker fusion measure described above; that is, the point of perceived equiluminance for red against a 4.92 cd/m^2 green. The remaining four luminance levels of the diamond were created by increasing diamond luminance in 3 cd/m^2 steps. For example, if an observer had an equiluminance
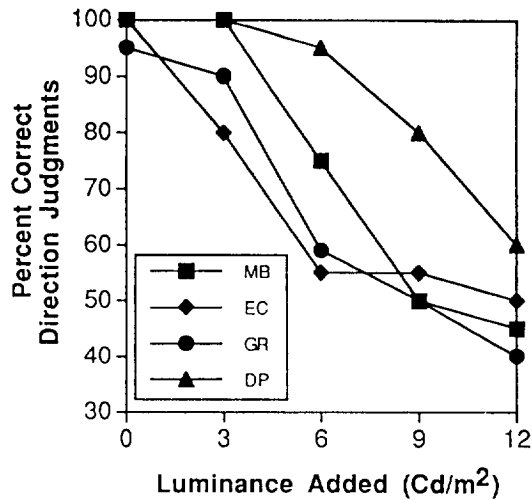
FIGURE 2. The results of experiment 1. The zero luminance column is the red–green isoluminance point for each subject. The 50% level indicates chance performance. Each symbol indicates the results from a different subject. Performance improves as the stimulus approaches isoluminance, suggesting that motion linking across edges is facilitated under low luminance contrast conditions.

point for red of 5 cd/m^2, then their five diamond luminances would be 5, 8, 11, 14 and 17 cd/m^2.

Procedure

On each trial, the diamond translated along a circular path in either a clockwise or counter-clockwise direction relative to a central fixation point. A circular motion path, or revolution, was chosen to maintain constant stimulus eccentricity and orientation. The diamond continuously translated, without changing its upright orientation, through 2.22 revolutions of the circular path in 1.33 sec, yielding a velocity of 1.67 rev/sec. Path radius was 0.4 DVA. Within each aperture, the visible line segment translated a maximum distance of 0.75 DVA with a mean velocity of 2.5 deg/sec. The diamond disappeared as soon as it stopped translating. The diamond had one of eight possible starting locations, each separated by 45 deg around the circular path. The direction of translation (clockwise or counter-clockwise) and the starting position were randomized across trials. As a result of this randomization and the aperture problem, it was not possible to determine the diamond's direction of translation from the motion of any single contour. Instead, the diamond's direction of translation could only be determined from a linkage of motion signals across the disconnected edges. According to a two-alternative forced-choice design, subjects indicated the perceived direction of diamond translation across trials. Viewing distance was fixed at 114 cm with a chin rest. No feedback was provided.

According to a within-subjects design, every subject viewed the translating diamond at five different luminance levels. Each subject completed 40 trials per diamond luminance level for a total of 200 trials. Subjects pressed one of two buttons on a computer keyboard to indicate whether the diamond translated in a clockwise or counter-clockwise direction.
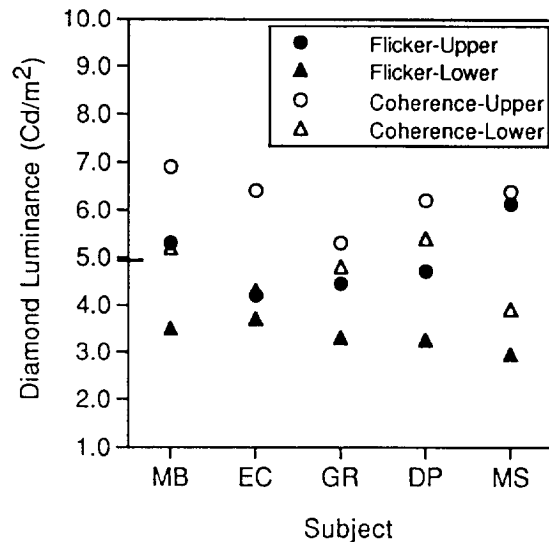

FIGURE 3. Isoluminance estimates for red against a 4.92 cd/m^2 green as measured by flicker fusion of a checkboard pattern and coherence judgments for the revolving diamond stimulus used in our experiments. The upper and lower limits are shown for each measure for five different observers. The small tick mark on the ordinate indicates photometric isoluminance.

Results and discussion

The results, shown in Fig. 2, demonstrate that subjects' accuracy on the direction discrimination task increased as the diamond's luminance contrast decreased. Subjects judged the diamond's direction of translation with near ceiling levels of accuracy as the red diamond approached isoluminance with the green background. As the red diamond's luminance increased, while the green background luminance remained constant, performance dropped to chance levels. Thus, while the magno-linking hypothesis predicts decreased motion linking with decreasing luminance contrast, this experiment finds the opposite pattern of results.

One of the difficulties associated with isoluminant displays is that behaviorally and physiologically measured isoluminance varies with the spatial and temporal characteristics of the display (e.g., Livingstone & Hubel, 1987; Logothetis et al., 1990; Schiller et al., 1991). We measured each subject's isoluminant point with a checkerboard display that differed significantly from our translating diamond display. We therefore undertook a second measure of each subject's isoluminant point using a coherence judgment of the same translating diamond display used in these experiments. Five subjects, four from experiment 1 and one from experiment 2, individually viewed the diamond display. On each of six trials, the green background was fixed at 4.92 cd/m^2 and the red diamond's luminance was initially set at 1.0 or 9.0 cd/m^2. According to the method of adjustment, subjects varied the diamond's luminance with a mouse device until the diamond first appeared rigidly coherent. Lower and upper coherence limits were determined and are shown, along with the values obtained from flicker fusion, in Fig. 3. Two aspects of these results are of interest. First, all observers reported

that the diamond appeared rigidly coherent over an average 1.5 cd range of luminance levels. This suggests that accurate performance in the direction discrimination task is associated with very low luminance contrast rather than precise isoluminance, if indeed such a single point exists. This interpretation is consistent with the gentle fall-off in performance obtained with increased diamond luminance in experiment 1. Secondly, the isoluminance estimates obtained with flicker fusion were consistently shifted downward from those obtained with coherence judgments. This shift is consistent with the hypothesis that isoluminance measures depend upon the spatio-temporal parameters of a display. Finally, since experiment 1 involved increasing luminance contrast from the isoluminance estimates obtained with flicker fusion, the isoluminance estimates obtained with coherence judgments were contained within the range of luminances used in this experiment.

The current findings appear to contradict some of the previous research on motion linking at isoluminance. For example, an array of diagonally positioned dots in an apparent motion display appears to move in a strongly correlated fashion when the luminance of the dots differs from the luminance of the background (Ramachandran & Anstis, 1983). However, these same dots appear to move incoherently when they are isoluminant with the background (Livingstone & Hubel, 1988). This finding has been used to suggest that the magno system, which is more sensitive to luminance contrast than color contrast, determines when parts of a visual image are grouped together and interpreted coherently. The difference between our results and those of previous researchers suggests that linking is a complex process involving multiple systems (Braddick, 1993; Stoner & Albright, 1993) and as such, is not reducible to a single, relatively early system such as the magnocellular system.

Theories of motion perception are often based on the assumption that the visual system links motion signals whenever such a linkage is consistent with the interpretation of a rigid object (Ullman, 1979). The four translating edges in our diamond stimulus were always consistent with the interpretation of a rigidly translating diamond. Yet, observers varied dramatically in their linkage of these motion signals.

Is the increased linkage of motion signals at low luminance contrast-specific to heterochromatic stimuli? Previous research suggests that it is not. When subjects view an achromatic version of the translating diamond stimulus, the perception of a coherent diamond again depends upon the luminance contrast of the display (Lorenceau & Shiffrar, 1992). As the luminance of the white diamond approaches that of the black background, accuracy in the same direction discrimination task increases. Thus, luminance contrast appears to be a robust, determining factor in the perception of both chromatic and achromatic displays.

One explanation of these luminance contrast effects is suggested by research on contour terminators. The perceived direction and speed of a translating line are

often determined by its terminators. When the terminators of a line or a group of lines are presented at high contrast, perceived line velocity is strongly influenced by the terminator velocity. However, when line terminators are difficult to localize, because they are presented at low contrast or their positions are jittered over time, perceived line velocity is determined by the velocity measured normal to the line's orientation rather than the terminator velocity (Castet et al., 1993; Kooi, 1993; Lorenceau et al., 1993; Shapley et al., 1995).

Accurate object recognition requires motion linking within but not across objects. Because terminators signal object boundaries, such discontinuities should determine when linking occurs. Consistent with this prediction, increasing evidence suggests that terminators play a critical role in the interpretation of object motion (e.g., Stoner & Albright, 1993). For example, when occlusion cues suggest that the ends of lines are extrinsic or accidental, motion linking is facilitated across those lines. Conversely, when occlusion suggests that the ends of lines are real or intrinsic, motion linking is inhibited (Shimojo et al., 1989). Terminator visibility also significantly influences motion linking. When displays consisting of multiple line segments, such as the dynamic split herringbone or the translating diamond, are presented in central vision or at high contrast, they appear incoherent. However, these same displays appear coherent when they are presented peripherally or at low contrast, when their terminators cannot be accurately localized (Adelson & Movshon, 1983; Lorenceau & Shiffrar, 1992). Finally, of most relevance to the current experiments, if one modifies a translating diamond display so that the line terminators, but not the intervening contour segments, appear at low contrast or in the presence of noise, the achromatic diamond appears coherent and direction discrimination improves significantly (Lorenceau & Shiffrar, 1992). Thus, it can be argued that when terminators are reliably localized and classified as intrinsic, they are used to segment images. This segmentation inhibits motion linking and may be the means by which the visual system avoids linking velocity estimates across different objects.

In the current translating diamond stimulus, reliance on the motion signals produced by the visible terminators would result in the perception of four diagonally translating line segments, since the line terminators always translated diagonally. That is, the reliable localization of the terminators may be associated with the local segmentation of the image and subsequent inhibition of motion linkage across the diamond's edges. If the terminators cannot be reliably localized, then they cannot be used to segment the image, thereby freeing the visual system to link the motion signals across the diamond's edges and as a result, interpret the display as a coherent diamond revolving in a particular direction.

The chromatic system is thought to have a lower spatial resolution than the luminance system (Merigan & Maunsell, 1993; Mullen, 1985). Thus, one way to interpret the current results is that the measurement of
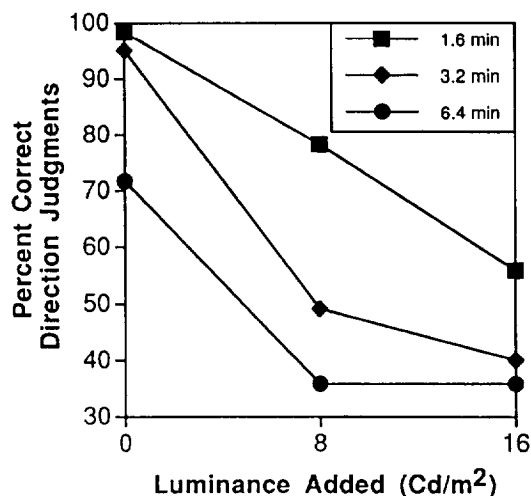
FIGURE 4. The results of experiment 2. Since all subjects showed the same response pattern, the data are collapsed across subjects. Each line indicates accuracy at a different diamond width. For every luminance level, increasing edge width decreased motion linkage.

terminator velocity is relatively degraded under near-isoluminance conditions (Lindsey & Teller, 1990; Troscianko, 1987). Since chromatic stimuli deliver less effective contrast than luminance stimuli (Smith & Pokorny, 1975), terminators in the red–green diamond stimulus might not be highly visible at low luminance contrast. The integration of ambiguous velocities across the diamond's edges may be facilitated in the absence of unambiguous velocities produced by clearly defined terminators (Lorenceau & Shiffrar, 1992). Such a theory predicts increased motion linkage across edges with decreased luminance contrast.

EXPERIMENT 2

Contour width

The above hypothesis was tested by increasing terminator visibility with increases in the width of the diamond outline. The rationale for this experiment was that terminators could be stimulated more effectively with wider red lines.

Methods

Three researchers from our laboratory volunteered to serve as subjects in this experiment. All had normal or corrected-to-normal vision. One subject had participated in the previous experiment while the other two subjects had not.

The stimulus consisted of the same translating red diamond outline viewed through four stationary apertures. As before, the partially occluded diamond translated clockwise or counter-clockwise against a 4.92 cd/m^2 green background. Before the experiment, the red–green isoluminant point was determined for each subject. During the experiment, the diamond's luminance and line width varied independently across trials. There were three possible luminance levels for the red diamond. For each subject, the lowest diamond luminance setting was their red–green isoluminance point, the second was

their isoluminance value plus 8 cd/m^2 and the third was isoluminance plus 16 cd/m^2. The three possible diamond line widths were 1.6 (also used in experiment 1), 3.2 and 6.4 minutes of visual angle. All other stimulus parameters were identical to those of the previous experiment. Thus, this experiment had a 3 × 3 within-subjects design such that on each trial, the diamond had one of three possible luminances and one of three possible outline widths. Width, luminance, direction of translation and starting position were randomized across trials. Each subject completed 360 trials (20 for each combination of direction, luminance and width) in two blocks. Again, on each trial the subjects' task was to indicate, according to a two-alternative forced-choice procedure, whether the diamond translated clockwise or counter-clockwise.

Results and discussion

The results, shown in Fig. 4, replicate the findings of experiment 1 since performance decreased with increased diamond luminance. The results also demonstrate that at each luminance level, performance decreased as edge width increased. This finding suggests that subjects' abilities to link motion signals across edges decreased as the terminators became more visible. This pattern of results suggests that the presence of perceptually salient terminators may inhibit the linkage of motion signals across an object's edges.

EXPERIMENT 3

Duration

Recently, several studies of motion perception have examined the influence of local image discontinuities across time. These investigations have demonstrated that translating gratings, plaid patterns and line segments viewed for short durations appear to change their direction of translation (Castet et al., 1993; Derrington et al., 1993; Freedland & Banton, 1993; Lorenceau et al., 1993; Shiffrar et al., 1995; Yo & Wilson, 1992). These temporal effects have been used to suggest that the visual mechanisms that analyze local image features or discontinuities are relatively slow and, therefore, only contribute to the interpretation of image motion after some delay. Could the same mechanisms responsible for changing the perceived direction of translating plaids and lines also be responsible for the current motion linking effects? If so, then short duration presentations of the translating diamond stimulus should limit the role of terminators in the interpretation of the diamond's motion and, as a result, enhance motion linking across the diamond's edges. This line of logic makes the unusual prediction that observers of the translating diamond displays initially perceive a coherently translating diamond and then lose that percept over time. To test this prediction, experiment 1 was simply replicated at a 166 msec stimulus duration.

Methods

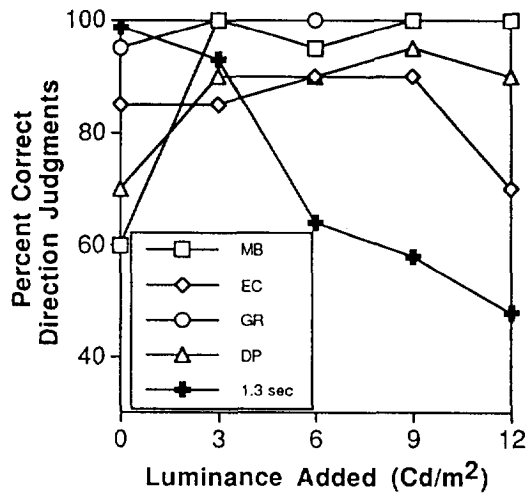The four observers from experiment 1 served as

FIGURE 5. The results of experiment 3. The outlined symbols indicate the data of individual subjects at the 166 msec stimulus duration. The solid symbols show the mean results from experiment 1 in which stimulus duration was 1.3 sec.

subjects in this experiment. The methodology of this experiment was the same as that in experiment 1 except that the translating diamond appeared for only 166 msec. The diamond's velocity remained constant at 1.67 rev/sec (same as in experiment 1) and, as a result, the diamond's path only covered 100 deg of the circular path on every trial. All other parameters were the same as those in experiment 1. That is, the luminance of the red diamond was randomly selected from one of five different levels. The exact luminance of each level depended upon that subject's red–green equiluminance point as measured by flicker fusion. The homogeneous green background had a constant 4.92 cd/m² luminance. Again, on each trial, the subject's task was to indicate whether the diamond's direction of translation was clockwise or counter-clockwise.

Results and discussion

The results, shown in Fig. 5, indicate that subjects consistently performed the direction judgment task with near ceiling accuracy levels except for a decrease at isoluminance. During debriefing, subjects reported that they had difficulty locating the isoluminant edges when they were presented for such a short duration. When the results of this experiment are compared with those from the longer, 1.3 sec stimulus duration of Experiment 1, performance is clearly superior at the shorter stimulus duration. This difference becomes especially evident with increasing diamond luminance. Since accurate performance in this task requires motion linking, these results suggest that motion linking across edges is facilitated at short durations.

One possible interpretation of these results depends on differences in the spatial extent of terminator translation at the two temporal durations. At the long duration, the diamond completed over two revolutions and as a result, the terminators visible within each aperture translated back and forth across a distance of 0.75 DVA. In the short

duration condition, the diamond completed less than half a revolution, and as a result, the terminators translated through a maximum of 0.375 DVA. Could the results of experiments 1 and 3 stem from this difference? To test this hypothesis, we conducted informal experiments in which the radius of the diamond's circular path decreased. This decreased the distance over which the terminators translated within each aperture. At the 1.3 sec stimulus duration, we found no change in the perception of the diamond's coherence nor its perceived direction of translation with decreases in terminator translation distance. Thus, time rather than the spatial extent of terminator translation, appears to best explain our results.

The enhanced performance at short durations also allows us to dismiss the role of eye movements in our displays since one would predict the opposite pattern of results if tracking facilitated velocity integration. Moreover, these behavioral differences are probably unrelated to the temporal differences between the magno and parvo systems, since the total transmission times to the visual cortex differ by only a few milliseconds (Lennie *et al.*, 1990). Finally, learning cannot explain our results. While the same four subjects participated in experiments 1 and 3, all subjects completed experiment 3 before participating in experiment 1. Instead, we conclude that if local discontinuities are analyzed by a relatively slow mechanism, then motion linking at short durations might result from a temporary absence of terminator influence in the motion integration/segmentation process.

GENERAL DISCUSSION

The first purpose of this series of experiments was to test the hypothesis that the magnocellular system determines what parts of an image define the same object and should be linked together. Although the actual functions of the magno and parvo systems are highly debatable (Livingstone & Hubel, 1988; Merigan & Maunsell, 1993; Shapley, 1990), we tested the magno-linking hypothesis as it was originally proposed (Livingstone & Hubel, 1988). Because observers were better able to link motion signals across the disconnected edges of a translating diamond near isoluminance than at higher luminance contrasts, our results do not support the magno-linking hypothesis. Instead, linking appears to be a complex process in which different image features influence linking to different extents (Shiffrar *et al.*, 1995). The motion linking process can be interpreted as a competition between unambiguous terminator velocities and ambiguous contour velocities (Lorenceau & Shiffrar, 1992).

The second purpose of these studies was to better understand how the visual system segments and integrates velocity estimates across image space. Our results suggest that, after some delay, the visual system relies on velocity estimates from thick, luminance-defined contour discontinuities to interpret object motion.

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