Vision Res. Vol. 33, No. 9, pp. 1207–1217, 1993
Printed in Great Britain.

0042-6989/93 $6.00 + 0.00

Different Motion Sensitive Units are Involved in Recovering the Direction of Moving Lines

JEAN LORENCEAU,* MAGGIE SHIFFRAR,* NORA WELLS,* ERIC CASTET*

Received 14 July 1992; in revised form 18 November 1992

We studied direction discrimination for lines moving obliquely relative to their orientation. Manipulating contrast, length and duration of motion, we found systematic errors in direction discrimination at low contrast, long length and/or short durations. These errors can be accounted for by a competition between ambiguous velocity signals originating from contour motion processing units and signals from line terminator processing units. The dynamic of this competition can be described by a simple model involving two different classes of processing units with different contrast thresholds, different integration time constants and different levels of response saturation.

Motion integration Aperture problem Terminators

INTRODUCTION

The computation of the true velocity (speed and direction) of translating objects is a difficult task for which several algorithms have been proposed (Fennema & Thompson, 1979; Poggio, Torre & Koch, 1989; Perrone, 1990). This difficulty arises from the ambiguity of individual velocity measurement (the "aperture problem", Horn & Schunck, 1981; Hildreth, 1984; Hildreth & Koch, 1987) which renders local readings insufficient to recover the true object velocity. A solution to this ambiguity can be computed by combining at least two different readings of velocity from two different orientations (Fennema & Thompson, 1979). Psychophysical (Adelson & Movshon, 1982; Lorenceau, 1987; Welch, 1989; Ferrera & Wilson, 1990) and electrophysiological (Movshon, Adelson, Gizzi & Newsome, 1986; Rodman & Albright, 1989) evidence has provided support for this scheme.

However, singular points in an image, such as corners or contour end points can be used to determine the true velocity of translating objects (Wallach, 1935; Nakayama & Silverman, 1988; Zucker, Iverson & Hummel, 1990). The use of singular points to solve the aperture problem has been assessed with translating Gaussian shaped lines (Nakayama & Silverman, 1988) gratings drifting behind apertures (Shimojo, Silverman & Nakayama, 1989) and partially occluded translating diamonds (Lorenceau & Shiffrar, 1992). Shimojo *et al.* (1989) distinguished extrinsic terminators produced by accidental occlusion that would not be used by the visual system to solve the aperture problem, and intrinsic terminators, corresponding to real end points that would constrain the solution to the aperture problem. Lorenceau and Shiffrar (1992), using disparate contours of a single object, found that intrinsic terminators are not reliably processed at medium contrast or in periphery and thus unable to signal local motion, therefore favoring a global interpretation.

In the frequency domain, terminators are characterized by a large distribution of energy across spatial frequencies and orientations in the Fourier plane. Therefore, terminators are likely to activate a large population of neurons selective to orientation and spatial frequency. In order to solve the aperture problem, the visual system should rely on the signals from these neurons, and ignore, minimize or constrain the ambiguous signals provided by neurons responding to the contour. If the type of neurons that process terminators is similar to that of neurons that respond to the contour (simple cells in V1, for instance), why should the visual system use the signals from the former rather than those provided by the latter to solve the aperture problem? In order for the visual system to use the signals provided at terminator location, it seems necessary that a subset of units with specific characteristics be activated. According to this view, terminators would be processed by feature detectors even if, at an early stage, they activate cells sensitive to their Fourier components. The aforementioned studies all suggest that end-stopped cells commonly encountered in the visual cortex, well suited to process the motion of terminators (Hubel & Wiesel, 1965; Gilbert, 1977; Orban, Kato & Bishop, 1979; Orban, 1984; Saito, Tanaka, Fukada & Oyamada, 1988; Dobbins, Zucker & Cynader, 1989) are involved in solving the aperture problem.

If specific units respond to terminators and to oriented contours, the existence and the nature of the interactions between these units remain open questions. Since the significance of terminator motion is fundamental to motion extraction and that of straight contours might be confusing, the interactions between units processing these different regions of the image should obey some

*Laboratoire de Psychologie Expérimentale, Université R. Descartes, Associé au CNRS, 28 rue Serpente, Paris 75006, France.

specific rules. To account for the significant influence of terminator motion, Hildreth (1984) has suggested that the unambiguous signals from terminators propagate along contours and constrain ambiguous readings of velocity in order to recover object motion. Although such process has been implemented in computational models of motion processing (Hummel & Biederman, 1992), to our knowledge, no electrophysiological or psychophysical data have been provided to directly support this scheme.

In the present paper, results of several psychophysical experiments are reported that provide additional evidence to support the hypothesis that reliance on terminator motion is critical for solving the aperture problem. Our data are compatible with the view that unambiguous responses to moving terminators constrain the ambiguous readings of velocity through a competitive process. A model is proposed to account for our results and the existence of a "propagation process" is discussed.

To shed light on the interactions between different readings of velocity from different regions of an image, we started with a simple question: how do observers recover the true velocity of lines moving in a direction oblique relative to line orientation? Given this simple stimulus, we speculated that motion processing units that could be activated by a moving line fall in three different categories. Some motion processing units could measure the velocity within a line (contour units thereafter). These units would face the aperture problem: the reading of velocity that would be available from such units would always be orthogonal to line orientation and thus inconsistent with the true velocity. Simple endfree cells could correspond to these type of units. A second type of motion processing unit could analyze the motion signals from terminators. For instance, units selective to the length and the orientation of a line could signal the true velocity. Endstopped cells, either symmetrical or asymmetrical (Orban *et al.*, 1979) could process terminator motion.* Finally, direction selective "blob" units that are insensitive to line orientation could be activated by a line as a whole (units with large circular receptive fields, for instance). These "blob" units could be activated by lines that fall within their receptive field and could correctly signal line velocity. These three hypothesized motion processing units are depicted in Fig. 1(a).

It is worth noting that these hypothesized units could behave differently depending on the stimulus. For instance a "blob" processing unit that correctly signal the motion of a short line could respond ambiguously to a longer line that covers its receptive field, thereby switching to a contour unit type.

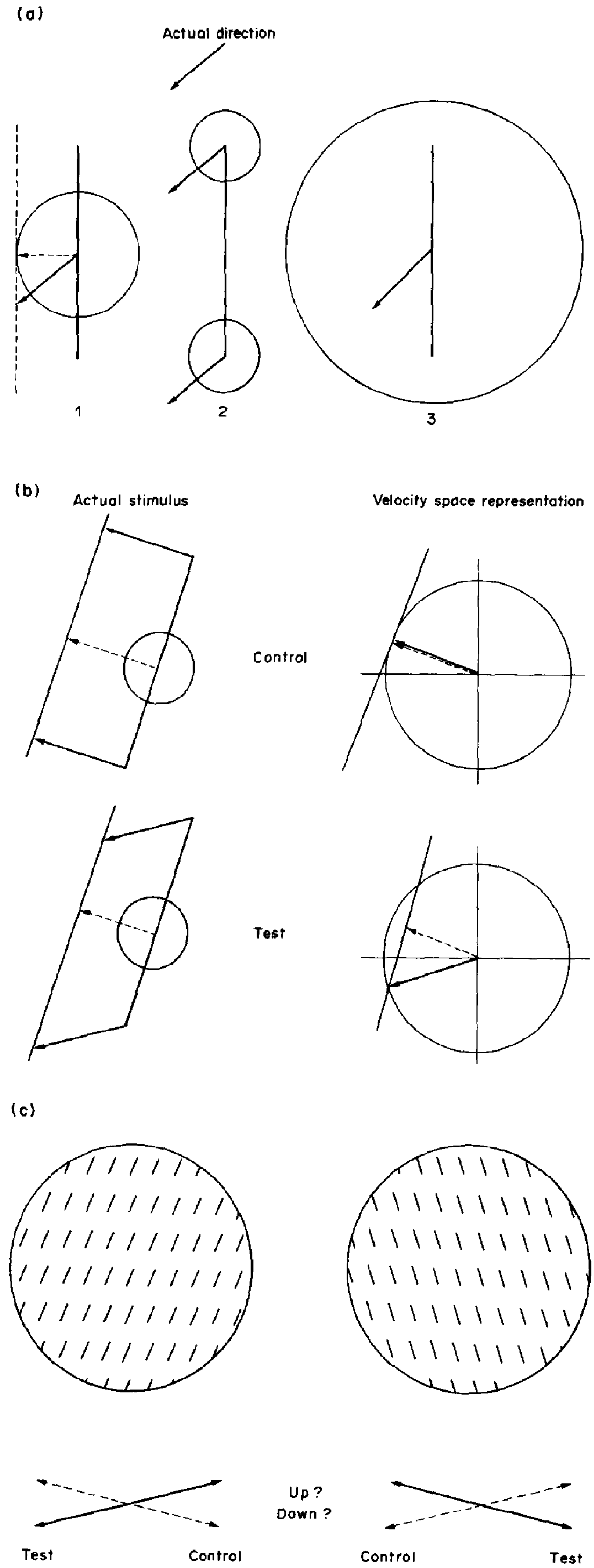


FIGURE 1. Schematic description of the stimuli and procedure used in all experiments. (a) Hypothetical motion processing units involved in processing the motion of moving lines: 1: contour unit, 2: terminator units, 3: "blob" unit. (b) Experimental design: motion of a single line in the control and test condition. Solid arrows represent the true direction, empty arrow show the component normal to line orientation. (c) Schematic description of the display: matrices of lines move normal to their orientation (control conditions, empty arrows) or obliquely relative to orientation (test conditions, solid arrows).

*The motion of a single terminator is insufficient to recover the true velocity of a moving line. The same terminator motion could be consistent with different types of motion (e.g. motion in depth). Thus, at least signals from two terminators are necessary to recover the true velocity. Coding both terminators of a single moving line could be realized by a single symmetrical or by two asymmetrical endstopped cells.

THE PARADIGM

To decouple the potential influence of these hypothetical motion units on the perceived direction of translating images, we measured direction discrimination for lines moving obliquely or perpendicular relative to their orientation. For instance, a line tilted 20 deg from vertical could move in a direction either 20 deg above or below a horizontal axis. Although the horizontal motion component is identical in both cases, the vertical motion components are in opposite directions. We asked observers to discriminate up/down directions of moving lines of different contrasts, different lengths and for variable durations of motion.

In *control* conditions, the true direction of motion was normal to line orientation. In this case, local readings of velocity made within the lines signal a motion identical to the motion signals available at the line endings. For these conditions, all types of motion processing units mentioned above should correctly signal the true direction of line translation. In *test* conditions, the direction of motion is oblique relative to line orientation. Local readings of velocity within a line signal a direction which is different from the veridical motion signal available at the line endings. For these conditions only the responses to terminator motion or that of hypothetical "blob" units could signal the true direction of moving lines. The control and the test conditions are depicted in Fig. 1(b, c).

GENERAL METHOD

Stimuli

The stimuli were displayed on a 1280 × 1024 resolution display (Sony GDM 1950) with a refresh rate of 60 Hz. The experiment was under the control of a computer (PC-AT 386). Special designed software (Lorenceau & Humbert, 1990) was used to edit and animate the stimuli. These consisted of matrices of lines of the same orientation. The use of matrices of lines rather than a single line minimizes the pure positional information that would otherwise be available to perform the task. However, in a subsequent control experiment a single line was used with results similar to those obtained with matrices of lines. Two different line orientations—+20 and −20 deg from vertical—were used. Direction, plus or minus 20 deg from horizontal was well above direction discrimination threshold (Ball, Sekuler & Machamer, 1983). An apparent motion was produced by redrawing the lines in adjacent locations with a frame rate of 30 Hz. The speed was maintained at 6.5 deg/sec throughout the experiments. Line width was 1.02 min of visual angle. The background had a luminance of 12 cd/m^2. The inspection field viewed from 57 cm was circular and covered 24 deg of visual angle. A fixation point at the center of the screen helped observers to fixate during trials. A chinrest was used to maintain head position during a session. Viewing was binocular.

Procedure

In all experiments, the method of constant stimuli was used together with a 2AFC procedure. At the beginning of a session, observers were told that they would have to indicate the perceived direction (upward or downward) of moving lines even though an oblique motion was perceived (i.e. observers had to neglect the horizontal motion component). They were asked to answer as quickly as possible at the end of each trial (response times were recorded) by using the up and down arrows of the computer keyboard and to maintain fixation during trials. Before the beginning of a session, observers ran 20 trials with feedback. No feedback was given during experimental sessions. A session, 400 trials, lasted 20 min. Two different sessions were performed on different days. Before a trial, the orientation of the lines and the level of the variable under investigation (contrast, length or duration) was chosen at random. Within a trial the direction of motion could be up-to-the-left, up-to-the-right, down-to-the-left or down-to-the-right across line orientation [Fig. 1(c)]. Since the direction of motion was not correlated to the orientation of the lines, orientation could not be used as a cue to predict the direction of motion. Using a strategy which combines orientation discrimination with leftward or rightward discrimination would lead to chance level performance.

EXPERIMENT I: EFFECT OF LINE CONTRAST

Recently, Lorenceau and Shiffrar (1992) used a moving diamond with invisible corners to study motion integration across space. These authors found that integration of contour motion was facilitated at medium to low contrast. At high contrast, performance on tasks requiring the integration of disconnected contours into a rigid percept was poor. Rather, a vivid impression of incoherent motion dominated. These authors interpreted this effect as evidence that the reliable processing of line endings (or terminators) disrupts the integration process. Additional experiments in periphery and with noisy terminator motion strengthened this interpretation. However, from their results, it is not known whether the perceived direction and speed of individual straight contours is directly affected by contrast. In the present paper, direction discrimination of moving lines is studied under a variety of conditions. In a subsequent paper (Castet, Lorenceau, Shiffrar & Bonnet, in press) we show that the perceived speed of moving lines depends on line orientation, length and contrast. If local readings of velocity within the lines are more salient than the motion signals produced by line endings or "blob" detectors, one expects systematic errors in direction discrimination, since only the direction normal to line orientation would be signaled by this set of motion processing units (i.e. the aperture problem). Assuming that the correct identification of the direction of moving lines depends upon the reliable processing of the motion of line terminators, then low contrast that weakens the response to terminators should result in systematic errors in direction discrimination in our test conditions. If, on the other hand, some kind of "blob" detector, insensitive to line orientation, signals the global line motion, no error in direction discrimination should be observed, or these errors should be similarly distributed in the *control* and the *test* conditions.

Stimuli and subjects

In this first experiment five levels of contrast were used (12, 25, 39, 52 and 70%). These were calculated as follows:

$$C\% = 100 \times (L \text{ lines} - L \text{ background})/L \text{ background}$$

where L is the luminance level as measured with a CS 100 Minolta photometer. Line length was at a constant 2.7 deg of visual angle. The duration of motion was 332 msec.

Within a block (400 trials), the contrast level, the line orientation and the direction were chosen at random for each trial. Control and test conditions were mixed within a block. Each observer performed two blocks of trials on different days. Thus, each point in the figures below represents 160 trials.

Four observers took part in this first experiment, two of them were unaware of the hypothesis under investigation. All had normal or corrected-to-normal vision.

Results and discussion

Since accuracy was independent of orientation, data for the two different orientations (+20 and −20 deg) were pooled together. Accuracy for the control and the test conditions is plotted for four observers in Fig. 2(a, b). Reaction times for the same conditions are shown in Fig. 2(c, d).

In the *control* conditions, the contrast (i.e. the luminance) of the lines has little effect on accuracy. Performance is near ceiling for all except the lowest contrast (12%). For this last contrast level, the visibility of the lines was poor. As a consequence, performance decreased and reaction times increased. For higher contrasts, reaction times decrease slightly as contrast increases which is in agreement with previous reports (Luce, 1986).

In the *test* conditions, performance is far below chance level for the lowest contrasts and increases with contrast up to 90% correct. Thus, at low contrast, observers reliably *misperceived* the direction of line motion. For the lowest contrast used (12%), performance is somewhat higher than at 29% contrast. This can be explained by the poor visibility of the lines at this low contrast: on some trials, observers could not see the stimulus and therefore responded at random (invisible

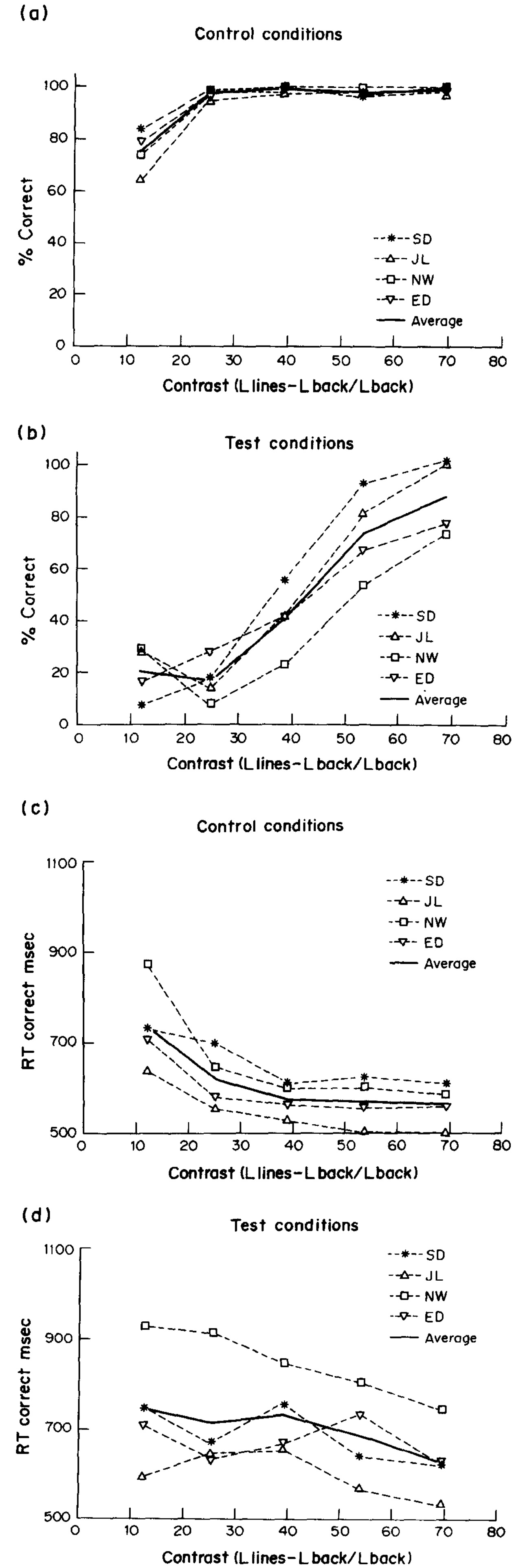


FIGURE 2. Accuracy for the discrimination of moving lines as a function of contrast for four subjects (dashed line) and average performance (continuous line): (a) accuracy in *control* conditions. (b) accuracy in *test* conditions. Reaction times in control conditions (c) and in test conditions (d).

lines would lead to chance level performance, i.e. 50%). At the intermediate levels of contrast used in this experiment, systematic errors in direction discrimination are observed. This indicates that observers reliably perceived a direction normal to line orientation. Reaction times for the correct responses [Fig. 2(b, c)] are slightly shorter in the control as compared to the test conditions. Since average reaction times are calculated on the basis of the correct responses alone, the comparison between control and test conditions might not be reliable. The difference in reaction time suggests, however, that observers needed more time to process correctly the direction in the test conditions. This point is addressed directly in Experiment III.

In the test condition, the vector normal to line orientation corresponds to a speed equal to 94% of the veridical speed. A 6% difference between two speeds is just discriminable with continuous motion and after training (McKee, 1981; De Bruyn & Orban, 1988). Under our conditions, observers did not report perceiving different speeds. If differences in apparent speed between the control and test conditions were reliable cues to perform the task, no systematic errors in direction discrimination should be observed, which is not the case.*

Because of the regular organization of the matrices of lines, low spatial frequency information exists in the display, mainly on the vertical axis. Note that this information alone is insufficient to perform the task because of the aperture problem that cannot be solved at these low spatial frequency. Similarly, virtual contours due to the alignment of line end points would move in the same direction in the control and test conditions. Thus, they would not provide information on the true direction of motion.

The systematic errors in direction discrimination of the lines at low contrasts suggest that motion units able to provide unambiguous responses were poorly activated as compared to units that face the aperture problem, i.e. motion units with receptive fields falling within the lines that signal a motion normal to line orientation. We suggest that at low contrast, their responses overcome the responses provided by line endings or "blob" detectors.

If "blob" units were primarily involved in signaling line motion, one would expect the same pattern of performance in the test and the control conditions since "blob" units are assumed to be unselective to orientation. Instead, we observed a strong asymmetry between the control and the test conditions. Lorenceau and Shiffrar (1992) provide an additional argument against the involvement of "blob" units: these authors studied motion integration across space with an occluded diamond whose visible sides had an heterogeneous luminance distribution. Luminance was either maximum at the line center and decreased smoothly toward the line endings or luminance was low at the center and increased toward the line endings. The overall luminance was equal in both cases. They found that integration of individual motion signals across space was more likely when luminance was low at the line endings. Since "blob" units should respond similarly in both cases—integrating the same luminance across their receptive field—we conclude from their results and the present data that it is unlikely that "blob" units are involved in coding the direction of moving lines, at least under our experimental conditions.

At high contrast in the test conditions, performance is near ceiling for all observers, suggesting that direction of terminator motion was unambiguously perceived. This further suggests the existence of a competition between units processing terminator motion and contour units that ambiguously signal the direction of motion. Does this competition depend on the number of units involved? In other words, are the responses of the different units pooled together prior to the competition level? Since the number of units activated by moving terminators should not strongly depend on line length whereas that of contour units should depend on line length, we addressed this question in the next experiment, using different line lengths.

EXPERIMENT II: EFFECT OF LINE LENGTH

To test the idea that a competition between the responses of contour units and that of line ending processing units accounts for the perceived direction of the lines, we replicated experiment I with lines of different lengths (0.3, 0.7, 1.3, 2.7 and 5.5 deg of visual angle). As line length increases, the number of contour units that are activated by the stimulus also increases, whereas the number of units processing terminator motion should remain approximately constant. Thus, the response of the overall population of contour units should increase while the response of the overall population of neurons activated by the motion of terminators should not. If a competition between contour and terminators units is involved in recovering the direction of moving lines in the test conditions, one expects accuracy to depend on line length. In the test conditions, accuracy should decrease with increasing line length since, as line length increases, an increasing number of neurons would signal a direction normal to line orientation, independent of the actual direction. In the control conditions, accuracy should be independent of line length since both contour and terminator units signal the actual direction of motion.

However, reducing line length also reduces the overall length visible on the screen, together with the mean luminance. In order to maintain these parameters, we changed the density of the lines so that the overall length and the mean luminance were unchanged as compared

*However, careful examination of the display with long duration of motion rendered this difference in speed noticeable at the lowest contrasts used (i.e. when direction was misperceived). It is worth noting that at low contrast and with free viewing conditions (long durations), one perceives a motion normal to line orientation whatever the actual direction. In addition, the lines appeared to slide along their orientation. This observation suggests that observers are not able to solve the "correspondence problem" (Ullman, 1981) under these specific conditions.

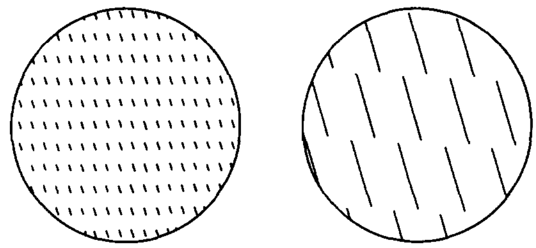


FIGURE 3. Examples of the stimuli used in experiment II. (a) Short lines, (b) long lines. Since a change in line length changes the overall luminance and the overall line length, the density of the lines was manipulated in order to maintain these parameters.

to experiment I. Thus, the ratio between the number of terminators and the overall length (i.e. the sum of all line's length) was manipulated (Fig. 3). For clarity, we refer hereafter to line length rather than to the ratio defined above.

Four observers took part in this experiment. They performed two blocks (400 trials) on different days. Within each block, the control and test conditions, together with the length, the line orientation and the direction of motion were chosen at random (see above section "procedure"). The contrast was fixed at a level (39%) that leads approximately to chance performance (i.e. 50 % correct responses) in experiment I and the same duration of motion (332 msec) was used.

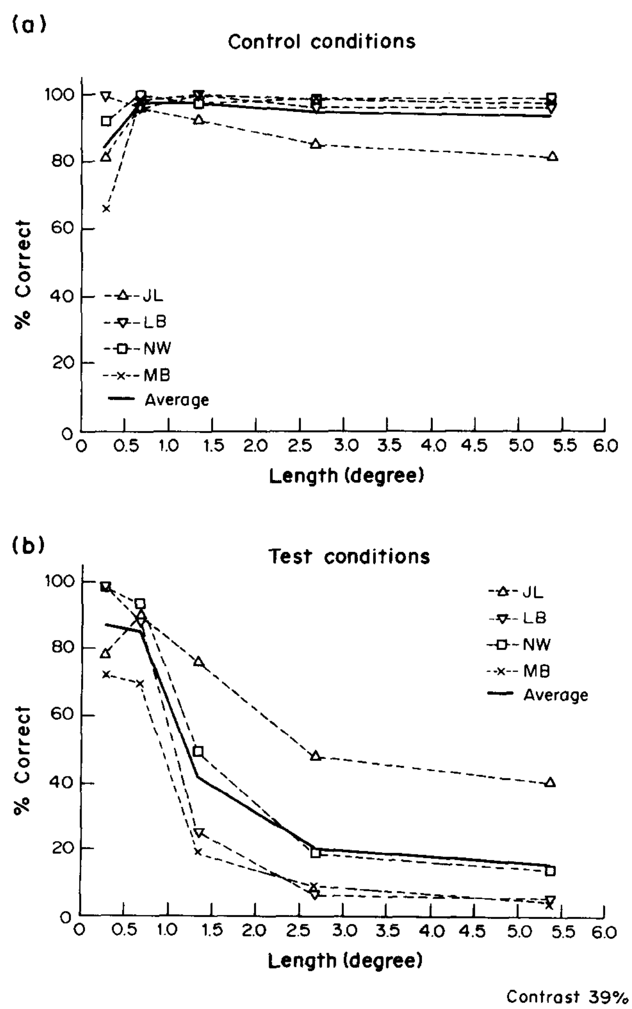


FIGURE 4. Accuracy for the discrimination of direction of moving lines as a function of line length. (a) Control conditions. (b) Test conditions.

Results and discussion

Since no systematic difference between orientations was observed, data for the two orientations were pooled together.

Accuracy is plotted as a function of line length for the control and the test conditions in Fig. 4(a, b). In the *control* conditions [Fig. 4(a)], performance is near ceiling for all observers. For the shortest length used, some observers complained that they could not always reliably see the stimulus. For these trials, they were told to answer at random. This explains why performance is somewhat lower for this particular length than for longer lengths.

In the *test* conditions [Fig. 4(b)], performance dramatically depends on line length. Accuracy is near ceiling for short lines and decreases as line length increases. Performance is far below chance level for medium and long lines. Thus, systematic errors were made by observers under these latter conditions. This suggests that, as in experiment I, observers perceived a direction normal to line orientation, whatever the veridical direction. Reaction times, not shown here, are roughly similar in the control and the test conditions.

Again, the results of this experiment are compatible with the existence of a competition between contour units and terminator processing units. For long lines the number of contour detectors that are activated is important. The overall response of these units would overcome the responses to terminator motion. For shorter lines fewer contour units would be activated by the stimulus. In this case, the response to terminator motion would dominate. However, one cannot exclude the possibility that, as line length decreases, a number of "blob" units are activated. These units could correctly signal the true direction and thus contribute to the increased performance observed for short lines. The steep decrease in accuracy as length increases is compatible with this view.

We mentioned above that in our display, the density of the lines increases as length decreases. Several authors (Sagi, 1990; Lorenceau & Boucart, 1992) have presented evidence that spatial interference between nearby elements of a texture increases with density. The spatial interference that could occur under our conditions might affect similarly the responses of both terminators and contour units, which should not influence performance. However, the results from Lorenceau and Boucart (1992) with moving figures embedded in stationary textures suggest that at high density the signal from terminators is specifically depressed. According to this view, it is unlikely that the high density used for the short lines in this experiment accounts for the present results, since a decrease in the response to terminator motion should result in a decrease in performance.

EXPERIMENT III: EFFECT OF DURATION OF MOTION

Studying the dynamics of recovery of the direction of moving lines may shed light on the underlying process. If, as we suggest, there exists a competition between the different units that process line motion, is this competition time dependent? In addition, does the dynamic of recovering the direction depend on line length and/or contrast?

To answer these questions, we replicated experiment I with five durations of motion (133, 232, 332, 432 and 531 msec. Two contrasts (39 and 70%) and two different lengths (1.3 and 2.7 deg) were used. Since the matrices of lines were larger than the test field, lines that disappear at one end were replaced by new lines at the other end.

Within a session four blocks of 200 trials each were performed, one block for each line length and each contrast. Within a block, the control and test conditions were mixed. For each trial, the direction and the duration of motion were chosen at random. Because the duration of motion could be as long as 531 msec, reaction times were not recorded. Three different observers performed four sessions on different days.

Results

The data for the two different orientations were pooled together. In the control conditions, accuracy is above 95% correct for all observers and does not significantly depend on duration nor on line length. For that reason, the data for the control conditions are not presented here. The results from three observers for the low contrast condition (39%) are plotted as a function of duration for the test conditions in Fig. 5(b). Data for two different line length are shown. In the test conditions, accuracy increases linearly with duration for all observers. Performance is below chance level for the shortest duration of motion, suggesting that observers systematically misperceived the direction of motion. Accuracy is better for short lines and worse for longer lines. This pattern of results holds for all observers although differences between observers can be large (see for instance observer MB who performed poorly at all durations).

The results from the same three observers, obtained using a higher contrast level (70%) are displayed in Fig. 5(a) as a function of duration. Accuracy strongly depends on duration in the test conditions. As a general trend, performance is better for this high contrast as compared with the low contrast conditions. Performance also depends on line length: for short lines, accuracy is better than for longer lines. Obvious ceiling effects appear at long duration for observers EC and ED. Data for observer MB are increased at this high contrast as compared to the low contrast conditions, although accuracy does not reach perfect discrimination at long duration.

The results indicate that direction discrimination strongly depends on duration of motion in the test conditions. This effect cannot be accounted for by a poor visibility of the lines at short durations, since the responses are not distributed at random: accuracy is near ceiling in the control conditions and far below chance level in the test conditions. The low level of performance in these later conditions suggests that observers consistently perceived a motion different from the true direction at these short durations. It is worth noting that for long durations and low contrast, observers did not perceive a straight path in the test conditions. Rather, they perceived a motion normal to line orientation at the beginning of the motion which smoothly turn into a motion oblique relative to line orientation.

The difficulty to determine the true direction suggests that tracking eye movements that could occur at long durations of motion did not help observers to perform the task. Moreover, if eye movements were used by observers in this task, no difference between long and short lines should be observed. It remains possible, as suggested by one of the reviewers, that the difference in accuracy for low and high contrast lines is due to the fact that high contrast terminators are necessary to initiate appropriate tracking eye movements, that could help observers to recover the true direction of motion at long durations. Although we cannot exclude this possibility, the potential influence of eye movements is, however, consistent with our interpretation that two different

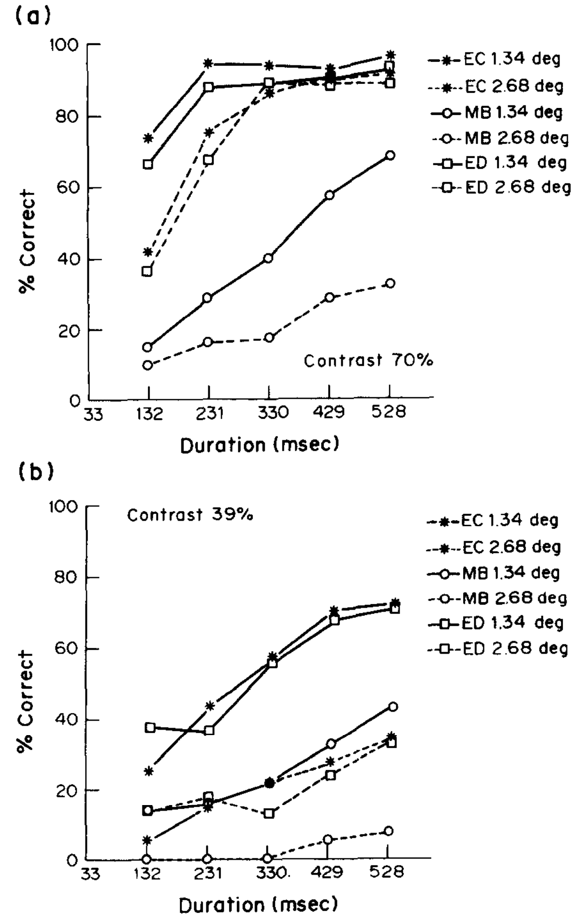


FIGURE 5. Direction discrimination as a function of duration of motion for two different line lengths for three obervers. (a) Low contrast conditions (39%). (b) High contrast conditions (70%).

types of units are involved in recovering the direction of moving lines.

In summary, the results are compatible with the existence of a dynamic competition between the response of terminator processing units and those of contour units. At the beginning of the motion, the response of contour units would overcome the response to terminators; the response to terminators would progressively override the responses of contour units, therefore allowing the recovery of the veridical direction.

A "WINNER TAKE ALL" MODEL

Using a simple "winner take all" model, we were able to simulate our data. The model relies on the involvement of two populations of units. One signals the motion of terminators, the other one signals ambiguous directions from the center part of the lines. The model considers the overall response of each population of units. These different units have different characteristics as suggested by the results of the three experiments presented above: (i) terminator processing units would have a lower contrast sensitivity than contour units (experiment I); (ii) the ratio between the overall response of terminator units and contour units would decrease with line length (experiment II); (iii) the time constant of integration of terminator units would be longer than that of contour units (experiment III). Thus, the response of each unit signaling either terminator motion or contour motion is a function of contrast and time. In the model, the probability of response of a single unit is described by the following function derived from that proposed by Quick (1974):

$$P_i = 1 - \exp[(-m/s(t)_i)^{\beta}] \quad (1)$$

with

$$s(t) = S/\exp[(-t/T_i)^{\beta}] \quad (2)$$

where P is the probability that the unit fires with its maximal response, m is the actual contrast, $s(t)$ is the contrast threshold of a unit at time t. Equation (2) is used to account for the fact that thresholds are time dependent (Bloch's law for contrast). In equation (2), t is the actual duration, T is the integration time constant of a unit, and S is the threshold for an infinite duration. The parameter β, set to 3 for all simulations in equation (1) and (2) is the slope of the psychometric function both along the contrast dimension and in the time domain.

For each type of unit, the activity of the overall population is calculated as the sum of each unit's activity according to equation (3):

$$A = \Sigma(a_i P_i) \quad (3)$$

where P_i is the probability calculated in equation (1) and a_i is the level of response saturation of each type of unit. This last parameter can be understood as the weight of each population of units (the weight of terminators units being larger than that of contour units). This parameter accounts for the fact that the visual system relies heavily on the motion of contour terminators (Wallach, 1976; Hildreth, 1984; Lorenceau & Shiffrar, 1992). The simulated dynamic of the competition between terminator units and contour units is shown in Fig. 6 for two different line lengths, as a function of contrast and duration. The probability of response of terminator units is displayed in Fig. 6(a). The probability of response of contour units is displayed for two line length in Fig. 6(b, c). Figure 6(d, e) shows the probability of response of the different units for two different line length. In the simulation, arbitrary contrast and time units were used. Thus, we indicate the ratios between the values chosen for each parameter rather than the absolute values. The ratio of contrast thresholds of terminators and contour units is around 3. The ratio between the integration time constants of the two types of unit is around 3. The weights of each type of unit were in a 10/1 ratio. However, the ratios could be greatly varied or noise could be added to each unit response without qualitative differences in the outputs. In the model, the population of units having the higher probability of response determined the perceived direction.

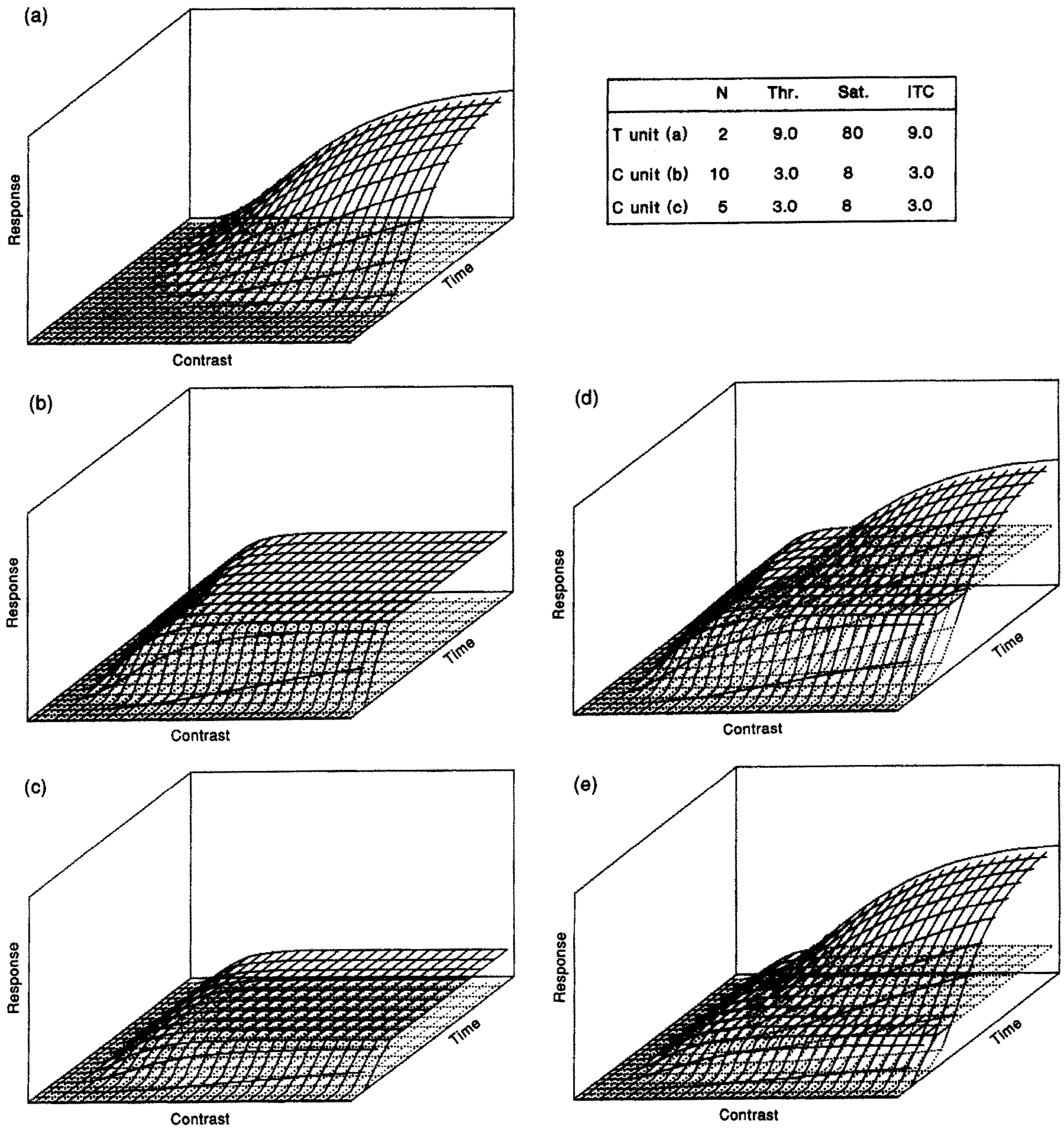
While this model does not provide a quantitative estimation of the characteristics of each type of units and does not specify the exact nature of the interactions between the different units, it did allow to test the plausibility of our interpretation of the data.

Several computational models of motion interpretation make use of terminators as important clues that allow to recover the motion of objects (Hildreth, 1984; Hildreth & Koch, 1987; Yuille & Grzywacz, 1988; Bülthoff, Little & Poggio, 1989). To our knowledge, these models do not incorporate different contrast sensitivity and different integration time constants for the different units of the networks. The present data and previous results from experiments on motion integration across space (Lorenceau & Shiffrar, 1992) suggest that incorporating these features in these models would be necessary to account for human perception of translating motion.

It is worth noting that our model is inadequate for motions involving rotations or deformation. With rotating motion, the direction signaled by terminators is congruent with that signaled by contour units. Since terminator processing units do not provide a better estimate of the true velocity than any other units there is no need that signals from terminators "constrain" other readings of velocity.

GENERAL DISCUSSION

We have presented experiments demonstrating that observers systematically misperceive the direction of lines moving obliquely relative to their orientation. Errors in direction discrimination occur at low contrast, long line length and short durations of motion. The distribution of errors in the control and test conditions suggests that errors are not due to either the visibility of the stimuli or to eye movements. When the direction is misperceived, observers see a motion component normal to line orientation rather than the veridical direction.



	N	Thr.	Sat.	ITC
T unit (a)	2	9.0	80	9.0
C unit (b)	10	3.0	8	3.0
C unit (c)	5	3.0	8	3.0

FIGURE 6. Simulation of the dynamic of the competition between contour and terminator processing units that would process line motion. *T*, terminator; *C*, contour; *N*, number of cells; Thr, threshold; Sat, maximal response of a single unit; ITC, integration time constant of a unit. (a) Overall response of 2 terminator units as a function of contrast and time. (b) Overall responses of 10 contour units (long lines). (c) Same as (b) for 5 contour units (short lines). (d) Output of the two types of units for long lines as a function of contrast and duration. (e) Same as (d) with short lines that involve less contour units. In the model, the greater activity of a population of units (continuous line) determines the perceived direction. See text for details.

From the results of experiment I (variable contrast), we argue that the information needed to perform the task (i.e. motion signals from terminators) is not available for the visual system at low contrast. This suggests that units able to process terminator motion have a lower contrast sensitivity than contour units that ambiguously signal the direction of contour motion. As the contrast level increases, the probability that terminator motion is reliably perceived increases. So does performance.

The results from experiment II (variable length) strengthen the hypothesis of a competition between terminator units and contour units. As line length increases the number of contour units able to respond to line motion also increases while that of terminator processing units would not. As predicted from the relative activity of the population of units involved in signaling motion, performance decreases in the test conditions.

Finally, experiment III (variable durations) enlightens the dynamic of the competition between the different types of units responding to line motion. The responses from contour units would dominate at short durations of motion. As duration of motion increases the responses to terminator motion would progressively overcome the responses from contour units. The time needed to complete this process appears to depend on contrast and line length.

The effect of duration on performance can be interpreted in two ways. The integration time constant of terminator units could be longer than that of contour units as implemented in the model described above. In that case, terminator units would respond with a delay to terminator motion as compared to the signal arising from contour units. This difference in the integration time constant could explain the effect of contrast and line length reported here: in order to reach a level of response able to compete with the responses of contour units, terminator units would have to integrate motion information for a longer time.

As an alternative, one could suggest that the integration of local velocity measurements through competitive interactions is a time consuming process. This idea was developed by Hildreth (1984) who proposed an algorithm that allows the recovery of the true velocity of moving contours by smoothing the velocity along contours [however, see Nakayama and Silverman (1988) for an extension of the algorithm]. She has, with others (Wallach, 1976; Nakayama & Silverman, 1988a, b), further suggested that the responses to the unambiguous motion of terminators propagates along contours. The results from experiment III seem compatible with this view: the unambiguous signal from terminators could propagate along the lines and constrain the ambiguous motion signals. The fact that one needs longer durations to recover the direction of longer lines could be explained by the fact that the propagation process would be time consuming. As line length increases the time needed to propagate the signals from terminators to the entire line would also increase. Although our data are compatible with this interpretation, they do not provide clear cut evidence of a propagation process in the visual system. It is worth noting that the two processes (different time constants together with a propagation process) may both be involved.

ELECTROPHYSIOLOGY

There is electrophysiological evidence to support the existence of two different types of units corresponding to the terminator and the contour units we invoked to account for our data. As a general rule simple cells that are directionally selective always prefer a direction of motion normal to their preferred orientation. These cells should ambiguously signal the direction of lines or bars moving obliquely relative to their orientation. On the other hand, end-stopped cells commonly encountered in area 17 and 18 (Gilbert, 1977; Rose, 1979; Orban, Kato & Bishop, 1979; Dobbins *et al.*, 1989) or cells in area 19 of cat visual cortex (Saito *et al.*, 1988; Tanaka, Ohzawa, Ramoa & Freeman, 1987) may well respond to the motion of terminators. In particular, Saito *et al.* described dot-responsive cells that are activated by moving dots or by the end of a bar moving through their receptive field, but that are unresponsive when an elongated bar covers the whole receptive field. These cells could correctly signal the direction of moving terminators. It should be noted here that differences in the response latencies of neurons are observed in area 19 of the cat (Duysens, Orban, van der Glas & Maes, 1982). However it is not known whether these differences are correlated with the functional properties of neurons in this area. In addition, endstopped cells require long stimulus duration (Duysens, Orban, Cremieux & Maes, 1985) and high contrast stimuli (De Weerd, Vandenbussche & Orban, 1990) to be optimally activated. Although we speculate that units in areas 17, 18 and 19 could be a neural substratum able to signal line motion, their relationships have not been, to our knowledge, studied in detail. Nevertheless, there exists anatomical pathways within (Gilbert & Wiesel, 1989) and across different visual areas (Felleman & Van Essen, 1991), that could subserve such interactions.

The existence of a propagation process remains highly speculative since it is not, to our knowledge, supported by experimental data. Nevertheless, recent electrophysiological studies (Gray & Singer, 1989; Gray, König, Engel & Singer, 1989) have reported a synchronization between the activity of visual neurons that could share similar characteristics with this hypothetical propagation process. Additional evidence from electrophysiological recordings of visual neurons are needed to test such possibility.

REFERENCES

Adelson, E. H. & Movshon, J. A. (1982). Phenomenal coherence of moving visual patterns. *Nature, 300,* 523–525.

Bülthoff, H., Little, J. & Poggio, T. (1989). A parallel algorithm for real-time computation of optical flow. *Nature, 337,* 549–553.

Ball, K., Sekuler, R. & Machamer, J. (1983). Detection and identification of moving targets. *Vision Research, 23,* 229–238.

Castet, E., Lorenceau, J., Shiffrar, M. & Bonnet, C. (1993). Perceived speed of moving lines depends on orientation, length, speed and luminance. *Vision Research.* In press.

De Bruyn, B. & Orban, G. A. (1988). Human velocity and direction discrimination measured with random dot patterns. *Vision Research, 28,* 1323–1335.

De Weerd, P., Vandenbussche, E. & Orban, G. (1990). Bar orientation discrimination in the cat. *Visual Neuroscience, 4,* 257-268.

Dobbins, A., Zucker, S. W. & Cynader, M. S. (1989). Endstopping and curvature. *Vision Research, 10,* 1371–1387.

Duysens, J., Orban, G. A., Cremieux, J. & Maes, H. (1985). Velocity selectivity in the cat visual system. III. Contribution of temporal factors. *Journal of Neurophysiology, 231,* 279–291.

Duysens, J., Orban, G. A., van der Glas, H. W. & Maes, H. (1982). Receptive field structure of area 19 as compared to area 17 of the cat. *Brain Research, 231,* 279–291.

Felleman, D. J. & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex, 1,* 1–47.

Fennema, C. L. & Thompson, W. B. (1979). Velocity determination in scenes containing several moving objects. *Computer Graphics and Image Processing, 9,* 301–315.

Ferrera, V. P. & Wilson, H. R. (1990). Perceived direction of moving two-dimensional patterns. *Vision Research, 30*, 273–287.

Gilbert, C. D. (1977). Laminar differences in receptive fields properties of cells in cat primary visual cortex. *Journal of Physiology, London, 268*, 391–421.

Gilbert, C. D. & Wiesel, T. N. (1989). Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex. *Journal of Neuroscience, 9*, 2432–2442.

Gray, C. M. & Singer, W. (1989). Stimulus specific oscillations in orientation columns of cat visual cortex. *Proceedings of the National Academy of Science U.S.A., 86*, 1698–1702.

Gray, C. M., König, P., Engel, A. K. & Singer, W. (1989). Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. *Nature, 338*, 334–337.

Hildreth, E. (1984). *The measurement of visual motion*. Cambridge, Mass.: MIT Press.

Hildreth, E. & Koch, C. (1987). The analysis of visual motion: From computational theory to neuronal mechanisms. *Annual Review of Neuroscience, 10*, 477–533.

Horn, B. K. P. & Schunck, B. G. (1981). Determining optical flow. *Artificial Intelligence, 17*, 185–203.

Hubel, D. H. & Wiesel, T. N. (1965). Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat. *Journal of Neurophysiology, 28*, 229–289.

Hummel, J. E. & Biederman, I. (1992). Dynamic binding in a neural network for shape recognition. *Psychological Review, 99*, 480–517.

Lorenceau, J. (1987). Apparent speeds and directions of coherent motion. *Journal of Physiology, London, 143P*, 9.

Lorenceau, J. & Boucart, M. (1992). A paradoxical enhancement of motion discrimination within texture. *Perception (Suppl.) 21*, 67a.

Lorenceau, J. & Humbert, R. (1990). A multiple purpose software package for editing two-dimensional animated images. *Behavior Research Methods, Instruments and Computers, 22*, 453–465.

Lorenceau, J. & Shiffrar, M. (1992). The influence of terminators of motion integration across space. *Vision Research, 32*, 263–273.

Luce, R. D. (1986). *Response times: Their role in inferring elementary mental organization*. New York: Oxford University Press.

McKee, S. P. (1981). A local mechanism for differential velocity detection. *Vision Research, 21*, 491–500.

Movshon, A. J., Adelson, E. H., Gizzi, M. S. & Newsome, W. T. (1986). The analysis of moving visual patterns. *Experimental Brain Research, 11*, 117–152.

Nakayama, K. & Silverman, G. H. (1988b). The aperture problem II: Spatial integration of velocity information along contours. *Vision Research, 28*, 747–753.

Orban, G. A. (1984). *Neuronal operations in the visual cortex*. Berlin: Springer.

Orban, G. A., Kato, H. & Bishop, P. O. (1979). End-zone region in receptive fields of hypercomplex and other striate neurons in the cat. *Journal of Physiology, 42*, 818–832.

Peterhans, A. & von der Heydt, R. (1989). Mechanisms of contour perception in monkey visual cortex. II. Contours bridging gaps. *Journal of Neuroscience, 9*, 1749–1763.

Perrone, J. (1990). A simple technique for optical flow estimation. *Journal of the Optical Society of America, A 7*, 264–278.

Poggio, J., Torre, V. & Koch, C. (1989). Computational vision and regularization theory. *Nature, 337*, 314–319.

Quick, R. F. (1974). A vector magnitude model of contrast detection. *Kybernetics, 16*, 65–67.

Rodman, H. R. & Albright, T. D. (1989). Single-unit analysis of pattern motion selective properties in the middle temporal visual area MT. *Experimental Brain Research, 75*, 53–64.

Rose, D. (1979). Mechanisms underlying the receptive field properties of neurons in cat visual cortex. *Vision Research, 19*, 533–544.

Sagi, D. (1990). Detection of an orientation singularity in Gabor texture: Effect of signal density and spatial-frequency. *Vision Research, 30*, 1377–1388.

Saito, H., Tanaka, K., Fukada, Y. & Oyamada, H. (1988). Analysis of discontinuity in visual contours in area 19 of the cat. *Journal of Neuroscience, 8*, 1131–1143.

Shimojo, S., Silverman, G. & Nakayama, K. (1989). Occlusion and the solution to the aperture problem for motion. *Vision Research, 29*, 619–626.

Tanaka, K., Ohzawa, I., Ramoa, A. S. & Freeman, R. D. (1987). Receptive field properties of cells in area 19 of the cat. *Experimental Brain Research, 65*, 549–558.

Ullman, S. (1981). The effect of similarity between line segments on the correspondence strength in apparent motion. *Perception, 9*, 617–626.

Versavel, M., Orban, G. A. & Lagae, L. (1990). Responses of visual cortical neurons to curved stimuli and chevrons. *Vision Research, 30*, 235–248.

Wallach, H. (1935). Ueber visuell wahrgenommene bewegungrichtung. *Psychologische Forschung, 20*, 325–380.

Wallach, H. (1976). *On perception*. New York: Quadrangle.

Welch, L. (1989). The perception of moving plaids reveals two processing stages. *Nature, 337*, 734–736.

Yuille, A. L. & Grzywacz, N. M. (1988). A computational theory for the perception of coherent visual motion. *Nature, 333*, 71–74.

Zucker, S. W., Iverson, L. & Hummel, R. A. (1990). Coherent compound motion: Corners and nonrigid configurations. *Neural Computation, 2*, 44–57.