Isolating the Effect of One-Dimensional Motion Signals on the Perceived Direction of Moving Two-Dimensional Objects

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A considerable body of evidence suggests the existence of a two-stage mechanism for the detection of global motion. In the first stage the motion of elongated contours is extracted and then at the second stage these one-dimensional (1D) motion signals are combined. What is the nature of the computation carried out in combining the 1D motion signals towards forming a global motion percept? We devised a set of stimuli that differentiate between different possible computations. In particular, they distinguish between a velocity-space construction (such as intersection of constraints) and a linear computation such as vector averaging. In addition, these stimuli do not contain two-dimensional (2D) motion signals such as line intersections, that allow unambiguous determination of global velocity. Stimuli were presented in uncrossed disparity relative to the aperture through which they were presented, to reduce the effect of line terminator motion. We found that subjects are unable to detect the veridical global direction of motion for these stimuli. Instead, they perceive the stimulus pattern to be moving in a direction which reflects the average of its 1D motion components. Our results suggest that the visual system is not equipped with a mechanism implementing a velocity-space computation of global motion.

Aperture problem Component motion Global motion

INTRODUCTION

Detection of a rigid object undergoing translational motion is a task human observers perform effortlessly in everyday life. However, the detailed processing of motion information involved in this computation is not fully understood. In particular, if the size of the object is significantly larger than the typical receptive field size of primary visual cortical cells, then the visual system must deal with the problem of integrating the local motion information carried by different cells of small receptive fields into a single global motion percept. A problem related to this is the aperture problem (Fenner & Thompson, 1979): the motion of a straight line moving behind an aperture is inherently ambiguous, in that only the velocity component perpendicular to the line's orientation is measurable. If an object is large enough so that the motion of its various parts, coded on different neurons, can be approximated by moving straight lines, each cell then carries only partial information about the global motion of the complete object. Information about the motion of any two differently oriented lines, however, is sufficient (mathematically) for determining the global velocity of the object, by way of a velocity-space construction, such as the intersection of constraints (IOC) algorithm (Adelson & Movshon, 1982; see Fig. 1). It has been suggested (Adelson & Movshon, 1982) that the visual system uses this possibility to compute the global velocity of images in two stages, first detecting the velocities of oriented contours belonging to the image and then at the second stage combining this information to produce the global image velocity through a neural implementation of the IOC algorithm.

Evidence for two stages in the motion computation has been obtained in several psychophysical experiments. Bonnet (1981), Adelson and Movshon (1982) and Movshon, Adelson, Gizzi and Newsome (1985) used techniques of contrast manipulation, adaptation and masking by noise to demonstrate that the coherent percept of two superimposed moving sine wave gratings as a single moving plaid involves at some intermediate stage mechanisms which are sensitive to the motion of its oriented components. More recently, Welch (1989) showed that the lower bound for speed discrimination of plaid motion is determined by these orientation sensitive mechanisms. Derrington and Suero (1991) elaborated the adaptation paradigm to show that adaptation to one of the component gratings can affect the perceived direction of motion of the plaid. There is strong
evidence, therefore, that the visual system does indeed use such a "two-stage process", first detecting the separate motions of elongated components of the image [one-dimensional (1D) motion signals] and then combining them into a single global [two-dimensional (2D)] motion signal.

However, the studies mentioned above did not address either of the following two issues: (1) what is the nature of the computation carried out on the component velocities in combining them to a single global velocity? As already noted by Adelson and Movshon, a linear operation such as averaging the component velocities in general would not result in the veridical global velocity. It was therefore assumed that what takes place is a velocity-space computation, which can be formalized as a nonlinear operation on the component velocity vectors. In all experiments mentioned above, plaid patterns which are the superposition of sinusoidal gratings at different orientations were used as stimuli. However, the nature of the plaid used in the studies by Adelson and Movshon (1982), Movshon et al. (1985), Welch (1989) and Derrington and Suero (1991) does not enable one to distinguish between the two possibilities of velocity-space computation vs velocity averaging. This is because the plaid employed in these studies were composed of two gratings of identical speeds, resulting in the global direction of motion lying along a symmetry axis of the pattern. For these specific cases, the linear operation of summing or averaging the component velocities would also lead to a correct result for the global direction of motion (although not of the global speed).

(2) What is the relative contribution of the motion of localized cues to the computation of direction and speed? Examples of localized cues are, in plaid, the areas of intersection of maxima or minima of the two gratings, sometimes referred to as "blobs" (Adelson & Movshon, 1982). This question is of much importance, since the motion of localized regions in the image is always veridical. While demonstrating that an orientation sensitive mechanism for the detection of motion exists, the studies mentioned above did not rule out the possibility that another mechanism, specializing in the detection of the motion of localized regions of luminosity gradient, might also contribute to the computation of global motion velocity. This mechanism may have different characteristic behavior than the component motion detectors (such as a lower sensitivity for the discrimination of speed).

Preliminary evidence that the perceived direction of motion may deviate from a correct combination of the 1D motion signals was obtained by Bonnet (1981) for the special case of orthogonal gratings ("gingham patterns"). More recently, Ferrera and Wilson (1990, 1991) and Yo and Wilson (1992) addressed in a series of studies the first question raised above, concerning the nature of global motion computation. They presented subjects with stimuli which they termed "type II plaid". The plaid consisted of two superimposed sinusoidal

![FIGURE 1. The aperture problem and the IOC solution. The motion of an elongated contour, whose endpoints lie outside the field of view, is inherently ambiguous since only the velocity component perpendicular to the contour (the 1D velocity) is measurable. The family of vectors which represent the possible velocities of a contour (solid arrows) end on a single constraint line (dashed line). The vector representing the object's global velocity ends at the intersection of the constraint lines (shaded arrow). In the special case when the contours are oriented symmetrically around the global velocity (a), the sum of the 1D velocity vectors lies along the global direction of motion. This, however, does not apply in the general case (b).](image-url)
gratings which move at different speeds so that the resultant 2D velocity of the plaid is substantially different from the two 1D component velocities, actually lying outside the region they delimit. They found that for short (80 msec) stimulus presentations, subjects perceived the plaids as moving in the direction of the sum of the 1D components, leading to deviations of up to 50 deg from the (mathematically) correct direction of motion. However, for longer presentation times (250 msec), the errors in perceived direction of motion decreased significantly, to 5 deg from the correct global direction. They concluded that the computation of global motion from 1D motion information deviates from an exact implementation of an IOC procedure. However, the extent of this deviation and the nature of the computation that is carried out on the 1D motion signals, is hard to assess using plaid patterns. This is because, as noted above, plaids contain localized features whose motion may be detected by other mechanisms and the relative contribution of these hypothesized mechanisms to the final motion percept is not known.

The experiments presented in the present study were designed to determine the nature of the computation carried out by the visual system when performing 1D to 2D motion integration in the absence of localized cues. As in the case of the type-II plaids, the global direction of motion of the stimuli we used deviated substantially from their 1D component velocities and from their vector sum. However, in addition, the stimuli did not contain the unambiguous motion signals of localized features which exist in plaids. Special care was taken to account for the effect of motion signals arising from line terminators, thereby isolating the effect of 1D motion signals on the perceived direction of motion. By this determination of the motion computation based on the 1D motion signals, we were able to infer the importance of localized features such as line terminators and isolated dots to global motion mechanisms.

Although lacking many of the clues abundant in everyday moving objects, the stimuli we used still contained enough velocity information for correct computation of the global direction of motion: if the visual system uses a velocity-space computation to produce a 2D velocity vector, then depriving it of other clues should have little effect. In this case, we would expect the visual system to compute correct 2D velocities (limited by the system’s acuity). If, on the other hand, the 2D velocity computation relies heavily on either the localized region motion clues, or on the 1D vector sum lying close to the global direction of motion, or on both, then the system should show large errors in motion perception. The experiments reported here support the second possibility.

METHODS

The stimuli comprised a set of differently oriented lines which all intersect at a single point. The lines were 45 sec arc (1 pixel) wide, of 100 cd/m² luminosity, drawn on a 40 cd/m² gray background; contrast [(L_{\text{max}} - L_{\text{background}})/L_{\text{background}}] was thus 1.5. Stimuli were generated by a Lexidata pg-90 graphics controller on a 19 in. Adage Monitor (1280 x 1024 pixels). Refresh rate was 60 Hz.

Line orientations changed in equal angular steps within a single quadrant with a step size of 9 deg. The set of lines was not presented in full, however, but rather only a portion of it was visible, as if through an aperture in an otherwise darkened screen. The location of the rectangular aperture was fixed on the screen throughout each trial and the location of the set of lines was changed from frame to frame, so as to mimic smooth translational motion in frontoparallel plane.

When a set of lines that belong to a single rigid object moves behind an aperture, two types of motion signals are produced. First, there are the velocities of the lines comprising the image, which we term the 1D signals. If the object moves with speed \( V \) in direction \( \theta \), then all 1D velocities are confined to lie within the half-plane \( (\theta - 90, \theta + 90) \). The speed of line \( i \) is given by \( V_i = V \cos(\theta - \theta_i) \), where \( \theta_i \) is the line’s direction of motion, which is perpendicular to its orientation and lies within the above half-plane. The magnitude of all 1D velocities is therefore smaller than or equal to the object’s speed, \( V \). The global velocity of the object can be recovered by using a velocity–space construction (such as IOC). In general, summing or averaging the 1D velocities results in a vector which does not coincide with the (mathematically) correct global velocity. However, in the special case where the lines comprising the object are oriented symmetrically around the global direction of motion, summing (or averaging) the 1D velocities results in a correct direction of motion (although an erroneous result for the speed). Another special case occurs when the lines comprising the object can be grouped into pairs of orthogonal orientations: summing the 1D velocities would again result in a correct global direction of motion. (Note, however, that the two cases differ in that the latter requires weighting of the direction of motion with speed before averaging.) The more the component velocities of an object approximate one or both of those conditions, the harder it is to distinguish between a velocity–space computation and some form of averaging of the component velocities. Therefore, in order to check whether the visual system is able to compute an object’s global direction of motion correctly from its 1D motion signals under unfavorable conditions, we construct the stimuli to be as different as possible from the above two conditions. (1) the orientations of the lines comprising the image were restricted to lie within a single quadrant, thus eliminating the possibility of orthogonal pairs. (2) The global velocity of the stimulus pattern was always along one of the major axes and therefore no pair of 1D velocities which lie symmetrically around the global direction of motion existed. A drawing of the stimulus pattern and its directions of motion used in the experiment is shown in Fig. 2(a).

The second class of motion signals produced when an object such as that of Fig. 2(a) moves behind an aperture are the motion of the line terminators along the aperture
FIGURE 2. The stimulus. (a) Schematic description of the form of the stimulus pattern used in the experiment and its possible directions of motion. The stimulus comprised a set of lines which intersect at a single point. The pattern was translated as a rigid body in one of four possible directions (arrows). Confining all line orientations to lie within a single quadrant and the motion direction to lie along the horizontal or vertical axes, prevents the generation of symmetrical or orthogonal pairs of 1D velocities by the stimulus pattern. The stimulus was only partially visible through a rectangular aperture and was presented in uncrossed disparity (16 min arc) relative to aperture boundaries. In (b) and (c) the areas visible through the aperture at onset and termination of stimulus motion are shown for two cases. Note that what is moving is the pattern, not the aperture! (b) Stimulus condition 1: the rectangular aperture is elongated perpendicular to the pattern’s direction of motion. (c) Stimulus condition 2: the aperture is elongated parallel to the pattern’s direction of motion.

To understand the stimuli more thoroughly, let us first consider the terminator motion signals. These signals originate from the motion of line intersections, but are eliminated in this study by the use of an aperture which hides the unique intersection point. The terminator motion signals are also confined to lie within the half-plane $(\theta - 90, \theta + 90)$. The direction of motion of the terminators is determined by the orientation of the aperture’s borders, $\theta_b$, and the speed of the terminator of line $i$ is given by $V_n = V_i \cos(\theta_i - \theta_b)$, where $V_i$ and $\theta_i$ are the magnitude and direction of the 1D velocity of the line. The global direction of motion can therefore not be recovered directly from the terminator motion signals, either in direction or in speed.

The terminator motion signals can, however, affect the perceived global velocity, as was already observed by Wallach (1935, 1976): a set of moving parallel oblique lines are perceived as moving vertically if viewed through a vertically elongated aperture, an effect known as the barber pole illusion. In this case of parallel lines, the terminator motion along the longer axis of the aperture have a stronger effect than the 1D velocity signals and dominate the perception of motion.

In order for the stimulus to enable us to distinguish between a motion percept dominated by the terminator signals and one which is determined primarily by the 1D signals, we take the aperture to be rectangular (1.7 x 5.1 deg) and orient its longer axis perpendicular to the pattern’s global direction of motion. Thus, if subjects perceive motion as directed along the aperture’s long axis it should be attributed to the effect of the terminator motion. We term this case stimulus condition 1. An example of the stimulus pattern and its motion behind the aperture in this case is shown in Fig. 2(b). We then compare it with the case where the long axis of the aperture is parallel to the pattern’s global direction of motion and term this case stimulus condition 2, an example of which is shown in Fig. 2(c).

First, let us remark that in pilot experiments we found that the tendency to see motion directed along aperture borders is not as compelling for the stimuli we used as in the case of a sine-wave grating or parallel stripes of the barber pole illusion. This was particularly true for stimulus condition 1. One possible reason for this is that in this case, the terminator speeds are different for the differently oriented lines (see details in next section) and therefore the strong uniform motion of all terminators is not present here. However, some bias towards judging the motion as directed along the aperture’s border still seems to exist for some observers and we therefore adopted a technique which was introduced by Shimojo, Silverman and Nakayama (1989). They demonstrated that when a set of parallel lines is presented in uncrossed disparity, as if behind a vertically elongated rectangular aperture, subjects perceive the motion as perpendicular to the line orientation, thus abolishing the barber pole illusion. All stimuli in the experiments to be described were therefore presented in uncrossed disparity of 16 min arc at a fixed viewing distance of 120 cm, by the use of prisms which directed a slightly shifted image to each of the two eyes.

A total of six subjects (three male, three female) participated in the experiment. They were all paid undergraduate students, unaware of the question under research. All had perfect or properly corrected eyesight and were found to have normal disparity vision. Subjects were verbally instructed that they were going to see translational motion of a rigid body which is partially hidden behind an aperture and were asked to report in what direction they perceive the object to be moving. Two of the subjects were shown a few examples of the full-screen stimulus at the beginning of the first three
sessions, with no significant difference between their responses and those of the other subjects.

Subjects fixated a point which was at a fixed location on the screen, at zero disparity. The aperture was randomly located to the right or left of the fixation point, with its border 30 min arc away from it, with equal probability. Each trial consisted of the following stages: the set of lines appeared within the aperture. Subjects fused the stimulus to their satisfaction and then struck a ready key to initiate the motion. The stimulus motion started after a random delay of 0.5–1 sec and lasted for 1.28–2.56 sec, depending on stimulus speed. The aperture was then darkened and an arrow appeared on the screen, with its tail located at the fixation point, pointing in a random direction. Subjects used the keyboard to adjust the arrow in the direction of perceived motion. They could use both clockwise and counterclockwise coarse (90 deg) or fine (1 deg) arrow movements. When subjects were satisfied with the arrow’s direction, they hit the ready key and the same stimulus appeared for a second time, followed by the arrow, pointing in the direction to which the subject had adjusted it in the first presentation. Only fine arrow movements were enabled this time, to allow for small corrections in the arrow’s direction.

In addition to the two stimulus conditions described above, presentations of stimuli composed of parallel lines were interleaved, for the purpose of isolating and quantifying the effect of terminator motion (see below).

Each stimulus was presented 48 times to each of the subjects, within four sessions of 12 repetitions of all stimulus conditions in each. Order of presentation was randomized and the stimuli were randomly rotated within the single quadrant.

Response data were subsequently folded back into a single quadrant.

RESULTS

Stimulus condition 1

The response of subjects to the first two stimuli we consider is shown in Fig. 3(a, b). For the data of Fig. 3(a), the stimulus pattern moved horizontally such that at its nearest location, the intersection point of the lines was at a distance of 0.8 deg from the aperture’s closest corner [upper left corner in Fig. 2(b)] and at its furthest location the distance was 4.8 deg. For Fig. 3(b), the motion was again horizontal and the nearest and furthest distances of the intersection point from aperture’s closest corner were 4.8 and 8.8 deg, respectively. Speed of pattern was 3 deg/sec in both cases. Data in Fig. 3 (and subsequently in Fig. 4) are presented in the following manner: the striped arrow points in the direction of the veridical global motion of the stimulus pattern (the set of lines). The solid arrow points in the direction of the line terminator motion, along the longer boundary of the aperture. The shaded regions identify the average direction of the 1D component motions (see below). Finally, the open white arrows demonstrate the direction of perceived motion as reflected in the individual subjects’ mean responses. Results for motion towards and away from the intersection point were averaged after no significant difference was found between the two cases for most of the subjects.

The first observation is that the perceived direction of motion deviates substantially from the (mathematically) correct global direction of motion. Subjects are thus unable to detect the global direction of motion of the stimuli we used. Instead, they point the arrow in a direction which is intermediate to the 1D velocities generated by the pattern’s motion. The results of Fig. 3 therefore suggest that the visual system is not equipped with a mechanism of computing the global direction of motion based on 1D motion information for general stimuli.

A few remarks should be made at this point. First, it should be emphasized that the stimuli of Fig. 3 contained, in principle, sufficient information for determining the pattern’s global motion from the 1D velocities: even at its farthest separation from the lines’ intersection point, the stimulus contained lines which produce 1D velocities separated by at least 18 deg in direction of motion (because three or more neighboring lines were visible through the aperture at all times) and 30% in speed, well above reported human limits (Orban, Wolf & Maes, 1984; McKee, Silverman & Nakayama, 1986). Furthermore, these were not brief presentations—the stimuli were on for a long duration of 1.28 sec, suggesting that the challenge posed by the stimuli to the visual system is not due to insufficient temporal processing.

Second, we note that the inability to detect the direction of motion veridically is a robust phenomenon, which does not depend on the specific parameters used for the stimuli of Fig. 3. We have found basically the same results after manipulating the contrast of the stimuli (in the range of 0.25–2.5), the density of the lines (angles between adjacent lines 3–9 deg) and the global speed of the patterns (1–8 deg/sec, traded off with stimulus duration). Removal of the fixation point and allowing subjects to use eye movements also maintained the same average perceived directions, but caused an increase of the SEs. Also, the authors’ personal observation and that of other non-naive observers, is that knowledge of the true global direction of motion does not help achieve a “correct” percept.

Lastly, an important qualitative observation is that along with the systematic errors in determining the global direction of motion (of which they are unaware), subjects reported that they did not perceive the stimulus pattern as rigid, but rather saw it “deforming”. We believe that this fact is in strong support of the claim that the visual system is not equipped with a mechanism to compute global velocity from the 1D component velocities for general (non-symmetrical) objects. There is evidence that when a rigid interpretation of motion exists, the visual system usually prefers it to other physically possible ones (Hildreth, 1984 and references therein). The fact that for the stimuli of Fig. 3 such an
interpretation, though existing, was not adopted by the system, strongly suggests that it is the inability to come up with the motion signal corresponding to the rigid interpretation which causes this unusual choice of a non-rigid interpretation. We shall return to this issue below.

A natural question to ask at this point is: what determines the response of the subjects for the stimuli of Fig. 3? What attributes of the stimulus determine the perceived direction of motion? In what follows we shall inspect separately the effect of three aspects of the stimulus: the proximity of the (invisible) intersection point of the lines to the aperture border, the content of the 1D motion and the effect of terminator motion signals.

Comparing the results of Fig. 3(a, b), one might think that the (slightly) more veridical judgment of the direction of motion for the stimulus of Fig. 3(a) may be related to the fact that the exposed region of the stimulus pattern is in this case more proximal to the lines'...
intersection point. However, we note that there is another difference between the two cases: the stimulus of Fig. 3(a) contains 1D component velocities which are closer to the global velocity vector than those of Fig. 3(b). Might the smaller errors obtained in Fig. 3(a) be attributed to that difference? The results presented in Fig. 3(c) confirm the latter conjecture: for the stimulus of Fig. 3(c), the lines which appear in the conditions of Fig. 3(a) but not in Fig. 3(b) were erased and the distance of aperture boundary from the intersection point was taken to be as in Fig. 3(a). Thus, the content of the 1D component velocities of the stimuli in Fig. 3(b, c) are identical, but the intersection point of the lines is far (4.8 deg) in Fig. 3(b) and near (0.8 deg) in Fig. 3(c). The results clearly indicate that proximity of the intersection point alone is not sufficient for a more veridical judgment of the global direction of motion [an insignificant difference of < 3 deg in the across-subject mean response is observed, with the response to the stimulus of Fig. 3(c) actually deviating more from veridical].

To check whether the perceived direction of motion can be accounted for solely by the 1D content of the stimuli, we calculated the following average 1D velocity:

\[ V_{1Dav} = \frac{\Sigma U_i}{l_i} \]

where \( U_i \) is a unit vector in the direction of motion of the \( i \)th line and \( l_i \) is the visible length of the line within the aperture. It should be noted that the nature of the stimuli we use is such that this weighted average changes continuously during stimulus motion: as the stimulus pattern moves "behind" the aperture, it uncovers different portions of the lines, some oriented lines disappear from the visible area and others appear into it in a continuous manner. The shaded areas in Fig. 3(a, b, c) denote the range of directions drawn by \( V_{1Dav} \) for each of the stimuli. The across-subject mean perceived direction falls within the shaded region for all three stimuli of Fig. 3. Furthermore, inspection of the data for each subject separately revealed that two of the subjects based their response on the "last impression" of stimulus motion: for them, the response to motion towards and away from the intersection point is significantly different (\( P < 0.05 \)) for the stimuli of Fig. 3(a) and matches to within 3 deg the two boundaries of the shaded area, as would be predicted by the average 1D motion near the end of the presentation period.

**Stimulus condition 2**

Aligning the aperture perpendicular to the direction of motion (above, stimulus condition 1) allowed us to differentiate between the terminator, 1D and global directions of motion. We found that the perceived
direction of motion most closely matched the average of the 1D motion signals generated by the stimulus. However, this procedure also poses a problem: since all 1D velocities lay intermediate between the global velocity and the terminator velocities, one may suspect that the perceived direction of motion results from some form of averaging of the global and the terminator motion signals, rather than being dominated by the 1D signals. Moreover, might it be that a (mathematically) correct computation of the global velocity is carried out by the visual system (based on the 1D velocity information), but that the terminator motion signals, which deviate by as much as 90 deg from it, interfere with the computation at some stage? This is easily checked by using stimulus condition 2 [see Fig. 2(c)], namely by presenting the same pattern as before, but this time orienting the aperture's long axis along the direction of motion. Now the veridical global motion (striped arrow) and the terminator motion (solid arrow) are in the same direction. Thus, response deviations cannot originate from an average between them. Figure 4 shows the results obtained for this case. The intersection point of the lines was at a minimal distance of 0.8 deg from aperture's closest corner and a maximal distance of 3.2 deg. Speed of pattern was 2 deg/sec. The average response of all subjects is shown in Fig. 4(a) and the individual mean responses of each of the subjects are shown in Fig. 4(b). The results clearly show, that in this case the perceived direction of motion still deviates from the true global direction of motion.

Although disproving the hypothesis of averaging the true 2D computed direction of motion with the terminator motion signals, the results of Fig. 4 raise questions as to the exact nature of motion processing taking place in this case. In contrast to the data of stimulus condition 1, here, it is no longer true that the perceived direction of motion always lies along the average of the 1D velocities: the across-subject average response lies outside the shaded area. Furthermore, inspection of individual subjects’ data reveals intersubject variability larger than that found for the cases of Fig. 3. As an example, the average response of subject OW lies close to the middle of the average-1D region, whereas that of subject SM lies outside it, pointing more towards the global and terminator direction of motion [two extreme open arrows in Fig. 4(b)]. What is the basis for these findings? Is the deviation due to the effect of terminator motion or to that of a 2D computed motion signal? Any suggested explanation should reconcile the differential effects under stimulus conditions 1 and 2, while at the same time accounting for the differences between individual subject responses in stimulus condition 2. We propose that, in addition to the effect of the 1D motion, the variable effect of terminator motion alone may explain all the data. Note that when the aperture's long axis is parallel to the global direction of motion, the terminator speed is equal for all line orientations:

\[ V_{\theta} = V \cos(\theta - \theta_i) \cos(\theta - \theta_t). \]

Estimating the effect of terminator motion

To check the hypothesis suggested above, we presented subjects with stimuli composed of parallel lines, using the same aperture size and disparity as for the stimuli of Figs 3 and 4. Lines were 20, 45 or 70 deg inclined, with inter-line distances of 0.8 deg (Stimulus presentations were interleaved with those of Figs 3 and 4. The stimuli were randomly rotated around the vertical and/or horizontal axis, as before, and the data were folded back for presentation.) Figure 5 summarizes the individual results of all subjects for the three stimulus orientations. The abscissa denotes the direction of motion perpendicular to the line orientations and the ordinate the subjects’ reported perceived direction of motion. The terminator motion is 90 deg for all cases. If the terminator motion signals had no effect at all, each subject’s response would lie along the diagonal. The stronger the subject is still affected by terminator motion, on the other hand, the more his/her responses should be shifted towards the horizontal 90 deg line.

\[ V_{\theta} = V \text{ for all } i \text{ when } \theta_i = \theta. \]

This is in contrast to stimulus condition 1, where each line produced a terminator motion of a different speed. It may therefore be, that the coherent motion of all the terminators in stimulus condition 2 produced a strong enough motion signal along the aperture borders that was not completely abolished for all subjects by the presentation of the image in uncrossed disparity. If this is indeed the case, one should find similar effects for stimuli composed of a set of parallel lines. i.e. for the barber pole illusion, since here, too, the terminators move coherently. Furthermore, quantification of the amount of remaining effect of terminator motion using parallel lines should enable us to isolate the influence of the 1D motion clues in the case of Fig. 4.
TABLE 1. Isolating the effect of 1D motion signals on the perceived direction of motion, individually for each subject

<table>
<thead>
<tr>
<th>Subject</th>
<th>a</th>
<th>b</th>
<th>r</th>
<th>Perceived direction (deg)</th>
<th>Isolated-1D direction (deg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>OW</td>
<td>0.81</td>
<td>0.15</td>
<td>0.99</td>
<td>35</td>
<td>27.7</td>
</tr>
<tr>
<td>OU</td>
<td>0.77</td>
<td>0.21</td>
<td>0.99</td>
<td>45</td>
<td>33.9</td>
</tr>
<tr>
<td>DR</td>
<td>1.05</td>
<td>0.22</td>
<td>0.99</td>
<td>46</td>
<td>25</td>
</tr>
<tr>
<td>NB</td>
<td>0.49</td>
<td>0.45</td>
<td>0.98</td>
<td>49</td>
<td>19.2</td>
</tr>
<tr>
<td>EO</td>
<td>0.27</td>
<td>0.52</td>
<td>1.0</td>
<td>53.7</td>
<td>25.5</td>
</tr>
<tr>
<td>SM</td>
<td>0.39</td>
<td>0.52</td>
<td>0.99</td>
<td>51.5</td>
<td>28</td>
</tr>
<tr>
<td>Mean</td>
<td>0.63</td>
<td>0.34</td>
<td>0.98</td>
<td>47.7</td>
<td>26.6</td>
</tr>
</tbody>
</table>

The left part of the table gives the a and b coefficients obtained from the data of Fig. 4 [see equation (2)], and the corresponding correlation coefficients. The right part of the table gives the perceived direction of motion in stimulus condition 2 for each subject separately (second column from the right; B in equation (2)), and the computed isolated-1D direction of motion (rightmost column, \( \theta_{ID} \) in equation (2)) based on subject's a and b values obtained from the parallel lines data.

We found that indeed the results are affected by the terminator motion signals. This effect is greater when the difference between the 1D and terminator signals is greater. The across-subject average perceived direction of motion is demonstrated in Fig. 5 by the dashed line. Inspecting the data for each subject separately, we find that as predicted, OW is only slightly affected by the terminator motion signals, whereas for SM the responses are indeed shifted towards the terminator direction of motion.

We used a phenomenological model which assumes that each subject's responses can be described as a weighted average of the 1D and the terminator motion signals:

\[
\theta_i = a\theta_{ID} + b\theta_t
\]  

(2)

where \( \theta_i \) is the perceived direction of motion, \( \theta_{ID} \) is the direction of motion of the 1D motion signals (which for the case of parallel lines is perpendicular to their orientation), \( \theta_t \) is the direction along the aperture's longer axis and a and b are coefficients which characterize each subject individually. (The convention used is that horizontal motion to the right is 0 deg, with the angle increasing counterclockwise. \( \theta_i \) is therefore always 90 deg.) Based on each subject's mean responses for the three different parallel lines orientations, a and b were obtained by linear regression and are given in Table 1.

We then used the magnitudes of a and b to isolate the values of \( \theta_{ID} \) for the subjects' individual mean responses to the stimuli of Fig. 4. Assuming the same phenomenological model holds in this case, these values represent the isolated effect of the 1D motion signals for stimulus condition 2. Results are summarized in the two rightmost columns of Table 1. The computed isolated-1D directions are plotted in Fig. 6. Referring back to Fig. 4, it is seen that by taking into consideration the remaining effect of the terminator motion signals (the extent of
which varies among subjects), the computed isolated-1D direction of motion falls within 1 deg of the region of the average 1D signals for all subjects. The across-subject mean isolated-1D direction of motion is 3.4 deg from the center of the shaded region in Fig. 6. We conclude that the perceived direction of motion is well characterized by the average of the 1D motion signals with an additional subject-dependent effect when coherent terminator motion is present.

**Addition of localized features to the moving image**

The stimuli described in the last three sections were all devised in order to isolate the perceived direction of motion generated by 1D motion signals alone. Next, we turn to examine what is the effect of adding non-ambiguous motion clues to the image.

Non-ambiguous motion clues arise when the image contains localized regions of luminosity gradient (e.g. isolated dots), which may be termed 0D motion clues, or when the image contains 2D form cues, such as terminated lines, intersecting lines, or lines of high curvature. The observations and results described below suggest that both 0D and 2D motion clues may play a crucial role in determining the motion percept.

When the lines comprising the stimulus pattern were replaced by dashed lines, we found that the perceived direction of motion turns into the correct global direction of motion of the stimulus. At the same time, a rigid interpretation of the stimulus pattern is observed. This effect occurs for a broad range of spacing between line dashes. It therefore seems that there are cases where the unambiguous motion clues can overcome the erroneous signal arising from the 1D motion signals and completely determine the perceived direction of motion.

In order to quantify how much 0D motion information is needed for this to occur, we used the original stimulus pattern made of solid lines (stimulus conditions 1 and 2), but added isolated dots in random locations to the gray background between the lines. These dots (2 x 2 pixels, same luminosity as the lines) moved together with the lines. It was found that the introduction of only a single visible isolated dot is sufficient for the motion percept to change abruptly into the correct global direction of motion. The average error of perceived direction was < 2 deg for all stimuli of conditions 1 and 2 (24 presentations each, SE 2 deg, results from two subjects). Here too, the presence of the dot turns the percept into one of rigid motion. This dramatic effect depends crucially on at least one dot being present within the area visible through the aperture throughout the stimulus motion.

**DISCUSSION**

The experiments reported here were devised to assess the ability of the visual system to compute the global direction of motion of a translating rigid object under unfavorable conditions. Although containing sufficient information for this computation, the stimuli were so designed that no 0D or 2D motion information was present and the 1D component velocities were such that their average deviated substantially from the veridical global velocity. Under these conditions, subjects were unable to perceive correctly the global direction of motion and instead determine the global motion to be directed along the average of the 1D motion signals. The possibility of interference of motion signals arising from line terminators in the process of computation was excluded.

Our results strongly suggest that the visual system is not equipped with a mechanism to compute veridically the global velocity solely from information of the component velocities produced by the objects’ motion. Although the conditions were unfavorable in terms of the content of 1D motion signals, all other stimulus conditions were specifically chosen so as to promote veridical perception of the direction of global motion. In particular, the stimulus pattern was presented through a single aperture, in foveal viewing conditions and for long presentation times of a second or more. Also, the stimulus was presented in uncrossed disparity relative to the aperture, to further reinforce the notion of coherent motion “behind” an occluder and reduce possible interference of line terminator motion in the computation (Shimojo et al., 1989).

Recently, Lorenceau and Shiffrar (1992) showed that if the effect of terminator motion is reduced, the visual system is able to integrate 1D motion signals into a correct coherent percept of global motion when an object (diamond) is presented behind an occluder, even when viewed through multiple apertures rather than a single one. The ways to reduce the interfering effect of terminator motion which they used (outlining the aperture boundaries or making them invisible but jagged, or presenting the stimulus at low contrast or in the periphery) did not include the use of disparity. However, we checked the case of presenting the diamond in uncrossed disparity relative to the apertures and found that indeed it allows the correct perception of the diamond’s motion. It is therefore unlikely that the failure of correct 1D motion integration for the stimuli presented here arises from a general inability to integrate 1D motion information from spatially segregated locations (i.e. for objects whose vertices are occluded). Rather, the results suggest that 1D motion integration does occur, but that the nature of the computation is better described as averaging the component velocities than as performing a velocity-space computation such as the IOC procedure (Adelson & Movshon, 1982). In the case of a diamond of orthogonal sides, averaging the 1D component velocities results in the correct global direction of motion, as indeed was observed by Lorenceau and Shiffrar (1992). However, when the component velocities are distributed anisotropically across space, large deviations of the average relative to the global velocity occur, as was found in the experiments reported here. Therefore, our results as well as those of Lorenceau and Shiffrar (1992) can be explained in terms of a mechanism of averaging the 1D motion signals.
A similar conclusion was recently suggested by Mingolla, Todd and Norman (1992). Their stimulus comprised an array of 64 alternating black and white circular apertures which contained coherently moving gray lines of two possible orientations. Subjects reported whether the prevailing motion contained an upward or downward component. They found that subjects’ responses were consistent with a pooling of the 1D motion signals rather than with the predictions of an IOC analysis. However, no account was given for the possible contribution to the global motion percept of the line terminator motion, whose average in the case of circular apertures is the same as that of the average of the entire pattern when present. The nature of the image motion when such an interpretation exists (Hildreth, 1984 and references therein). [For a discussion of counter examples see Nakayama and Silverman (1988a, b).] For the stimuli we used, integrating the 1D signals in a (mathematically) correct manner goes together with finding an interpretation of the stimulus pattern as motion of a rigid object. Therefore this procedure should be more, rather than less preferable. Furthermore, it was found that when the unambiguous motion of line terminators or isolated dots was added to the image, the visual system indeed adopts this direction of motion as that of the lines, too, thereby binding them into a single rigid object. Finally, let us note that we observed similar systematic errors in the perceived direction of motion for a stimulus made of a continuous surface of varying luminosity

\[ L(x, y) = L_0 + L_1 \cos(k \cdot \tan^{-1}(y/x)) \]

\[ (L_0 = 70 \text{ cd/m}^2; L_1 = 30 \text{ cd/m}^2; k = 20, 40) \]  

(as if “interpolating” the luminosity between the lines), when the surface moved behind an aperture so that the origin was hidden. In this case, the possibility that the visual system deliberately chooses not to bind the 1D motion signals together is even less plausible. because the system interprets as disparate rather than performing a global computation on the 1D motion signals they produce. We do not believe this to be the case for several reasons. First, as already noted, the visual system usually shows preference to a rigid interpretation of image motion when such an interpretation exists (Hildreth, 1984 and references therein). [For a discussion of counter examples see Nakayama and Silverman (1988a, b).] For the stimuli we used, integrating the 1D signals in a (mathematically) correct manner goes together with finding an interpretation of the stimulus pattern as motion of a rigid object. Therefore this procedure should be more, rather than less preferable. Furthermore, it was found that when the unambiguous motion of line terminators or isolated dots was added to the image, the visual system indeed adopts this direction of motion as that of the lines, too, thereby binding them into a single rigid object. Finally, let us note that we observed similar systematic errors in the perceived direction of motion for a stimulus made of a continuous surface of varying luminosity

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(as if “interpolating” the luminosity between the lines), when the surface moved behind an aperture so that the origin was hidden. In this case, the possibility that the visual system deliberately chooses not to bind the 1D motion signals together is even less plausible, because this stimulus pattern appears to be unitary when at rest.

Therefore, we conclude that our data imply that the visual system does not have the ability to link 1D motion signals by an IOC-like computation when only 1D signals are present in the stimulus pattern even when these signals arise from a compact region of visual space.

Next we address the question, why should the visual system not implement a velocity–space computation of global motion from component motion signals? We first note in this respect that a highly nonisotropic sample of orientations is probably rare in real world scenes and therefore averaging the component velocities is not a substantially inferior strategy to one of performing velocity–space computation. Furthermore, translatory motion of rigid objects is only a small subset of moving scenes analyzed by human observers in everyday life and an averaging mechanism may be the better compromise between the various optimal strategies in each of the cases: what seems to be a failure from a limited point of view, may actually be a sign of optimizing the system over a larger space of possible stimuli.

However, going back to the assumption that a velocity–space construction, being the general correct solution for rigid translatory motion, would be a desirable strategy to implement, a few more concrete remarks should be made. First, a velocity–space construction demands a reliable representation of not only the direction, but also of speed of the component velocities. Contrary to the case of direction of motion, where much evidence exists both from physiology and psychophysics for high acuity and reliable representation, for speed there may be strong limitations on the reliability of representation (Orban, Kennedy & Maes, 1981a; b; Thompson, 1982). Although human performance in discrimination of speed is good (McKee et al., 1986; Welch, 1989), it may actually be the performance in absolute judgment of speed that sets the limit for the purpose of a velocity–space construction.

A more important reservation may be that, strictly speaking, a velocity–space construction is a global computation rather than a local one, in the sense that information from spatially segregated locations should be carefully integrated. Consider, e.g. an object whose boundary changes orientation gradually over space. To obtain better accuracy, it is then preferable to integrate 1D motion signals arising from more distant parts of the object. This may not be an easy task to implement physiologically. We note that in the experiments reported here the stimuli contained orientations differing by up to 45 deg within a region of < 1.5 deg and yet systematic errors in the perceived global velocity were observed.

It may therefore be concluded, that a necessary condition for correct integration of 1D motion signals requires that the image contain different orientations within overlapping regions in space. Whether this condition is also sufficient in general, is not yet known. Note, however, that the latter statement basically means that 2D features in the form of line (or grating) crossings must be contained in the image for correct global motion detection to occur. This may indicate, that for correct perception of global motion the visual system relies on mechanisms which specialize in the detection of general 2D or 0D features, such as line terminators, isolated dots and local regions of luminosity changes. Similar suggestions were recently made by Derrington and Badcock (1992) and by Wilson, Ferrera and Yo (1992). Note that indeed, in our preliminary experiments on isolated dots added to the stimuli of Fig. 2, the 0D motion signals appeared to be able to “capture” the motion of the entire pattern when present. The nature
of integration of 1D with 0D motion signals is an important quantitative question raised by the present experiments.

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