Vision Res. Vol. 33, No. 14, pp. 1921–1936, 1993
Printed in Great Britain.

0042-6989/93 $6.00 + 0.00

Perceived Speed of Moving Lines Depends on Orientation, Length, Speed and Luminance

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Received 22 October 1992; in revised form 9 February 1993

In this study, the perceived speed of a tilted line translating horizontally (for a duration of 167 msec) is evaluated with respect to a vertical line undergoing the same translation. Perceived speed of the oblique line is shown to be underestimated when compared to the vertical line. This bias increases: (1) when the line is further tilted, (2) with greater line lengths, (3) with lower contrasts, and finally (4) with a speed of 2.1 deg/sec as compared to a higher speed of 4.2 deg/sec. These results may be accounted for by considering that two velocity signals are used by the visual system to estimate the speed of the line: the translation of this line (this signal does not depend on the line's orientation) and the motion component normal to the line (this signal depends on orientation). We suggest that these two signals are encoded by different types of units and that the translation signal is specifically extracted at the line endings. We further suggest that these signals are integrated by a weighted average process according to their perceptual salience. Other interpretations are considered at the light of current models dealing with the two-dimensional integration of different velocity signals.

Apparent speed Aperture problem Velocity integration Terminators Vector average

INTRODUCTION

Recovering the actual motion of a continuously moving contour can be formally represented by the extraction of a two-dimensional velocity field that assigns a direction and a magnitude of velocity to each point in the image. This task is not trivial for the visual system. Early motion detectors have spatially limited receptive fields and measure therefore a velocity signal which is local. They must consequently face the so-called "aperture problem": an orientation- and direction-selective unit does not signal the true local motion, but only the component of motion normal to the contour traversing its receptive field (Wallach, 1935). This local reading is ambiguous in the sense that it does not specify the velocity component tangent to the contour. As a consequence of this ambiguity, the measurement of the true global motion requires the combination of the primary local signals extracted at different locations along the contour. Although a set of local signals provides considerable constraint on the possible global motions, some additional assumptions on the physical plausibility of the computed motion are needed to guarantee a unique solution. Different assumptions result in specific algorithms of integration, and may yield different solutions for the same physical movement (e.g. three-dimensional motion with deformation). The validity of an assumption relies then in its ability either to predict the actual motion, or to compute a velocity field that looks like the misperception reported in perceptual studies. For instance, the algorithm used by Hildreth (1984) does not permit the recovery of the true velocity field of an ellipse rotating around its centre: instead, the computed field presents a radial component which should result in the deformation of the moving ellipse, as far as this computation underlies the final percept. This perceived non-rigidity has indeed been reported, which constitutes an argument in favour of Hildreth's model.

When a contour is undergoing a pure translation in the fronto-parallel plane, two types of misperceptions may occur independently or concurrently. First, this contour may be perceived with a global velocity (direction and speed) different from that of the actual velocity. Second, it may be seen as a non-rigid figure, that is with a computed velocity field made up of different vectors. Such misperceptions have indeed been reported.

Recently, it was shown that the perceived direction of straight lines translating with a direction non-perpendicular to their orientation is biased towards the motion component normal to the line under some conditions (Lorenceau, Shiffrar, Wells & Castet, 1993). In the same vein, a planar curve undergoing a translation in the image plane appears sometimes as highly non-rigid (Nakayama & Silverman, 1988a, b). It is as though the visual system would accept some local velocity vectors as such (those in the region of non-rigidity), without constraining them to be integrated in the global curve translation.

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These kinds of misperceptions regarding pure translations provide some constraints on the models of motion perception concerning the problem of two-dimensional velocity integration, and they should help to distinguish between them. For instance, the computed velocity field based on Hildreth's (1984) algorithm is always similar to the actual motion. However, other models have been used to predict misperceptions of pure translation under some conditions. Perrone (1990) proposed a model which integrates local measurements using a voting scheme and at least qualitatively predicts direction misperceptions under some circumstances. Wilson, Ferrera and Yo (1992), using vector averaging, proposed a model which integrates Fourier and non-Fourier components and which applies to superimposed translating gratings (plaids). This model successfully predicts observed plaid-direction errors (Ferrera & Wilson, 1990) and plaid-speed errors (Ferrera & Wilson, 1991). The model of Yuille and Grzywacz (1988) predicts the perceived non-rigidity reported by Nakayama and Silverman (1988a,b) with translating planar curves (see also Grzywacz & Yuille, 1991).

The crucial issue raised by these results concerns the conditions impeding the normal components of motion to be integrated, i.e. constrained, in a final unique rigid percept corresponding to the true motion. Nakayama and Silverman (1988a) argued that the local signals may be difficult to combine when they come from detectors not sufficiently different in their orientation tuning. This would render the global motion intepretation very uncertain because of the inherent noise embedded in each individual velocity signal. In order to overcome this difficulty, the use of feature points such as terminators, corners or points of high curvature, seems preponderant and would permit the recovery of the true velocity field by constraining the local signals. Indeed, Nakayama and Silverman (1988b) showed that the non-rigidity of two-dimensional figures was reduced by adding line terminators on the moving contour. Lorenceau *et al.* (1993) provided evidence that the bias in perceived direction towards normal components for translating lines was reduced in conditions favouring the processing of moving line ends. The use of feature points to solve the aperture problem has also been assessed when moving contours distributed across space are translated with a common velocity (Wallach, 1935, 1976; Shimojo, Silverman & Nakayama, 1989; Lorenceau & Shiffrar, 1992).

Altogether, these results suggest that the motion of feature points, as opposed to the motion of little portions of the contour, is given a great weight at the stage where all velocity signals must be combined. They further suggest that terminators' motion would be processed by specific motion detectors different from the classical units with elongated receptive field such as those described in the primary visual cortex.

Recovering the global velocity of a moving contour also means recovering its speed. This issue is investigated in the present study with a simple question which is a complementary approach to the work of Lorenceau *et al.* (1993): namely, is the perceived speed of a straight line translating with a direction not perpendicualr to its orientation influenced by the local readings extracted along the line? If such a bias in apparent speed exists, does it depend on the relative perceptual salience between line terminators and the contour itself?

The speed sensitivity of the human visual system is quite good as revealed by psychophysical studies. With single vertical lines undergoing translation, McKee (1981) reported that speed differences of 5% could be detected at medium speeds and with sufficient durations. Is this performance sufficient to detect the difference between the translation speed of a line oblique with respect to its trajectory and the speed readings normal to the line orientation? This speed difference is 6% for a line oriented 20 deg from the vertical and moving horizontally. Thus, this line, and also lines closer to horizontal, provide a speed difference between the translation signal and the normal components signal which should be detected by the visual system. Then, making allowance for these two potential signals does make it plausible that an oblique line in translation implies the integration of different speeds.

The issue of speed-integration was studied with single lines translating horizontally. The apparent speed of a comparison tilted line was judged by reference to a standard vertical line, whose speed was constant, and was accordingly varied with a staircase procedure. Except for the orientation, the standard and the comparison stimuli were identical, so that they only differed in their ability to activate motion detectors responsive to other directions than that of the line's translation.

GENERAL METHODS

Stimuli

The stimuli were white lines of different length, orientation and speed, translating horizontally either leftward or rightward. Their luminance was 131 cd/m^2. The background was grey with a luminance of 2.5 cd/m^2. Luminance was measured with a home-made photo-multiplier calibrated with respect to a CS 100 Minolta photometer. The room was dimly illuminated.

The standard was a vertical line with a speed of 2.1 or 4.2 deg/sec [Fig. 1(a)]. The comparison stimulus was a tilted line with an orientation of 30, 45 or 60 deg above the horizontal [Fig. 1(b)]. These orientations corresponded respectively to angles θ between the direction of local velocity vectors and translation vectors of 60, 45 or 30 deg. The comparison and the standard lines had the same length: 0.21, 0.88 or 1.76 deg of visual angle.

The occurrence of eye movements was limited by the short mean duration (167 msec) used in all experiments (Westheimer, 1954; Robinson, 1965) and by the randomisation of the motion direction in each temporal interval of each trial. As an aid to maintain fixation, a fixation point in the form of a red cross was displayed below the trajectory of the line.

Attempts were made to minimize the use of distance and duration cues in estimating apparent speed. For

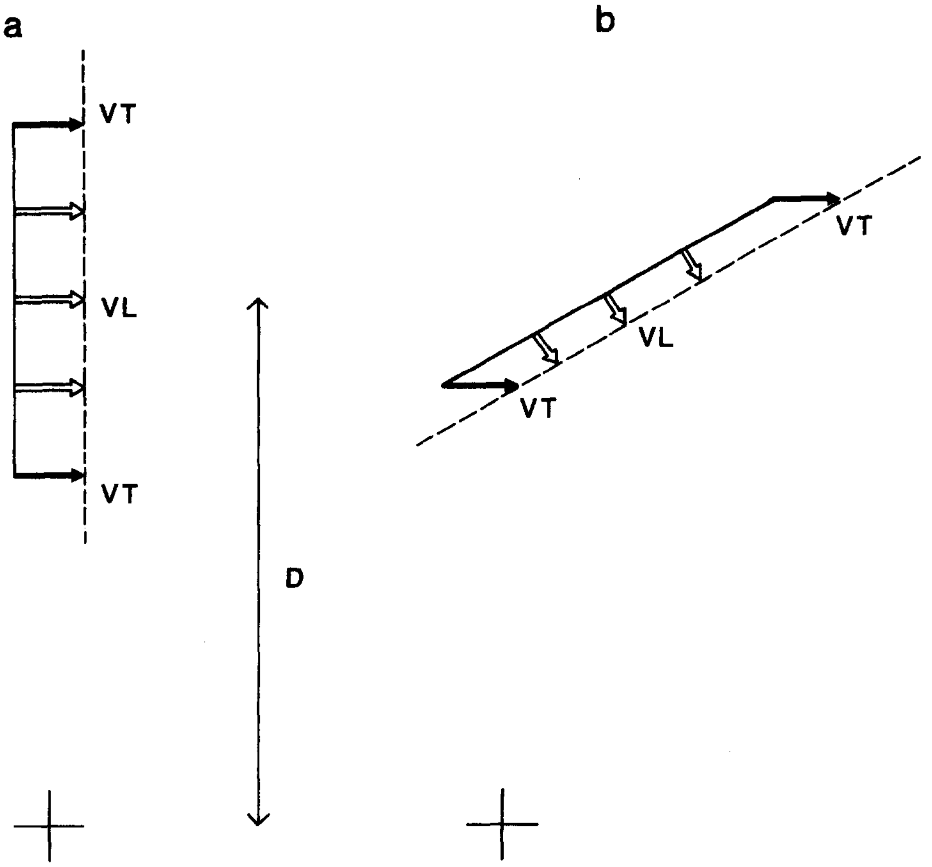

FIGURE 1. Spatial configuration of two temporal intervals of the 2AFC procedure. A line is drifted horizontally above a fixation cross. Its translastion velocity is represented by the solid vectors V_T. The local orthogonal component of motion is represented by open vectors (V_L). The centre of the line, whatever the line length, moved on the same trajectory whose vertical distance D to the fixation cross was 1.32 deg. (a) Temporal interval containing the standard moving line which was always vertical ($V_L = V_T$) with constant speed across trials. (b) Temporal interval containing a tilted comparison line ($V_L < V_T$). Line's speed is varied by a staircase procedure. In this figure, the comparison's speed equals that of the standard as it was the case at the beginning of each staircase.

each presentation, the duration was randomly varied within a range of $\pm 10\%$ around the mean duration. In addition, the starting point of the trajectory was randomly chosen within a range of 0.42 deg centred on the middle of the screen.

Whatever the line's length, its centre always moved on a horizontal trajectory whose vertical distance to the fixation point (labelled D in Fig. 1) was constant (1.32 deg).

Stimuli were displayed on a Sony RGB 19″ monitor (GDM-1950) with a 1024 × 1280 pixels resolution and 60 Hz refresh rate. The monitor was controlled by a computer (PC 386-AT). Specially designed graphic software (Lorenceau & Humbert, 1990) was used to drive an Adage PG 90/10 graphics card.

Observers viewed the stimuli binocularly with natural pupils at a distance of 87 cm. An adjustable chinrest was used to stabilize the head.

Procedure

A temporal two-alternative forced-choice (2AFC) paradigm was used in conjunction with a staircase procedure. On each trial, two moving lines, the standard and the comparison, were presented sequentially in random order separated by an interval of 400 msec. After each trial the observer indicated which of the two lines appeared to be drifting faster by pressing one of two response buttons. The standard line had the same speed in all trials. The speed of the comparison line varied across trials according to a staircase procedure. Observers were not explicitly instructed to estimate the perceived horizontal speed. However, it seems likely that this task was implicitly implied by the horizontal motion of the standard vertical line.

PILOT EXPERIMENT

A pilot experiment consisting in an extensive speed discrimination task was performed by all observers before carrying out the main experiments. This aimed at ensuring: (1) that speed sensitivity would be high enough to detect the speed difference between the translation speed and speed readings normal to the line, and (2) that performance would not change during the main experiments. This training was performed until each observer reached a given criterium value as described below.

The standard and the comparison stimuli were similar vertical lines that subtended 0.88 deg. The standard had a speed of 2.1 deg/sec. A block contained two staircases converging respectively on 0.29 and 0.71 thresholds according to a transformed up-down method (Levitt, 1971). In the 0.71 staircase, if the observer's response was false, the comparison's speed was increased at the next presentation of this staircase, and speed was only decreased when the observer responded "faster" for two successive presentations of the same speed. The starting values of each staircase were respectively -20 and $+20\%$ of the standard speed. Auditory feedback was provided after each trial to indicate the correctness of the response. This feedback was not provided in the actual experiments. Two blocks formed a session.

The differential threshold (DT) was defined as the half difference between the 0.29 and 0.71 levels. The relative differential threshold (or Weber fraction) was the ratio of DT to the mean of the 0.29 and 0.71 levels.

Sessions were continued for an observer until its Weber-fractions reached a stable level of $<13\%$. This level corresponds approximately to the performance reported in previous studies bearing on speed discrimination for the duration and speed employed here (McKee & Welch, 1985; de Bruyn & Orban, 1988; Snowden & Braddick, 1991). This percentage is also the speed difference between local speed and translation speed for a line oriented 30 deg from the vertical ($\theta = 30$ deg). Thresholds improved over time by a factor of about 3 for the three observers who had never practised motion psychophysical tasks (SD, LF and AMD), and only by 2 or even less for the remaining observers all accustomed to similar tasks.

EXPERIMENT 1

The general purpose of this experiment is to test whether the perceived speed of an oblique line in translation is biased towards local speed-readings normal to the line. The predictions corresponding to such a bias are best understood by considering Fig. 1(b): a tilted line is shifted horizontally to the right with a translation that is represented by the vector $\mathbf{V_T}$. The speed of any local reading $\mathbf{V_L}$ elicited by this line in motion is determined by the "constraint" dashed line. If local velocities are not properly integrated, one would predict that they should reduce the perceived speed of the line, because the magnitude V_L is shorter than the magnitude V_T of the translation (note that whereas a vectorial quantity is indicated by bold characters, its magnitude is represented by plain text).

In conditions in which local velocities are more or less taken as such, a second prediction can be made concerning the effect of line orientation on apparent speed. Indeed, tilting a line towards horizontal, i.e. increasing the angle θ between a given line translation $\mathbf{V_T}$ and the direction of its local vectors $\mathbf{V_L}$ reduces the magnitude of $\mathbf{V_L}$ with respect to V_T ($V_L = \cos(\theta)*V_T$). Thus, any speed underestimation should become more important when the orientation of the line approaches the axis of the trajectory, i.e. when the ratio of V_L to V_T is reduced.

In order to test whether the horizontal translation signal was specifically carried by the terminators, we increased the number of units supposed to respond to the orthogonal component of motion by increasing the length of the line. In our view, this should result in a relative decrease of the terminators' signal and consequently in a greater bias of perceived speed, provided that the translation signal is essentially signalled by the terminators. These effects were studied with different speeds to make sure that the results could not be interpreted as just reflecting a particular speed difference between local speeds and terminators' speeds.

For these three reasons, the apparent speed of a tilted line moving horizontally was assessed in this experiment for three orientations, three lengths and two speeds of this line.

Procedure

The standard line (vertical) had the same speed in all trials. The speed of the comparison line (oblique) varied across trials according to a staircase procedure.

A block consisted of three interleaved staircases each attributed to a different orientation of the line. The interleaving was randomized with the following constraints: every 15 trials, each of the three conditions were presented five times, and no condition was allowed to be presented more than three times in succession. This permitted an homogeneous presentation of the three conditions across trials, without the observers being able to anticipate which condition would be presented next. A block was ended after 12 reversals had occurred in each of the three independent staircases.

Each staircase was run according to a simple up-down method (Dixon & Mood, 1948) converging on a 0.5 threshold. A "comparison faster than standard" response decreased the comparison's speed and a "slower" response had an inverse effect. At the beginning of each staircase, the standard and comparison speeds were equal, and the comparison speed was then varied by a step of 20%. This step was halved after the first reversal, and halved again after the second reversal where it was kept constant until the end of the series. The mean of the last six reversal points was taken as the 0.5 threshold (Wetherill & Levitt, 1965).

Within a session, two blocks were peformed for each of the three line length conditions, resulting in six randomly ordered blocks. In each session, the standard speed was constant. Observers performed three sessions for each of the two standard speeds (2.1 or 4.2 deg/sec).

Five observers participated in the first experiment, three of them were unaware of the hypothesis under study. All had normal or corrected to normal vision.

Results and discussion

Relative perceived speed was defined as the ratio of the standard speed to the comparison speed (Vs/Vc). In Fig. 2, relative perceived speed is plotted against V_L/V_T (the ratio of the orthogonal component's speed V_L to the

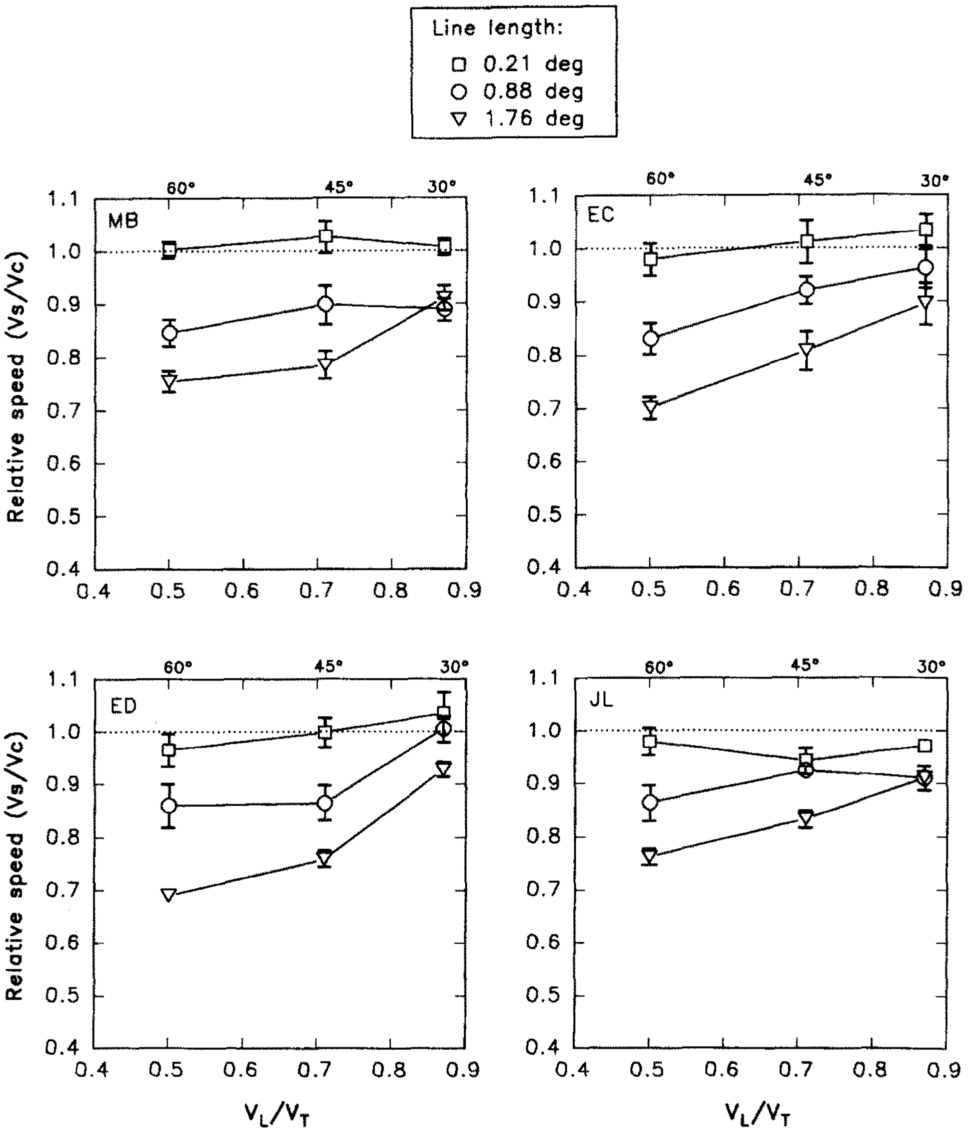

FIGURE 2. Results of Expt 1 for the standard speed of 2.1 deg/sec and for four observers with line length as a parameter (indicated by the legend in the box). Relative perceived speed is plotted against the ratio of the local speed to the translation speed (V_L/V_T). The upper horizontal axis shows the three angles θ between V_L and V_T corresponding to the three line orientations used in our study [$V_L/V_T = \cos(\theta)$]. The horizontal dotted line (Vs/Vc = 1) represents veridical match between the standard and the comparison. The vertical bars indicate standard errors.

terminator speed V_T). To allow clear representation of the data, the angle θ between V_L and V_T corresponding to each value of V_L/V_T appears in the upper horizontal axis. With this notation, $V_L/V_T = \cos(\theta)$. The use of V_L/V_T as abscissa emphasizes our hypothesis that apparent speed should depend on the relative magnitude of V_L with respect to V_T. The results are represented at a standard speed of 2.1 deg/sec in Fig. 2 for four observers (MB, EC, ED, JL), and at a standard speed of 4.2 deg/sec in Fig. 3 (with one more observer SD). All data have been averaged across observers since the variability between them was low. They are shown on Fig. 4 for the two standard speeds (2.1 and 4.2 deg/sec) used in Expt 1 with the same notations as in Figs 2 and 3.

For all observers and for the two standard speeds, the speed of the comparison tilted line is lower than that of the vertical standard, except for the shortest length (squares). This bias increases either with line orientation or line length.

Effect of line orientation. For the long (inverse triangles) and intermediate (circles) lengths, apparent speed declines when the orientation of the line deviates from the vertical, i.e. when the angle θ between the local velocities and the translation vector increases. In other words, the perceived speed of the tilted line is decreased when the speed of local readings (V_L) is reduced by gradually tilting the line towards the horizontal axis of the translation (and hence decreasing V_L/V_T since the translation is constant whatever the orientation). This result is in agreement with our initial hypothesis that local readings would be taken as such by the visual system and would bias the estimate of the translation speed towards lower values. If speed estimation entirely relied on local estimates however, results would fall on the dashed-dotted lines in Fig. 4. This is obviously not

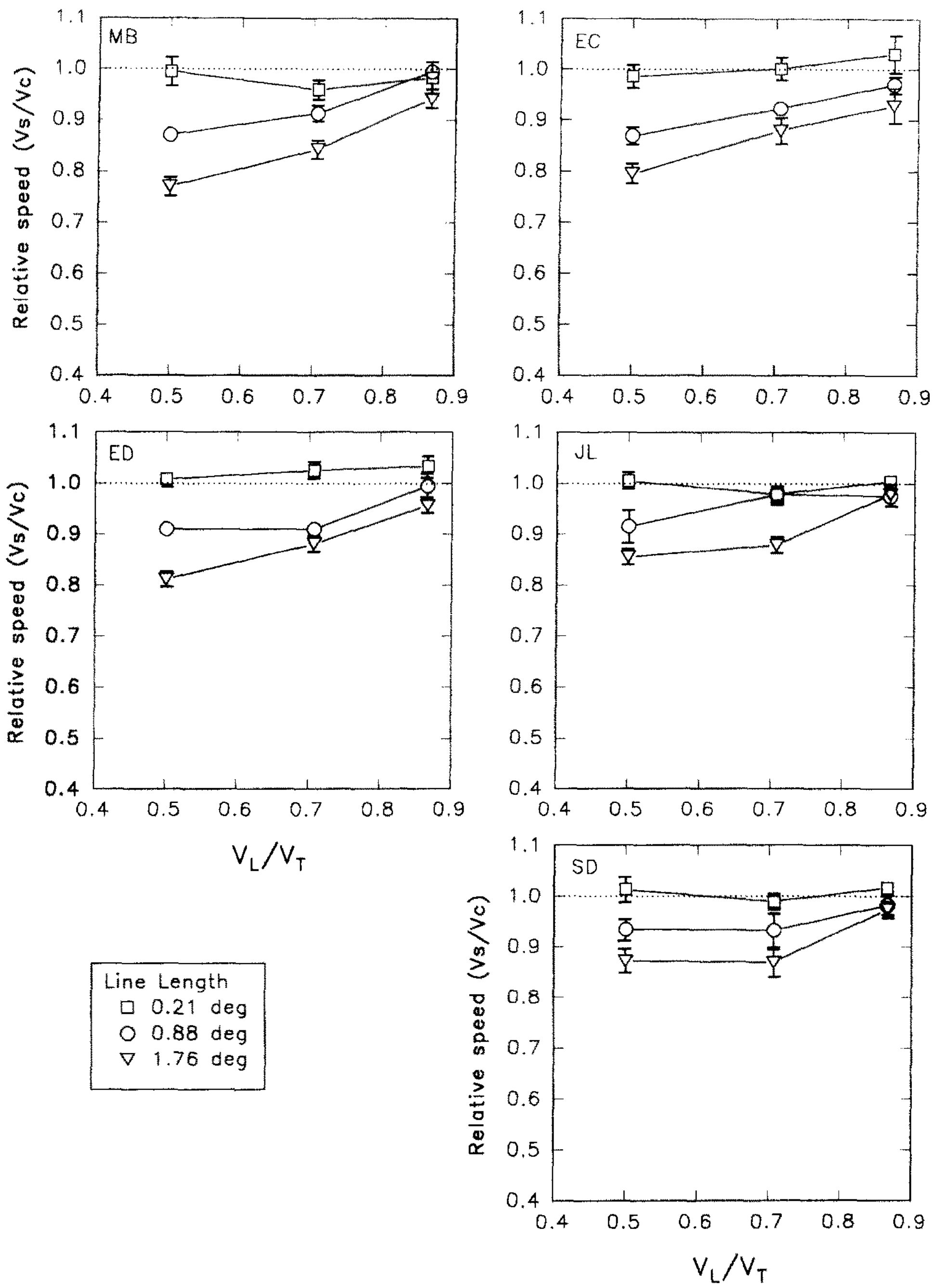

FIGURE 3. Results of Expt 1 for the standard speed of 4.2 deg/sec and for five observers with line length as a parameter (indicated by the legend in the box). Notations are the same as in Fig. 2.

the case, which suggests that these local speeds are integrated with the translation speed at some stage, and yield a compromise estimate between both.

These results suggest that two motion signals are extracted at an early stage in our display: local velocity (V_L) and translation velocity (V_T). These two signals are then combined and yield, in our experimental conditions, an apparent speed whose magnitude lies between V_L and V_T. The precise nature of the translation signal is however not clear. Is it a motion signal specifically extracted at the line terminators? Or is it due to other mechanisms? One possibility would be for instance to detect the horizontal translation all along the line with Reichardt-type detectors correlating elements of like orientation (here oblique with respect to the detector axis). Indeed, such a correlation process was demonstrated by van den Berg, van de Grind and van Doorn (1990). The first hypothesis however, involving specific terminators' motion, is the only one to predict that increasing the line length would result in a differential processing of the translation signal and the local signals. This prediction is based on the potential enhancement of the activity representing the component of motion normal to the line by virtue of a greater number of units recruited along the line, whereas the terminators' motion should not benefit of this increased length. In contrast, the second hypothesis would not predict any difference concerning a change in the efficiency of both signals since both would benefit equally of a length increase.

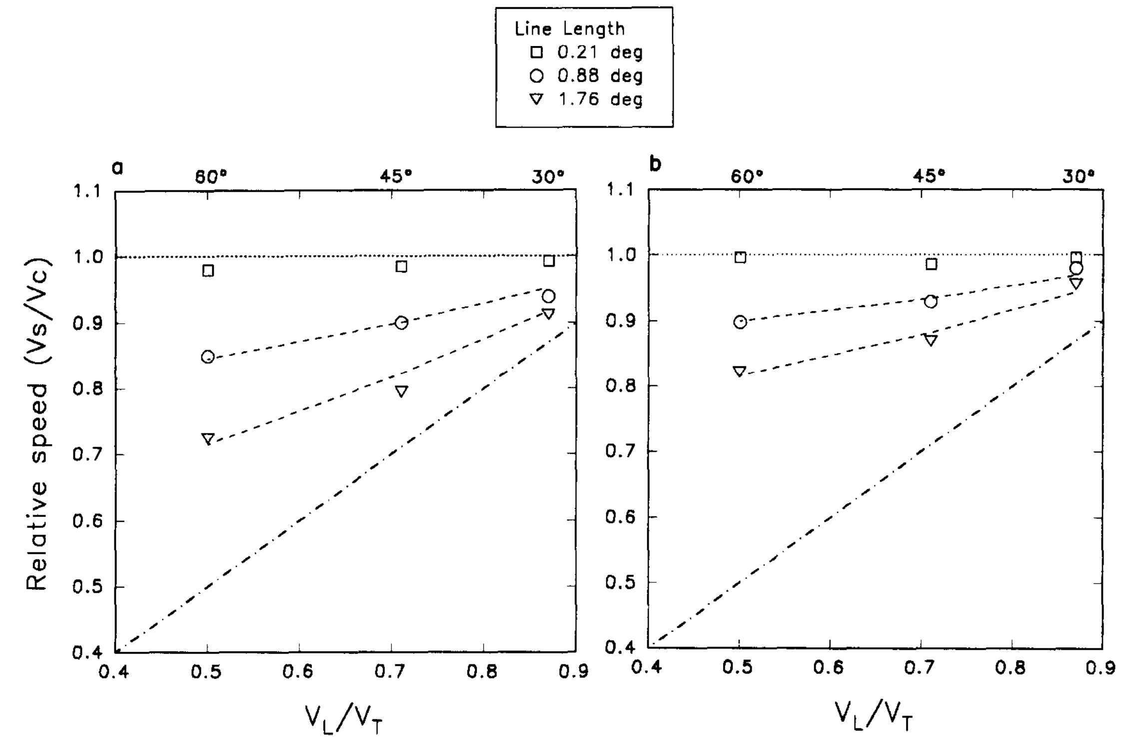

FIGURE 4. Results of Expt 1 averaged across observers for the two standard speeds with line length as a parameter (indicated by the legend in the box). Relative perceived speed is plotted against the ratio of the local speed to the translation speed (V_L/V_T). The upper horizontal axis shows the three angles θ between V_L and V_T corresponding to the three line orientations used in our study. For the medium (circles) and long (triangles) lengths, experimental points are adjusted with dashed lines according to the predictions of the weighted average hypothesis (see text). The two weights (α and β) corresponding to the average vector associated with each adjusted line are tabulated in Table 1. If perceived speed was solely determined by the normal component V_L, results would lie on the 45 deg oblique line (dot-dashed line).

We therefore tested these hypotheses by evaluating the perceived speed of the tilted line for three different lengths.

Effect of line length. Figure 4 shows that apparent speed is reduced for all orientations when the line length is increased from the shortest (squares) to the longest (triangle). For the shortest line length (squares), the tilted comparison line has the same apparent speed as the vertical standard speed (Vs/Vc about 1).

This increased speed underestimation with longer lines indicates that only readings normal to the contour are pooled along the line before being integrated, whereas the translation signal seems not to be. This is conveniently described by an interaction between a specific terminators' motion, that does not benefit from the increasing length, and local readings. When line length is increased, the normal component of motion becomes therefore relatively more salient than terminators' motion in the combination process. Conversely, when the length becomes very short (our shortest line subtends 0.21 deg of visual angle), the normal component becomes so weak compared to the line endings motion that it is discarded from the integration process, and cannot bias perceived speed anymore (circles). This failure of the normal component to be integrated explains also why the shortest line has the same apparent speed regardless of its orientation.

Pooling perpendicular to the direction of motion has already been described by van Doorn and Koenderink (1982). These authors have shown how enlarging the width of a stroboscopically moving dot pattern could be effective in enhancing its threshold signal to noise ratio, although pooling in the direction of movement is much more efficient (see also McKee & Welch, 1985). Whether the same type of pooling process is at work here is however unclear because of the different methodologies used in both studies. Most notably, the presentation of the moving dot pattern, limited only by the response of the subject, was much longer than the one used in our study (167 msec). It is then possible that the pooling process occurring with our display may operate on a faster time scale.

Some computational models explicitly use the spatial pooling of early motion signals. In Perrone's (1990) model for instance, the motion signals elicited by long edges of a moving object are over-represented. Consequently, the computed velocity of the moving object does not usually yield the actual motion. Instead, a bias towards the velocity of the longest lines is shown to occur.

Alternatively, instead of interpreting these results as due to an absolute increase of the local signals influence by virtue of spatial pooling, one could argue that terminators in fact lose their influence because they would be presented more peripherally as line length increases. Indeed, the integration of terminators' motion was shown to be much impeded at an eccentricity of 7 deg (Lorenceau & Shiffrar, 1992).

It seems unlikely that the length effect reported here may be explained by the smallest influence of terminators, although this interpretation cannot be completely ruled out. First, the centre of the lines whatever their length is always presented at the same eccentricity ($D = 1.32$ deg, Fig. 1) which always makes the lower terminator closer to the fovea when length is increased. Second, the eccentricity of the upper terminator is relatively small (<2 deg for the longest line). Thus, a reasonable prediction is that the stronger signal of the lower terminator should at least compensate for the slightly weaker signal of the upper terminator.

Finally, this length effect is in qualitative agreement with the work of Lorenceau *et al.* (1993). This study showed that the bias towards the direction of local readings was more pronounced when line length was increased, and already proposed an interpretation based on the spatial pooling of local readings.

Effect of speed. Inspection of Fig. 4 reveals that the results concerning orientation and length effects are qualitatively the same with the standard speeds of 2.1 and 4.2 deg/sec. However, the bias in apparent speed is more important with the speed of 2.1 deg/sec both for the medium length [$F(1,3) = 18.15$; $P = 0.02$] and the long length [$F(1,3) = 35.82$; $P = 0.009$]. In this case, in contrast to the length effect, it is *a priori* not clear whether this increased bias results from an absolute degradation of terminators' motion or from an increase of the local components' signal *per se*. In the first hypothesis, it could be argued for instance that the units processing local readings are tuned to lower speeds than those processing terminators. Instead of this *ad hoc* hypothesis however, we suggest that lower speeds produce a signal normal to the contour which is stronger than the translation signal. This predominancy would occur for two reasons that might be non-exclusive. First, the normal component of motion could be weightier at lower speeds because spatial pooling occurs more easily when speed is decreased. This is suggested by considering the results of van Doorn and Koenderink (1982) already mentioned (their Fig. 3). These authors report an elevation of the thresholds associated with higher speeds. This loss of sensitivity indicates somehow a degradation of the pooling process with greater speeds. We propose that the same mechanism, less spatial pooling along the line at greater speeds, takes place in our study. It would thus explain why the relative weight of the orthogonal component is lower for a speed of 4.2 deg/sec than for a speed of 2.1 deg/sec. The second intepretation is not in terms of interaction between local normal readings and terminators' signals, but rather between motion detectors with different spatial scales. There is psychophysical evidence that motion detectors integrate energy over regions whose extents are proportional to the speed they are tuned to (e.g. van de Grind, Koenderink & van Doorn, 1986). As a consequence of the poorer spatial resolution with higher speeds, the units responding to the horizontal translation of a tilted line would become relatively more numerous than the units responding to the normal component of motion. Thus a model that integrates motion over multiple spatial scales (e.g. Smith & Edgar, 1991) by favouring the most active population could be also consistent with our results.

EXPERIMENT 2

The first experiment provided evidence that the perceived speed of a tilted line translating horizontally was judged lower than a vertical line moving with the same translation. This decrease of apparent speed was stronger when the line was made more oblique, that is when the local speed readings were shorter. This bias was also greater when the length of the line was longer, or its speed lower. We interpreted these findings as evidence that the terminators' motion *per se* along with the orthogonal components of motion are early signals that interact with different relative weights.

In order to reinforce this hypothesis, we wished to know if another simple attribute of the moving contour, supposed to alter specifically the processing of the terminators, would result in a lower apparent speed of the line by allowing more relative influence to the local signals. Lorenceau and Shiffrar (1992) and Lorenceau *et al.* (1993) have shown how low contrast levels of moving contours could make the motion signals of terminators less salient in tasks involving the integration of different velocities. Therefore, the luminance was manipulated in this experiment in order to generalise our finding that estimating the perceived speed of a moving contour relies on a combination process involving two types of signals: local perpendicular components and terminators' motion.

Stimuli and procedure

The standard and comparison lines had the same length (0.88 deg of visual angle), and same luminance that could take one of five levels (3.8, 5.2, 7, 10.6 or 131 cd/m^2). The highest level was the one used in Expt 1. The comparison line had an orientation of 30 deg above the horizontal ($\theta = 60$ deg). The standard speed was 2.1 deg/sec.

During the first session, the starting speed of the comparison-stimulus was the same as that of the standard, and for subsequent sessions it was set at +10% of the standard speed to accelerate staircase convergence. After the first reversal, the step (10% of standard speed) was halved and kept constant. Then the up-down procedure was run until six reversals were achieved. The estimate was the mean of the six last reversals. In all other respects, the stimuli and procedure were the same as in Expt 1.

Three observers, one of the authors, and two naive observers (LF, AD) who had never practised psychophysical tasks, served in this experiment. The two naive observers had beforehand gone through extensive training in the speed discrimination task already described.

Results and discussion

The relative perceived speed of the tilted line is plotted against its luminance for three observers on Fig. 5. The

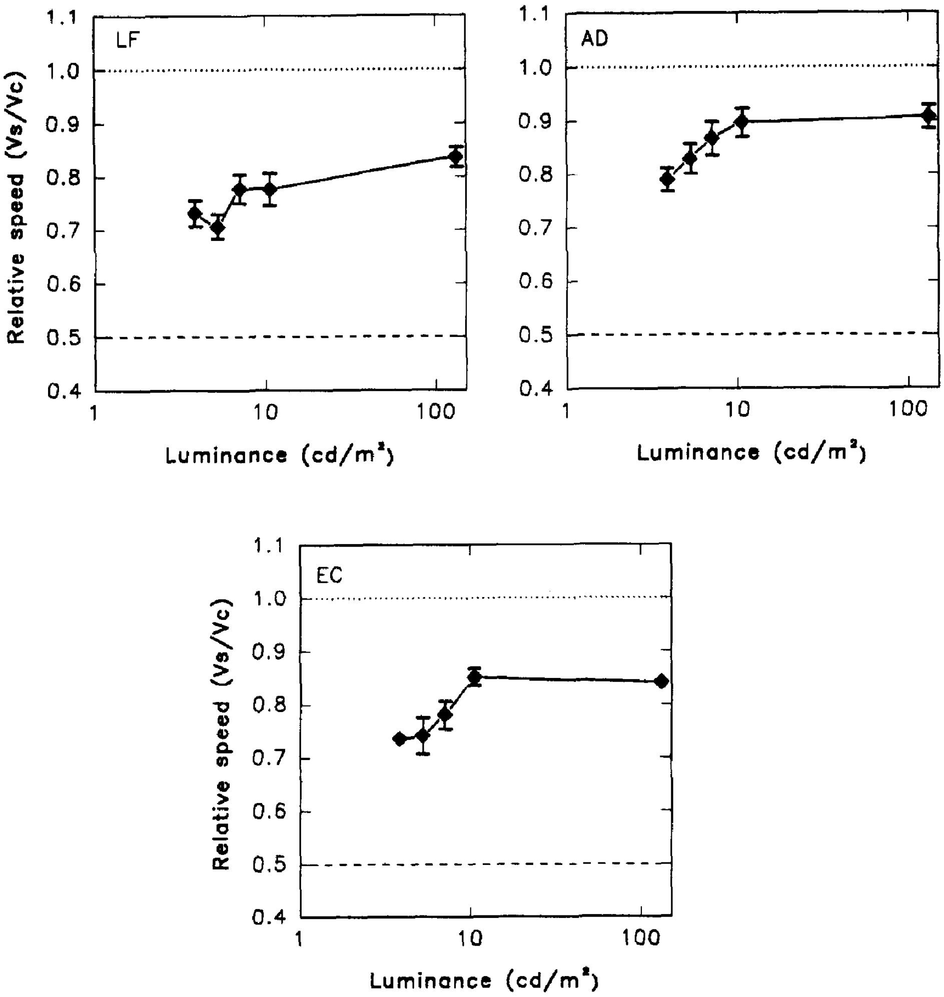

FIGURE 5. Results of Expt 2 for three observers. Relative perceived speed is plotted as a function of the line luminance (logarithmic scale). The horizontal dotted line (Vs/Vc = 1) represents veridical match between the standard and the comparison. If perceived speed was solely determined by the normal component V_L, the results would lie on the dashed line. Vertical bars indicate standard errors.

first point to be noted is the speed underestimation for all luminance levels used: all experimental points lie below the thin dotted line representing perfect matching with the standard (Vs/Vc = 1). Since the standard and the comparison had identical luminance, these results cannot be accounted for by the lower apparent speed of low contrast stimuli reported by Thompson (1982) and Stone and Thompson (1992). With the highest level (131 cd/m^2), the decrease in perceived speed is similar to that obtained in Expt 1 with the same level (between 0.8 and 0.9). With lower luminance levels, apparent speed decreases indicating a progressive higher influence of the orthogonal component of motion at a subsequent stage of combination. If perceived speeds were uniquely determined by local readings, the results would lie on the 0.5 dashed line ($V_L/V_T = 0.5$ with this line orientation). While the relative influence of local motions and terminators' motions stays constant between about 10 and 131 cd/m^2, the relative influence of the normal component becomes progressively greater with lower luminance levels. For observer LF, the effect of luminance is non-monotonic for the lowest levels because of the very low visibility he reported in these conditions after the experiments.

This progressively greater bias toward orthogonal components with lower luminance levels was already reported in our previous work (Lorenceau *et al.*, 1993) where it was revealed by measuring the perceived direction instead of the apparent speed of translating lines. This misperceived direction with lower luminance was also reported here, although not measured, by all observers when asked about it at the end of the experiment.

The effect of luminance on the integration of different velocities was also studied by Lorenceau and Shiffrar (1992) with an outlined diamond moving behind non-visible apertures. From a computational point of view, recovering the true motion of this stimulus implied the integration of the components of motion normal to the visible parts of the diamond that were distributed across space. It also meant "ignoring" the velociites of the line terminators (resulting from the occlusion by the apertures) which were not correlated with the true motion. The results showed that correct recovery was only possible with low luminance levels. This suggested that low contrast renders terminators' motion less salient and permits the integration of the local readings normal to each contour in a final global coherent percept.

Altogether, these results may be interpreted in three ways. First, the influence of luminance could be due to its differential effect on two types of early detectors which process respectively the terminators' motion and the local orthogonal motion, as first proposed by Lorenceau and Shiffrar (1992). They suggested that the response of terminators' motion was carried out by detectors with higher contrast thresholds than that of detectors responding to oriented contours. Accordingly, lower contrasts would diminish the probability of signaling terminators' motion much more than the probability of signalling local velocity readings.

Alternatively, it could be hypothesized that the spatial pooling of local signals along the line, demonstrated in Expt 1, is in fact responsible for the effect of luminance. The loss of visibility induced by lower luminance levels could be the same at an early stage in both terminators' detectors and normal components' detectors. However, the signal normal to the contour would be less altered than terminators' motion by virtue of spatial pooling.

A third alternative may be envisaged if the translation signal was detected by more global processes. One could argue that motion detectors tuned to large scales in the order of the line length would be responsible for analysing the motion of the line as a whole. The existence of such detectors is supported for instance by the motion capture effect described by Ramachandran and Cavanagh (1987). This hypothesis is indeed compatible with our results provided that large scale detectors are less sensitive than smaller detectors activated by local normal signals.

WEIGHTED AVERAGE HYPOTHESIS

We now present a simplified quantitative model which aims at formalizing the integration of different velocities in order to obtain a final velocity estimate. So far, our data on apparent speed have been stated in qualitative terms. We have assumed, on the basis of these results, that two primary motion signals are available in our display: the true translation motion of the line ($\mathbf{V_T}$), and local components normal to the contour ($\mathbf{V_L}$). Although reliance on the translation motion alone would permit to recover the true velocity field of the moving line, the visual system defaults towards local readings in our experimental conditions. This results in a final velocity estimate which is a compromise between the translation motion and local orthogonal signals.

Intuitively, this qualitative characterization seems to be consistent with an averaging process of the velocity vectors $\mathbf{V_T}$ and $\mathbf{V_L}$. In addition, vector averaging is an attractive tentative model because it permits the assignment of different relative weights to both signals ($\mathbf{V_T}$ and $\mathbf{V_L}$), thus describing their respective perceptual saliences. Therefore, we set out to compare our results in Expt 1 with quantitative predictions based on a weighted average of the translation motion and local readings.

We first review some of the basic definitions of vector calculus applied to our display. Figure 6 represents the upper part of an oblique line undergoing a translation $\mathbf{V_T}$ rightward. The vector $\mathbf{V_L}$ is a local reading normal to the contour. Both vectors are "attached" to the upper line terminator to allow a vector construction as in a velocity space. The vector labelled $\mathbf{Va_1}$ is the average vector of $\mathbf{V_L}$ and $\mathbf{V_T}$ in the usual sense. In this case, it is often referred to as a mean vector. It is obtained by taking the half diagonal of the parallelogram constructed with $\mathbf{V_L}$ and $\mathbf{V_T}$. Using vectorial notation, this leads to the expression: $\mathbf{Va_1} = \frac{1}{2}*\mathbf{V_L} + \frac{1}{2}*\mathbf{V_T}$. Other vectors can be calculated by assigning different weights to $\mathbf{V_L}$ and $\mathbf{V_T}$, so that the resultant average vector $\mathbf{Va_i}$ has its terminal point "sliding" along the segment (dashed line) joining both terminal points of $\mathbf{V_L}$ and $\mathbf{V_T}$. The more weight is given to $\mathbf{V_T}$, the more the average vector "slides" upwards.

In the general case, we have:

$$\mathbf{Va_i} = \alpha*\mathbf{V_L} + \beta*\mathbf{V_T} \tag{1}$$

with $\alpha + \beta = 1$.

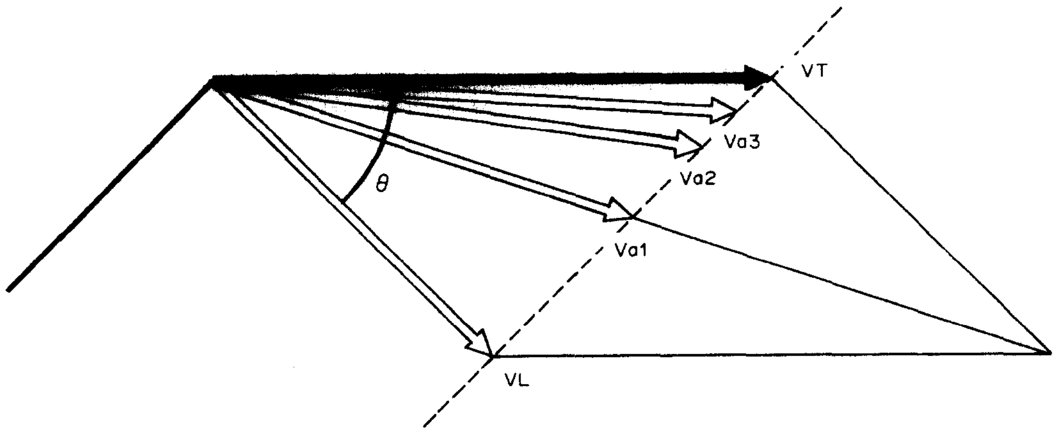

FIGURE 6. Upper part of a tilted moving line illustrating the weighted average calculus. The translation of the line is represented by the solid vector $\mathbf{V_T}$ attached to the upper line terminator. The components of motion perpendicular to the contour is represented by the open vector $\mathbf{V_L}$. The vector $\mathbf{Va_1}$, the half diagonal of the parallelogram constructed with $\mathbf{V_L}$ and $\mathbf{V_T}$, is an equally weighted average (the mean) of $\mathbf{V_L}$ and $\mathbf{V_T}$. As the relative weight α assigned to $\mathbf{V_L}$ is reduced, the resultant average vector $\mathbf{Va_i}$ "slides" along the dashed line towards $\mathbf{V_T}$ ($\mathbf{Va_i} = \alpha*\mathbf{V_L} + \beta*\mathbf{V_T}$ with $\alpha + \beta = 1$). $\mathbf{Va_2}$ and $\mathbf{Va_3}$ correspond respectively to weights α of $\frac{1}{2}$ and $\frac{1}{4}$.

In Fig. 6, only three average vectors among all possible have been represented: $\mathbf{Va}_1$ already defined, $\mathbf{Va}_2 = \frac{1}{4}*\mathbf{V}_L + \frac{3}{4}*\mathbf{V}_T$, and $\mathbf{Va}_3 = \frac{1}{8}*\mathbf{V}_L + \frac{7}{8}*\mathbf{V}_T$. The shift from $\mathbf{Va}_1$ to $\mathbf{Va}_2$, as well as from $\mathbf{Va}_2$ to $\mathbf{Va}_3$, corresponds to the division by 2 of $\mathbf{V}_L$'s weight. These three average vectors have been chosen to illustrate graphically the effect caused by a two-fold decrease of $\mathbf{V}_L$'s weight. Note also that they are constructed with α inferior to β to remind that terminators are often given a great functional role in the integration of different velocities (Hildreth, 1984; Shimojo *et al.*, 1989; Lorenceau & Shiffrar, 1992).

As mentioned above, we wish to know whether the magnitude of any average vector $\mathbf{Va}_i$ is consistent with the apparent speed of our display in Expt 1. More precisely, we assume that a given line length produces a constant weighting of $\mathbf{V}_L$ and $\mathbf{V}_T$ regardless of the orientation of the line. To assess numerically this prediction, the magnitude of the vector $\mathbf{Va}_i$ corresponding to a given set of weights has to be calculated in function of the line orientation. In fact, since we are interested in relative speed, we have to calculate Va_i/V_T (indeed V_T is the translation speed of the tilted comparison line) which is exactly the value predicted for relative perceived speed. Moreover, since we have chosen to plot the data of Expt 1 against V_L/V_T, we would like to express Va_i/V_T as a function of V_L/V_T to permit direct graphical comparison. This is achieved with simple vector calculus (as shown in the Appendix) by deriving the following function from equation (1)

$$Va_i/V_T = \sqrt{\{\beta^2 + (\alpha^2 + 2*\alpha*\beta)\ (V_L/V_T)^2\}}. \qquad (2)$$

This function permits now to answer the question: what is the average vector associated with each line length under the assumption of vector averaging in Expt 1? For the medium and long line lengths, the data have been fitted with the function (2) by adjusting the parameters α and β. The best fit is represented by dashed lines in Fig. 4 for the long and medium lengths at two standard speeds, and the parameters of these adjustments are displayed in Table 1. Inspection of Fig. 4 shows that experimental points lie close to the predictions. This is consistent with the hypothesis that each line length results in the adoption of a different set of relative weights that stays constant for all orientations of the contour employed here. Then the magnitude of the corresponding average vector would be computed, yielding lower values when the line becomes more oblique.

More geometrical insight into the aspect of the vectors corresponding to the fitted parameters is provided by considering for instance the vector $\mathbf{Va}_2$ ($\frac{1}{4}*\mathbf{V}_L + \frac{3}{4}*\mathbf{V}_T$) in Fig. 6. This vector turns out to be close to the average vector computed for the long contour (triangles) with a standard speed of 4.2 deg/sec [Fig. 4(b)].

TABLE 1. Relative weights of $\mathbf{V}_L$ and $\mathbf{V}_T$ as estimated in Expt 1 with a weighted average hypothesis

	Standard speed			
	2.1 deg/sec		4.2 deg/sec	
	α	β	α	β
Medium length	0.21	0.79	0.14	0.86
Long length	0.41	0.59	0.25	0.75

The adjusted weights (Table 1) express quantitatively two results that were already reported in Expt 1. First, for the two speeds used, we note that a two-fold increase in the line length multiplies the weight α attached to $\mathbf{V}_L$ by a factor of about 2. Second, the weight α of the orthogonal component is about 1.6 times lower for a speed of 4.2 deg/sec than for a speed of 2.1 deg/sec with the two lengths. In addition, it is simply verified, with this vector-description, that the relative weight assigned to the terminators' motion is always greater than that given to local readings.

This quantitative approach does not claim to provide a general model of velocity integration. In its present form, it offers a simple description of the results of Expt 1. The main assumption of this model is that the two signals that must be fed into the combination stage are the vector quantities $\mathbf{V}_L$ and $\mathbf{V}_T$. The relative strength of both signals depends on the filtering characteristics and on the pooling properties of early motion detectors. In this sense, the relative weights α and β reflect the effect of many confounded factors.

One of these factors might be the luminance of the lines, as suggested by the results of Expt 2. Actually, the bias in apparent speed increases with lower luminance levels which implies that α and β depend on luminance. Another factor might be the duration of presentation. Recently, Yo and Wilson (1992) showed that some misperceptions with two-dimensional patterns could disappear when the duration of presentation was increased. We also presented similar effects of duration with oblique lines in translation: the bias towards local orthogonal readings diminished with longer durations and finally disappeared with a duration of about 500 msec (Lorenceau *et al.*, 1993). In this latter work, in contrast to the present one, the model we proposed was better adapted to take into account the properties of early motion-extraction processes. This model included different contrast sensitivity functions, and different time constants, for the two populations supposed to process the signals $\mathbf{V}_L$ and $\mathbf{V}_T$.

The quantitative predictions made here in order to test the averaging hypothesis are based on the use of three different orientations for each condition in Expt 1. One could question whether the averaging strategy would hold for other orientations and especially for those close to horizontal. Figure 7 shows, for three observers, the predictions (in dashed lines) extrapolated from their individual performances in Expt 1 as a function of all possible angles between $\mathbf{V}_L$ and $\mathbf{V}_T$. The notation is the same as in Fig. 4. Open symbols represent the measurements obtained in Expt 1. According to these predictions, the perceived speed of lines very close to horizontal (small values of V_L/V_T) should be greatly under-estimated. This misperception is predicted, even for horizontal lines, because the model assumes that any signal $\mathbf{V}_L$, even when it has a very small magnitude, is

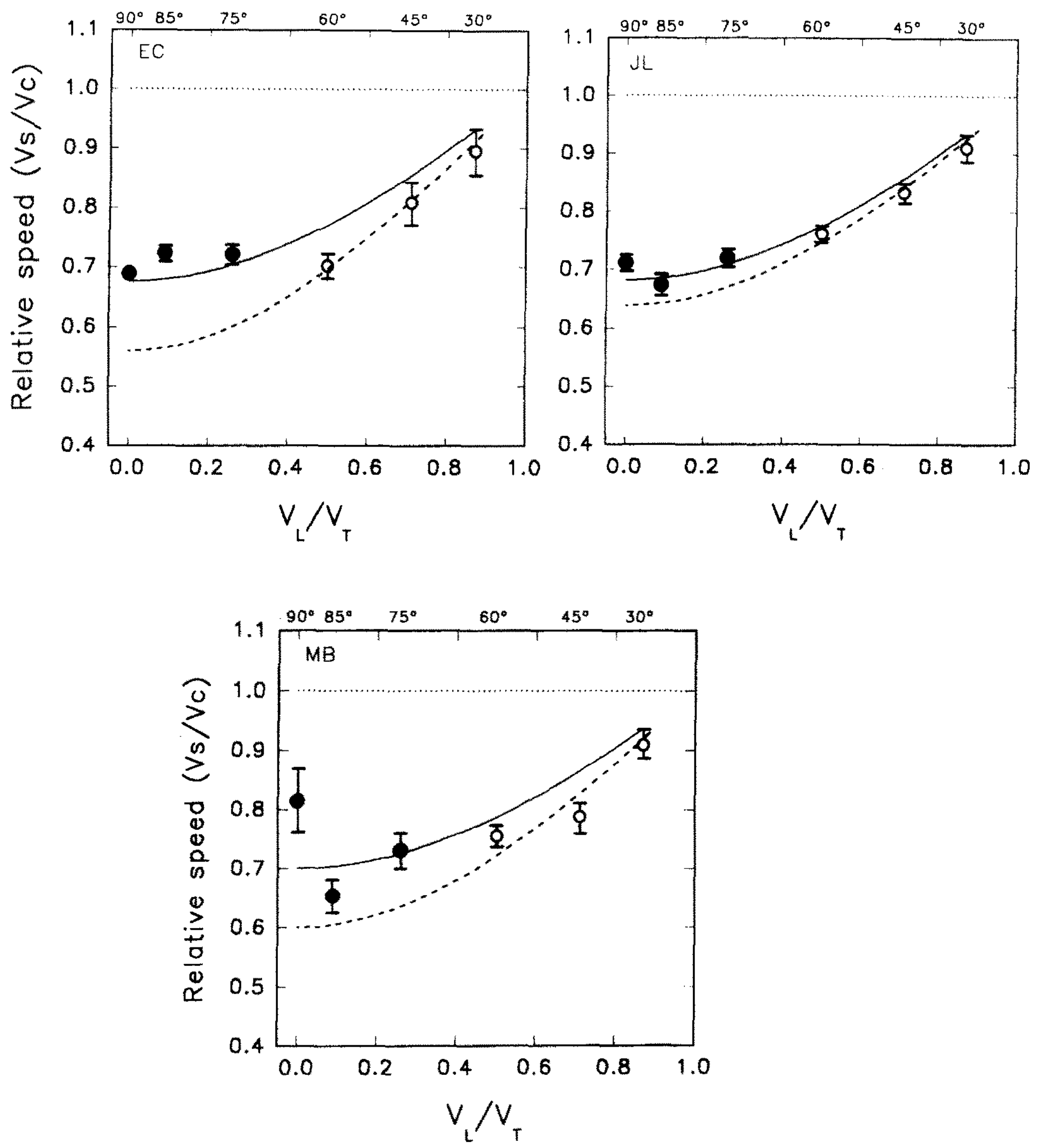

FIGURE 7. Effect of line orientation on apparent speed for three observers with one line length and one standard speed. The three measurements already made in Expt 1 are represented by open symbols. These data are adjusted with dashed lines according to the predictions of the weighted average hypothesis. Additional measurements with lines close to horizontal are represented by solid symbols. The six experimental points are fitted by solid lines according to the averaging model. Standard speed, 2.1 deg/sec; line length, 1.76 deg.

still able to activate velocity mechanisms. However, there are reasons to doubt the validity of this prediction. First, reliable velocity coding implies spatio-temporal recruitment of motion detectors (McKee & Welch, 1985), a process which should be relatively more difficult as the line becomes more oblique. Second, low speeds are known to be relatively less precisely encoded than medium ones (McKee, 1981; de Bruyn & Orban, 1988; Snowden & Braddick, 1991). At the extreme, one could even wonder whether the task of judging the speed of very oblique lines still implies a two- rather than a one-dimensional integration of velocities. At first sight, a horizontal line moving horizontally seems to imply the integration of only one-dimensional velocity signals across space. If it was the case, the predictions of the averaging model should not be reliable with small V_L signals, and this model should be modified to incorporate the dependence of α on line-orientation.

In order to answer these questions, we made some additional measurements using the same procedure and the same stimuli as in Expt 1. The effect of line-orientation on perceived speed was assessed for three additional angles ($\theta = 75$, 85 and 90 deg). Note that the angle of 90 deg corresponds to an horizontal line. Only one line length (1.76 deg) and one speed (2.1 deg/sec) were used. The results are shown in Fig. 7 with solid symbols for three observers (observer MB was unaware of the purpose of the experiment). The apparent speed of the lines close to horizontal, along with the horizontal line itself, is clearly underestimated with respect to the vertical line. Although there is some inter-subject variability, the data seem to indicate a certain stabilization of the bias in apparent speed with small values of V_L/V_T. How do these data fit with the averaging predictions? When compared with the extrapolation from the three points measured in Expt 1 (dashed lines), the present data indicate a moderate saturation of the effect, especially for observer EC. This is not the case, however, when all orientations are included in the adjustment (solid lines). Then, the data seem compatible with an averaging of V_L and V_T that implies less bias towards V_L. In this latter case, although the fit is obviously less accurate, the hovering perceived speed is in keeping with the predictions of the averaging hypothesis for all orientations (except for observer MB with the horizontal line).

Despite some inter-subject variability, these results are broadly consistent with an averaging model without further embellishment. It seems therefore that the underestimation reported with the lines close to horizontal may also be interpreted as a bias of the translation signal towards local slow speeds. The underestimation of the horizontal line further suggests that the null component of motion orthogonal to the line is encoded and incorporated in the averaging process. This encoding is consistent with the idea that any system of directionally selective detectors must have a characteristic null response when no movement occurs (Barlow & Hill, 1963).

Finally, it must be noted that, according to the vector averaging model, a bias in apparent speed for oblique lines should be closely correlated with a bias in apparent direction. This prediction cannot be tested on the basis of the work of Lorenceau *et al.* (1993) on misperceived directions. In fact, in this latter study, the direction-bias was estimated by its probability of occurrence instead of its apparent direction. Moreover, the main purpose of this previous study was not to test the possibility of an averaging process, so that only one orientation of the oblique lines was used. This of course prevents us from comparing the data obtained in this way with the averaging predictions. Therefore, we think that the question whether direction and speed are processed independently or not should be further investigated.

To sum up, in conditions in which the normal component can be optimally extracted, clearly with the orientations used in Expt 1, it seems that an integration process relying on a weighted average of two signals, the translation motion and the local normal readings, may explain the effect of line orientation. In this context, the relative weighting of both signals would represent the efficiency with which these signals serve as inputs for the combination stage.

GENERAL DISCUSSION

Our experiments present conditions under which a straight oblique line undergoing an horizontal translation is apparently slower than a vertical line moving at the same velocity. This misperception increases when the line is tilted towards the horizontal. The apparent speed of the tilted line also reduces with greater line length, with lower speeds, or with lower luminance levels. The dependence of apparent speed on line orientation indicates that local speed readings, whose magnitude become shorter with more tilt, are taken as such by the visual system, thus drawing the final integrated speed towards lower estimates.

How do these results fit with current models of motion perception? A model based on a voting scheme (e.g. Perrone, 1990) for integration across space predicts the effect of line length, and can also predict the greater bias with lower speeds if it is assumed that low speeds permit better spatial pooling. However, the effect of luminance is not compatible with this type of models, because if all votes were equal, then lowering the luminance should not change the bias. In order to account for this effect, a model which integrates by averaging over spatial scales (e.g. Smith & Edgar, 1991) is more suitable, provided that large and small detectors have different contrast sensitivities. According to this view, large motion detectors detecting the translation signal would be relatively more affected by low luminance levels. Such integration over multiple spatial scales would also predict the speed effect if one assumes that detectors tuned to high speeds have large receptive fields (van de Grind *et al.*, 1986), and thus process the whole oblique line as a blob. One finding does not seem consistent with this latter model, however. In fact, it does not predict that increasing the line length would enhance the component of motion normal to the line as was effectively reported in Expt 1. Similarly, is the model of Wilson *et al.* (1992), which uses a vector averaging integration algorithm of Fourier and non-Fourier motion inputs, compatible with our data? In its current form, this model considers that non-Fourier motion is a texture boundary motion that must be extracted over regions much larger than those needed with Fourier motion. Given this formulation, it seems unclear how to derive a prediction for our stimuli which do not contain such texture boundary motion. Finally, we propose that the involvement of the line endings as specific motion "carriers" of the translation signal comes closest to explaining the data reported here and in previous studies (Lorenceau & Shiffrar, 1992; Lorenceau *et al.*, 1993).

There is electrophysiological evidence that feature points, such as line terminators or line discontinuities, could be processed by specific detectors. This processing could be related to the activity of end-stopped cells (Hubel & Wiesel, 1965; Orban, Kato & Bishop, 1979; Dobbins, Zucker & Cynader, 1989; Versavel, Orban & Lagae, 1990). In addition, a number of neurons show specific responses to many different pattern discontinuities in the area V2 of the monkey (von der Heydt & Peterhans, 1989; Peterhans & von der Heydt, 1989) and in the area 19 of the cat (Saito, Tanaka, Fukada & Oyamada, 1988; Tanaka, Ohzawa, Ramoa & Freeman, 1987).

We propose a tentative model for the rules governing the combination of different velocities. This model postulates a weighted average process of early motion signals and makes predictions that are consistent quantitatively with our present results, and at least qualitatively with previous ones (Lorenceau *et al.*, 1993). Other studies bearing on the integration of different velocities have argued in favour of averaging processes between early motion signals. Studies using moving random-dot stimuli have clearly shown that direction information (van Doorn & Koenderink, 1982; Williams & Sekuler, 1984; Watamaniuk, Sekuler & Williams, 1989; Williams, Tweten & Sekuler, 1991) as well as speed information (Watanamiuk & Duchon, 1992) could be averaged by the visual system. Using spatially dispersed contours moving within visible apertures, Mingolla, Todd and Norman (1992) also noticed that a vector average measure of velocity signals normal to these contours was consistent with their results.

Averaging of speed information is also suggested, in our opinion, by the results of Ferrera and Wilson (1991) with plaid motion stimuli. Plaids are classically used to study the integration of two different motion signals. Actually, these stimuli are composed of two superimposed moving gratings having different orientations, and appearing as a unique rigid moving plaid under particular conditions. However, it has already been remarked that the regions where the light and dark extrema of the individual gratings coincide form conspicuous nodes which could contribute, at an early level, to the analysis of motion (e.g. Derrington & Badcock, 1992). One consequence of making allowance for the motion of the nodes is that three signals, instead of two should be integrated by the visual system. With this simple assumption, the results of Ferrera and Wilson (1991) may be consistent with an integration process relying on vector averaging. These authors have measured the perceived speed of plaids with respect to moving standard gratings of different spatial frequencies. When the standard pattern was a grating of the same spatial frequency as the components of the plaid, the perceived speed of the plaids was slower than that of the nodes and larger than that predicted by the single components. This finding may be interpreted, at least qualitatively, in terms of an average measure of the components' velocities and of the nodes' velocity.

In agreement with this interpretation, there is an additional striking feature of Ferrera and Wilson's (1991) data that could be related to ours: namely, apparent speed decreases with greater angles between the components, that is with lower component speeds while nodes speed stays constant. This finding suggests that lower component-speeds could be responsible for drawing the final apparent speed of the plaid towards lower estimates. We suspect therefore that the same mechanisms could be at work in these studies and in ours, insofar as the motion of the nodes and of the terminators are considered to be relevant signals for the visual system in order to compute a final velocity.

In the same study however (Ferrera & Wilson, 1991), the perceived speed of plaids was predicted by the nodes' motion vector whenever the standard grating had the same spatial frequency as the spatial frequency of the nodes forming the plaid. To interpret the absence of vector averaging in this case, we suggest as pointed out by Mingolla *et al.* (1992) that the speed of the nodes was rendered more "accessible" by the use of a standard grating of the same spatial frequency as that of the nodes. In these conditions, the nodes' motion would become more emphasized relative to the components' motion in the integration process. Note that this variable perceptual salience of the nodes may be equivalent to that of the terminators which we have already reported, and could also depend on the same factors.

This idea may be pursued by considering the data concerning plaid-direction errors. These errors are classically defined with respect to the so-called intersection of constraints rule (IOC) as proposed by Adelson and Movshon (1982). The IOC solution is the only global motion consistent with the velocities of its two constituent gratings (components) assumed to be translating rigidly in the fronto-parallel plane.

The perceived direction of moving plaids has been studied more extensively than their perceived speed. Ferrera and Wilson (1990) found that type II plaids (both components lie on the same side relatively to the IOC resultant) were perceived with a direction different from that of the IOC predicted direction. Actually, the perceived direction was biased towards the vector sum direction (by about 5 deg). Note that when considering only direction, vector sum and vector mean direction are equivalent. These authors then suggested that averaging of both component motions was carried out concurrently with the intersection-of-constraints rule.

More recently, Yo and Wilson (1992) studied how the perceived direction of type II plaids was affected by their duration, contrast and eccentricity, and a model accounting for these data was proposed (Wilson *et al.*, 1992). Their three main results are the following.

(1) In peripheral vision, the perceived direction of type II plaids deviates by up to 40 deg from the IOC prediction. This deviation is smaller than that which would have been produced if direction judgements had been based on vector summation or on the direction of the faster component.

(2) At low contrasts (5 and 10%) in foveal viewing, the perceived direction of plaids is grossly biased toward the vector average of both components.

(3) At higher contrasts, this bias still occurs for short durations (< 90 msec) and becomes smaller, i.e. closer to the IOC motion, only after a time lag (150 msec).

These data present a great resemblance with our previous results (Lorenceau *et al.*, 1993). We showed that the perceived direction of lines translating in a direction not perpendicular to their orientation could be biased towards local readings extracted along the lines. This bias occurred at low contrasts or with short durations of presentation, and progressively disappeared when contrast or duration was increased. We interpreted these findings as evidence that the motion of terminators was less reliably processed at low contrast levels or at short durations, which rendered the local normal signals more pregnant in the final velocity estimation. The effect of peripheral viewing on velocity integration has also been studied by Lorenceau and Shiffrar (1992). They demonstrated that the true motion of an outlined diamond seen behind invisible apertures could be better recovered at 7 deg of eccentricity than in the fovea. In order to extract the true global motion, this task necessitated reliance on the motion-components normal to the lines and not on the motion of line terminators. Thus the integration of the terminators' motion seemed relatively reduced in the periphery.

Altogether these data obtained with single lines are akin to those obtained with plaids by Yo and Wilson (1992). Indeed, with both types of stimuli, there is a similar effect of contrast, duration and eccentricity on the strength of the bias towards normal components. It seems thus very likely that similar integration processes may be at work in both cases. These processes have been modelled by Wilson *et al.* (1992) and have successfully predicted the plaid-direction errors. A key feature of this model is that normal components of motion are averaged with the signal constituted by the motion of illusory contours which are created by the alignment of the plaids' nodes.

Could we interpret the plaid-direction errors by taking into account the motion signal elicited by feature points such as the nodes? It is known that the motion of the nodes in a plaid is equivalent to the motion of its IOC resultant. If we assume that the nodes in the plaids are (like the line-terminators) more or less salient depending on contrast, duration or eccentricity, we may try to describe the work of Yo and Wilson (1992) in the following way. In conditions in which the nodes are not optimally processed (low contrast, large eccentricity or short duration), the perceived direction would depend primarily on the motion of the components, and otherwise it would depend on a compromise between the components and the nodes. Only when the nodes are conspicuous features (high contrasts and long duration) would they overcome the bias due to the components and constrain the plaid motion to the IOC predicted direction.

It is noteworthy that the difference between Wilson *et al.* (1992) model and our interpretation relies partly on the nature of the signal used to counteract the components' motion. We agree that the texture boundary motion, obtained after squaring of the plaid and appropriate filtering, is a plausible candidate. Another non-Fourier motion candidate, however, may be the nodes motion, and could be processed concurrently.

To summarize, we have reviewed some important plaid-motion results and pointed out their resemblance with our single lines data. From the model developed by Wilson *et al.* (1992) to account for plaid-misperceptions, it is however not clear how to derive quantitative predictions for single moving lines. Therefore, we suggest that the allowance for nodes' motion in plaids may help bridging the gap between results involving different stimuli such as random dot moving stimuli, plaid-stimuli and moving contours.

Finally, the speed bias reported in this study, corresponding to a speed underestimation with respect to the line's translation, fits well with the directional bias reported in the work of Lorenceau *et al.* (1993) with oblique moving straight lines. In addition, the effects of line luminance and line length on the strength of this bias are qualitatively similar in both studies. This convergence of results is an incentive to further quantitative investigation of the correlation between speed- and direction-coding for moving two-dimensional patterns.

REFERENCES

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

Barlow, H. B. & Hill, R. M. (1963). Evidence for a physiological explanation of the waterfall phenomenon and figural aftereffects. *Nature, 200,* 1345–1347.

van den Berg, A. V., van de Grind, W. A. & van Doorn, A. J. (1990). Bilocal motion detectors are selective for orientation. *Journal of the Optical Society of America A, 7,* 933–939.

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

Derrington, A. M. & Badcock, D. R. (1992). Two-stage analysis of the motion of 2-dimensional patterns, what is the first stage? *Vision Research, 32,* 691–698.

Dixon, W. J. & Mood, A. M. (1948). A method for obtaining and analyzing sensitivity data. *Journal of the American Statistical Association, 43,* 109.

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

van Doorn, A. J. & Koenderink, J. J. (1982). Temporal properties of the visual detectability of moving spatial white noise. *Experimental Brain Research, 45,* 189–195.

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

Ferrera, V. P. & Wilson, H. R. (1991). Perceived speed of moving two-dimensional patterns. *Vision Research, 31,* 877–893.

van de Grind, W. A., Koonderink, J. J. & van Doorn, A. J. (1986). The distribution of human motion detectors properties in the monocular visual field. *Vision Research, 26,* 797–810.

Grzywacz, N. M. & Yuille, A. L. (1991). Theories for the visual perception of local velocity and coherent motion. In Landy, M. & Movshon, J. A. (Eds), *Computational models of visual processing* (pp. 119–133). Cambridge, Mass.: MIT Press.

von der Heydt, R. & Peterhans, E. (1989). Mechanisms of contour perception in monkey visual cortex. II. Lines of pattern discontinuity. *Journal of Neuroscience, 9,* 1731–1748.

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

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.

Levitt, H. (1971). Transformed up-down methods in psychoacoustics. *Journal of Acoustical Society of America, 49,* 467–477.

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 on motion integration across space. *Vision Research, 32,* 263–273.

Lorenceau, J., Shiffrar, M., Wells, N. & Castet, E. (1993). Different motion sensitive units are involved in recovering the direction of moving lines. *Vision Research, 33,* 1207–1217.

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

McKee, S. P. & Welch, L. (1985). Sequential recruitment in the discrimination of velocity. *Journal of the Optical Society of America A, 2,* 243–251.

Mingolla, E., Todd, J. T. & Norman, J. F. (1992). The perception of globally coherent motion. *Vision Research, 32,* 1015–1031.

Nakayama, K. & Silverman, G. H. (1988a). The aperture problem I: Perception of non-rigidity and motion direction in translating sinusoidal lines. *Vision Research, 28,* 739–746.

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., 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.

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

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.

Ramachandran, V. S. & Cavanagh, P. (1987). Motion capture anisotropy. *Vision Research*, *27*, 97–106.

Robinson, D. A. (1965). The mechanics of human smooth pursuit eye movement. *Journal of Neurophysiology*, *180*, 569–591.

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.

Smith, A. T. & Edgar, G. K. (1991). Perceived speed and direction of complex gratings and plaids. *Journal of the Optical Society of America A*, 1161–1171.

Snowden, R. J. & Braddick, O. J. (1991). The temporal integration and resolution of velocity signals. *Vision Research*, *31*, 907–914.

Stone, L. S. & Thompson, P. (1992). Human speed perception is contrast dependent. *Vision Research*, *32*, 1535–1549.

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.

Thompson, P. (1982). Perceived rate of movement depends on contrast. *Vision Research*, *22*, 377–380.

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.

Watamaniuk, S. N. J. & Duchon, A. (1992). The human visual system averages speed information. *Vision Research*, *32*, 931–941.

Watamaniuk, S. N. J., Sekuler, R. & Williams, D. W. (1989). Direction perception in complex dynamic displays: The integration of direction information. *Vision Research*, *29*, 47–59.

Westheimer, G. (1954). Eye movement responses to a horizontally moving visual stimulus. *Archives of Ophthalmology*, *52*, 932–941.

Wetherill, G. B. & Levitt, H. (1965). Sequential estimation of points on a psychometric function. *British Journal of Mathematical and Statistical Psychology*, *18*, 1–10.

Williams, D. W. & Sekuler, R. (1984). Coherent global motion percepts from stochastic local motions. *Vision Research*, *24*, 55–62.

Williams, D. W., Tweten, S. & Sekuler, R. (1991). Using metamers to explore motion perception. *Vision Research*, *31*, 275–286.

Wilson, H. R., Ferrera, V. P. & Yo, C. (1992). A psychophysically motivated model for two-dimensional motion perception. *Visual Neuroscience*, *9*, 79–97.

Yo, C. & Wilson, H. R. (1992). Perceived direction of moving two-dimensional patterns depends on duration, contrast and eccentricity. *Vision Research*, *32*, 135–147.

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

Acknowledgements—This research was supported by a Direction des Recherches Etudes et Techniques grant, and in part by a CNRS-NSF International Program grant (859).

APPENDIX

Vector calculus is used to obtain the magnitude of a vector $\mathbf{Va_i}$ defined by equation (1) with an angle θ between $\mathbf{V_L}$ and $\mathbf{V_T}$ (Fig. 6). A vectorial quantity is noted with bold characters, whereas its magnitude is represented by normal ones

$$\mathbf{Va_i} = \alpha * \mathbf{V_L} + \beta * \mathbf{V_T} \tag{1}$$

with $\alpha + \beta = 1$.

By taking the square of both sides of equation (1), we obtain:

$$(\mathrm{Va_i})^2 = \alpha^2 * \mathrm{Vl}^2 + \beta^2 * \mathrm{Vt}^2 + 2 * \alpha * * \beta * (\mathbf{V_L} \cdot \mathbf{V_T})$$

and

$$(\mathrm{Va_i})^2 = \alpha^2 * \mathrm{Vl}^2 + \beta^2 * \mathrm{Vt}^2 + 2 * \alpha * * \beta * \mathrm{V_L} * \mathrm{V_T} * \cos(\theta) \tag{1'}$$

substituting $\cos(\theta) = \mathrm{V_L}/\mathrm{V_T}$ into (1′):

$$\mathrm{Va_i^2} = \mathrm{Vt}^2 * (\beta^2 + (\alpha^2 + 2 * \alpha * \beta) * (\mathrm{V_L}/\mathrm{V_T})^2)$$

and finally:

$$\mathrm{Va_i}/\mathrm{V_T} = \sqrt{(\beta^2 + (\alpha^2 + 2 * \alpha * \beta)\ (\mathrm{V_L}/\mathrm{V_T})^2)}. \tag{2}$$