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DIRECTION PERCEPTION IN COMPLEX DYNAMIC DISPLAYS: THE INTEGRATION OF DIRECTION INFORMATION

SCOTT N. J. WATAMANIUK,[1] ROBERT SEKULER[2] and DOUGLAS W. WILLIAMS[3]

[1]Department of Psychology, [2]Departments of Neurobiology/Physiology, Psychology and Ophthalmology, and [3]Departments of Neurobiology/Physiology and Psychology, Northwestern University, Evanston, IL 60208, U.S.A.

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Abstract—We created random-dot cinematograms in which each dot's successive movements were independently drawn from a Gaussian distribution of directions of some characteristic bandwidth. Such a display, comprising many different, spatially intermingled local motion vectors, can produce a percept of global coherent motion in a single direction. Using pairs of cinematograms, direction discrimination of global motion was measured under various conditions of direction distribution bandwidth, exposure duration, and constancy of each dot's path. A line-element model gave an excellent account of the results: (i) over a considerable range, discrimination was unaffected by the cinematogram's direction distribution bandwidth; (ii) only for the briefest presentations did changes in duration have an effect; (iii) so long as the overall directional content of the cinematogram remained unchanged, the constancy or randomness of individual dots' paths did not affect discrimination. Finally, the line-element model continued to give a good account of the results when we made additional measurements with uniform rather than Gaussian distributions of directions.

Motion perception   Line-element model   Discrimination   Direction

INTRODUCTION

Though motion perception does depend upon spatially local processes, under certain circumstances global processes make an important contribution. For example, the human visual system can integrate different, spatially-intermingled motion vectors into a global percept of motion in a single direction (Adelson and Movshon, 1982; Williams and Sekuler, 1984). Such integrated percepts may offer important clues to the mechanisms of motion perception. To exploit such clues we have followed the tradition of using discrimination performance to probe underlying psychophysical mechanisms (e.g. Graham, 1965; Wilson and Gelb, 1984). Specifically, we were interested in how easily observers could discriminate between two different global motions when each had resulted from the integration of many different motion vectors.

Our stimuli were random dot cinematograms in which each dot took an independent two-dimensional random walk with steps of constant size. The direction any dot moved, from one display frame to the next, was independent of the dot's previous movements as well as the movements of other dots. All dots chose their directions of movement from the same probability distribution. Williams and Sekuler (1984), using uniform distributions of directions, showed that the resulting global percept of motion depends upon the range of the distribution. Specifically, uniform distributions with ranges of directions less than 180° tend to produce a perception of global motion in the approximate direction of the distribution's mean even though the random perturbations of each dot are evident. As the range increases further, the perception of global motion diminishes, until at the limit, a uniform distribution with 360° yields a percept of only local random motion of individual dots. In this present study, we measured the discriminability of the direction of global motion using the Gaussian distributions of directions.

To anticipate, our results show that direction discrimination of the global motion percept is influenced by both the bandwidth of the controlling direction distribution and duration of the stimuli, but not by the paths travelled by individual dots over time. As will be shown later in the discussion, our data are consistent with a line-element model described previously by Williams *et al.* (1988).

METHODS

Stimuli

Stimuli were 256 computer-generated dots plotted on an x–y cathode ray tube (CRT) display with a relatively fast, P4, phosphor. A mask, with a circular aperture 8 deg in diameter, covered the face of the CRT. This aperture allowed only about 130 of the 256 dots to be visible at any one time. The density of dots was 2.56 dots per square degree of visual angle. Each dot subtended 6 min. Luminance of a single dot was about 0.82 cd/m^2. The luminance of the mask was 0.07 cd/m^2; the veiling luminance was 0.03 cd/m^2.

Stimuli were presented at a frame rate of 17.5 Hz. The initial screen location of each dot was randomized for each presentation, rendering the pattern of dots an unreliable clue to direction. From frame to frame, each dot's movements were controlled by a predefined distribution of directions stored as an array of x- and y-increments. The predefined distribution of directions was Gaussian.* The computer read the increment values for a dot's movements from the array, added the increments to the dot's current position and transmitted the dot's new x- and y-position to the CRT display via precision, 12-bit digital-to-analog converters. This provided a display with more than 40,000 addressable points per square degree of visual angle. The spatial density of this addressable matrix allowed us to produce equal displacements regardless of direction. Each displacement was 0.46 deg; at our framerate of 17.5 Hz, this created effective dot velocities of 8 deg/sec.

Supported and restrained by a chin-headrest, the seated observer viewed the CRT monocularly from a distance of 57 cm. The non-preferred eye was covered by a translucent patch. The height of the CRT was set so that the center of the aperture was at approximately eye level and observers were required to maintain fixation on a dot located at the center of the aperture. Push-buttons connected to the computer initiated each trial and signalled the observer's responses.

*Because of the discrete nature of the display, it was not possible to present a continuum of directions. We approximated a Gaussian distribution by sampling at one degree intervals.

Observers

One of the authors (SW) and four university students served as observers for all experiments. Except for SW, all observers were naive to the purposes of the present experiments and had normal, or corrected-to-normal, visual acuity. Those who required corrective lenses wore them for all experiments.

Procedure

Stimuli were presented in a two-alternative forced-choice procedure. Though the durations of the paired test intervals varied from condition to condition, on any single trial the two were always of equal duration. Interstimulus interval was fixed at 500 msec.

Different distributions of directions governed motion in the two intervals of each trial. One test interval, picked at random, was governed by a distribution whose mean direction was 90 deg (upwards); we'll refer to this stimulus as the standard. Motion in the other test interval was governed by a distribution whose mean was greater than 90 deg (that is, counterclockwise of upwards); we'll refer to this stimulus as the comparison. The observer had to identify the interval in which the global direction of motion was upwards. Note that for all stimuli, the mean velocity was in the same direction as the mean dot-displacement.

A session consisted of six blocks, 48 trials each. A block of trials was characterized by one combination of direction bandwidth and test-interval duration. In order to produce a large range of discrimination performance, from chance to near perfection, six comparison stimuli with different mean directions were used in each block. Trial-wise feedback was provided, with a low tone signalling an incorrect response. Approximately 4 sec elapsed between trials. Over any 48-trial block, the standard stimulus appeared equally often in the first and second intervals.

EXPERIMENTS

Experiment I. Bandwidth and duration

This experiment examined direction discrimination as a function of (i) the directions present in the stimulus, and (ii) stimulus duration. Four ranges of directions were used, each defined by a different Gaussian distribution of directions. The distributions had standard deviations (SD)

Table 1. Bandwidths and mean directions of stimuli with Gaussian and uniform direction distributions

	Mean directions	
	Standard	Comparison
Standard deviations of Gaussian distributions		
0.0 deg (unitary motion)	90 deg (upwards)	91, 92, 93, 94, 95, 96
17 deg	90 deg	91, 92, 94, 95, 96, 98
34 deg	90 deg	92, 94, 95, 96, 98, 100
51 deg	90 deg	92, 95, 97, 99, 102, 105
Ranges of uniform distributions		
1 deg (unitary motion)	90 deg (upwards)	91, 92, 93, 94, 95, 96
31 deg	90 deg	91, 92, 93, 94, 95, 96
91 deg	90 deg	91, 92, 93, 96, 99, 102
161 deg	90 deg	92, 94, 95, 100, 105, 110

of 0.0†, 17, 34 and 51 deg. Larger standard deviations, or bandwidths, imply a greater range of directions was simultaneously present in the cinematogram. All standard deviations used produced global motion in the approximate direction of the mean of the distribution.

A pilot study showed that discrimination varied with bandwidth. So, to span the psychometric functions of each bandwidth, sets of comparison stimuli with different means were needed. Table 1 lists the six comparison means associated with each bandwidth. Five durations of presentation, 3, 6, 9, 12 and 25 frames, were completely crossed with the four bandwidths. For each combination of bandwidth and duration, an observer was tested on a total of 288 trials.

Analysis

Responses were aggregated to yield the percentage correct for each combination of standard and comparison. The percentage correct responses for individual observers were then fit by the Quick (1974) psychometric function, given by

$$\Psi(S) = 1 - 2^{-(kS)^P}, \quad (1)$$

where S is the separation in mean direction between the standard and comparison stimulus, measured in deg, $1/k$ is the difference between standard and comparison means at which $\Psi(S)$ equals 0.5 (chance performance), and P determines the maximum slope of the function in the neighborhood of 75% correct. This function provided good fits to the observed data (mean r^2 for 100 data sets was 0.89). Discrimination thresholds, defined as the difference between standard and comparison mean directions sufficient to yield 75% correct, were evaluated from the fitted psychometric functions. Threshold values were then treated by analysis of variance (ANOVA)‡ including a trend analysis on the two variables.

RESULTS

Discrimination thresholds, averaged over observers, are plotted as a function of bandwidth

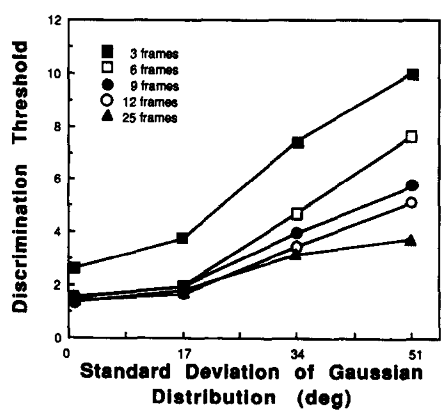

Fig. 1. Discrimination thresholds (see text for definition) for five durations, averaged over observers, plotted as a function of stimulus distribution standard deviation (SD). Notice that at all SDs, the three-frame thresholds are higher than all others. At the two smallest stimulus SDs, thresholds are identical for durations of six frames or more. For these same durations, thresholds diverge at larger SDs. At the two largest SDs, there seems to be a systematic change in thresholds with duration; thresholds decrease as duration increases.

†The Gaussian distribution with a standard deviation of 0.0 deg signifies motion in which all dots moved in parallel paths in the same direction.

‡The evaluation of discrimination thresholds produced two extremely large values that were substantially different from the others. These extreme values were due to a lack of monotonicity in two observers' data for a particular bandwidth-duration combination. These two values were excluded from the ANOVA conducted on the bandwidth and duration data.

in Fig. 1. As the figure shows, discrimination thresholds for each duration increased with stimulus bandwidth. Generally, discrimination thresholds changed relatively little as stimulus SD was increased from 0.0 to 17 deg, but changed substantially with further increases. This observation was confirmed with a trend analysis of the data averaged over durations, which yielded significant linear and non-linear components ($F_{1,2} = 5520.72$ and $F_{2,4} = 8.45$, both $P < 0.05$). Notice that at the smallest bandwidths, the discrimination thresholds for the four longest durations are indistinguishable. However divergence does occur as bandwidth gets larger. In contrast, the results at the shortest duration, three frames, differ from those of other durations at all bandwidths. This interaction between bandwidth and duration was confirmed by the ANOVA ($F_{12,24} = 13.03$, $P < 0.05$). This implies that as bandwidth grows, it may take longer to perceive the global flow. It is clear however, that regardless of bandwidth, discrimination thresholds obtained with the briefest presentations are consistently higher than those obtained with longer ones.

To more clearly show the effect of duration, we have replotted the data as a function of duration in Fig. 2. The figure shows a progressive decrease in discrimination threshold as a function of duration (linear trend $F_{1,2} = 256.74$, $P < 0.05$). However, the decrease in threshold with duration also contains non-linear components ($F_{3,6} = 14.72$, $P < 0.05$). A larger decrease occurred when duration was increased from three to six frames than when duration was increased from 12 to 25 frames. Moreover, discrimination thresholds for the two

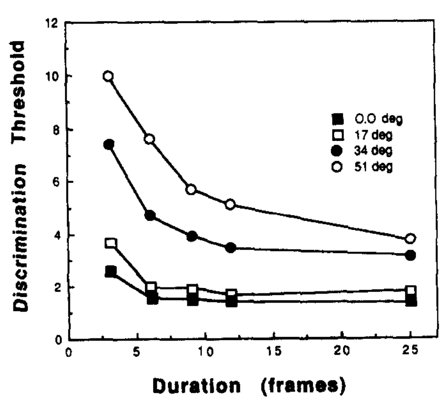

Fig. 2. Discrimination thresholds (see text for definition) for four stimulus distribution standard deviations, averaged over observers, plotted as a function of duration. Note that for the two smallest distribution SDs (filled and unfilled squares), thresholds have reached an asymptotic minimum after a duration of only six frames.

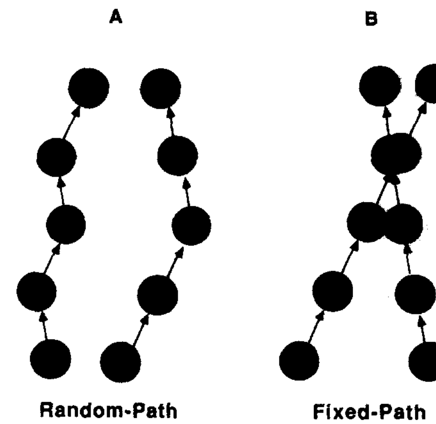

Fig. 3. Two types of individual dot motion, random-path (A) and fixed-path (B). Note that only two directions of local motion are present in both A and B and that the vector-sum of the directions is the same in both cases.

smallest bandwidths seemed to reach an asymptotic level between 6 and 25 frames of duration. In contrast, for the largest bandwidth, each increase in duration produced a further decrease in the discrimination threshold.

Experiment II. Effective dot path

In Expt I, discrimination thresholds increased as bandwidth increased. However, because several aspects of the stimuli covary with bandwidth, that experiment does not allow unequivocal inferences to be made about the cause of the threshold increase. By definition, the number of directions contained in a stimulus increases with bandwidth. So, as bandwidth increases, the path taken by any single dot contains a greater *variety* of directions. This greater variety might itself have increased the variability of the perceived global direction, thereby impairing global direction discrimination for the stimulus as a whole. We wanted to determine, therefore, how discrimination performance might vary with the number of directions occurring in each dot's path.

To answer this question, we created two stimuli that produced very different individual dot paths but had the same aggregate direction distribution. Both types of stimuli are illustrated in Fig. 3. In one, dots took a two-dimensional random walk as described earlier. Because each dot's path was random, within limits imposed by the distribution bandwidth, we'll refer to such a stimulus as the *random-path* type. Such paths are represented in panel A for two different dots. In the other type of stimulus, a different scheme generated a dot's path. Once a dot had randomly chosen a direction for its first displacement, it continued to move in that same direction for the entire presentation. Because each dot moved along its own characteristic fixed path, we'll refer to such a stimulus as the *fixed-path* type. Such paths are represented in panel B for two different dots. Note that although the aggregate direction distributions for both stimuli are identical, the variability of their dot paths are very different. In the *random-path* stimulus, the controlling distribution of directions creates differences between different dots' paths, and also introduces randomness to any single dot's path. In the *fixed-path* stimulus, the controlling distribution affects only differences between different dots' paths.

The two stimulus types were used to produce three test conditions. In one condition, both presentations within a single trial were fixed-path stimuli (fixed-path condition). In a second condition, both presentations were random-path stimuli (random-path condition). In the third condition, one random-path and one fixed-path stimulus were presented on each trial (combined condition). In this last condition, the two types of motion were completely crossed with respect to which served as the standard or comparison and also their presentation order.

Discrimination performance was measured for six separations between the standard and comparison mean directions: 2, 4, 5, 6, 8 and 10 deg. All stimuli had a Gaussian direction distribution with a standard deviation of 34 deg. Each stimulus was presented for nine frames. This bandwidth and duration were chosen because in previous experiments this combination produced a moderate level of performance. This ensured some latitude for discrimination performance to improve or grow poorer as condition varied from random-path to fixed-path. Observers were the same as those in Expt I.

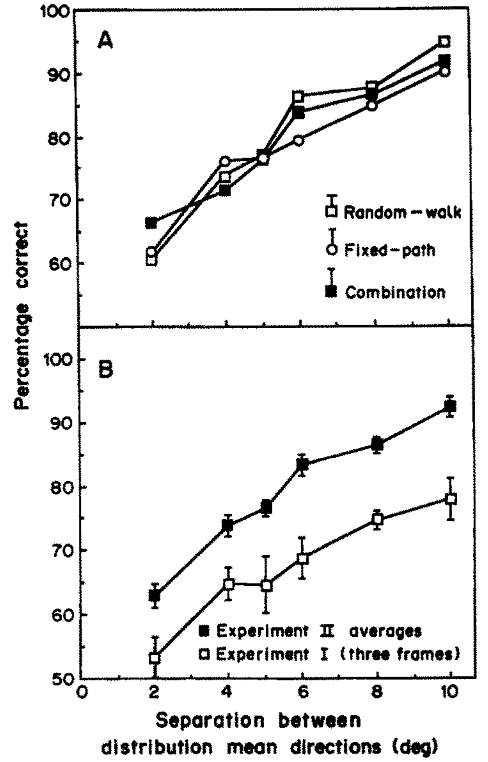

Fig. 4. Percentage correct judgments as a function of mean direction separation. Data are averaged over all observers. (A) Data are presented for three dot-path conditions. Average standard error bars are provided in the legend for each condition. Notice that the three different conditions yield quite similar results. (B) Data, averaged over the three dot-path conditions, are presented with data from Expt I. These Expt I data were obtained using the same stimulus bandwidth but presented for only three frames. Standard error bars are provided on each curve. Note that the three-frame data from Expt I are far below the averaged data from Expt II.

RESULTS

The data, averaged over observers and represented as percentage correct, are plotted as a function of the difference in mean direction between the standard and comparison stimuli in Fig. 4A. The figure shows that all three conditions yielded similar discrimination ($F_{2,8} = 1.22$, $P > 0.05$).

At the duration used in this experiment, nine frames, the two types of motion were different. However, if one looked at the stimuli through a narrow time window, in particular, examining only a single pair of successive frames, the minimum needed to define motion, the two types of stimuli would be indistinguishable. We were concerned, therefore, that this short-term similarity between stimuli might account for the similarity in performance with the two types of motion. This concern would be serious if performance had become asymptotic at a presentation of just two frames. Then, observers would have extracted all the necessary stimulus information before any real differences between stimulus types could have become manifest. But for our experiments this concern is not justified.

Results from Expt I show that asymptotic performance in Expt II would certainly have required presentations longer than just two frames. In Fig. 4B we have plotted the average of the earlier results for the stimulus with an SD of 34 deg presented for three frames, the shortest presentation used. The averaged results from the present experiment, for both stimulus types, are also plotted in that figure. Recall that all cinematograms in that earlier experiment were of the type we've labelled "random path". Note that performance with presentations of only three frames in Expt I was far below that obtained in Expt II, with nine frames. Therefore, within just two frames, observers in Expt II had not extracted all the necessary information to determine the direction of motion. So, the identity of random-path and fixed-path stimuli over the first two frames of presentation cannot explain the lack of performance difference between the stimuli at nine frames.

The results of Expt II suggest that individual dot paths over frames are not being used by the visual system in determining the direction of global perceived motion. Rather, perceived global direction seems to depend only upon the *distribution* of directions of motion present from one frame to the next. That is, the visual system keeps track of the directions created by any one displacement but does not keep track of the successive movements, over frames, of individual dots.

DISCUSSION

As stated earlier, one of the major objectives of this research is to account for our results with a line-element model of direction discrimination. Before discussing the model, it will be useful to relate our results to those in the literature and discuss the implications that these results hold for research in motion perception.

We have found that direction discrimination of random-dot cinematograms depends upon certain stimulus dimensions. First, increasing stimulus bandwidth decreases direction discrimination. Further, increasing stimulus duration results in an improvement in discrimination performance. However, in developing its representation of global direction, the visual system appears to disregard information about the paths that individual dots take.

The visual system also seems to disregard some information contained in the stimulus' velocity. To appreciate this point, note that the upward vector of velocity covaried with the mean direction of the stimulus. In particular, the magnitude of this upward vector was proportional to the sine of the mean direction. So, if subjects could extract the magnitude of this upward vector they could have performed the discrimination using velocity information rather than direction information *per se*. To determine if this were the case, we ran a control experiment in which dot velocity was rendered unreliable as a cue for direction discrimination. In this control experiment, stimulus velocity was independently randomized for the two intervals of each two-alternative forced-choice trial by changing dot speed. For each interval, speed was chosen randomly, without replacement, from a set of three quite different speeds, 4, 6 and 8 deg/sec. The results with randomized speeds were essentially the same as those obtained previously with unchanging speed. So, random variation of speed between intervals of a trial does not affect direction discrimination. Note that this randomization changed the magnitude of the upward velocity vector by far more than would have resulted from changing mean direction alone. As a result, we can conclude that subjects, in our main experiments, were not basing their discriminations on velocity cues.

The results of our two main experiments relate to previous work in motion perception. Williams and Sekuler (1984), using stimuli similar to that used here, found that global motion in a single direction was always seen when the range of the uniform direction distribution was less than or equal to 180 deg. Experiment I showed that, although unidirectional global motion was always perceived, as the bandwidth of the direction distribution increased so did the discrimination threshold. The present results suggest that although coherent global flow can be created by any one of a wide range of bandwidths, the precise direction seen may not be as predictable. In other words, the directional bandwidth controls the precision with which the perceived direction matches the mean of the direction distribution.

Experiment I also provided some indication of the integrative power of the visual system in determining direction of motion. Figure 1 showed that direction discrimination did not change significantly when the bandwidth of the stimulus was raised from $SD = 0.0$ to $SD = 17$ deg. This occurred even though the two distributions produced highly distinguishable patterns of movement. The visual system seems to extract and integrate directional information just as easily from stimuli containing many different directions (the stimulus with an SD of 17 deg contained 79 different directions of motion) as it does with only a single direction present.

But bandwidth was not the only variable that influenced discrimination. Stimulus duration also had an impact: as the duration of the stimuli increased, direction discrimination improved. This implies some sort of temporal summation in the process that governs perceived direction of motion. Note that the number of frames needed to reach asymptotic performance is not the same for all bandwidths: as bandwidth decreases, fewer frames are needed to produce asymptotic performance.

Experiment II examined the effect of dot path on discrimination. The results showed that when direction distributions were identical, whether the dots took random walks or followed fixed but different paths, discrimination was unchanged. Previously, Williams and Sekuler (1984) showed that the global percept of motion does not depend on the spatial relationship between local motion vectors over time. Our findings agree with this view: when many vectors of motion are present, the direction of global motion is determined by the *distribution* of directions rather than by the individual dot paths.

The result also has some methodological, as well as theoretical, implications. Some researchers, utilizing random dot displays, have purposely limited the lifespan of individual dots to restrict the directional information contained within a single dot path (e.g. Mather and Moulden, 1980, 1983). The present result, that individual dot paths do not affect direction discrimination, suggests that this control may not always be necessary. When the stimulus is comprised of many random dots, the visual system does not necessarily utilize information about the consecutive movements of individual dots.

THEORY

A line-element model of direction discrimination

As stated earlier, one of our objectives was to account for global direction discrimination with a line-element model. Line-element models have been successful in accounting for several visual discrimination tasks involving dimensions such as wavelength and spatial-frequency (Graham, 1965; Wilson and Gelb, 1984; Wilson and Regan, 1984; Wilson, 1985). A line-element model has also been useful for predicting the conditions under which random dot displays with very different direction distributions would be *metameric*, that is indistinguishable perceptually despite their considerable physical differences (Williams *et al.*, 1988).

Any line-element model has three defining characteristics. First, it postulates mechanisms whose sensitivity profiles span the stimulus dimension of interest. For any stimulus, the total response of a mechanism is the sum of that mechanism's individual response to each component of the stimulus. Second, discrimination between two stimuli depends upon the change in a mechanism's response as a result of a change in stimulus components. Finally, the differences in responses to two stimuli are pooled over all mechanisms. This implies that the discriminability of two stimuli is a function of a scalar value (Graham, 1965).

An example of a line-element model is one Williams *et al.* (1988) used to predict which set of discrete directions of motion would have to be mixed in order to generate a percept that was indistinguishable from one generated by a stimulus containing a broad band of directions of motion. This model comprised a set of direction selective mechanisms, and the response of the model depended only upon the component directions of the stimulus. Our data show that direction discrimination also depends only upon the *distribution* of *directions* and not the distribution of velocities or the paths of individual dots. These results, together with the previous success of the Williams *et al.* (1988) line-element model, made it reasonable to attempt to fit the present data with the same model.

In the remainder of the discussion, we will describe the basic structure of the line-element model that we used to account for the present data. Parameters of the model will be estimated using data obtained for stimuli with Gaussian distributions of directions presented for 12 frames. The same parameters will then be used to account for data obtained with different presentation durations and predict results for stimuli that had uniform, rather than Gaussian, direction distributions.

Description of the model

The basic structure and assumptions of the present model are the same as those used to account for motion metamers (Williams *et al.*, 1988). The present model assumes that the full range of directions (360 deg) is spanned by a small number of evenly-spaced mechanisms. All mechanisms have the same Gaussian-shaped response profile (equation 2) and each mechanism only responds to a particular range of directions. The center-to-center separation between any two adjacent mechanisms is equal to their half-amplitude half-bandwidth (one-half of a mechanism's full bandwidth measured between the points where its response profile is at one-half of its full height).

More formally, the sensitivity of the ith mechanism, centered at θ_i, to direction of motion θ is given by

$$S_i(\theta) = \exp\{-[(\theta - \theta_i)/h]^2 \ln 2\}\,, \quad (2)$$

where h is the half-amplitude half-bandwidth of the mechanism. The response of the ith mechanism to a distribution of directions, $D(\theta)$, is given by

$$R_i(D) = \sum_{\theta=1}^{360} S_i(\theta)\,\mathrm{pr}\{D(\theta)\}, \quad (3)$$

where $S_i(\theta)$ is the ith mechanism's sensitivity to direction θ, and $\mathrm{pr}\{D(\theta)\}$ is the proportion of dots in distribution $D(\theta)$ that move in direction θ.

To predict the discriminability of any two distributions, $D(\theta_1)$ and $D(\theta_2)$, with different mean directions, one calculates the difference, for each mechanism, between its responses to the two distributions

$$\Delta R_i = R_i\{D(\theta_1)\} - R_i\{D(\theta_2)\}. \quad (4)$$

These differences are then pooled for all the individual mechanisms according to a Qth norm rule:

$$\Delta R = \left\{\sum_{i=1}^{M} |\Delta R_i| Q\right\}^{1/Q} \quad (5)$$

where M is the number of mechanisms. ΔR represents the total difference between the responses to the two stimuli generated within the visual system. Note that this method of pooling allows for the effects of probability summation (Quick, 1974).

The variable Q determines the way response differences, ΔR_i, for each mechanism will be combined. If $Q = 1$, all ΔR_i's are weighted equally and the system would be taking the simple sum of all ΔR_i's. If $Q > 1$, the larger values of ΔR_i are weighted more heavily than smaller values; if Q = infinity, the model acts as a peak detector, taking only the single largest value of ΔR_i into account.

In order to relate the predicted values of ΔR to the data obtained in Expt I, we used a psychometric function of the form:

$$Y(\Delta R) = 1 - 2^{-(k\Delta R)^P}, \quad (6)$$

where k is equal to the value of $1/\Delta R$ at $Y(\Delta R) = 0.50$ and P is related to the slope of the psychometric function.

The model as described above has four free parameters, two of which we fixed on *a priori* grounds. Previous researchers, Wilson and Gelb (1984), have shown that when $Q = 2$, a line-element model provides good fits to spatial-frequency discrimination data when the stimuli are presented under *sustained* temporal conditions. The temporal modulation of their sustained stimulus was Gaussian with a $1/e$ time constant of about 250 msec. Following Wilson and Gelb, we decided to use $Q = 2$ in order to fit the data we obtained at a duration of 12 frames, since at this duration, thresholds for the three smallest standard deviations first reached asymptotic levels. The decision left three free parameters, k, P and M, the number of mechanisms.

We set $M = 12$ in accordance with Williams *et al.* (1988) who found that a model with 12 mechanisms accounted for metameric relations between cinematograms that contained a wide range of directions and cinematograms that contained just a few directions. Having fixed Q and M, we estimated the optimum values for k and P by a least-mean-squares fit to Expt I data presented for 12 frames. Table 2 shows the chi-square (χ^2) goodness-of-fit values obtained for best-fits to the present data. All χ^2 values are well below the critical value suggesting that the model fit the data well.

Table 2. χ^2 values of model fits to four Gaussian stimuli and predictions for four uniform stimuli presented for 12 frames

Observer	Gassian distribution	Uniform distribution
CC	8.35	24.92
CP	7.73	9.21
DA	4.88	7.63
JW	12.93	17.38
SW	4.16	5.60
critical $\chi^2_{0.95}$	33.9 (d.f. = 22)	36.4 (d.f. = 24)

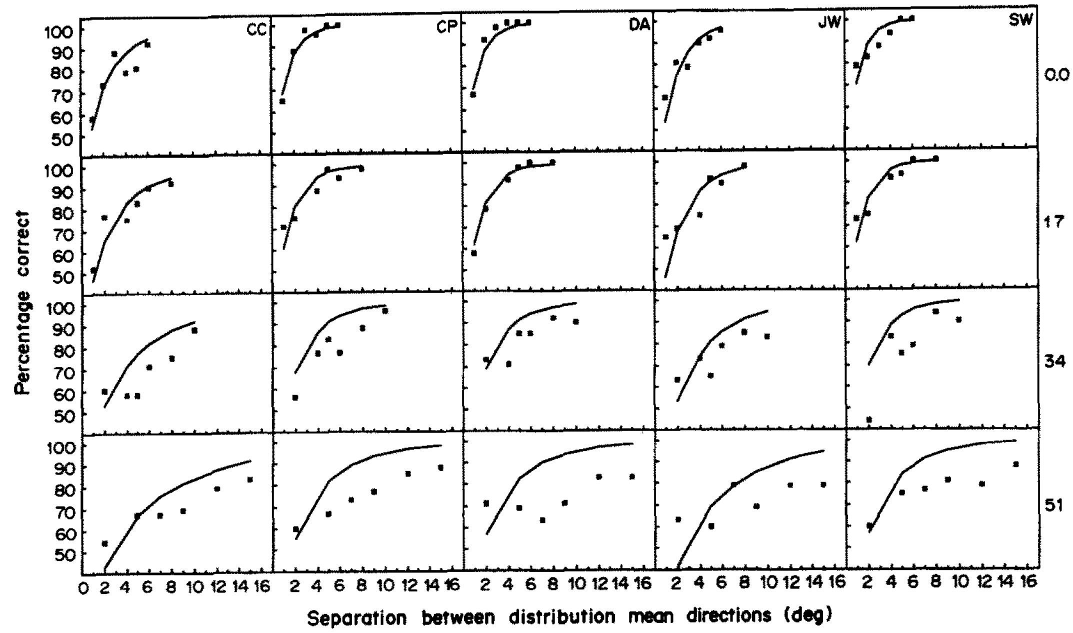

Fig. 5. Data for four stimuli with Gaussian distributions of directions with different standard deviations (SD), presented for a duration of six frames. Data are represented by the filled squares while the solid curves represent fits from a 12-mechanism line-element model with $Q = 2$. Each row of graphs represents data for a single stimulus distribution SD; each column provides a single observer's data. Note that the slope of the data gets shallower as the distribution SD increases and that the model fits follow this trend of the data.

Model fits for various durations

The model as described above, provided a satisfactory account of data obtained for stimuli presented for a long duration, 12 frames, with $Q = 2$. Since the 6-, 9-, 12- and 25-frame conditions seemed to be grouped together (see Fig. 1), the same parameters used to fit the 12-frame data were also used to fit the 6-, 9- and 25-frame data. The predicted values along with the observed data for the 6-frame condition, for all observers, are presented in Fig. 5. Those for the 9-frame condition appear in Fig. 6 while those

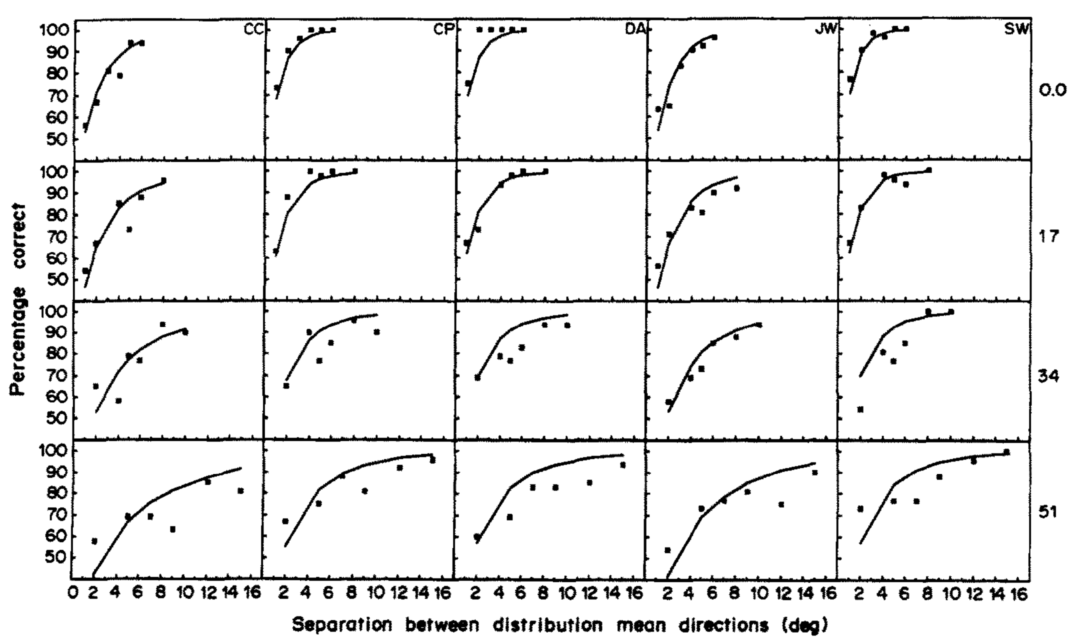

Fig. 6. As in Fig. 5, but for a duration of nine frames.

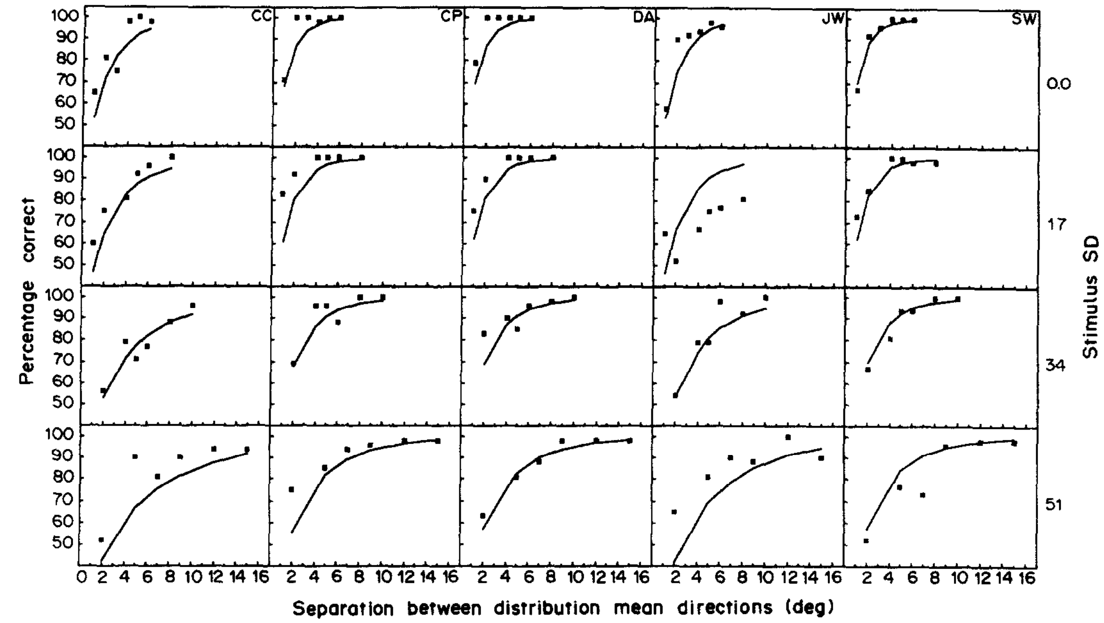

Fig. 7. As in Fig. 5, but for a duration of 25 frames.

for the 25-frame condition appear in Fig. 7. Data are shown by the filled squares and the model by the lines. For all three duration conditions, the model captures the trend of the data. χ^2 goodness-of-fit values for the 6-, 9-, and 25-frame data appear in Table 3. The χ^2 values for all observers were below the critical value.

Discrimination thresholds obtained at durations of six frames or greater appear to be grouped together (see Fig. 1). However, for the shortest presentation, three frames, discrimination was poorer. Since a model of direction discrimination should account for this effect of duration, we sought to use the present model to predict discrimination for this very short stimulus duration.

Previously, Wilson and Gelb (1984) demonstrated an empirical relation between Q and stimulus duration. They found that a line-element model with $Q = 2$ predicted spatial-frequency discrimination when the stimuli were presented in sustained temporal conditions. When the stimulus was only presented for about 125 msec (transient condition), $Q = 2$ did not give a good account of the data, but $Q = 6$ did. Since the duration of three frames, in msec, was close to that of the transient condition described by Wilson and Gelb, we used $Q = 6$ to predict discrimination in the three-frame condition. The values of k, M and P remained fixed at the values previously estimated.

Figure 8 compares the model fits to the 3-frame data for all observers, measured for various stimulus standard deviations. Data are represented by filled squares and the model calculations by the lines. Across any row, all the graphs show data for a single standard deviation; within any column, graphs are for a single observer. Table 3 lists the χ^2 values for each observer. Since there were four standard deviations crossed with six separations, there were a total of 24 data points per person used in the calculation of χ^2. As can be seen, all but one of the χ^2 values are below the critical value. In-

Table 3. χ^2 values of model fits to four Gaussian stimuli presented for durations of 3, 6, 9 and 25 frames

Observer	3 frames	6 frames	9 frames	25 frames
CC	27.62	12.93	11.35	13.03
CP	18.47	10.72	5.15	10.65
DA	24.00	14.66	7.03	5.78
JW	50.17	19.10	7.78	23.40
SW	18.47	15.64	8.35	3.87
critical $\chi^2_{0.95}$	35.2 (d.f. = 23)	36.4 (d.f. = 24)	36.4 (d.f. = 24)	36.4 (d.f. = 24)

Note: Value underlined exceeded critical χ^2.

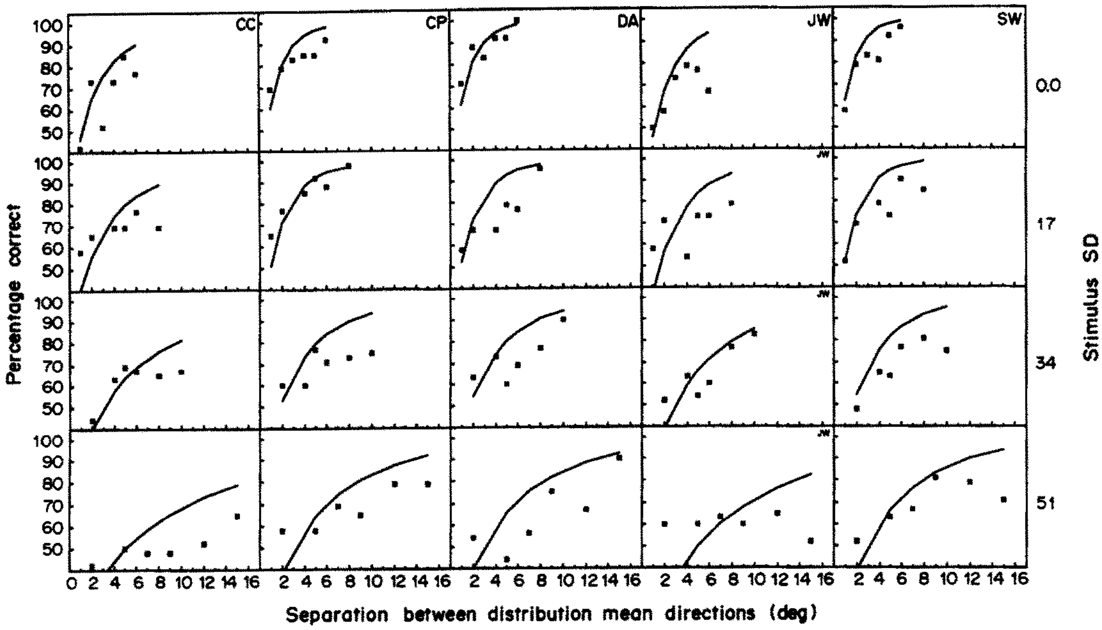

Fig. 8. Data for four stimuli with Gaussian distributions of directions with different standard deviations (SD), presented for a duration of three frames. Data are represented by the filled squares while the solid curves represent fits from a 12-mechanism line-element model with $Q = 6$.

spection of Fig. 8 shows that although the general trend of the data is captured by the model, the fits are not particularly good for the largest standard deviation. The fits would not have been appreciably improved by increasing Q beyond its set value of six since predictions change little as Q is raised above this value. This relatively poor fit to the data can not be reconciled at this time.

Discrimination with uniform distributions

We next sought to determine whether the model parameters developed for long-duration stimuli with Gaussian direction distributions (Expt I) could also account for performance with a different distribution of directions. So we measured direction discrimination, for the same observers as before, now using stimuli with *uniform* direction distributions. The uniform distributions had ranges of 1, 31, 91 and 161 deg. As we did earlier with the Gaussian stimuli, discrimination was measured for six separations between mean directions, yielding 24 data points per person (separation values for each uniform distribution are found in Table 1). All stimuli were presented for 12 frames.

Figure 9 compares the predictions of the 12-mechanism model to data obtained with the four uniform stimuli for all observers. This is a parameter free fit to the data, the parameters having been determined in fitting the model to the long-duration Gaussian data. Data are represented by the filled squares and predictions by the lines. Inspection of the figure shows that qualitatively, the model captures the trends in the observed data well. χ^2 goodness-of-fit values were evaluated, for each observer, using all 24 points obtained with the uniform stimuli. The χ^2 values for each observer for the fitted data (Gaussian stimuli) and predicted data (uniform stimuli) are found in Table 2. For all observers, the χ^2 values were well below the critical value. Thus the same parameters that earlier gave a good account of data with long-duration Gaussian stimuli, also give a good account of data with long-duration uniform stimuli.

Summary of model results

For all observers, a line-element model with 12 mechanisms and $Q = 2$, provided a good fit to data obtained with Gaussian direction distributions presented for 12 frames. Consistent with the idea that durations of six frames or greater fall into the same group (see Fig. 1), the same parameters that provided good fits for the 12-frame data also provided good fits for the 6-, 9-, and 25-frame data. For the briefest stimuli, three frames, the model required that $Q = 6$. Finally, the same parameter set estimated for Gaussian direction distributions, presented for

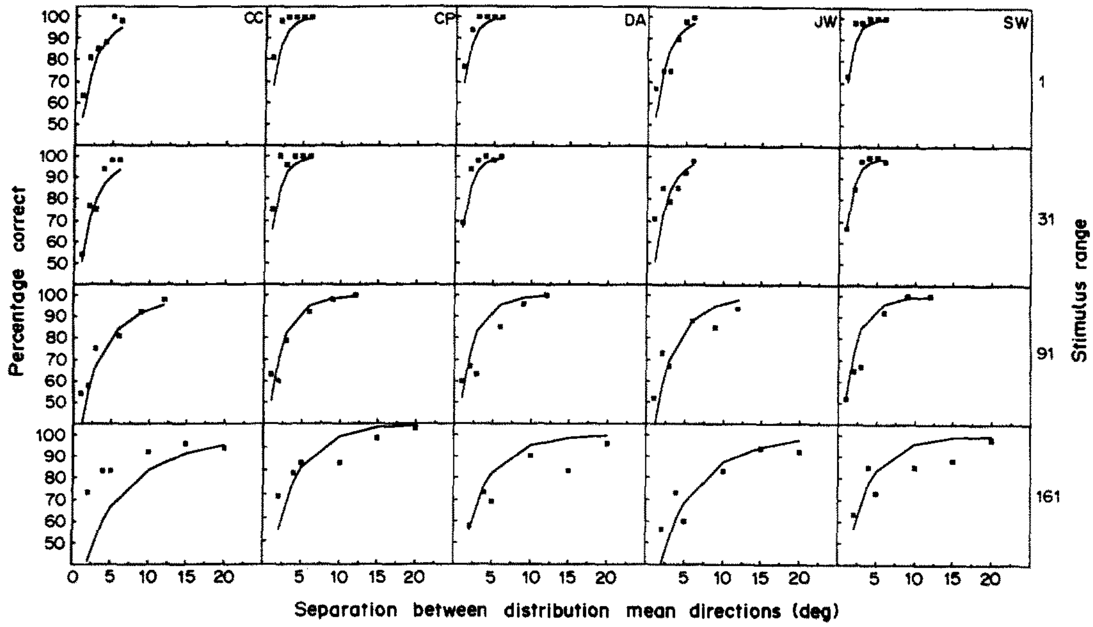

Fig. 9. Data for four bandwidths of uniform stimuli presented for 12 frames. Data are represented by the filled squares while the solid curves represent predictions from a 12-mechanism line-element model with $Q = 2$. Model parameters were evaluated from fitting data obtained for four stimuli with different Gaussian distribution standard deviations presented for 12 frames. Each row of graphs represents data for a single stimulus bandwidth; each column provides a single observer's data. As in the previous figures, the slope of the data gets shallower as the bandwidth increases; this trend is captured well by the model predictions.

12 frames, did a good job of predicting discrimination with four *uniform* distributions, presented for 12 frames.

Further research

This research raises further questions about the ability of the visual system to integrate direction information. Although we have considered discrimination obtained with durations of six frames or greater as a group, it is apparent that for stimuli with large bandwidths there is a systematic change in discrimination with duration (see Fig. 1). The present model, though adequate as a first approximation of the integration process, does not account for this bandwidth-duration interaction. Further research is needed to refine the model to account for this effect.

One aspect that has not been touched on here is the integration of information between the two eyes. In the present experiments, all stimuli were presented monocularly. An experiment that could help establish the locus of the integration would be to present part of the distribution of directions to each eye and measure the perceived direction of motion. By varying the relative proportion of the overall distribution shown to each eye and its directional content, we could establish how the visual system integrates motion information between the two eyes and how dissimilar the two stimuli must be before the integration system fails and rivalry results.

Another question of interest is whether color has an effect on the integration of direction information. Recent physiological research has shown that the cells in the Medial Temporal area (MT), which are particularly responsive to complex moving stimuli (Newsome *et al.*, 1986), seem little influenced by color (Livingstone and Hubel, 1987). If MT neurons were involved in the detection and integration of direction information, then one could psychophysically test whether the color of the components of the moving stimuli affect the perceived direction of motion.

A final question concerns the power of the system to integrate various directions. In particular, how similar must component directions of a stimulus be in order for integration to occur? We have shown that people can discriminate the global direction of motion produced by a distribution of directions, with a high degree of accuracy, even when the bandwidth is quite large. However, we also know that if two very different directions of motion are presented simultaneously, the observer perceives both directions of motion but with the separation between them exaggerated (Marshak and Sekuler, 1979). Stimuli similar to ours could be used to examine the continuum between perceiving a single global direction of motion (integration) and simultaneously perceiving several different separate directions of motion (segregation). To explore this continuum, one could present stimuli containing many different directions, sampled at various spacings, and measure whether observers perceived a single global direction.

CONCLUSIONS

To summarize the findings and implications of the present studies: increasing stimulus bandwidth decreases direction discrimination. Increasing stimulus duration results in an improvement in discrimination performance. In developing its representation of global direction, the visual system appears to disregard information about individual dot paths. A line-element model with 12 mechanisms accounts for direction discrimination for a wide variety of stimulus bandwidths and durations. The model required a systematic change in Q, the parameter that reflects the mode of pooling across mechanisms, to account for the change in discrimination with duration. A Q of 6 was required for the shortest duration while a Q of 2 was required for longer durations. A possible mechanistic way to interpret the change in Q with duration is that as duration decreases, fewer of the mechanisms' responses enter into the pooled, overall response.

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