

Temporal and Spatial Integration in Dynamic Random-Dot Stimuli

SCOTT N. J. WATAMANIUK,*† ROBERT SEKULER*‡

Received 23 October 1991; in revised form 24 March 1992

Random-dot cinematograms comprising many different, spatially intermingled local motion vectors can produce a percept of global coherent motion in a single direction. Thresholds for discriminating the direction of global motion were measured under various conditions. Discrimination thresholds increased with the width of the distribution of directions in the cinematogram. Thresholds decreased as the duration of area of the cinematogram increased. Temporal integration for global direction discrimination extends over about 465 msec (9.3 frames) while the spatial integration limit is at least as large as 63 deg² (circular aperture diameter = 9 deg). The large spatial integration area is consistent with the physiology of higher visual areas such as MT and MST.

Motion Direction discrimination Temporal integration Spatial integration Global motion Random dots

INTRODUCTION

When moving targets are time sampled and displayed as a sequence of frames, motion perception improves when the length of the sequence exceeds two frames. This improvement has been demonstrated for various aspects of motion perception including visibility (Burr, 1981), the maximum step size at which motion can be seen (Nakayama & Silverman, 1984; Snowden & Braddick, 1989b), detection of motion within a noisy display (van Doorn & Koenderink, 1983; Downing & Movshon, 1989), speed discrimination (McKee & Welch, 1985), motion interpolation (Morgan & Watt, 1982), and vernier acuity (Morgan, Watt & McKee, 1983). With random-dot cinematograms comprising distributions of many different directions, Williams and Sekuler (1984) found that the probability of perceiving coherent global motion improved with increased duration up to about 440 msec (11 frames at 25 Hz). Using similar stimuli, Watamaniuk, Sekuler and Williams (1989) found that direction discrimination reached asymptote at a duration of about 580 msec (10 frames at 17 Hz).

The present experiments were designed to measure systematically the time and space over which motion information is integrated. The stimuli were random-dot cinematograms in which dots took independent two-dimensional random walks of constant step size. The direction that any dot moved, from frame to frame, was

independent of the dot's previous movement and the movements of other dots. All dots within a single stimulus chose their movements from the same probability distribution. These stimuli, comprising many different spatially-intermingled directions, result perceptually in global motion in a single direction, approximating the mean of the intermingled directions.

Note that our stimuli were designed to put the greatest possible demands on the spatial and temporal integrative capacity of the visual system. Because a new sample of directions is drawn for each frame, the aggregate of directions of movements at any moment is an approximation of the underlying distribution. As a result, a more faithful approximation of the directions in that underlying distribution can be developed if the visual system integrates directions over many dots and over several frames. Although we have demonstrated that spatial and temporal integration occurs in random-dot stimuli for both direction and speed (Watamaniuk *et al.*, 1989; Watamaniuk & Duchon, 1992), the present determine the limits of that integration.

To anticipate our results, direction discrimination thresholds decrease as the stimulus duration increases, up to about 500 msec (10 frames). Also, thresholds decrease as the spatial extent of the stimulus display increases, up to a diameter of at least 9 deg (area = 63 deg²). Finally, discrimination thresholds increase as the range of directions in the cinematogram increases.

*Department of Psychology, Northwestern University, Evanston, IL 60208, U.S.A.

†To whom all correspondence should be addressed at present address: Smith-Kettlewell Eye Research Institute, San Francisco, CA 94115, U.S.A.

‡Present address: Department of Psychology and Center for Complex Systems, Brandeis University, Waltham, MA 02254, U.S.A.

METHODS

Observers

The first author (SNJW), one undergraduate and one graduate student served as observers for all experiments.

All observers had previous experience as participants in visual experiments. Except for SNJW, all observers were naive to the experiments' purposes. All observers had corrected-to-normal visual acuity.

Stimuli

Stimuli were random-dot cinematograms composed of 256 dynamic random dots generated by a computer. The dots were plotted on an x - y display (Tektronix 604 monitor with P-4 phosphor), at a rate of 20 frames per sec. For all experiments, dots took two-dimensional random walks of constant step size (0.6 deg). With this step size and the geometry of addressable points on the display, the mean direction of the stimulus could be changed in 0.5 deg increments. The two-dimensional random walks were created in the following way. For every frame anew, each dot's movement was chosen from a predefined Gaussian distribution of directions* stored as an array of increment values. Gaussian distributions with different standard deviations (SDs) were used in different conditions. The increment array held 256 pairs of values, each consisting of an x -axis increment and a y -axis increment. From this array, the computer chose randomly, with replacement, increment values for the dots' movements. Sampling with replacement results in a distribution of directions for any one frame that was a random sample of the underlying direction distribution.

After 256 x - and y -samples had been drawn, the chosen increments were added to the dots' current positions and the dots' new x - and y -positions were transmitted to the cathode ray tube (CRT) display via high speed digital-to-analog converters. The initial screen location of each dot was randomly determined at the beginning of each sequence of frames. This constantly shifting spatial array made it impossible for an observer to base a direction judgment on information about dot pattern.

Apparatus

Experiments were conducted in an isolated, darkened room, with a CRT positioned on an elevated platform fastened to a table. A mask, with a circular aperture, was attached to the face of the CRT. For most experiments the mask measured 9 deg of visual angle in diameter when seen from the viewing distance of 57 cm. This mask allowed the observer to see about 163 of the 256 dots at any one time. Each dot subtended 0.05 deg of visual angle and had a luminance of 0.27 cd/m².† The luminance of the surrounding mask was 0.07 cd/m² while the veiling luminance was 0.03 cd/m². These luminance values produced a stimulus that was easily seen but not so bright as to produce afterimages when viewed at the

longest duration. Each experimental session started with a 5 min period to adapt an observer's visual system to the dim illumination.

With chin resting comfortably in a chin cup, the observer sat facing the display. Additional support was provided by a head restraint mounted on the table. Viewing was binocular. The height of the CRT placed the center of the display at approximately eye level. Push-buttons connected to the computer initiated each trial and also signaled the observer's responses.

Procedure

All experiments used the same psychophysical procedure: a two-alternative forced-choice staircase. Each trial consisted of two stimulus presentations separated by an inter-stimulus interval of approx. 500 msec. The distribution of increments sampled in order to create one stimulus, the standard stimulus, had a mean direction of 90 deg (upwards). On average, this stimulus should be expected to generate global motion in an upwards direction. The distribution of increments sampled to create the other stimulus, the comparison stimulus, had a mean direction slightly greater than 90 deg. On average, this stimulus would produce global motion somewhat counterclockwise from upward. On half the trials, randomly chosen, the standard stimulus occupied the first interval. The observer had to determine if the global motion of the second stimulus was to the left (counterclockwise) or right (clockwise) relative to the global motion of the first stimulus.

Each staircase began with a comparison stimulus whose mean was 20 deg counterclockwise from upward. This large difference between standard and comparison stimuli was generally easy to distinguish under all stimulus conditions. Four successive correct responses were required to decrease the difference between the mean directions while one incorrect response increased the difference. The difference between the mean directions was decreased by 3 deg for each set of four correct responses until the observer made one error. Thereafter the difference between the mean directions changed by only 0.5 deg. This procedure continued until ten reversals were recorded. The up-down decision rule tracked the 84% on the psychometric function (Wetherill & Levitt, 1965). The direction discrimination threshold was determined by averaging only the last six reversals.

The computer sounded a tone to signal its readiness to present a stimulus; then the observer could press a button to initiate a trial. After the trial's two stimuli had been presented, the observer responded by pushing one of two buttons, left or right, corresponding to the perceived direction of the second stimulus relative to the first. An inter-trial interval of about 2 sec separated trials.

EXPERIMENT 1. TEMPORAL INTEGRATION

This experiment was designed to estimate the integration time for global motion perception. Direction

*The discrete nature of the display made it impossible to present a continuum of directions. We approximated a Gaussian distribution by sampling at 1 deg intervals.

†This value was obtained by plotting a matrix of non-overlapping dots (center-to-center spacing was 0.06 deg) at the same frame rate as used in the experiments. The luminance of this matrix was then measured with a Minolta luminance meter.

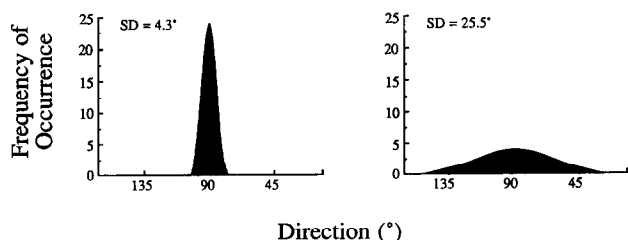


FIGURE 1. Representations of the two Gaussian direction distributions, SDs of 4.3 and 25.5 deg, used in the first two experiments. Frequency of occurrence is plotted as a function of motion direction.

discrimination thresholds were measured for 15 different stimulus durations, ranging from 150 to 1250 msec (3–25 frames). Thresholds for two distribution SDs, 4.3 and 25.5 deg, were evaluated at each duration. Figure 1 shows the two Gaussian direction distributions schematically. Aperture diameter was held constant at 9 deg (area = 63.6 deg²) and mean density of dots was fixed at 2.56 dots/deg².

Results

Figure 2 shows the results for three observers with direction discrimination threshold (deg) plotted as a function of stimulus duration. Each data point is the average of four threshold estimates (24 staircase reversals), ± 1 SE are plotted on each point. Notice that for all observers, thresholds decreased as duration increased. Also note that for both SDs, thresholds seem to level out after an initial decline. To evaluate the point at which the data asymptote, two lines were fit to the data for each SD for each observer (Bogartz, 1968). For all observers, two lines fit the data better than one line, with the root mean-squared error ($\sqrt{\text{MSE}}$) decreasing on average by about 35%. The point at which the two lines intersect was taken as the temporal integration limit.

The temporal integration limits for SD = 4.3 deg were 421, 436 and 489 msec (8.43, 8.72, and 9.78 frames) while

those for SD = 25.5 deg were 464, 529 and 450 msec (9.29, 10.58, and 9.00 frames) for observers SW, BT and SS respectively. Notice that the limits are quite similar across SDs and observers. Because of their similarity, the six temporal limits were averaged to obtain a mean integration time of 465 msec (9.3 frames).

Though this temporal integration limit is quite long, it is close to the values reported by other researchers, using similar but not identical stimuli. Williams and Sekuler (1984) found, for a similar presentation rate, that the probability of perceiving global motion did not improve if the stimulus lasted longer than 440 (11 frames) msec. Watamaniuk *et al.* (1989) found that direction discrimination reached asymptote after about 580 msec (10 frames).

EXPERIMENT 2. SPATIAL INTEGRATION

This experiment was designed to measure the effect of stimulus area on the discrimination of global motion's perceived direction. Direction discrimination thresholds for nine different display areas were measured. The circular displays had diameters of 4–9 deg, in 0.5 deg steps, corresponding to areas ranging from 12.5 to 63.6 deg². Thresholds for two distribution SDs, 4.3 and 25.5 deg, were evaluated at each display area. We measured thresholds for two different SDs to determine if the spatial integration limit, like the temporal integration limit, was constant across SD. Duration was constant at 400 msec (8 frames) while mean dot density was held at 2.56 dots/deg².

Results

Figure 3 shows discrimination thresholds (deg) for each of the three observers plotted as a function of aperture size (area). Each data point is the average of four threshold estimates (24 staircase reversals), ± 1 SE are plotted on each point. In general, discrimination

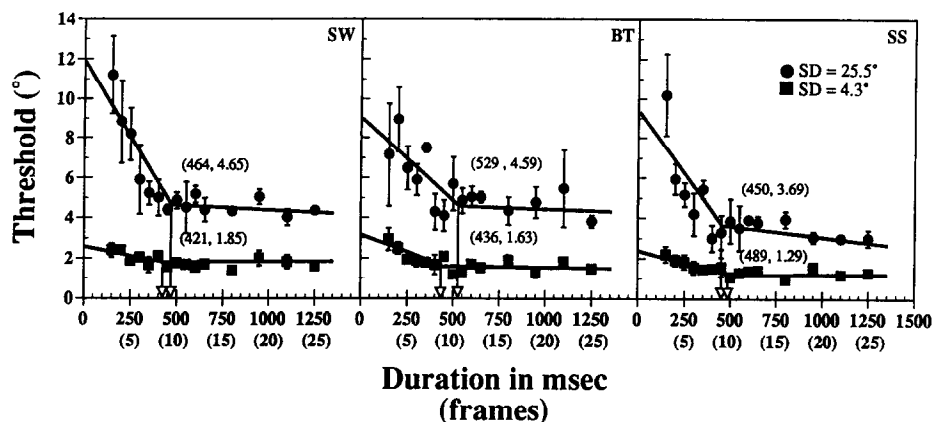


FIGURE 2. Direction discrimination thresholds, in deg, plotted as a function of duration in msec (frames). Each panel shows data for a single observer for each of two SDs. Each point is the average of four threshold estimates (24 staircase reversals). ± 1 SE are plotted on each point. Solid squares (■) show data for an SD = 4.3 deg while the solid circles (●) plot data for an SD = 25.5 deg. Aperture diameter was held constant at 9 deg (area = 63.6 deg²) and density was 2.56 dots/deg². For all observers, thresholds decrease as duration increases and seem to reach asymptote. Two intersecting lines were fit to each curve (Bogartz, 1968) to establish the point at which slope changes. Arrows extending to the x-axis and coordinates above each data set indicate the point of intersection of the two fitted lines. Notice that across both SD and observers, the point at which discrimination performance changes slope is similar. Because of their similarity, the average of the six intersection points, 465 msec (9.3 frames), was taken as the temporal integration limit.

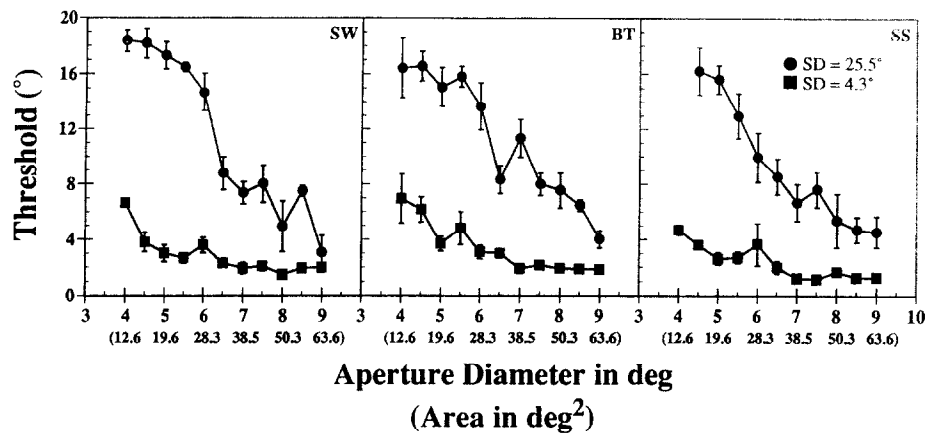


FIGURE 3. Direction discrimination thresholds, in deg, plotted as a function of aperture diameter in deg (area in deg^2). Each panel shows data for a single observer for each of two SDs. Each point is the average of four threshold estimates (24 staircase reversals). ± 1 SE are plotted on each point. Solid squares (■) show data for an SD = 4.3 deg while the solid circles (●) plot data for an SD = 25.5 deg. Duration was held constant at 400 msec (8 frames) and density was 2.56 dots/ deg^2 . Notice that for all observers, thresholds decrease as area increases. Also notice that for SD = 4.3 deg, thresholds seem to reach asymptote while those for SD = 25.5 deg continue to decrease over the entire range of stimulus area.

thresholds decrease as display area increases. But notice that changing stimulus area affects the thresholds for the small SD differently than those for the large SD. Here, when the SD is small, 4.3 deg, thresholds decrease and then level out once the area reaches about 40 deg^2 . However, when the SD is large, 25.5 deg, the threshold continues to drop as area increases, up to the largest area tested.

It should be pointed out that in this experiment, we did not control for retinal eccentricity. In fact, since observers always fixated the center of the stimulus, more of the periphery was stimulated as the stimulus diameter increased. It could be argued that the improvement in performance with increasing stimulus area is due to the activation of the periphery which may be more sensitive to motion. To check this, a control experiment measured direction discrimination for an SD = 4.3 deg with an annular aperture (i.d. = 4 deg; o.d. = 6 deg; annular area = 15.7 deg^2) for observer SW. The discrimination threshold obtained with the annular aperture was 11.05 deg (SE = 1.69 deg), far worse than any of the thresholds obtained with a circular aperture—even though the area covered by the annulus was larger than that of the smallest circular aperture. This suggests that

simply activating more peripheral mechanisms cannot account for the improvement in performance as stimulus area increases.

EXPERIMENT 3. STANDARD DEVIATION

In each of our first experiments, discrimination was measured in conjunction with two different stimulus SDs. In all conditions, thresholds tended to be higher for the larger SD than for the smaller SD. The following experiment used a wide range of different SDs in order to ascertain how stimulus SD affects the threshold for direction discrimination.

Direction discrimination thresholds were measured for nine different stimulus SDs: 0.0, 4.3, 8.5, 12.8, 17.0, 22.5, 25.5, 29.6, and 34.0 deg. Thresholds were measured with a constant duration of 400 msec (8 frames), with a constant display diameter of 9 deg (area = 63.6 deg^2) and constant density of 2.56 dots/ deg^2 .

Results

Figure 4 shows direction discrimination thresholds (deg) as a function of stimulus SD for each of the three

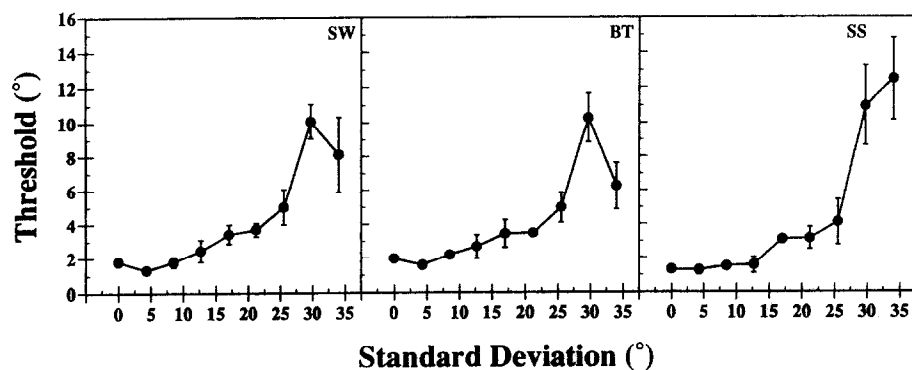


FIGURE 4. Direction discrimination thresholds, in deg, plotted as a function of stimulus SD in deg. Each panel shows data for a single observer. ± 1 SE are plotted on each point. Aperture diameter was held constant at 9 deg (area = 63.6 deg^2), duration was constant at 400 msec (8 frames) and density was always 2.56 dots/ deg^2 . Notice that for all observers, thresholds increase as SD increases. Also notice that the data follow a relatively shallow slope until SD reaches about 20 deg after which it rises more sharply.

observers. Each data point is the average of four threshold estimates (24 staircase reversals) and is plotted with ± 1 SE. Overall, discrimination thresholds increase gradually with SD. At the largest SDs the individual differences among observers make it difficult to settle on a single clear description of the results. For two observers, SW and BT, thresholds jump abruptly at SD = 25 deg and then decrease slightly. Observer SS shows a comparable jump at SD = 25 deg but no decline thereafter.

DISCUSSION

A possible artifact?

Since the two stimuli on each trial had different mean directions, the two stimuli would also have slightly different mean velocities in an upwards direction. We were concerned that this difference in velocity might have contributed to our observers' ability to discriminate direction. For example, compared to the upward velocity of a standard stimulus, which always had a mean direction of 90 deg, a comparison stimulus with a mean direction of 92 deg would have an upward velocity approx. 0.06% less (this is the most extreme case, when SD = 0.0). However, this velocity difference is so small that its usefulness as a cue would be nil. McKee (1981) found that the threshold for discriminating stimulus speeds was nearly 100 times higher, about 5%. In fact, the comparison stimulus would need to have a mean direction of about 72 deg to produce a 5% change in upward velocity from the standard. Thus it is extremely unlikely that our observers could have successfully based their direction judgments on velocity information.

Stimulus duration

Experiment 1 showed that discrimination performance improved with longer durations. The threshold for discrimination of global direction decreased as stimulus duration increased, reaching a minimum at about 465 msec (9.3 frames) and remaining constant thereafter. We take this value as an estimate of the time over which the visual system is able to integrate motion information, as it is consistent with those found by other researchers using comparable cinematograms (e.g. Williams & Sekuler, 1984; Watamaniuk *et al.*, 1989).

In this experiment, frame rate was held constant so that increasing duration, by increasing the number of frames, simultaneously increased both the length of the motion sequence in time and the number of direction samples. The present experiment cannot determine if one of these factors is more important than the other for the processing of motion information (although these two factors could be disentangled by measuring performance at various frame rates). The literature seems to show that both sources of information play a role in improving performance. For example, Williams and Sekuler (1984) showed that for frame rates between 10 and 25 Hz, detecting coherent motion did not improve after about 11 frames. When expressed in terms of time, temporal

summation ranged from 440 to 1100 msec. Using similar stimuli, Watamaniuk *et al.* (1989) showed that global direction discrimination reached asymptote after about 10 frames or 580 msec. Using a different stimulus, Snowden and Braddick (1989a), reported that for frame rates below 20 Hz, the signal-to-noise ratio required to discriminate leftward from rightward motion, reached a minimum after only 5–6 frames (about 300 msec). However, for a frame rate of 50 Hz, performance continued to improve after 8 frames (160 msec). Snowden and Braddick suggest that two types of facilitative processes may be acting in these situations; a cooperative process (i.e. "sequential recruitment"—Nakayama & Silverman, 1984; McKee & Welch, 1985) and one based on the activation of motion units of different size and with different temporal properties. They posit that activation of different sized units can only occur when the frame rate exceeds 25 Hz. Thus, when frame rates are high, both types of facilitation can occur and allow performance to improve more quickly and possibly over more extended motion sequences (i.e. more frames).

The differential contribution of the two types of facilitative processes hypothesized by Snowden and Braddick seems to explain why performance in their experiments varied with frame rate. However, neither type of facilitation can resolve the discrepancy between the 10-frame temporal integration limit found in the present study and others (Watamaniuk *et al.*, 1989; Williams & Sekuler, 1984) and the 6-frame integration limit found by Snowden and Braddick (1989a). We believe that differences in the algorithms used to generate the displays may account for differences in temporal integration limits. In our study, a single dot's direction of motion varied unpredictably from frame to frame, making it impossible to extrapolate the ensembles' aggregate direction from the motion of any single dot. Snowden and Braddick measured the relative proportion of signal dots moving in a single direction among randomly placed noise dots needed to do their discrimination task. The signal dots moved in a single direction of motion, rather than a distribution of directions such as we used. Like samples from any noisy process in which the noise is uncorrelated among samples, successive samples (frames) of our stochastic cinematograms would yield ever better approximations to the underlying distribution of directions. It may be that with noisy stimuli, the number of direction samples play a larger role in determining performance than the length of the motion sequence in time.

Stimulus area

Experiment 2 showed that discrimination performance increases with stimulus area and that, with appropriate stimuli, the human visual system can integrate direction information over areas at least as large as 63 deg². But our estimate of the area over which integration occurs was not the same for the two stimulus SDs we used. For the smaller SD, 4.3 deg, the thresholds decreased and then leveled out when stimulus area

reached about 40 deg². However, for the larger SD, 25.5 deg, the threshold decreased over the entire range of areas, all the way up to 63.6 deg².

Why does the area over which information is integrated depend upon stimulus SD? This pattern of results is curious because at first glance it implies that for the same discrimination task, the visual system changes its integration area depending upon the stimulus' directional characteristics. This seems unlikely. A more physiologically plausible way to explain the present results is to hypothesize that the integration area is constant but that internal noise sets a lower limit on the direction discrimination threshold. Thus, the expectation is that performance will improve until the spatial integration limit is reached or until the limit set by the internal noise is reached. Now, for SD = 4.3 deg, performance improves as area increases until thresholds fall to between 1 and 2 deg (see Fig. 3). We hypothesize that these lowest thresholds represent the limit in performance set by the internal noise of the visual system and thus increasing area further does not result in still lower thresholds. However, as Fig. 3 shows, thresholds for SD = 25.5 deg do not reach the putative 1–2 deg limit, instead performance improves over the entire range of areas tested. This suggests that the spatial integration limit is at least as large as 63.6 deg².

Our estimate of the spatial integration area of the visual system is large especially when compared to measures of spatial summation of luminance. Traditional estimates of spatial integration for foveal contrast detection, at luminances comparable to those used here, are always < 1.0 deg² (Blackwell, 1946; Thomas, 1978). But other researchers have also found large integration areas in motion processing. Downing and Movshon (1989) measured the effect of stimulus area on a motion detection task in which observers had to choose which of four patches of randomly moving dots contained a set of signal dots moving in a single direction. They found that performance improved as the target areas increased up to about 25 deg². Their estimate is smaller than ours but this may be due to differences in experimental procedures and stimuli. However, both Downing and Movshon's and our estimate of spatial integration are much larger than that expected from the traditional measures of the spatial summation of luminance.

Stimulus standard deviation

Our final experiment systematically investigated the effect of SD on discrimination threshold. Discrimination thresholds were measured for nine stimulus SDs ranging from 0.0 to 34.0 deg. Consistent with the first two experiments, thresholds increased with SD (see Fig. 4). In addition, performance changed little until the SD reached about 15 deg, after which it declined steadily. Dramatic increases in threshold were observed when SD became larger than 25 deg. This pattern of results may be due to two factors: internal noise and incomplete coherence.

As stated in the discussion about area, it is reasonable to assume that internal noise will limit performance until the stimulus noise (proportional to SD) becomes larger

than the internal noise. Once the stimulus noise exceeds that of the internal noise, performance should change in proportion to the stimulus noise (Geisler, 1989). Our data show this trend. Thresholds are fairly constant up to an SD of about 15 deg, presumably because internal noise is limiting performance, after this point stimulus noise exceeds the internal noise and thresholds rise gradually with SD up to about 25 deg. However, once SD becomes > 25 deg, thresholds make a dramatic increase. This abrupt change in threshold is not expected in the context of signal detection theory. Some other factor must have come into play to produce this abrupt change.

One such factor that may have influenced our observers' performance is incomplete coherence. We use the term incomplete coherence to refer to a situation in which the width of the direction distribution is increased beyond a putative coherence limit so that some of the direction components of the stimulus are not integrated completely. Williams and Sekuler (1984) found that the probability of seeing coherent global motion, as a function of the width of the direction distribution, did not follow a step function going from coherence to incoherence. Instead their psychometric functions had steep but finite slopes showing that there was a gradual transition from complete coherence to complete incoherence. Thus, it seems that there is a weakening of coherence (i.e. some directions are not integrated completely), as the direction distribution gets broader, before the global percept is destroyed completely. A more sensitive assay of global motion, such as direction discrimination, might reveal the weakening of coherence in the form of decreased precision before the global percept is lost. In the present experiments, our large SD stimuli may have had wide enough direction distributions to produce incomplete coherence. Thus although the global motion percept was not lost, the inability to integrate some directions completely may have caused a precipitous decrease in the precision of the perceived mean direction. This could have caused the dramatic rise in thresholds as SD increased beyond 25 deg.

Further support for incomplete coherence comes from Movshon, Adelson, Gizzi and Newsome (1985) who showed a transition in coherence with plaid stimuli as a function of the contrast of the grating components. They found that at particular contrasts, sometimes the gratings cohered and at other times they did not (see also Welch & Bowne, 1989).

Physiological speculations

We suspect that the rather complex direction-integration process necessary to perceive global motion occurs in higher visual processing areas such as the middle temporal area (MT) and the medial superior temporal area (MST). One indication that MT neurons are capable of the kind of processing needed in the present task is that they respond to complex pattern motion. Movshon *et al.* (1985), using moving plaids as stimuli, found that cells in V1 encoded the motion of each of the oriented components while a population of MT neurons encoded the resultant motion of the plaid pattern.

The physiology of these higher-level cells also supports temporal and spatial integration in motion perception. Mikami, Newsome and Wurtz (1986) have demonstrated temporal integration in MT neurons by showing that multiple displacements of an apparent motion stimulus are necessary to elicit a strong directional response. In addition, if one assumes that the spatial extent over which direction information can be integrated is dependent upon the receptive field sizes of the neurons encoding the direction of global motion, MT and MST neurons could also support large spatial integration. The receptive fields of MT neurons are, on average, 100 times the size of those in V1 (Gattass & Gross, 1981) while those of MST are larger still, some covering a whole quadrant or more (Van Essen, Maunsell & Bixby, 1981). Further support comes from Sclar, Maunsell and Lennie (1990) who found that the contrast needed to make MT cells reach one half of their maximum response decreased as the size of the stimulus increased up to 300 deg². If perception of stochastic cinematograms like ours requires the kind of integrative processing attributed to cells in MT or MST, the size of receptive fields in those areas may well account for the large integration areas that we and others have found for motion tasks.

CONCLUSION

To summarize, when the task is to discriminate the direction of global motion, the visual system integrates over long times and large areas. Our temporal integration limit of about 465 msec (9.3 frames) agrees with that found by other investigators for comparable motion tasks. However, our estimate of the area over which integration operates is larger than any previously reported, though it is consistent with the physiology of motion-selective cells in cortical areas believed to be involved in integration of diverse motion signals. Finally, the gradual rise in discrimination thresholds as SD is increased (up to about 25 deg) may reflect the interaction of internal noise processes with the statistical characteristics of the stimuli. A model of direction discrimination of global motion in which performance is dependent upon stimulus statistics and the internal noise processes of the responding visual system is qualitatively supported by our data. In another paper, we develop a quantitative statistical ideal observer model that takes into account the temporal and spatial limits found here (Watamaniuk, 1992). As a preview, the ideal observer model with two free parameters, a scaling factor and an internal noise factor, provides good fits to direction discrimination data obtained at many durations, areas and SDs.

REFERENCES

- Blackwell, H. R. (1946). Contrast thresholds of the human eye. *Journal of the Optical Society of America*, 36, 624–643.
- Bogartz, R. S. (1968). A least squares method for fitting intercepting line segments to a set of data points. *Psychological Bulletin*, 70, 749–755.
- Burr, D. C. (1981). Temporal summation of moving images by the human visual system. *Transactions of the Royal Society of London B*, 211, 321–339.
- van Doorn, A. J. & Koenderink, J. J. (1983). Spatiotemporal integration in the detectability of motion. *Vision Research*, 23, 47–56.
- Downing, C. J. & Movshon, J. A. (1989). Spatial and temporal summation in the detection of motion in stochastic random dot displays. *Investigative Ophthalmology and Visual Science (Suppl.)*, 30, 72.
- Gattass, R. & Gross, C. G. (1981). Visual topography of striate projection zone (MT) in posterior superior temporal sulcus of the macaque. *Journal of Neurophysiology*, 46, 621–638.
- Geisler, W. S. (1989). Sequential ideal-observer analysis of visual discriminations. *Psychology Review*, 21, 267–314.
- 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.
- Mikami, A., Newsome, W. T. & Wurtz, R. H. (1986). Motion selectivity in macaque visual cortex. II. Spatiotemporal range of directional interactions in MT and V1. *Journal of Neurophysiology*, 55, 1328–1339.
- Morgan, M. J. & Watt, R. J. (1982). Effect of motion sweep duration and number of stations upon interpolation in discontinuous motion. *Vision Research*, 22, 1277–1284.
- Morgan, M. J., Watt, R. J. & McKee, S. P. (1983). Exposure duration affects the sensitivity of vernier acuity to target motion. *Vision Research*, 23, 541–546.
- Movshon, J. A., Adelson, E. H., Gizzi, M. S. & Newsome, W. T. (1985). The analysis of moving visual patterns. In Chagas, C., Gattass, R. & Gross, C. (Eds), *Pattern recognition mechanisms* (pp. 117–1151). New York: Springer.
- Nakayama, K. & Silverman, G. H. (1984). Temporal and spatial characteristics of the upper displacement limit for motion in random dots. *Vision Research*, 24, 293–299.
- Sclar, G., Maunsell, J. H. R. & Lennie, P. (1990). Coding of image contrast in central visual pathways of the macaque monkey. *Vision Research*, 30, 1–10.
- Snowden, R. J. & Braddick, O. J. (1989a). The combination of motion signals over time. *Vision Research*, 29, 1621–1630.
- Snowden, R. J. & Braddick, O. J. (1989b). Extension of displacement limits in multiple-exposure sequences of apparent motion. *Vision Research*, 29, 1777–1787.
- Thomas, J. P. (1978). Spatial summation in the fovea: Asymmetrical effects of longer and shorter dimensions. *Vision Research*, 18, 1023–1029.
- Van Essen, D. C., Maunsell, J. H. R. & Bixby, J. L. (1981). The middle temporal visual area in macaque: Myeloarchitecture, connections, functional properties and topographic representation. *Journal of Comparative Neurology*, 199, 293–326.
- Watamaniuk, S. N. J. (1992). An ideal observer for discrimination of the global direction of dynamic random dot stimuli. *Journal of the Optical Society of America A*. In press.
- 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, 49–59.
- Welch, L. & Bowne, S. F. (1989). Neural rules for combining signal from moving gratings. *Investigative Ophthalmology and Visual Science (Suppl.)*, 30, 75.
- 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.

Acknowledgements—This research was supported by grant AFSOR-85-0370 and ASFOR-89-0243. This work was presented at the 1990 meeting of the Association for Research in Vision and Ophthalmology.