



Recruitment Mechanisms in Speed and Fine-direction Discrimination Tasks

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Received 24 October 1996; in revised form 18 February 1997

The minimum information necessary to specify motion requires a change in position across time. Previous studies have shown that human motion measurements improve with more than two frames of motion. This study clarifies how motion information is integrated to produce the best speed and direction discrimination. Using random-dot kinematograms, fine-direction discrimination thresholds and speed discrimination thresholds are assessed as a function of dot lifetime. Specifically, we ask if performance on both tasks depends on dot lifetime in the same manner. If both speed and direction discrimination performance improve the same way with increasing dot lifetime, this would indicate that both tasks have the same integration limit and both tasks may depend on the same underlying mechanisms. Experiment 1 shows that for both tasks a four-frame dot lifetime is necessary for observers to reach asymptotic threshold levels. The absolute level of performance improves with increasing stimulus duration or signal-to-noise ratio, but the integration limit itself does not vary. Experiment 2 examines whether this integration limit is constrained by the number of frames or by the temporal duration of the dot lifetime. The data in Experiment 2 suggest that both a minimum number of samples and a minimal temporal integration period determine the integration limit for recruitment mechanisms. The results suggest that speed and fine-direction discrimination depend upon the same underlying motion mechanisms. These results are discussed in relation to possible underlying physiological substrates and computational models of motion measurement. © 1997 Elsevier Science Ltd

Temporal integration Motion Speed discrimination Direction discrimination Random dots

INTRODUCTION

Humans can coarsely discriminate large changes in direction or speed with just two frames of motion, but to make more precise motion measurements more frames are necessary (Sperling, 1976; Lappin & Bell, 1976; Lappin & Fuqua, 1982; van Doorn & Koenderink, 1982a,b, 1984; Ramachandran & Anstis, 1983; Nakayama & Silverman, 1984; van Doorn *et al.*, 1985; McKee & Welch, 1985; De Bruyn & Orban, 1988; Snowden & Braddick, 1989a,b, 1990, 1991; Fredericksen *et al.*, 1993, 1994a,b,c; Grzywacz *et al.*, 1995; Watamaniuk *et al.*, 1995; Todd & Norman, 1995). The improvement in performance that is seen with increased stimulus duration or number of stimuli in an apparent motion sequence has been described as sequential or temporal recruitment (Nakayama & Silverman, 1984; McKee & Welch, 1985; Snowden & Braddick, 1989a,b, 1990). Although there is general agreement that the simplest motion unit detects correlated inputs across space and time (Adelson & Bergen, 1985; van Santen & Sperling, 1984; Watson &

Ahumada, 1985), precisely how motion information is combined is still debated. Motion detectors appear to be arranged within a network in such a way that signals which indicate similar speeds and directions are enhanced by either integration within detectors, or summation across detectors, or both.

The term "recruitment" has been used to describe both the integration of motion signals within a single detector and the integration of motion information across detectors. Distinguishing between these two types of integration schemes is important for adequately describing how these motion detectors are arranged and interact within a network. Probability summation calculations are one method for distinguishing integration within, rather than across, motion detectors. If the improvement in performance which is seen with increased stimulus duration is worse than the combined improvement in performance for two independent samples that are half that stimulus duration, then integration has probably occurred across multiple motion detectors, but not very efficiently. If the improvement is equal to that expected based upon probability summation, than maximally efficient integration has occurred across motion detectors. If, however, the improvement is better than what would be expected based upon probability summation,

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then it is likely that the integration of motion signals has occurred within a single motion detector.

Researchers also disagree on whether sequential recruitment is limited by the number of samples of a motion or its temporal extent (McKee & Welch, 1985; Snowden & Braddick, 1989a; Fredericksen *et al.*, 1993, 1994a). McKee & Welch (1985) found that speed discrimination thresholds improved up to stimulus durations of 80–100 msec for a bar stimulus moving at 15 deg/sec. This temporal limit did not vary with changes in the framerate of the motion stimulus. These numbers are consistent with the integration limits for speed discrimination found by (De Bruyn & Orban, 1988) and (Snowden & Braddick, 1991) using different motion stimuli with a range of speeds. However, when Snowden & Braddick (1989a,b) examined discrimination thresholds for opposed directions of motion (right vs left directions), they found very different integration characteristics for apparent motion stimuli with short and longer temporal asynchronies (20 msec vs 50 and 100 msec). The spatial displacement size was kept constant across the different temporal asynchronies, while the number of displacements was varied systematically. With the 20 msec temporal asynchrony condition, thresholds showed no signs of asymptote, even at their longest displacement sequence of 8 frames (a stimulus duration of 160 msec). At the longer temporal asynchrony conditions (50 and 100 msec), thresholds reached their minimum between 4 and 6 frames (stimulus durations ranging from 200 to 600 msec). Although different limits were found for short and longer temporal asynchrony conditions, there was no consistent temporal integration limit across the different speeds.

Snowden & Braddick (1989a) pointed out that, as the number of frames in an apparent motion sequence increase, two types of correlation within the motion sequence increase as well. The first type (small-sized detectors) measures motion across two contiguous frames of motion (e.g., frames 1 and 2, 2 and 3, etc.). Snowden & Braddick (1989a) suggested that motion from these small-sized detectors is combined by a co-operative process such that the motion system develops a bias for detecting similar motion signals on subsequent frames. The second type (larger-sized detectors) measures motion across non-contiguous frames (e.g., frames 1 and 3, 1 and 4, etc.). These detectors are tuned to larger spatial and temporal delays. They suggested that the presence of different-sized detectors explains the different integration characteristics for the short and longer temporal asynchronies. Psychophysical data from van Doorn and colleagues provide extensive evidence for motion detectors with varying spans and time delays (van Doorn & Koenderink, 1982a,b, 1984; van Doorn *et al.*, 1985; Fredericksen *et al.*, 1993, 1994a,b,c). Snowden & Braddick (1989a) suggested that these larger-sized detectors can detect and integrate correlated motion signals for up to 80 msec delays. In their 20 msec temporal asynchrony condition, both the small- and larger-sized detectors could contribute to the improve-

ment in performance seen with increased stimulus duration. For their longer temporal asynchrony conditions (50 and 100 msec), only the small-size detectors could contribute to performance because the delays across non-contiguous frames were above the 80 msec limit. When they eliminated the contribution of larger-sized detectors from their stimulus by limiting the dot lifetime to two frames, they found that the integration characteristics for the 20 msec temporal asynchrony condition became similar to those for the longer temporal asynchrony conditions (50 and 100 msec). From these data, Snowden & Braddick (1989a) concluded that a number of frames limit is a more appropriate description of sequential recruitment than a limit in time.

Eliminating the contribution of larger-sized detectors from motion measurement is extremely useful in determining the spatial and temporal characteristics of the small-sized detectors (Snowden & Braddick, 1989b, 1990, 1991; Fredericksen *et al.*, 1993, 1994a,b,c; Todd & Norman, 1995). However, the human motion system clearly uses both types of correlation to make precise motion measurements (Snowden & Braddick, 1989a). Any computational model which accommodates sequential recruitment must include the contribution of both large- and small-sized detectors. Because both kinds of correlation increase with increasing duration, it can be difficult to determine the relative contributions of these two mechanisms to sequential recruitment. The solution in some studies (Snowden & Braddick, 1989a; Fredericksen *et al.*, 1993, 1994a,b,c) has been to selectively eliminate the larger-sized detectors by limiting the dot lifetime to two frames. In this way, the correlation across non-contiguous frames is completely removed. Increases in stimulus duration only increase the relative contribution of small-sized detectors. This tells us nothing about the integration characteristics of the larger-sized detectors. One way to examine the relative contributions of the larger-sized mechanisms without also varying the activity in the small-sized mechanisms is to keep the total number of frames in the apparent motion sequence constant and vary the dot lifetime.

Figure 1 illustrates how information from the two types of correlation can contribute to the measurement of motion. When the dot lifetime is limited to two frames, motion can only be detected across contiguous frames of correlated motion (first row of detectors). In this way, the degree of correlation across pairs of frames is constant as long as the stimulus duration remains the same. If there are larger-sized motion mechanisms that detect information across larger number of frames, longer dot lifetimes should elicit better performance, even with no change in stimulus duration. Small-sized mechanisms should still contribute to the motion measurement, but their contribution should be constant across different dot lifetimes. The point at which performance does not improve further with increased dot lifetime will indicate the maximum span over which larger-sized recruitment mechanisms operate.

Figure 1 illustrates two important points about this

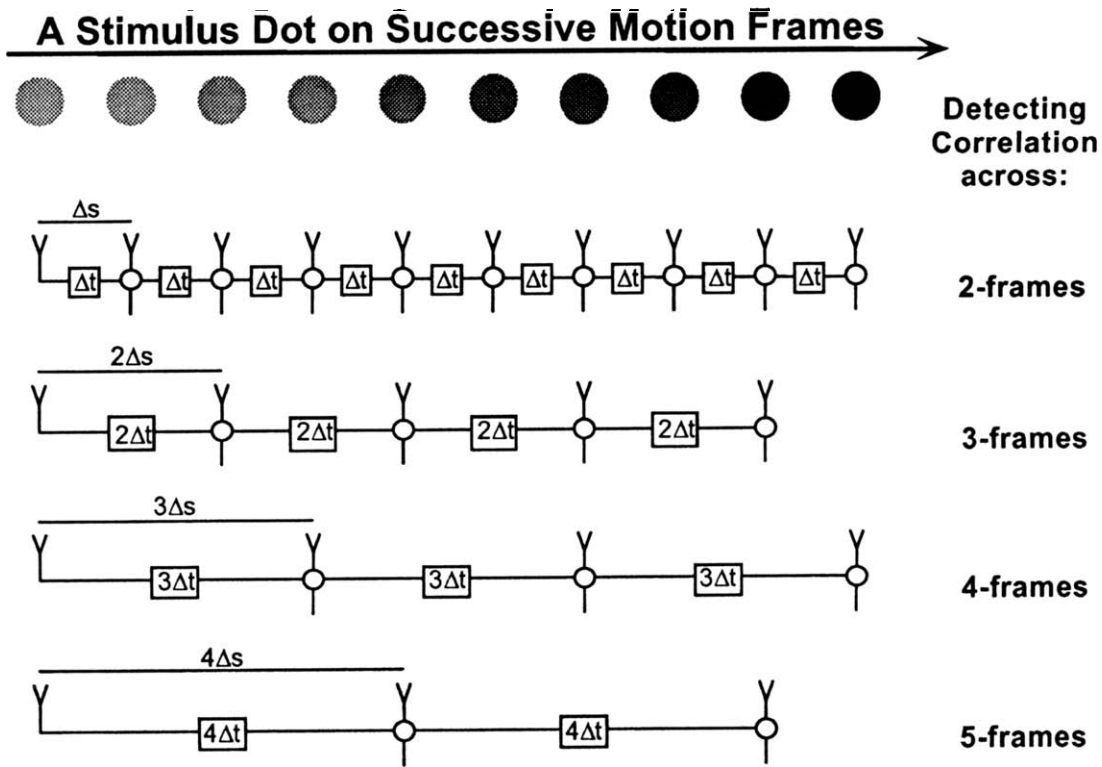


FIGURE 1. A schematic of potential integration mechanisms for the measurement of motion. The dots represent sequential frames of motion across space and time that a dot could undergo. The bilocal motion detectors represent potential mechanisms over which the visual system can integrate motion to achieve the best measurement. The Δs indicates the spatial span and the Δt indicates the temporal span of the detectors. The detectors across rows are sensitive to the same speed because the temporal and spatial spans of the detectors increase proportionally. When the dot lifetime is limited to two frames, motion can only be detected across contiguous frames of correlated motion (top row of detectors; see Methods). As the dot lifetime is increased, the correlation across non-contiguous frames of motion further apart in space and time can potentially contribute to the motion measurement (other rows of detectors). As long as the stimulus duration does not change, the amount of correlation across two frames is constant, regardless of the dot lifetime. This figure is intended to illustrate the degree of correlation that exists across motion frames. This study does not examine whether the motion system uses all of these detector types (two-frame, three-frame, four-frame, etc.). The goal is simply to determine the maximum span (or correlation) of the larger-sized detectors where motion measurements are at their best.

strategy for revealing the maximum span of the larger-sized motion mechanisms. With a constant stimulus duration, as the dot lifetime increases the relative number of larger-sized mechanisms that can detect motion decrease. A fall-off in improvement could indicate that the maximum span of the larger-sized motion mechanisms has been reached or that motion mechanisms with larger spans are not sufficiently stimulated to affect performance. Performance at different dot lifetimes for several stimulus durations will need to be examined to be certain that the latter is not a viable explanation. The second point this figure reveals is that increasing the dot lifetime does not eliminate the contributions of mechanisms with smaller spans to performance. Rather, performance with a four-frame dot lifetime stimulus is determined by the effects of two-, three-, and four-frame correlations in the motion signal. This study does not examine whether the motion system uses all of these detector types. The goal of this study is simply to determine the maximum span (or correlation) of the larger-sized detectors.

Sequential recruitment has been observed in both

speed and direction tasks. Very few researchers, however, have examined the characteristics of the motion mechanisms involved in speed and direction discrimination using comparable stimulus parameters. This makes it difficult to assess whether the same mechanisms are operating in the two types of tasks. The results from the few studies which directly compared speed and direction tasks have been mixed (De Bruyn & Orban, 1988; Watamaniuk *et al.*, 1989; Watamaniuk & Duchon, 1992; Smith *et al.*, 1994; Hiris & Blake, 1995). Watamaniuk & Duchon (1992) showed that for random-dot kinematograms, the human motion system integrates a distribution of different speeds in the same way that it integrates a distribution of different directions (Watamaniuk *et al.*, 1989). Further, Smith *et al.* (1994) showed that for both speed and direction tasks the removal of low spatial frequencies from random-dot displays has no effect on the perceived global motion. De Bruyn & Orban (1988) data, however, suggest that the human motion system integrates information across a larger area for speed discrimination than for fine-direction discrimination. In addition, Hiris & Blake (1995) have shown that perceived

coherence for random-dot kinematograms which contain distributions of different directions or speeds is differentially affected by the addition of speed and direction noise. Thresholds for displays containing distributions of directions were unaffected by the addition of speed noise, whereas the addition of direction noise to displays with distributions of speeds significantly elevated thresholds.

A number of studies have examined the spatial and temporal characteristics of motion detectors using coarse direction discrimination tasks (e.g., right vs left) (van Doorn & Koenderink, 1982a,b, 1984; van Doorn *et al.*, 1985; Snowden & Braddick, 1989a; Fredericksen *et al.*, 1993, 1994a,b,c). While these studies reveal critical information about the characteristics of individual motion detectors, discrimination tasks for opposed directions of motion may not require extensive integration within and/or across motion detectors (De Bruyn & Orban, 1988). The differences in integration across motion detectors exhibited for opposed direction discrimination compared with that of fine-direction and speed discriminations (De Bruyn & Orban, 1988) may show parallels with the coarse local and precise global motion mechanisms that Bravo & Watamaniuk (1995) and Watamaniuk (1996) have suggested are involved in speed and direction discrimination. Snowden & Braddick's (1989a) assertion that larger-sized detectors only contribute to performance when the temporal asynchrony between motion frames is short may not be correct when the task requires more precise discriminations. Furthermore, their conclusion that a number of frames limit is a more accurate description of sequential recruitment than a limit in time may only be appropriate for coarse discrimination tasks. This may explain why McKee & Welch (1985) found a constant stimulus duration limit in their speed discrimination task. Speed discrimination involves much more precise motion measurements than opposed-direction discrimination.

This study examines the influence of non-contiguous correlated frames (larger-sized detectors) on precise motion measurements and attempts to determine whether the same mechanisms are involved in precise speed and direction discriminations. Our results suggest that the same mechanisms are involved in the integration of speed and fine-direction information and that sequential recruitment indicates integration within motion detectors, rather than a combination of information across detectors. Larger-sized recruitment mechanisms are constrained by two types of limits: a minimum number of frames and a minimum amount of time. Speed and fine-direction discrimination thresholds improve until the dot lifetime reaches four frames and 60 msec.

EXPERIMENT 1

The purpose of Experiment 1 is to examine the relative contributions of small- and larger-sized recruitment mechanisms to performance in speed and fine-direction discrimination tasks. To assess this, speed and fine-direction discrimination thresholds are examined as a function of dot lifetime. The stimulus duration is held

constant for different dot lifetimes to keep the contribution of the small-sized detectors to the measurements constant across different dot lifetimes. The degree of correlation across any two frames does not change with longer dot lifetimes (see Fig. 1). We assume that for two-frame dot lifetimes, only small-sized detectors can operate (Snowden & Braddick, 1989a,b). At longer dot lifetimes, larger-sized detectors can contribute to the motion measurement. The point at which the thresholds asymptote for the different conditions indicates the span over which larger-sized detectors can operate (or further contributions no longer improve thresholds). Additionally, if thresholds asymptote at similar points for speed and fine-direction across different stimulus durations and signal-to-noise ratios, then this suggests that the same mechanisms contribute to the measurement of the two aspects of motion.

Methods

Observers. Both authors and one naïve observer participated in this experiment. The two authors served as observers for the control tasks. All observers had normal or corrected-to-normal vision. Each observer was well practiced in each condition before formal collection of data occurred. Practice ensured that the observer's discrimination thresholds reflected the best and least variable performance.

Apparatus. Random dot kinematograms were computer generated and displayed on a Tektronix 608 oscilloscope with P-31 phosphor. All dots were drawn within a circular aperture of 9 deg visual angle. Observers viewed the stimuli binocularly through a 57 cm-long circular tube in a dimly lit room. Their heads were stabilized with a chin rest and forehead restraint. Observers adjusted the chair and the chin rest's height so the center of the aperture was at approximately eye level. Designated keys on a computer keyboard and mouse buttons served to initiate each block of trials and record the observer's responses. Feedback was provided by a high pitch tone that sounded after each incorrect response.

Stimuli. Random dot kinematograms were composed of an average of 200 ($\pm 20\%$) dynamic random dots for all speed and fine-direction discrimination conditions. In the orientation control task, the kinematograms had an average of 80 ($\pm 20\%$) dynamic random noise dots and 20 ($\pm 20\%$) stationary line elements. The average dot densities were 3.14 dots per square degree in the former conditions and 1.57 dots per square degree in the latter task. Each dot subtended 3 min arc of visual angle.

The luminance of a single dot with a refresh rate of 50 Hz, the average framerate in this experiment, was measured with a PR-650 Spectra Colorimeter through an aperture lens of 0.51 mm in diameter. A stationary calibration dot remained on the screen for approximately 1 sec. Two different luminance values were measured. One was based on the voltage applied to the screen for the dots in the experiment. This measurement (667.8 cd/m^2) is misleading because the experimental dots remained in one location for only one frame. We, therefore, adjusted

the voltage value until the perceived brightness of the stationary calibration dot approximately matched the perceived brightness of the moving dots in the displays. This second measurement (8.96 cd/m^2) better characterizes the luminance of the dots used in this study. Luminance values were chosen to be comfortably above threshold, but allow for minimal visual persistence of the dots on the screen. The background luminance was below the measurement capabilities of the photometer.

Dots were plotted on a CRT display at an average rate of 50 Hz. A subset of the dots were signal dots which moved coherently in one direction at an average speed of 8 deg/sec. The direction of motion was always horizontal in the speed discrimination task and centered on horizontal for direction discrimination. The direction of motion was randomized (left or right) from trial to trial to minimize the effect of anticipatory eye movements (Kowler & Steinman, 1981). Each signal dot maintained a particular trajectory across a specified number of frames. The specified number of frames defined the signal dot lifetime after which each signal dot became a noise dot and was replotted in a random screen position. For a two-frame dot life, the identity of each signal dot changed every two frames until the stimulus duration was complete. For a five-frame dot life, the signal dots became noise dots every five frames. At the completion of each dot life, new signal dots were selected from the noise dots. These new signal dots were shifted relative to their previous positions as noise dots. To illustrate this point further, for a five-frame lifetime the signal dots moved coherently in one direction and one speed on Frames 1–5. On Frame 6, those dots were replotted in random locations. The new set of signal dots were chosen from noise dots in Frame 5 and lived from Frame 5 to Frame 9, becoming noise dots on Frame 10. In this way, there was no interruption in the signal information on the frame following the completion of a dot lifetime (e.g., between Frames 5 and 6). A constant proportion of signal dots was in motion throughout the stimulus duration, even though the identity of those signal dots changed each time a dot lifetime ended. This process of signal–noise replacement was repeated until the specified stimulus duration was complete. Noise dots were randomly positioned at new X–Y coordinates within the aperture from frame to frame (i.e., flicker noise) (Williams & Sekuler, 1984; Newsome & Pare, 1988).

For long dot lifetimes, there are two ways to deal with the signal dots reaching the screen edge before the lifetime is complete. One is to have the signal dots “wrap around” and reappear on the other screen edge, but this reduces the dots’ effective lifetime and reduces the effective signal-to-noise ratio. Because of this we chose to restrict the signal dot locations so their trajectories would not go past the screen edge. For long dot lifetimes this could result in inhomogeneities in signal dot placement on the screen (e.g., for rightward motion there were more signal dots on the left side of the screen at the beginning of the display and more signal dots on the right side of the screen at the end). We were not concerned

with this problem because the inhomogeneity could not help observers perform our tasks—small changes in speed or in direction were not affected by the inhomogeneity. This would be more important for a rightward vs leftward direction task.

The density of the dots in the display was varied ($\pm 20\%$), but signal-to-noise ratios were kept constant. Pilot data revealed that in order for the discrimination thresholds to reach reasonable performance levels, a minimum of 20% signal was necessary. Thresholds for 20 and 40% signal-to-noise ratios were examined in the speed and fine-direction discrimination tasks.

Procedure

Speed and fine-direction discrimination tasks. Discrimination thresholds were measured using the method of constant stimuli. For any one block of trials, either five or seven speeds or directions were chosen in a narrow range around the mean speed or mean horizontal direction. One of those speeds or directions was chosen on each trial in a pseudo-block randomized fashion from the possible speeds or directions in the set. Each speed or direction could be chosen only twice randomly within successive blocks of 10 (five possible stimuli) or 14 (seven possible stimuli) trials. The observer then judged whether the motion of the signal dots in that trial was faster or slower than the mean speed (speed discrimination) or up or down from horizontal (fine direction discrimination). Observers were given 10 practice trials to familiarize them with the set of stimuli before each block of 150 trials. Thresholds were measured over several sessions.

Each datum point for each dot lifetime was based on at least 300 responses. The proportion of trials in which the observer responded “faster” or “up” for each of the five or seven stimulus values in the set was used to generate a psychometric function. To estimate the threshold and its standard error, a cumulative normal curve was fit to the psychometric function using Probit analysis (Finney, 1964). Threshold was defined as half the stimulus increment that produced a change in the response rate from 25% to 75% correct ($d' = 0.68$). Standard errors were also estimated by Probit analysis and were generally 10–15% of the threshold value.

Two signal-to-noise ratios (20 and 40%) and three stimulus durations (100, 200, and 400 msec) were examined in speed and fine-direction discrimination tasks. Dot lifetime was varied across blocks of trials within a session. Dot lifetimes from two to twelve frames were examined with stimulus durations of 200 and 400 msec. For 100 msec stimulus duration, dot lifetimes were from two to six frames. The six- and twelve-frame dot life displays for the 100 and 200 msec stimulus durations, respectively, corresponded to the situation where signal dots never changed to noise dots. The signal-to-noise ratio, the average stimulus duration, and type of task were kept constant within a session.

To help mask spatial and temporal cues other than speed in the stimulus, duration was varied randomly from

trial to trial. The variation ($\pm 20\%$) in stimulus duration produced maximum durations of 120, 240 and 480 msec. For the same reason, each speed in the stimulus set was varied by changing both the frame-to-frame size of the spatial offset and the temporal asynchrony. For each stimulus presentation, a spatial offset and temporal asynchrony was chosen in a block randomized fashion from a set of five for each speed in the set. These five values varied around the mean spatial offset and temporal asynchrony by $\pm 20\%$. For example, the mean spatial offset and temporal asynchrony for an 8 deg/sec stimulus was 9.6 min arc and 20 msec, respectively. However, the spatial offsets for this speed ranged from 7.68 to 11.52 min arc and the temporal asynchronies ranged from 16 to 24 msec. This meant that neither the distance between dots on successive frames nor the temporal asynchrony alone were reliable cues to stimulus speed. The number of dots on the screen was also varied (while keeping the signal-to-noise ratio constant) because shorter temporal asynchronies resulted in the perception of more dots on the screen. These variations were only relevant in the speed task; the signal dots' temporal aspects could not provide cues to stimulus direction. These stimulus variations in the speed task do contribute variability to the observers' responses on a trial-by-trial basis. For this reason, stimulus duration and number of dots were varied for the direction task to keep the speed and direction displays comparable in noise content.

Orientation control task

In this task, observers judged whether lines were oriented clockwise or counterclockwise relative to horizontal. The lines were designed to mimic the moving signal dots' trajectories in the direction task. Each line was composed of the same number of dots in the same positions that signal dots would be found in the direction task. Longer dot lifetimes produced longer lines that were visible for longer durations. Thus, a two-frame dot life produced line elements composed of two dots, half as long and replaced twice as often as the lines composed of four dots for a four-frame dot life. Thresholds for different dot lifetimes were measured with displays of 200 msec stimulus duration and 20% signal. Signal refers to the proportion of line elements to noise dots independent of the number of dots within each line. Orientation thresholds were compared with direction-discrimination thresholds for both 20 and 40% signal.

Because the dots making up the lines remained stationary in the same X - Y positions throughout each dot lifetime, perceived luminance increased with increasing dot life. To match the perceived brightness of line elements to the noise dots in the display, the luminance of the signal dots in this task was decreased systematically with increasing length of dot lifetime. To adjust the brightness of the signal dots without adjusting the brightness of the noise dots in the orientation control task, a slightly different method of signal-noise replacement was utilized. Signal dots were not replaced by noise dots at the end of their dot lifetimes. Rather, a subset of

dots remained signal dots throughout the trial. Their X - Y positions were changed to other random X - Y positions at the end of each dot lifetime. It was necessary to stagger the time at which the signal dots completed their dot lifetimes so there was constant signal information in all frames of the trial. Half the signal dots were randomly repositioned one frame prior to when their dot life should end in their first dot lifetime of a trial. The other half were repositioned on the next frame that completed their dot life. After the first dot lifetime, both sets of dots were repositioned on the frame that completed their dot life.

Noise control task

Direction discrimination thresholds were measured using random-walk noise (Williams & Sekuler, 1984). The noise dots took two-dimensional random walks with a constant step size. Signal dots moved coherently along trajectories of a particular direction and speed. Signal dots were replaced by noise dots at the end of each dot lifetime as previously described, but the amount of flicker within the display was kept constant (at zero) across blocks of trials with different dot lifetimes. Stimuli with 40% signal and 200 msec duration were used. Thresholds for two- and eight-frame dot lifetimes were measured and compared with the fine-direction thresholds found with flicker noise.

Results and discussion

Speed and fine-direction discrimination tasks. Speed discrimination thresholds measure the smallest change in speed that can be reliably discriminated, whereas fine-direction discrimination thresholds measure the smallest change in direction. Therefore, different axes are necessary to plot the two types of thresholds. Figure 2 shows examples of speed and fine-direction discrimination thresholds as a function of dot lifetime for two observers. The speed thresholds are plotted relative to the left axis and the direction thresholds are plotted relative to the right axis. The pattern of results, illustrated in this figure, is similar across the two tasks at all stimulus durations (100, 200, 400 msec) and signal-to-noise ratios (20 and 40%) for all three observers. Even though the units of measure are different, we can evaluate whether speed and fine-direction discriminations are similar by comparing: (1) the integration limits for the two tasks (number of frames); (2) the relative improvement in thresholds (y -intercept) with increases in signal-to-noise or stimulus duration for the two tasks; and (3) the relative change in rate of improvement (slope) in thresholds with a change in the signal-to-noise or stimulus duration for the two tasks.

To evaluate where the discrimination thresholds asymptote for each observer in each task, two lines were fit to the data for each stimulus duration and signal-to-noise ratio (Bogartz, 1968). The point at which these two lines intersect was taken as the integration limit. To evaluate improvement in thresholds, changes in the slope of the descending limb and the y -intercept for the asymptotic line of the function with increases in stimulus

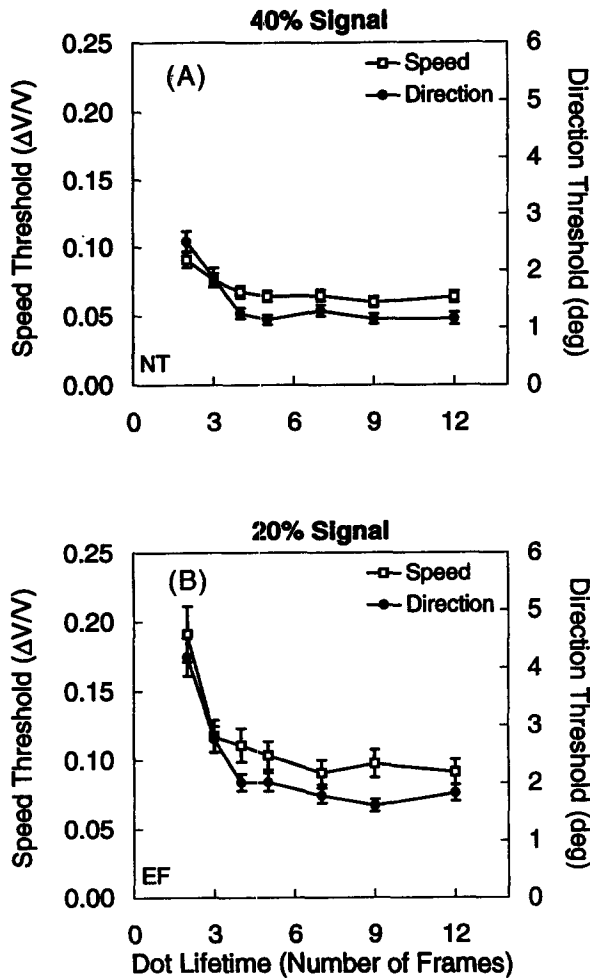


FIGURE 2. Speed and fine-direction discrimination thresholds for two observers, plotted as a function of dot lifetime. The open squares represent speed discrimination Weber fractions ($\Delta V/V$). The closed circles represent fine-direction discrimination thresholds in degrees of visual angle. Error bars indicate ± 1 standard error. (A) Data from one observer for a stimulus duration of 200 msec and a signal-to-noise ratio of 40%. (B) Data from another observer for a stimulus duration of 200 msec and a signal-to-noise ratio of 20%. Note that the curves for speed and direction are similar in shape for both observers and that the thresholds are higher overall with the lower signal-to-noise ratio. The effect of signal-to-noise ratio is constant across and within observers; thresholds are lower for the higher signal-to-noise ratio.

duration or signal-to-noise ratios were compared across the two tasks. Neither the slopes nor the y-intercepts can be compared directly across the two tasks, but both these values can be converted into normalized ratios and then compared. The slopes and y-intercepts of every fitted function were normalized by dividing each slope or y-intercept by the smallest slope or y-intercept, respectively, for each observer.

Integration limits within each task (fine-direction and speed) were similar across observers and conditions. The average integration limits were $4.05 (\pm 0.14)$ frames for fine-direction discrimination and $4.11 (\pm 0.09)$ frames for speed discrimination. Figure 3 shows discrimination thresholds as a function of dot lifetime at different stimulus durations for two observers. There is a vertical shift downward in both speed and direction thresholds

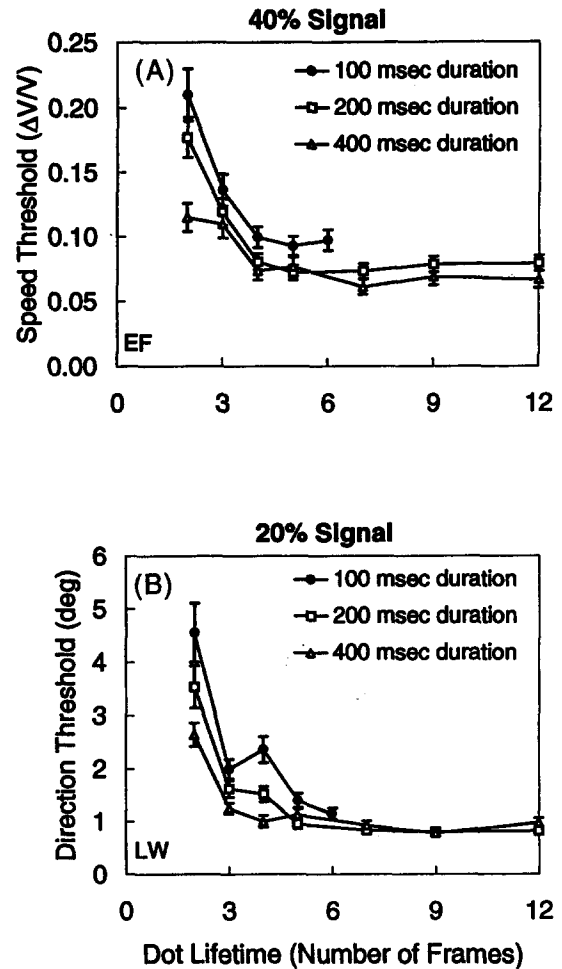


FIGURE 3. A comparison of discrimination thresholds at three stimulus durations (100, 200, 400 msec) for two observers, plotted as a function of dot lifetime. Speed discrimination Weber fractions ($\Delta V/V$) for one observer are shown in (A). Fine-direction discrimination thresholds in degrees of visual angle for another observer are shown in (B). Standard error bars (± 1) are provided on each point. The data are from signal-to-noise ratios of 40% in (A) and of 20% in (B). Note there is a small but systematic shift downward in thresholds for both speed and direction as stimulus duration increases.

with increasing stimulus duration, but the integration limit does not change systematically. This vertical shift is reflected mostly in a decreasing slope for the descending limb of the function with increased stimulus duration. The extent to which the slopes decreased as a function of stimulus duration was similar in the two tasks. For the 40% signal condition, slopes decreased with increased stimulus duration by a factor of 2.78 for direction and 2.14 for speed. For the 20% signal condition, the decrease was only by a factor of 1.32 for direction and 1.30 for speed. Except for the increase in stimulus duration from 100 msec to longer durations, the magnitude of the asymptotic thresholds (as reflected by the y-intercepts) did not decrease appreciably with increased stimulus duration for either speed or fine-direction discrimination. This might reflect the visual system's "central noise" limit (Bowne, 1990), where improvement in the signal had little effect because performance was at its maximum.

Likewise, as illustrated in Fig. 2, increasing the amount of signal in the displays produced a vertical shift downward in thresholds but did not change the integration limit. Overall, the slopes were steeper for the 20% signal condition compared with the 40% signal condition. The average 20 to 40% slope ratio was somewhat larger in the direction data (1.39) than in the speed data (1.17). The y-intercepts were higher overall for the 20% signal condition compared with the 40% signal condition in both tasks. For direction discrimination, the average y-intercepts decreased from 2.21 (± 0.42) deg for 20% signal to 1.29 (± 0.14) deg for 40% signal, corresponding to a ratio of 1.72. For speed discrimination, the y-intercepts decreased from 0.101 (± 0.003) $\Delta V/V$ for 20% signal to 0.076 (± 0.007) $\Delta V/V$ for 40% signal, corresponding to a ratio of 1.33.

If the threshold improvement seen with increasing dot lifetime were simply the result of probability summation of signals across independent detectors, the thresholds for three-frame dot lifetime should equal the combined threshold of two independent samples of two-frame dot lifetime detectors. When we calculated the expected thresholds for the three-frame dot lifetime, we found that 55% of the three-frame dot lifetime thresholds for fine-direction and speed discrimination were less than that predicted from probability summation.* This suggests that at least some of threshold improvement seen with increasing dot lifetime was due to enhanced signal detection within individual detectors.

The similarities between the various speed and direction measures suggest that the same integration mechanisms are operating in both tasks. Thresholds asymptote at a dot life of approximately four frames (80 msec) for both tasks at all stimulus durations and signal-to-noise ratios tested.

As outlined in the Introduction, we assume there are multiple different-sized motion detectors that integrate information across two or three or more frames. In a multiple frame sequence, several detectors sensitive to two-frame motion will be activated. In our experiment, the number of small-sized detectors (sensitive to two-frame motion) activated at a particular stimulus duration is constant and independent of dot lifetime. This is because the degree of correlation across any two frames does not change with longer dot lifetimes. As dot lifetime increases, motion detectors sensitive to longer sequences can become active. This means that improved performance with longer dot lifetimes at a particular stimulus duration must be due to larger-sized detectors. Whether these detectors are simply sensitive to two dots located further apart in space and time or if they are sensitive to multiple dot sequences is not clear. The probability summation calculations suggest that these detectors may be sensitive to multiple dot sequences, similar to motion energy units (Adelson & Bergen, 1985).

Comparisons of the thresholds for the two-frame dot lifetime reveal lower thresholds with increasing stimulus duration and signal-to-noise ratios. This suggests that there is an increase in the number of small-sized detectors that contributed to the motion measurement. However, even at the longest stimulus duration tested (400 msec), larger-sized detectors are necessary for asymptotic performance. The constant integration limit of approximately four frames for speed and fine-direction discrimination across stimulus durations suggests that four frames is the longest span over which larger-sized detectors operated. The size of the largest detectors does not change when stimulus duration is changed. Rather, the number of detectors that contribute to the measurement increase to produce an overall vertical shift downward in thresholds. Put another way, a stimulus aspect that may be expected to affect performance at long dot lifetimes is the number of the long dot-lifetime sequences that fit into the stimulus duration. There will be more five-frame sequences in the 400 msec duration than in the 100 msec duration and the number of long sequences could change where best performance will be found. On the contrary, though performance is slightly improved with longer stimulus durations, the number of frames needed for asymptotic performance is the same across a factor of four difference in duration.

Orientation control task. If observers base their direction judgments on the spatial orientation of the dots' trajectories, then the thresholds for a static orientation task should correspond to those of the direction task. Figure 4 compares orientation discrimination thresholds to fine-direction discrimination thresholds as a function of dot lifetime for two observers. For the orientation task, the dot lifetime determined the length of the lines in the display, as well as the lines' duration. (See Methods for further details.) At a two-frame dot lifetime, orientation discrimination thresholds for both observers were close to 10 deg of rotation. Thresholds for fine-direction discrimination at this dot lifetime were much better than the orientation thresholds (between 2 and 4.5 deg of rotation). Increasing the dot lifetime improved thresholds in both tasks, but orientation thresholds improved over a greater range of dot lifetimes than the direction thresholds. For dot lifetimes greater than two frames, thresholds for static orientation were consistently lower than the fine-direction thresholds. These results suggest that observers are using different types of information in the orientation and direction tasks. Fine-direction discrimination thresholds are not limited by the orientation information available from the signal dots' trajectories.

Noise control task. There was twice as much flicker in a two-frame dot lifetime display compared with one with a four-frame dot lifetime. This was because the signal dots in a two-frame display were replaced twice as often as those in a four-frame display. The improvement we saw with increasing dot lifetime could have been due to a decrease in the amount of flicker, and not the activation of larger-sized detectors. One way to show that this was

*Calculations were based on the equation $T_3 = 1/\sqrt{(1/T_2^2 + 1/T_2^2)}$, where T_3 was the three-frame dot lifetime threshold and T_2 was the two-frame dot lifetime threshold.

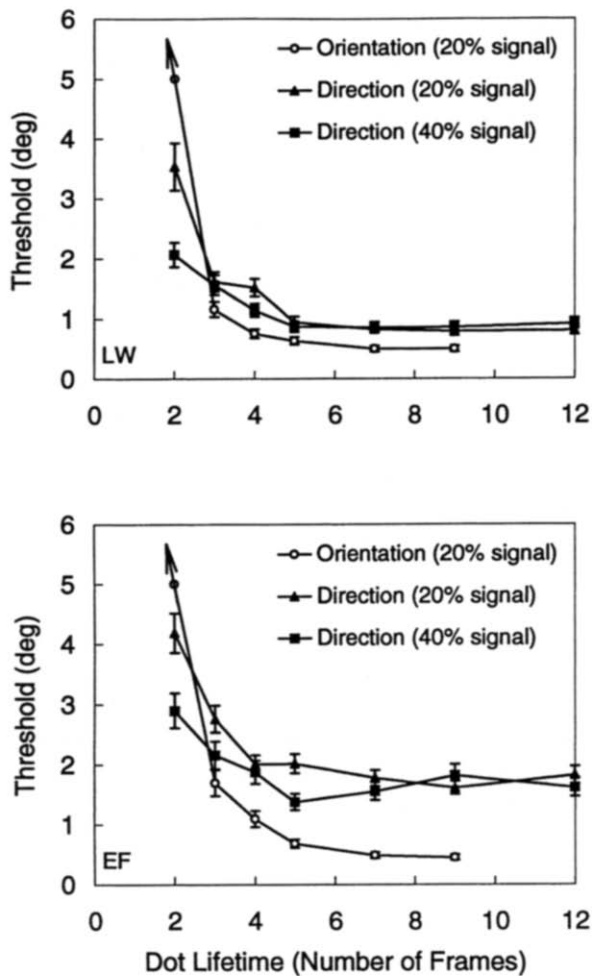


FIGURE 4. Orientation discrimination thresholds and fine-direction discrimination thresholds at two signal-to-noise ratios (20 and 40%) for two observers, plotted as a function of dot lifetime. Standard error bars are provided on each point. The stimulus duration for this control task was 200 msec. Orientation discrimination thresholds for both observers at a two-frame dot lifetime were close to 10 deg of visual angle. At dot lifetimes longer than two frames, orientation discrimination thresholds are smaller than those for direction discrimination at both signal-to-noise ratios for both observers.

not the case was to remove the flicker in the displays by replacing flicker noise with random-walk noise. Fine-direction thresholds at two- and seven-frame dot lifetimes with flicker noise are compared with those with random-walk noise in Fig. 5. Removing flicker from the displays did not change the thresholds in a consistent way across dot lifetimes for both observers. This indicates that the improvement in thresholds with increased dot lifetimes (Figs 2 and 3) is not due to the decrease in the amount of flicker in the displays.

An alternative way to show that the amount of flicker in the displays did not produce the changes in the thresholds across the two dot lifetimes is to compare the thresholds from the main experiment with equal amounts of flicker. A display with 40% signal and a two-frame dot lifetime contained twice as much flicker but also twice as much signal, as a display with 20% signal and a four-frame dot lifetime. So, if we assume a trade-off between

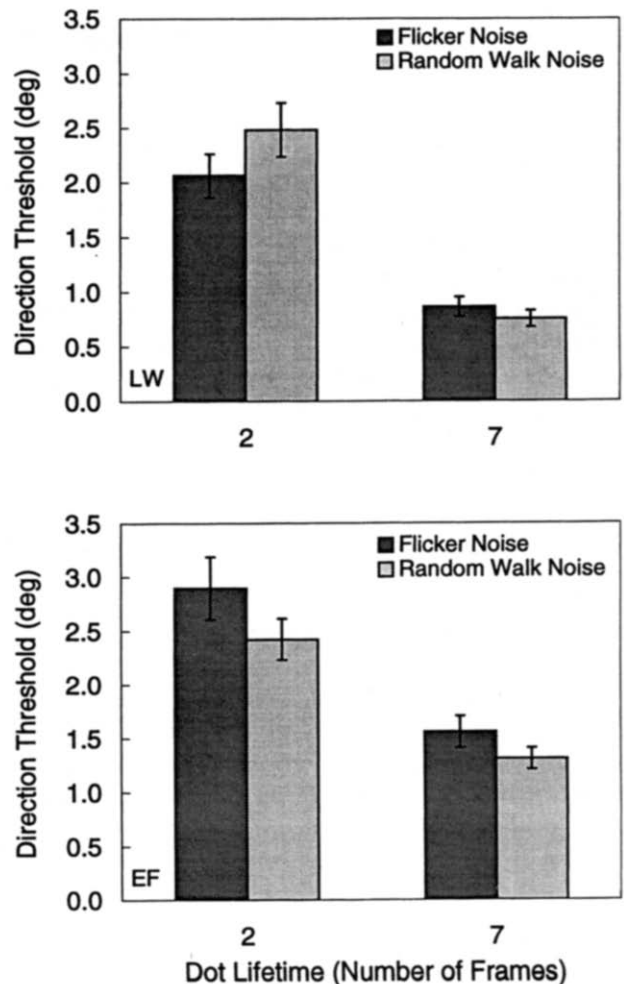


FIGURE 5. A comparison of fine-direction discrimination thresholds with flicker noise displays and random walk noise displays at two dot lifetime conditions for two observers. Standard error bars are provided on each bar. The signal-to-noise ratio was 40% and the stimulus duration was 200 msec. Direction thresholds for both types of noise displays are very close at each dot lifetime for both observers.

signal and flicker noise, these two conditions are equated. This comparison across each observer at each stimulus duration in the main experiment shows that thresholds for two-frame dot lifetimes were higher, relative to those for four-frame dot lifetimes in all but one comparison. This, along with the results from the noise control task, suggests that the improvement in performance with increasing dot lifetimes in the speed and fine-direction tasks cannot be due simply to the reduction of flicker in the displays. Rather, increasing the dot lifetime allows both small- and larger-sized detectors to contribute to the motion measurement.

EXPERIMENT 2

Experiment 1 suggests that the same mechanisms are involved in the integration of speed and fine-direction information. Thresholds for speed and fine-direction discrimination change in a similar manner with changes in signal-to-noise ratio and stimulus duration. The

integration limit of approximately four frames (or 80 msec) corresponds to the relative span over which larger-sized detectors can operate. However, the integration process could be limited by the number of frames (four), the amount of time (80 msec), or the amount of space (38.4 min arc) over which the motion signal occurred.

The purpose of Experiment 2 is to elucidate what is the underlying nature of this integration limit. If the integration limit is simply one of having enough samples of motion, then increasing the frame temporal asynchrony should have little effect on the point of asymptote. The integration limit should be four frames, regardless of the temporal asynchrony. If the limit is the amount of time over which the motion is sampled, decreasing or increasing the temporal asynchrony between motion samples should shift the point of asymptote to larger or shorter dot lifetimes, respectively. Alternatively, the limit could be spatial, where the larger-sized motion detectors are limited by the amount of visual space that they can integrate across.

To assess the type of integration limit present in the larger-sized detectors, speed and fine-direction discrimination thresholds are examined as a function of dot lifetime with motion defined by either longer (35 msec) or shorter (10 msec) framerates compared with that of Experiment 1 (20 msec). The speed also varied: 2 deg/sec for the longer framerate and 8, 16 or 32 deg/sec for the shorter framerate. This variation in speed allows us to examine changes in temporal asynchronies without having corresponding changes in spatial displacement size along the trajectories of motion. The displacement size for the 2 deg/sec condition is almost half (4.2 min arc) and the temporal asynchrony almost double (35 msec) those for the 8 deg/sec condition (9.6 min arc and 20 msec) in the first experiment. With the 16 deg/sec condition, the displacement size is equal (9.6 min arc) and the temporal asynchrony half (10 msec) those for the 8 deg/sec condition (9.6 min arc and 20 msec) in the first experiment. The 32 deg/sec condition has a displacement size that is double (19.2 min arc) and a temporal asynchrony half (10 msec) those for the 8 deg/sec condition (9.6 min arc and 20 msec) in the first experiment. A comparison of asymptotes for the 8 deg/sec condition with different displacement sizes (9.6 vs 4.8 min arc) and temporal asynchronies (20 vs 10 msec) in both experiments allows us to examine changes in the integration limit at a constant speed. To anticipate, our results show two types of integration limits: a minimum number of frames and a minimum amount of time.

Methods

Observers. Both authors and three naïve observers participated in this experiment. All observers had normal or corrected-to-normal vision. Each observer was well practiced in each condition before formal collection of data occurred.

Apparatus and stimuli. The apparatus was identical to that used in the first experiment. Except for the framerate,

all details about the stimulus conditions are identical to those of the speed and fine-direction discrimination tasks of the first experiment. The dots were plotted with X-Y coordinates on a CRT display at an average rate of either 28.57 Hz for the 2 deg/sec condition or 100 Hz for the 8, 16 and 32 deg/sec conditions. These numbers corresponded to 35 and 10 msec framerates. Because of the draw-time limitations for the 8, 16 and 32 deg/sec conditions, the kinematograms were composed of 100 ($\pm 20\%$) dynamic random dots.

The luminance of a single dot with refresh rates of 28.57 and 100 Hz, the two framerates used in this experiment, was measured with a PR-650 Spectra Colorimeter in an identical manner to that of the first experiment. A stationary calibration dot remained on the screen for approximately 1 sec. Two different luminance values were measured for each framerate. One was based on the voltage applied to the screen for the dots in the experiment. These measurements (391.4 cd/m^2 for 35 msec and 1340 cd/m^2 for 10 msec) are misleading because the experimental dots remained in one location for only one frame. Voltage values were adjusted until the perceived brightness of the stationary calibration dot matched the perceived brightness of the moving dots in the display. The adjusted voltage values (5.12 cd/m^2 for 35 msec and 17.68 cd/m^2 for 10 msec) better characterize the luminances of the displays for the two framerates used in this experiment. As in the first experiment, luminance values were chosen to be comfortably above threshold but allow for minimal visual persistence of the dots on the screen. The background luminance was below the measurement capabilities of the photometer.

Procedure

Number of frames vs integration time limit. Experiment 1 suggests that the integration limit was unaffected by changes in stimulus duration. To examine the same range of dot lifetimes and a comparable stimulus duration as in Experiment 1, two stimulus durations (175 and 350 msec $\pm 20\%$) were used with the 2 deg/sec condition (35 msec framerate). These durations allowed us to test dot lifetimes from two to six frames and two to twelve frames, respectively. Speed and fine-direction discrimination thresholds were examined at both stimulus durations for two signal-to-noise ratios (20 and 40%).

The framerate for the 8 and 16 deg/sec conditions (10 msec) was half that of the 8 deg/sec condition (20 msec) of the first experiment. This permitted sampling across a greater range of dot lifetimes than the 8 deg/sec condition of the previous experiment with the same stimulus duration. Dot lifetimes were tested over a range of 2–17 frames. Speed and fine-direction discrimination thresholds were measured for the 16 deg/sec speed at a stimulus duration of 200 msec and signal-to-noise ratio of 40%. Only fine-direction discrimination thresholds were measured for the 8 deg/sec speed at a stimulus duration of 200 msec and signal-to-noise ratio of 40%. All other details of the procedure were identical to

those in Experiment 1. These thresholds were compared with those in the first experiment.

Spatial-integration limit control

The displacement size for the 16 and 8 deg/sec conditions of the first experiment were equivalent in size (9.6 min arc), but their framerates differed (10 and 20 msec, respectively). The framerate for the 32 deg/sec condition was equivalent to that of the 16 deg/sec condition (10 msec), but the displacement sizes differed (19.2 and 9.6 min arc, respectively). This control condition allowed us to disambiguate spatial and temporal limits. If the point of asymptote for the 32 deg/sec condition remained the same as that of the 16 deg/sec condition, then a temporal limit would be revealed. If, however, the point of asymptote shifted to a shorter dot lifetime, a spatial limit would be revealed. Fine-direction discrimination thresholds were measured for displays with 40% signal and 200 msec stimulus durations. To obtain speed discrimination thresholds for the 32 deg/sec condition, a larger range of temporal asynchronies would have been necessary. Equipment limitations prevented us from generating this range, so we did not measure $\Delta V/V$ for the 32 deg/sec condition. Dot lifetimes were tested over a range of 2–17 frames. These thresholds were then compared with the 16 deg/sec fine-direction discrimination thresholds.

Results and discussion

Number of frames vs temporal-integration limit. The two-line fit to threshold as a function of dot lifetime, as described in Experiment 1, was used to evaluate discrimination threshold asymptotes for each observer in each task for 2, 8, 16, and 32 deg/sec conditions. In order to sample the same range of dot lifetimes as the 8 deg/sec condition in Experiment 1, the stimulus duration for the 2 deg/sec condition was lengthened to 350 msec. The data from Experiment 1 suggest that stimulus duration and signal-to-noise ratio had no effect on the integration limit, and this was confirmed with data collected at 175 msec stimulus duration and two signal-to-noise ratios (40 and 20%) for the 2 deg/sec stimulus.

As in Experiment 1, for two stimulus durations (175 and 350 msec) and signal-to-noise ratios (40 and 20%), asymptotic threshold levels were similar for speed and fine-direction discrimination for both observers. The top panel of Fig. 6 compares speed and direction discrimination thresholds at 20% signal and 350 msec stimulus duration for one observer. We observed similar changes in thresholds with changes in stimulus duration and signal-to-noise ratio in these data, as we did in Experiment 1. The comparison of speed and fine-direction thresholds was not the focus of Experiment 2, so these similarities across stimulus duration and signal-to-noise ratios will not be discussed further.

The critical comparisons for Experiment 2 are the integration limits for speed and fine-direction discrimination with motion displays of different temporal asynchronies. Figure 7 compares the average integration

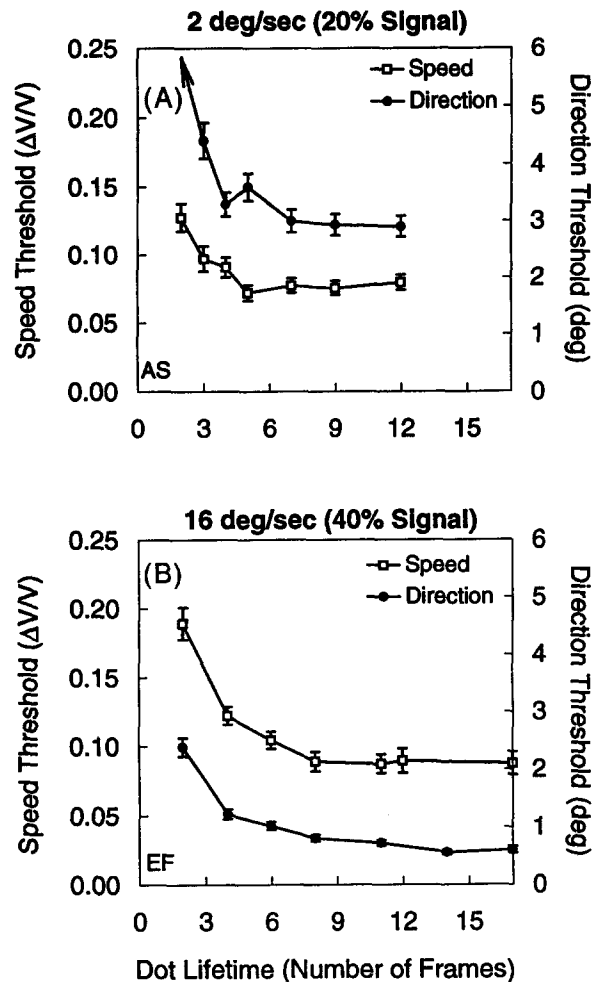


FIGURE 6. Speed and fine-direction discrimination thresholds for two observers, plotted as a function of dot lifetime. The open squares represent speed discrimination Weber fractions ($\Delta V/V$). The closed circles represent fine-direction discrimination thresholds in degrees of rotation. Standard error bars are provided on each point. (A) Data from one observer at 2 deg/sec with a stimulus duration of 350 msec and a signal-to-noise ratio of 20%. (B) Data from another observer at 16 deg/sec with a stimulus duration of 200 msec and a signal-to-noise ratio of 40%. Thresholds were sampled at lifetimes from two to twelve frames for the 2 deg/sec condition and from 2 to 17 frames for the 16 deg/sec condition. Note that the framerate for 2 deg/sec is 35 msec and that for 16 deg/sec is 10 msec. The curves for speed and direction are similar within each panel, but are different across the two panels.

limits across observers for the speed and fine-direction tasks at each speed and framerate used in Experiments 1 and 2. Even though the framerate for the 2 deg/sec condition (35 msec) was almost double that of the 8 deg/sec condition (20 msec), the integration limit in number of frames did not change. The average integration limits were $4.33 (\pm 0.14)$ frames for speed discrimination and $4.08 (\pm 0.11)$ frames for fine-direction discrimination. This suggested that the number of frames of motion, regardless of the temporal asynchrony determined where these thresholds asymptote. The data for the 8 and 16 deg/sec conditions, however, suggest that this was not always the case.

The shapes of the curves depicted in the bottom panel of Fig. 6 and the average integration limits shown in Fig.

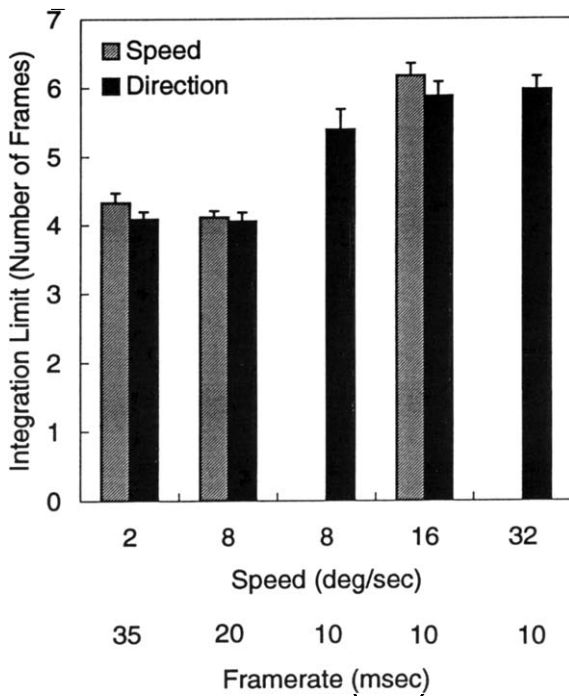


FIGURE 7. Integration limits in number of frames averaged across all observers and conditions for speed and fine-direction discrimination tasks are shown for each speed and framerate tested in Experiments 1 and 2. The average integration limits for 2 and 8 deg/sec conditions are similar (approximately four frames), even though the framerates are nearly a factor of two different. The average integration limits for 8, 16 and 32 deg/sec conditions are similar (approximately six frames) with identical framerates of 10 msec.

7 for the 16 deg/sec condition are very different from those of the 8 and 2 deg/sec conditions. The integration limits for the 16 deg/sec condition were $6.17 (\pm 0.19)$ frames for speed discrimination and $5.87 (\pm 0.21)$ frames for fine-direction discrimination. Even though both the displacement sizes (9.6 vs 4.8 min arc) and temporal asynchronies (20 vs 10 msec) of the 8 deg/sec condition from both experiments were different, a comparison of these conditions allowed us to examine the integration limit as a function of framerate without confounding changes in speed. The integration limit for the 8 deg/sec condition (10 msec framerate) from this experiment was $5.39 (\pm 0.29)$ for fine-direction discrimination. Together, these data suggest that a temporal integration limit of approximately 60 msec, rather than a number-of-frames limit, is present in these tasks.

It appears that two types of integration limit determine the point of asymptote for the thresholds in these tasks. Lengthening the temporal asynchrony to 35 msec produced no shift in the point of asymptote, but shortening the temporal asynchrony to 10 msec shifted the point of asymptote to longer dot lifetimes. The first observation suggests that a minimum number of four frames is necessary, regardless of the time over which those motion samples occur. The second observation shows that further integration can occur above this four-frame limit if a minimum time period (temporal limit) has not elapsed.

Spatial-integration limit control. The data from Experiments 1 and 2 cannot be explained solely by limitations in the *spatial* extent over which motion samples could be integrated. The dot displacement size for the 2 deg/sec condition (4.2 min arc) was less than half that of the 8 deg/sec condition (9.6 min arc) of the first experiment, but the data revealed similar asymptotes. The 16 deg/sec condition had an identical dot displacement size to that of the 8 deg/sec condition (9.6 min arc), but the points of asymptotes were different. If the first type of limit were spatial, the number of frames limit would have increased with smaller displacements (2 deg/sec condition) and remained the same when the displacement sizes were identical (16 deg/sec), not the reverse.

The recruitment mechanisms in the 16 deg/sec condition integrated across a larger spatial extent (as illustrated by the longer dot lifetime asymptotes) than either the 8 or 2 deg/sec conditions. It is possible that the second type of limit was spatial and not temporal, as we have described. The average integration limits for the three observers were $5.97 (\pm 0.19)$ frames and $6.02 (\pm 0.14)$ frames for the 32 and 16 deg/sec conditions, respectively (see Fig. 7). Even though the displacement size of the motion samples was doubled for the 32 deg/sec condition (19.2 min arc), the point of asymptote did not change. The framerates for the two speeds are identical (10 msec), so these data confirm that the second integration limit is temporal in nature.

GENERAL DISCUSSION

Several conclusions can be drawn from the results of these experiments. The data suggest that the same underlying integration mechanisms are used by the visual system for discriminating fine differences in speed and direction. Thresholds for both tasks improve in a similar manner with changes in dot lifetime across different stimulus durations, signal-to-noise ratios, and framerates. Although the observers' absolute levels of performance improve with increases in stimulus duration or signal-to-noise ratio, the maximum span of integration for the larger-sized detectors does not change. Improvement in absolute threshold levels is probably due to an increase in the number of detectors that information is pooled across. The distinction between integration within detectors as compared with pooling across detectors is similar to the distinction made by Fredericksen *et al.* (1994a,b) between integration and summation, respectively. Sequential recruitment in our experiments indicates integration within motion detectors rather than some combination of information across detectors.

Our finding that speed and fine-direction discrimination use the same underlying recruitment mechanisms conflicts with data from some studies. Hiris & Blake (1995) suggested that the differential effect of speed noise on perceived coherence for direction displays compared with direction noise on coherence for speed displays was due to a difference in ability of the two types of motion to affect higher-level grouping processes.

Alternatively, we suggest that the difference that they showed may be due to a difference in the relative effectiveness of the two types of noise introduced into the displays. Their data show that discriminating a display with a bandwidth of directions or speeds from a display containing no distribution of directions or speeds improved when the bandwidth was increased for both aspects of motion. However, there is no obvious way to equate the speed and direction variability that they introduced in the noise conditions. These results may point to a difference in higher-level grouping processes or they may simply show that the two types of noise were not equally effective. Smith *et al.* (1994) did not have this problem because they introduced the same high-pass, filter noise into their speed and direction displays. In their study, they showed that the perceived global motions for the two aspects of motion were equally unaffected by the noise.

De Bruyn and Orban's conflicting data (1988) are puzzling because their study was very similar to ours. They measured speed and fine-direction thresholds for random dot patterns as a function of stimulus size and duration for a range of velocities. Their stimuli were moved continuously by means of mirror stepper motors, rather than in apparent motion as in our displays. Speed and fine-direction discrimination thresholds were equally affected by changes in speed and size of the stimulus, but showed differences for changes in stimulus duration. Direction discrimination performance asymptoted at shorter stimulus durations than speed discrimination performance, indicating that the amount of pooling was less for fine-direction than speed. Because De Bruyn & Orban (1988) used continuous motion displays while we systematically varied dot lifetime, we can only compare our data for the longest dot lifetimes across different stimulus durations to theirs. Our data do not show a difference in the absolute levels of improvement for speed and fine-direction discrimination as a function of stimulus duration. One possibility for this discrepancy is that their fine-direction task effectively may have been an orientation discrimination task. Westheimer & Wehrhahn (1994) showed that fine-direction discrimination thresholds for a dot in essentially continuous motion (sampling rate of 2 msec) were very similar to those for orientation of line elements that have similar temporal and spatial extents. Unlike our displays, De Bruyn & Orban (1988) used dot patterns that contained no noise. Their orientation control task may not have been appropriate because the full trajectory was not given—only the first and last dot positions of the display were shown. An orientation control task where the entire trajectory was represented (such as ours) might have been a better stimulus to show what spatial orientation information was available in their displays.

Experiment 1 compares the integration limits for discriminating fine differences in speed and direction to determine whether the same or different mechanisms are used in two types of tasks. It reveals nothing about the underlying nature of the limits. Experiment 2 is designed

to explore the characteristics of the integration limits. The data reveal that two limiting factors determine the extent over which motion information can be integrated. Performance continues to improve until the dot lifetime reached both four frames and a time period of 60 msec. This suggests that larger-sized detectors integrate information across four frames regardless of the time over which these motion samples occur. They then continue to integrate above this four-frame limit until a time period of 60 msec has elapsed.

A framerate limit is a somewhat misleading way to define the temporal structure of motion detectors. If we consider motion energy units (Adelson & Bergen, 1985), coarsely sampled motion may simply not be as effective a stimulus as finer sampled motion because the amount of signal falling within the receptive field of a detector may not be adequate. Another way that using framerate can be misleading is when considering continuous motion. In an apparent motion sequence, as the spatial displacements between frames reduce, the frames become difficult to differentiate and there may need to be 20 frames to enable the observer to detect any motion at all. In the limit of continuous motion, framerate means nothing and one can only speak of spatial or temporal effects on performance.

The current study suggests that motion detectors are sensitive to multiple motion frames, not just to two frames. We are able to evaluate the extent of those detectors because we kept the degree of correlation across contiguous frames of motion constant, while varying the dot lifetime. Fredericksen *et al.* (1994b,c) data revealed a similar dependence on framerate for asymptotic threshold performance. When motion stimuli had long frame asynchronies, thresholds asymptoted at longer stimulus durations than with stimuli with short frame asynchronies. Similarly, Snowden & Braddick (1990) found differences in threshold performance for apparent motion when the spatial displacements between frames were small, compared with those that were large. They examined the proportion of errors as a function of displacement size and number of frames. The dot-lifetime of the signal dots was either limited to two frames or was continuous. For small displacements, performance did not improve with more frames if the dot lifetime was limited to two frames, but improved if the dot lifetime was continuous. For large displacements, the performance improved with more frames under both dot lifetime conditions. These and other studies (Fredericksen *et al.*, 1994b,c; Snowden & Braddick, 1990) used coarse direction discrimination tasks to obtain threshold measures. While De Bruyn & Orban (1988) suggested that the relative extent over which motion is integrated in coarse discrimination tasks may have been substantially less than in fine discrimination tasks, the limiting factors for both coarse and fine discrimination tasks appear to be similar. It is possible that different motion mechanisms are involved in the two types of discriminations, as Bravo & Watamaniuk (1995) and Watamaniuk (1996) suggest. However, the limiting factors for the two types of tasks are the same.

The two integration limits that we found and the differences seen in Fredericksen *et al.* (1994b,c) data and Snowden & Braddick (1990) data may reflect different underlying physiological substrates that had different integration characteristics. Newsome *et al.* (1986) attempted to find a correlation between motion perception and physiology by comparing human psychophysical data with responses of direction-selective cells in areas MT and V1 of awake, behaving rhesus monkeys. Newsome *et al.* (1986) measured the largest possible spatial displacement size between frames of apparent motion to elicit direction-selective responses for several speeds. The same stimuli were then shown to human observers. The maximum spatial displacement size for each speed which elicited a perception of motion was then measured. Newsome *et al.* (1986) found a speed-dependent correspondence between the physiological responses and the psychophysical measurements. For faster speeds (>8 deg/sec), the psychophysical maximum displacement size measures were similar to the direction-selective behavior of MT cells, but not V1 cells. For slower speeds (<8 deg/sec), the psychophysical displacement size measures were similar to the responses of V1 cells.

Mikami *et al.* (1986) further examined whether the spatial and temporal limits of direction-selective cells in areas MT and V1 were similar. They showed that MT and V1 direction-selective cells had similar temporal limits, but MT direction-selective cells could tolerate much larger spatial limits than V1 direction-selective cells and retain their direction selectivity. Responses from MT direction-selective cells were best at relatively constant temporal intervals of 60–100 msec, except at much higher speeds (16 and 32 deg/sec) where the optimal temporal interval dropped to 40–60 msec (Newsome *et al.*, 1986). The displacement size of the motion did not affect these relatively constant temporal limits. Unlike MT cells, responses from V1 cells depended more strongly on the combination of the spatial and temporal intervals used (Newsome *et al.*, 1986).

These physiological data (Mikami *et al.*, 1986; Newsome *et al.*, 1986) are quite suggestive of different underlying physiological substrates for our results from different speeds. The temporal limit of 60 msec that we found for the 16 and 32 deg/sec conditions is quite similar to the temporal limit that Mikami *et al.* (1986) found for their direction-selective MT cells. Similarly, our number of frame limit is consistent with the integration characteristics of motion processing for V1 cells. This argues that the four-frame limit we find for the slower speeds is the result of different temporal characteristics of the mechanisms encoding slow speeds compared with those for faster speeds. However, these results could also be the result of inadequate sampling for any particular motion detector, so several detectors contributed to optimal performance.

While there are several models of motion detection (e.g., van Santen & Sperling, 1984; Adelson & Bergen, 1985; Watson & Ahumada, 1985), most were not

designed with sequential recruitment in mind, with the notable exception of Snippe & Koenderink (1994). Their model dealt with recruitment across multiple frames of apparent motion by combining Reichardt detectors (without the opponent stage) with different spatial and temporal spans into multi-input detectors. In other words, their motion detectors had interconnected subunits tuned to the same direction and speed that sum motion information along trajectories. Models of sequential recruitment (van Doorn & Koenderink, 1982a,b, 1984; Snowden & Braddick, 1989a, 1990) suggested that the outputs of bilocal Reichardt detectors having different temporal and spatial spans but tuned to the same speed were combined via some sort of cooperative pooling network along a single direction. What differentiates these models from the Snippe & Koenderink (1994) model was in the nature of the interconnections between spatial detectors. In the Snippe and Koenderink model, the detectors were hard wired together into multi-input integrators. In the other recruitment models (van Doorn & Koenderink, 1982a,b, 1984; Snowden & Braddick, 1989a, 1990), bilocal Reichardt detectors were independent of each other at the input stage and their outputs were combined in a cooperative network.

Although we have described our results in terms of Snowden & Braddick (1989a) small- and larger-sized recruitment mechanisms, it is improbable that separate detectors respond to these two types of correlations. Rather, the integration limits in this study reflect recruitment or temporal summation within individual motion detectors. Physiological studies (Emerson *et al.*, 1987, 1992) suggest that motion energy units described cell activity more accurately than two-input motion detectors (e.g., Reichardt detectors). Other motion detector models (e.g., Adelson & Bergen, 1985; Fredericksen *et al.*, 1994a,b,c) could also exhibit recruitment across multiple frames of apparent motion as long as the stimulus remained within the detector's receptive field. The more of the receptive field that is filled by the stimulus, the greater its output will be. These models are similar to the Snippe & Koenderink (1994) model, in that combinations across more than two frames of motion are intrinsic to the detector itself without requiring further integration. These models would be consistent with Mikami *et al.* (1986) finding that direction-selective cells responded best to motion stimuli that extend over multiple frames.

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Acknowledgements—Portions of this work were presented at the 1995 meeting of the Association for Research in Vision and Ophthalmology. The authors wish to thank Scott Watamaniuk for his helpful discussions of this research and comments on an earlier version of this manuscript. This research was funded by Brown University.