Stimulus configuration determines the detectability of motion signals in noise

Preeti Verghese, Suzanne P. McKee, and Norberto M. Grzywacz

Smith Kettlewell Eye Research Institute, 2318 Fillmore Street, San Francisco, California 94115

We measured the detectability of moving signal dots in dynamic noise to determine whether local motion signals are preferentially combined along an axis parallel to the direction of motion. Observers were asked to detect a signal composed of three dots moving in a linear trajectory among dynamic noise dots. The signal dots were collinear and equally spaced in a configuration that was either parallel to or perpendicular to their trajectory. The probability of detecting the signal was measured as a function of noise density, over a range of signal dot spacings from 0.5° to 5.0°. At any given noise density, the signal in the parallel configuration was more detectable than that in the perpendicular configuration. Our four observers could tolerate 1.5–2.5 times more noise in the parallel configuration. This improvement is not due merely to temporal summation between consecutive dots in the parallel trajectory. Temporal summation functions measured on our observers indicate that the benefit from spatial coincidence of the dots lasts for no more than 50 ms, whereas the increased detectability of the parallel configuration is observed up to the largest temporal separations tested (210 ms). These results demonstrate that dots arranged parallel to the signal trajectory are more easily detected than those arranged perpendicularly. Moreover, this enhancement points to the existence of visual mechanisms that preferentially organize motion information parallel to the direction of motion. © 2000 Optical Society of America [S0740-3232(00)02009-3]

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1. INTRODUCTION

Recently, several studies have explored how the human visual system combines local oriented signals. For instance, a smooth contour made up of a string of similarly oriented Gabor patches is easily detected in a background of randomly oriented patches.[1,2] Polat and Sagi[3,4] studied this interaction more closely by measuring contrast detection thresholds for the central patch in a three-patch string. The central patch was most detectable when the two flanking patches were collinear with it and was much less detectable when the flanks were orthogonal. The bounding contours of natural objects typically change slowly, so this enhanced sensitivity for collinear targets, or for targets with gradual changes in orientation, likely depends on some process that identifies object contours.

Do similar interactions between local signals occur for orientation in space–time, i.e., motion? Natural objects in motion rarely change direction abruptly. Therefore evidence for a process that enhances motion in a consistent direction is not surprising. Indeed, a substantial body of results indicates that there is an enhancement of motion signals along the direction of motion.[5–14] Some, but not all, of these results can be explained by summation within a single local motion energy unit.

Van Doorn and Koenderink[7] measured detection thresholds for a rectangular random dot patch moving coherently in dynamic white noise and showed that thresholds were lower when the patch was elongated in the direction of motion than when it was elongated in the direction perpendicular to motion. They attributed the improvement along the direction of motion to the recruitment of motion units at a variety of scales. Fredericksen *et al.*[15] replicated their experiments with limited lifetime dots that they argued stimulated only a single scale; they still found that the thresholds were lower for patches elongated along the direction of motion. On the basis of these results, they concluded that the primary motion units were somewhat elongated along the axis parallel to their directional tuning. Although their estimates of receptive field width are comparable with the values obtained by Anderson and Burr,[16] they concluded that the units are not circularly symmetric. This is opposite to the findings of Anderson and Burr,[16] who based their estimate of circularly symmetric receptive fields on contrast thresholds for direction discrimination as a function of stimulus width and height.

Not all studies of motion have shown enhanced detectability along the direction of motion. Nakayama *et al.*[17] found that the minimum threshold for detecting differential motion in random dots was smaller when the amplitude of motion was modulated along the axis of motion (compression) than when it was modulated orthogonal to the axis of motion (shear). They interpreted their results as showing that spatial integration within the motion system is greatest in a direction orthogonal to the direction of motion. It seems likely that the minimum motion threshold depends on the receptive field structure of the primary motion units, particularly integration within subfields, which are known to be oriented orthogonally to the direction of motion. Other studies that show en-

hanced detectability parallel to the direction of motion undoubtedly reflect the operation of a different neural substrate, perhaps involving some combination of the primary motion units as was originally argued by van Doorn and Koenderink.[7]   We shall now consider evidence from a very different paradigm used to demonstrate this same enhancement of motion signals parallel to the direction of motion.

In a visual search task, Watamaniuk *et al.*[12] showed that a single dot moving in a consistent direction is easily detected among noise dots moving in random directions from frame to frame (Brownian motion).   Their main reason for using Brownian motion noise was to conceal the signal dots, thus making the search more difficult, because the noise dots move in ways that mimic the signal motion.

This visual search task has some aspects in common with the original signal-in-noise paradigm of van Doorn and Koenderink.[7]   Contemporary models of visual search[18–20] use a signal-to-noise framework to explain target detection among distractors.   In this case, the trajectory dot is the signal, and the noise dots in Brownian motion are the distractors.   In a two alternative forced-choice task, the search model calculates the largest motion signal in each interval and chooses the interval with the larger signal (maximum rule).   The trajectory dot is detected when it generates a local motion signal that is larger than any of the competing local motion signals generated by the numerous noise dots.   As the number of noise dots increases, the probability increases that the noise will generate a motion signal larger than that generated by the trajectory, leading to an incorrect choice. However, the stimulus in Watamaniuk *et al.*[12] differs in one important aspect from that in the earlier study by van Doorn and Koenderink.[7]   In the study by Watamaniuk *et al.* the signal was a single dot that appeared at an unknown location amid Brownian noise dots, whereas in the van Doorn and Koenderink study, the signal was co-extensive with the noise throughout a rectangular test patch.

Verghese *et al.*[14] explored whether this visual search model could explain the enhanced detectability of an extended trajectory.   We used a local motion model composed of independent motion energy units[21] followed by a decision stage to calculate the detectability of the trajectory dot in noise.   Our calculations show that the output of motion energy detectors followed by a maximum rule explains the detectability of brief (100 ms) trajectories but cannot explain the detectability of an extended trajectory. Inherent in our version of the local motion model is the assumption that motion units have circular receptive fields.

Although physiological and psychophysical measurements of receptive field dimensions[16,22,23] support the assumption of circular symmetry, we did consider alternative aspect ratios.   A second-stage unit centered on the trajectory and elongated in the direction of motion would indeed respond more strongly to the signal than would a circularly symmetric first-stage unit.   The second-stage unit could be formed by a simple combination of the outputs of the circular first-stage detectors.   Such a unit might see the entire trajectory, but it would also see all

the noise falling within the combined detectors; generally, the signal would increase linearly, while the noise would increase as the area of the first-stage units, resulting in a lower signal/noise ratio.

An alternative is a matched trajectory detector at the first stage, having a high aspect ratio elongated in the direction of motion such that it sees all of the signal and little of the noise.   The problem arises when we consider that ours is a search task: noise everywhere and signal in a single location, moving in an unknown direction.   To detect the signal, these elongated units must tile the whole display area.   If we assume a constant spacing between these units (twice their space constant along their width and height dimensions), more of the elongated units would be needed to tile the display, compared with the highly efficient tiling associated with circularly symmetric units.   The larger the number of units, the higher the probability that the response to noise will exceed the signal response.   Our simulations with aspect ratios up to 10 suggest that units elongated along the motion direction cannot predict human performance for detecting extended trajectories in noise.

In addition, we have other results that challenge the elongated-unit explanation.   This type of unit cannot explain the detectability of a trajectory on a slowly changing path.   Earlier studies[12,14] found that the trajectory dot is still quite easily detected if the path changes direction gradually, forming a circular path or a shallow sawtooth.

One explanation that does account for the detectability of extended trajectories, including slowly changing paths, is a network that propagates interactions between units tuned to roughly similar directions of motion.[13,24,25]   A network monitors the activities of local units and selects those with the largest local activation.   Network units propagate activation to other units if their preferred direction roughly points to those units.   Note that this network is assumed to operate at a stage after motion is encoded by the primary motion units and that its activity does not alter the response of these primary units.   Nevertheless, activation of this network could enhance detection of suprathreshold stimuli that lie along the same motion trajectory.   We tested this hypothesis in the following experiments.

Our stimulus was a triplet of dots.   These dots were arranged either perpendicular to or parallel to the direction of motion.   If indeed there is an interaction along the direction of motion, then the parallel configuration should be more detectable.

We provide a road map to guide the reader through the experiments and controls that we performed.   The first experiment compares the detectability of parallel and perpendicular triplets in noise and shows that the parallel configuration is more detectable.   We take a brief detour to show that the differences in detectability of the two configurations cannot be attributed to small differences in eccentricity.   The next experiment investigates whether the enhanced detectability of the parallel configuration is due to temporal summation between consecutive dots that fall in approximately the same spatial location.   Our final experiment compares the detectability of the parallel and perpendicular triplet with the summation of three independent trajectories across space.

2. EXPERIMENT 1: EFFECT OF STIMULUS CONFIGURATION

A. Methods

The experiments were done on an Amiga 4000 with a CyberVision graphics card, connected to a 17-in. Nanao multisynch monitor. The stimuli were dots that subtended 2 arc min, at a viewing distance of 1 m. The luminance of the background was 45 cd/m^2. The high luminance for the background obscured any spatial pattern that might have resulted from phosphor persistence.

Experiment 1 is similar to the signal-in-noise paradigm of Watamaniuk *et al.*[12] with the single signal dot replaced by a triplet of signal dots. The signal dots that made up the triplet were collinear and equally spaced in a configuration that was either parallel to or perpendicular to their trajectory (Fig. 1). The center dot of the triplet was constrained to pass within $\pm0.25°$ of fixation. The signal triplet moved in one of eight directions, randomly picked on each interval.[26] Thus the perpendicular and parallel triplets could take one of the eight configurations shown in Fig. 1. Each signal dot was displaced in a consistent direction by 0.17° on every frame. This corresponded to a velocity of 12 deg/s, given the 71-Hz frame rate of the display monitor. Each noise dot was displaced by the same amount as the signal on each frame, but its direction was randomly sampled from 360°. As the signal and noise dots had the same step size and frame rate, it was impossible to discriminate between them on the basis of a pair of frames. The luminance of the dots was 130 cd/m^2, yielding a Michelson contrast of 50%. The display duration was 300 ms. The display area was a circular region 12.6° in diameter. The number of dots in this area determined the dot density. In our experiments the number of dots varied from 100 to 1024, corresponding to noise dot densities that ranged from 0.8 to 8.2 dots/deg^2.

The center-to-center spacing of the dots in the triplet varied from 0.5° to 5°. For spacings between 0.5° and 2.5°, observers viewed the display at a distance of 1 m. As the dots moved at 12 deg/s, this spacing range corresponded to a temporal delay of 42 to 210 ms between consecutive dots of the parallel triplet. Owing to technical limitations on display dimensions, the viewing distance was 0.5 m for larger spacings from 3° to 5°. At the closer viewing distance the dots moved at a speed of 24 deg/s, so the temporal delay corresponded to 125 to 210 ms at dot spacings of 3° to 5°.
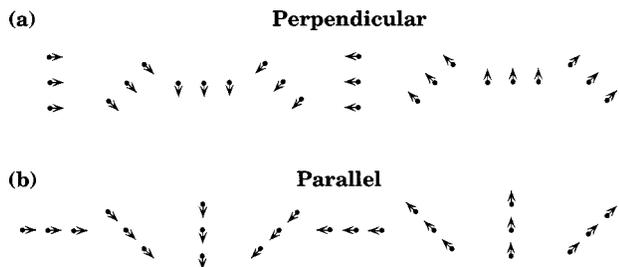

Fig. 1. Configuration of signal dots. The signal was a collinear triplet of dots that was arranged along one of eight orientations at 45° intervals. The dots in the triplet moved rigidly along a path that was either perpendicular to or parallel to the triplet configuration, as depicted in (a) and (b), respectively. The dots in the triplet had a uniform center-to-center spacing, which ranged from 0.5° to 5°.
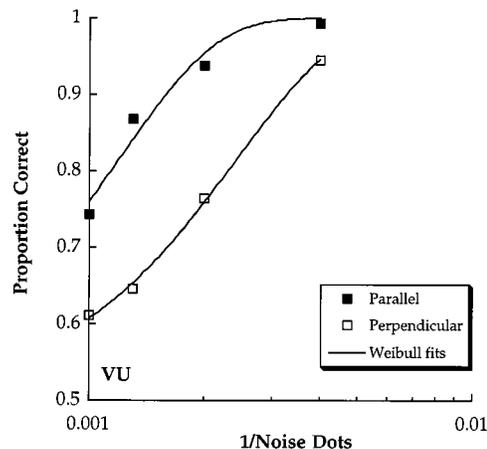

Fig. 2. Psychometric functions for the parallel and perpendicular configurations. The proportion correct is plotted versus the reciprocal of the number of noise dots. Open and solid symbols plot data for the perpendicular and parallel conditions, respectively. The center-to-center spacing of the dots in both configurations was 1°. Continuous curves are Weibull fits to the data. Thresholds were estimated as the noise level corresponding to 82% correct.

We measured thresholds for the parallel and perpendicular configurations, using a two-alternative forced choice procedure with two temporal intervals. One of the intervals, picked at random, contained the signal in noise, whereas the other interval contained noise alone. Observers were asked to choose the interval with the signal. They did not have to identify its direction or say whether it was a parallel or perpendicular triplet. Feedback was provided. The parallel and perpendicular conditions were interleaved in a block of 96 trials, with 6 trials for each of the 16 configurations shown in Fig. 1. As the orientations of these configurations were matched in the parallel and perpendicular cases, it was not possible to distinguish the cases on the basis of static cues alone. Each block was run at a fixed spacing and noise density. At each spacing, the proportion correct was measured at several noise densities to yield a psychometric function from which we estimated threshold. The raw data were fit with a Weibull function, and threshold was taken to be the noise density that corresponded to 82% correct, separately estimated for each of the two stimulus configurations. In the maximum-likelihood fitting procedure that we used, we allowed the threshold, α, and the log–log slope, β, to vary while keeping the guessing rate, γ, and the finger error parameter, δ, fixed at 0.5 and 0.01, respectively.

B. Results and Discussion

Figure 2 plots typical psychometric functions for the parallel and perpendicular configurations. The proportion correct is plotted versus the reciprocal of the number of noise dots in the stimulus field. The center-to-center spacing of the dots in the triplet for both configurations was 1°. The open and solid symbols plot data for the perpendicular and parallel configurations, respectively, and the smooth curves through the data represent Weibull fits. Each point on the psychometric function represents a total of 96 trials measured across two blocks of trials. The psychometric function for the parallel configuration

lies clearly to the left of that for the perpendicular configuration, indicating that the former is much more detectable than the perpendicular configuration; i.e., the parallel configuration can tolerate a larger number of noise dots. Figure 3 summarizes our results for four observers over a range of interdot spacings. The open squares plot the thresholds for the parallel configuration, and the solid squares plot the thresholds for the perpendicular configuration. As is evident, the parallel configuration has much lower thresholds than the perpendicular configuration. This is true for all our observers at all of the spacings that we measured. In short, the parallel configuration is significantly more detectable than the perpendicular configuration. We obtained almost identical results when we repeated these experiments with randomly replotted noise instead of Brownian noise.

For comparison, Fig. 3 also shows thresholds for a single dot. Since spacing is not defined in this case, we arbitrarily plot single dot thresholds as a horizontal dashed line. Typically there is a marked improvement in thresholds from one dot to three dots, even in the perpendicular configuration. We return to this issue in Section 4.

C. Eccentricity Effect?

One potential explanation for why the parallel configuration is more detectable is that the mean eccentricity of its dots is smaller. Grzywacz *et al.*[13] reported that increasing eccentricity produced quite steep declines in the detectability of a single trajectory dot. In the context of our moving stimuli, eccentricity refers to the *closest point of approach* of a trajectory to fixation. The center dot of the parallel and the perpendicular configurations always had the same eccentricity and were presented closest to fixation (±0.25°). By design, all three dots in the parallel configuration followed the same path. In the perpendicu-

lar condition the flanking dots followed separate motion paths, whose separation from the center dot depended on dot spacing. Thus the flanking dots of the perpendicular configuration necessarily lay at relatively more eccentric locations. To balance the eccentricities in the two conditions, we ran the following control. We first measured detectability of a single dot as a function of eccentricity for the noise levels used in this experiment. We then used the detectability-versus-eccentricity function to equate the detectability of the three dots in the parallel and perpendicular configurations, as described below.

For this control experiment the eccentricity of the center dot of the perpendicular configuration was constrained to be 1° from fixation, while that of the flanking dots depended on dot spacing. For instance, at a spacing of 1°, one of the flanking dots passed through fixation and the other passed through a point 2° from fixation. From the measured detectability of a single dot at each of these eccentricities, we calculated the total detectability of the perpendicular configuration, assuming d' additivity (independence) of the individual trajectories. We then calculated the equivalent eccentricity of the parallel triplet (interpolating between measured values, if necessary) by assuming that all three dots in the parallel configuration had the same eccentricity; i.e., the closest point of approach for all the dots in the parallel triplet was the same. Note that this assumption underestimates the eccentricity of the parallel triplet for spacings larger than 1.5° as only the center dot of the parallel triplet actually passes through this point. Thresholds for two observers, SPM and PV, were measured for dot spacings of 1°, 1.5°, 2°, and 2.5°. The ratio of sensitivities of the parallel and perpendicular configurations in this eccentricity control was not significantly different from the case when the central dot passed within ±0.25° from fixation. Thus it appears that differences in mean eccentricity between the
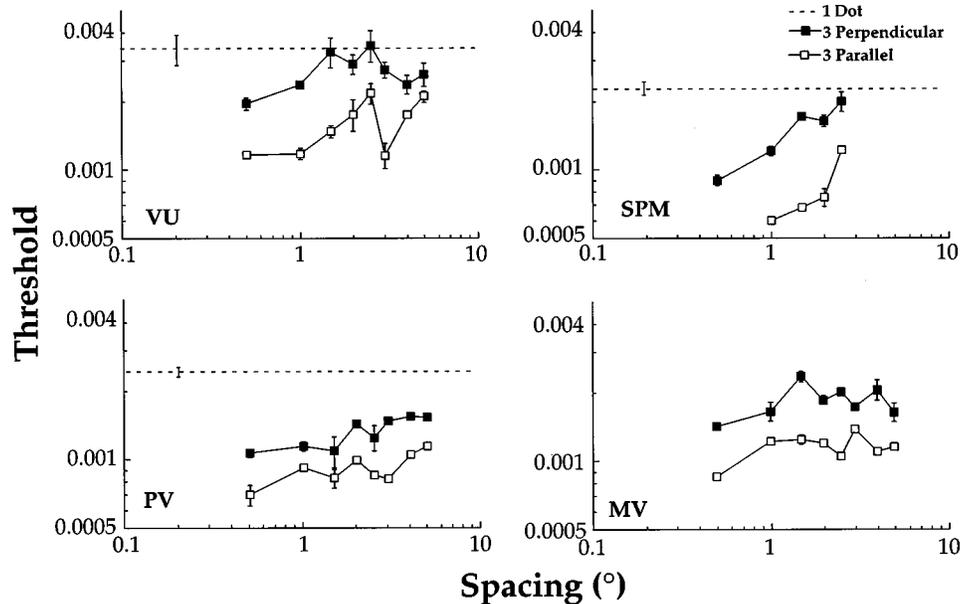

Fig. 3. Thresholds for the parallel and perpendicular configurations in Brownian noise. Open and solid squares plot the thresholds for the parallel configuration and the perpendicular configuration, respectively, as a function of dot spacing. Horizontal dashed line plots threshold for a single dot. The parallel configuration has much lower thresholds than the perpendicular configuration, over the entire range of dot spacings. Error bars represent ±1 standard deviation of the estimate of threshold.

parallel and perpendicular configurations in the main experiment cannot account for the higher detectability of the parallel triplet.

3. EXPERIMENT 2a: TEMPORAL SUMMATION

We are assuming that the subjects are detecting the parallel triplet on the basis of its effects in the motion system. However, the detection could be based on an entirely different cue, namely, the increased contrast or luminance produced by the superposition of dots at the same spatial position, i.e., temporal summation between consecutive dots. This possibility is illustrated in Fig. 4(a), which is a space–time plot. Each diagonal set of dots represents the different spatial positions of a single dot over time. The topmost horizontal row shows the parallel triplet at one instant of time. At a later instant in time, one dot of the parallel triplet can appear in the same location as a preceding dot and the responses to these dots could sum. For the 0.5° spacing illustrated in Fig. 4(a), it takes four frames for two dots to be in approximately the same location. (The dashed line shows that the dots are never quite in the same location.) To evaluate the contribution due to the spatial coincidence between two dots in the triplet, we measured temporal summation between two pulses that were presented at the same location, as a function of the onset asynchrony or delay between them. This configuration is illustrated in Fig. 4(b).

A. Methods

The experimental setup was the same as the one used in the trajectory experiment. The pair of dots were each flashed on for a single frame (14 ms), with a variable delay between their onsets. The dots had the same dimensions as those used in the trajectory experiment. Contrast thresholds for detection were measured in a yes–no paradigm. At each delay, performance was measured as a function of contrast. Performance at each delay and contrast value was measured over a minimum of two blocks (192) trials. The proportions of hits and false alarms were converted to detectability values (d') and plotted as a function of contrast. To estimate contrast threshold, we fit a power function of the form[27]

$$d' = \left(\frac{c}{c_{\text{thresh}}} \right)^b$$

where c is the contrast, c_{thresh} is the contrast for which $d' = 1$, and b is the log–log steepness.

We estimated the contrast threshold at each delay from a psychometric function of percent correct versus contrast. Contrast sensitivity was taken as the reciprocal of contrast threshold. We defined the summation index at a given delay as the ratio of sensitivities for a pulse pair to that for a single pulse.

B. Results

Figure 5 plots the temporal summation indices, for our four observers, as a function of the delay between the pulses. The error bars represent the standard error of
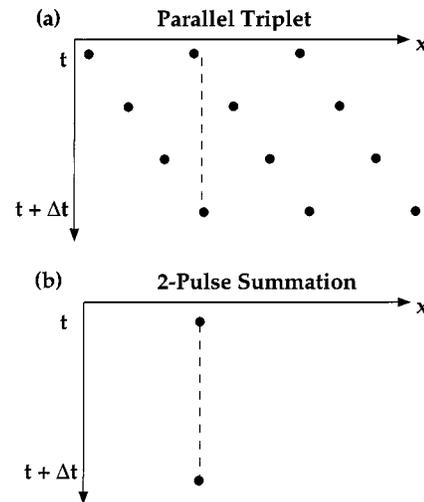

Fig. 4. (a) Space–time (x–t) plot of the parallel signal triplet. The top row of dots shows the triplet at one instant of time. At a time Δt later, one of the dots in the triplet could be in the same spatial location as a previous dot, and the responses to these two dots could sum. (b) A space–time plot of the configuration to measure temporal summation. Two dots are flashed in the same location, and contrast thresholds are measured as a function of the temporal delay between them.

the contrast threshold across blocks of trials. These temporal summation functions for dots resemble summation data found with sinusoidal gratings.[28] There is a facilitation between the two pulses at delays shorter than 50 ms. For delays between 50 and 100 ms this facilitation disappears; two observers even show inhibition at these delays. At longer delays the pulse pair is more detectable than a single pulse, which is consistent with probability summation. Also plotted is the ratio of sensitivities of the parallel and perpendicular configurations as a function of the temporal separation between consecutive dots in the triplet. The ratio is derived from the data in Fig. 3, which plots noise thresholds as a function of the spacing between dots. As the dots moved at a fixed speed, a given spacing corresponds to fixed temporal delay between consecutive dots in the parallel triplet. The two ratios—the temporal summation index and the ratio of sensitivity in the parallel configuration to sensitivity for the perpendicular configuration—are comparable because they are measures of the relative sensitivity to the spatial coincidence of two pulses with respect to that of a single pulse. For all four observers, the ratio of sensitivities of the parallel and perpendicular configurations lies above the temporal summation function, showing that the increased detectability of the parallel configuration cannot entirely be explained by temporal summation.

However, it is possible that the *three* dots in the parallel triplet could sum. One dot in the triplet could be in the same spatial location as the two preceding dots of the parallel triplet. To evaluate the contribution of the near-spatial coincidence of the three dots, we measured temporal summation between three pulses as a function of the delay between them. The stimulus consisted of three dots sequentially flashed in the same location, with the same temporal interval between the first two dots and the last two dots. Delay was once again defined as the temporal separation between consecutive dots. The experi-

mental paradigm and data analysis were similar to that for the two-pulse temporal summation experiment. Figure 6 plots temporal summation for three pulses as a function of delay. Superimposed on the same plot is the ratio of sensitivities of the parallel and perpendicular configurations. The ratio lies above the three-pulse summation data for both observers. Thus even three-pulse summation cannot account for the enhanced detectability of the parallel configuration. Note that the improvement in detectability shown by these threshold data represent an upper bound on temporal summation, since suprathreshold summation for contrast is modest or nonexistent.[29]

One might ask why we consider only temporal summation between the two or three dots that fall in roughly the same spatial location and not the other dot positions that lie in the vicinity of this location, since these neighboring dot positions could fall within the receptive field of the same detector. For instance, in Fig. 4(a) we consider only

summation between the two dots marked by the dashed line and not the dot positions that lie on either side of the dashed line. Instead, we should consider summation within a unit that responds to a particular region of space–time. In Fig. 7(a) we have superimposed a box, corresponding to a spatial area of 0.9° and a temporal period of 50 ms, on top of the moving parallel configuration with a spacing of 0.5° (shown by black dots in the diagram). The spatial–temporal window, represented by the box, contains approximately eight stimulus dots. Note that the four dots on the main diagonal of the box represent the motion of a single trajectory dot—a motion that is common to both the parallel and the perpendicular configurations. Here we are trying to determine what extra signal might be generated by the parallel configuration, when compared with the perpendicular configuration, to explain the difference in detectability. The four dots that land in the corners of the box could represent
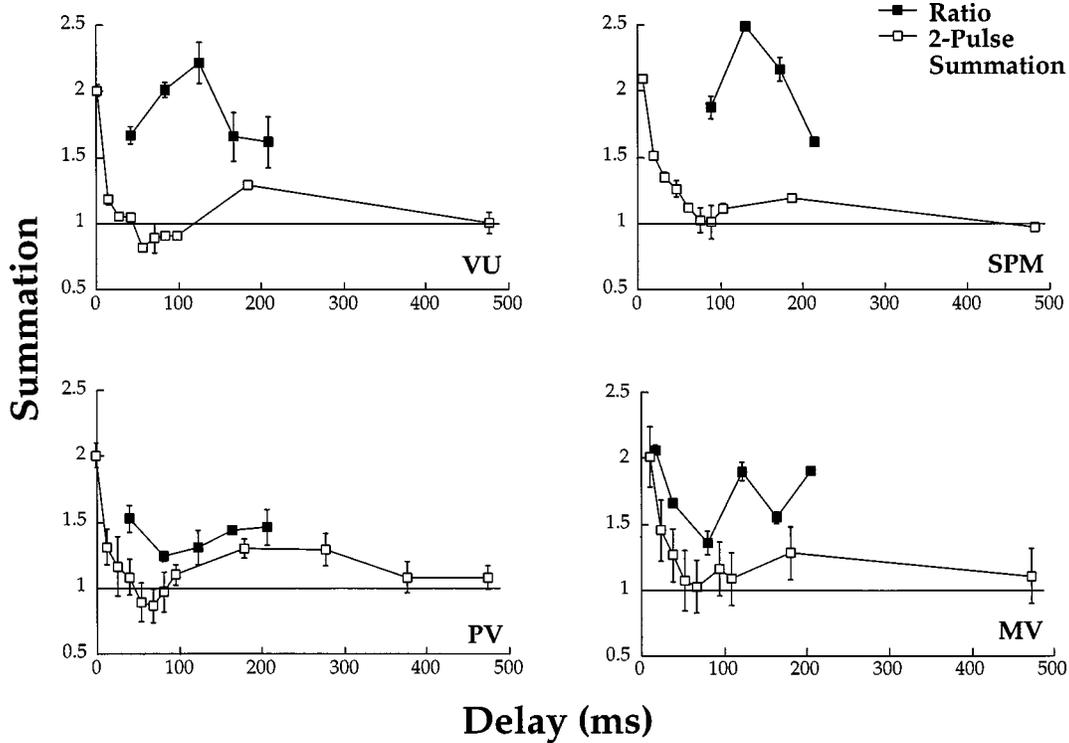

Fig. 5.   Temporal summation functions for our four observers.   Open squares plot summation (the ratio of sensitivity to a pulse pair at a given delay to a single pulse) as a function of the delay between the pulses.   Solid squares plot the ratio of sensitivities of the parallel and perpendicular configurations.
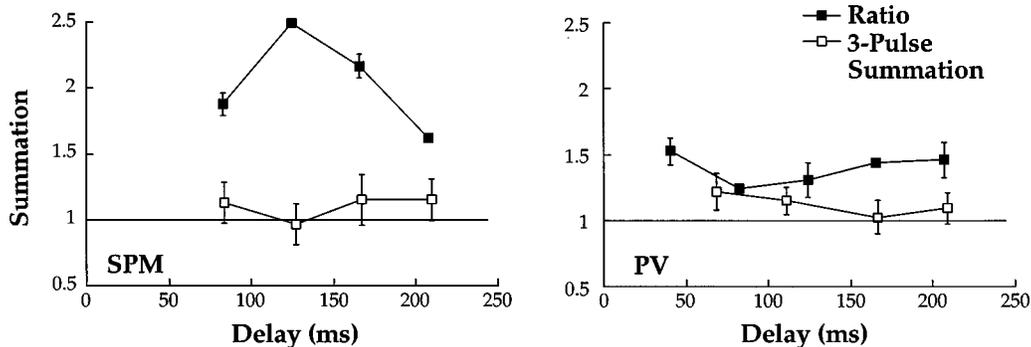

Fig. 6.   Open squares plot temporal summation between three pulses as a function of delay.   Solid squares plot the ratio of sensitivities of the parallel and perpendicular configurations.
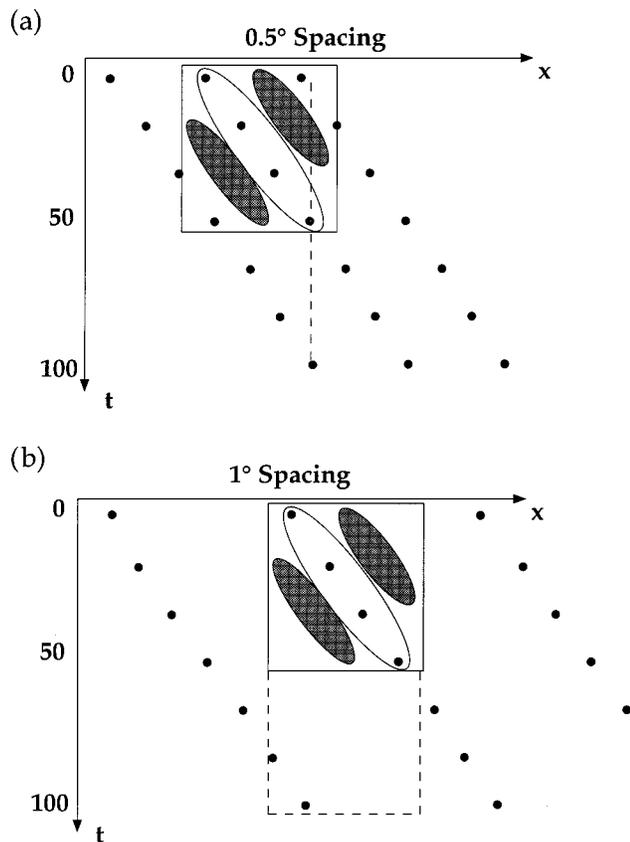
Fig. 7. Space–time $(x–t)$ plot of the parallel configuration at dot spacings of (a) 0.5° and (b) 1.0°, respectively, with a local motion unit superimposed. The size of the motion unit in the x dimension is 0.9°, which is the full width at half-height of the optimal motion unit (see text). The summation duration of 50 ms is based on the temporal summation function of Fig. 5. The dashed outline in (b) represents a summation duration of 100 ms. Each diagonal row of dots represents the displacement of a single dot over time.

this extra signal, if the unit passively summed any stimulus falling within its spatial–temporal window. If the detector is a motion unit (white and gray ellipses) with positive and negative lobes, then where the dots fall is bit more critical. Nevertheless, one could argue on the basis of this diagram that the parallel configuration should be slightly more detectable at this spacing than the perpendicular configuration. Once we include probability summation among several independent units responding at different times during the 300-ms stimulus duration, this small enhancement might be sufficient to explain the large difference in the detectability of the two triplet configurations, at least at this 0.5° spacing or at smaller spacings where even more stimulus dots will fall within the spatial–temporal window.

However, it is difficult to make this type of explanation work for a larger spacing. The lower half of Fig. 7 shows the same spatial window superimposed on the parallel triplet configuration with a 1° spacing; there are no additional stimulus dots falling within the box. Perhaps we have underestimated the temporal summation period (the vertical dimension of the box). The diagrammed summation is 50 ms, corresponding to the positive segment of the temporal summation functions we measured with dot tar-

gets (Fig. 7). Motion units are thought to have a temporal response of ~80–100 ms, the latter half of which is inhibitory. A bright dot falling within the negative lobes of the spatial receptive field, during the inhibitory portion of the temporal response function could lead to an increased response. Whether a bright dot arriving as late as 85–100 ms in this sequence would actually enhance a unit's response is hard to determine without actual calculations with appropriate spatial and temporal filters. Certainly, there is no plausible temporal summation period for local motion units that would explain the observed difference in the detectability of the parallel and perpendicular triplets at spacings greater than 1°.

What about the spatial summation region (the horizontal dimension of the box)? In previous studies we have calculated the optimum size for detecting a single trajectory dot in noise, according to two different criteria.[13,14] Both calculations produced the same result for the speed (or hop size) used in this study—the 0.9° size shown in the diagram. It is possible that the optimum size is different for a triplet of trajectories, but any increase in size of a conventional motion detector with a circular profile (and orthogonal preferred axes for orientation and motion direction) would favor the perpendicular trajectory much more than the parallel trajectory. This is because the dots in the perpendicular configuration are orthogonal to the direction of motion and thus stimulate a motion unit better than the dots in the parallel configuration, which, at any given time, fall in spatial regions of varying sensitivity and polarity. It might seem that the optimal unit for detecting the parallel triplet would be one elongated spatially only along the direction of motion (the x dimension in our diagram) without any increase in the y dimension. In the Introduction we explained why this type of unit is not flexible enough to handle all the trajectory results. Furthermore, our simulations with detectors that have elongation ratios as high as 10:1 showed that elongated units did not significantly increase the detectability of an extended trajectory over circular units. These elongated units had width-to-length ratios ranging from 2 to 10; i.e., they were a factor of 2 to 10 larger along the motion axis than along the orthogonal (preferred orientation) axis. The lack of improvement with elongated units is largely because the number of detectors required to tile the display area increased with elongation ratios. In summary, any type of motion unit that sums over a large spatial region is not optimal because it typically sees more noise than signal as size increases. (The noise dots that we used to obscure the signal trajectory are not shown in Fig. 7.) Instead, an ensemble of small motion units of roughly similar direction preference, which sum selectively along the direction of motion, is much better suited to detecting the parallel triplet.

4. EXPERIMENT 2b: MULTIPLE OBSERVATIONS

We have considered temporal summation between the dots in the triplet at a single location. We next consider the interaction of the triplet trajectories across space and compare the detectability of the parallel and perpendicular configurations to the predicted improvement in perfor-
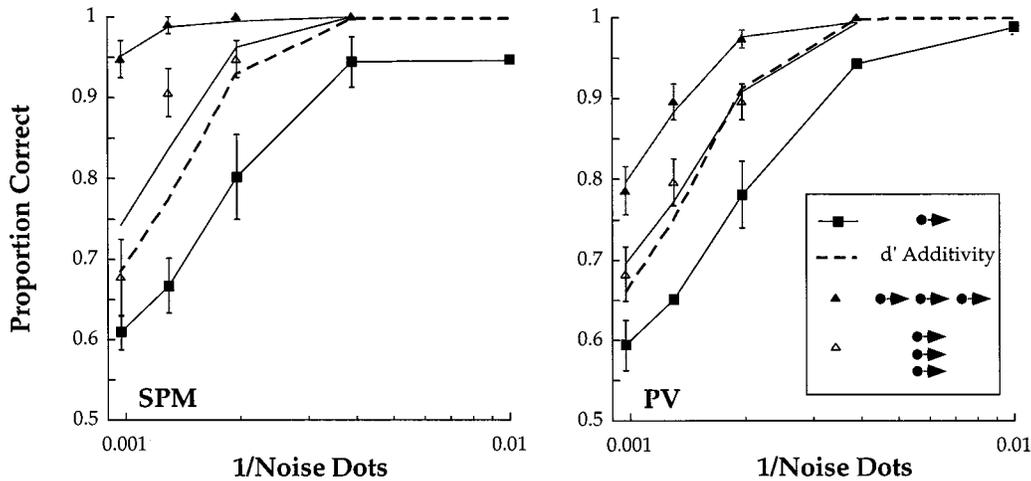
Fig. 8.   Psychometric functions for various configurations of the signal.   Solid squares plot the probability of detecting a single signal trajectory.   The dotted curve is the predicted improvement for the detection of three dots, assuming that the three dots are combined independently.   Solid and open triangles plot the probability of detecting the parallel and perpendicular configurations, respectively. Solid curves are Weibull fits to the data.   Each data point represents a minimum of 192 trials measured over two blocks.   Error bars represent ±1 standard error of the percent correct estimate across blocks of trials.
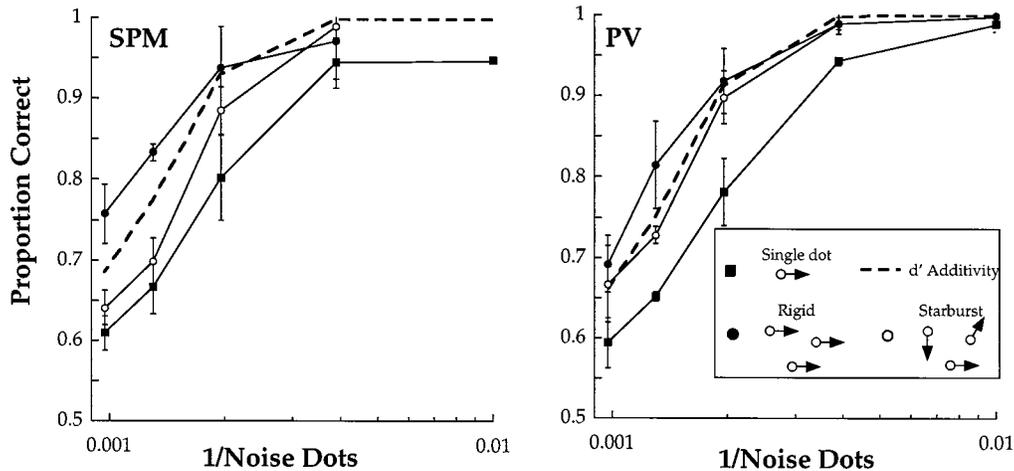

Fig. 9.   Psychometric functions for the rigid and starburst configurations of three signal trajectories.   Solid squares and the dashed curve are replotted from Fig. 8 and are the probabilities of detecting a single signal trajectory and the probability summation prediction for three independent signal trajectories, respectively.   Solid and open circles plot the probability of detecting the three signal trajectories in the rigid and starburst configurations, respectively.   The solid curves are Weibull fits to the data.   Each data point represents a minimum of 192 trials measured over two blocks.   Error bars represent ±1 standard error across blocks of trials.

mance for three independent trajectories.   To generate such a prediction we measured the probability of detecting a single dot moving in a consistent direction among noise dots.   The graphs in Fig. 8 are psychometric functions for two observers.   The solid squares plot the proportion correct for detecting a single signal dot.   The dashed curve is the predicted improvement for the detection of three dots based on the d' additivity equation for multiple signals,[30]

$$d_3' = d_1' \sqrt{3},$$

where d_3' and d_1' are the detectabilities of three dots and one dot, respectively.[31]   The solid triangles plot data for the detectability of the parallel configuration, which is significantly better than even the d' additivity prediction. The open triangles show data for the perpendicular con-

figuration, which seem to be slightly better than the d' additivity prediction for observer SPM and consistent with this prediction for observer PV.   In both the parallel and the perpendicular configurations, the center-to-center spacing of the dots was 1°.   To determine whether the near-agreement with d' additivity was fortuitous or due to the fact that the dots in the perpendicular configuration were treated independently, we did the following experiment.

We compared the detectability of three signal dots that moved either rigidly or in independent directions.   We called these two cases the rigid and the starburst configurations, respectively.   In the rigid configuration, the three signal dots were randomly placed with the constraint that the spacing between any dot and its nearest neighbor was 1°–1.25°.   This was achieved by placing the first dot such that at the midpoint of its trajectory it

was in a $2° \times 2°$ box centered on fixation. The second and third dots lay on the circumference of a circle $1°$–$1.25°$ in radius, such that their angular separation from the first dot was at least $60°$. All three dots moved in the same direction. In the starburst configuration, the three signal dots moved independently in one of eight directions. The only constraint on the placement of the three dots in this configuration was that at the midpoint of their trajectories, they had to be in the same spatial arrangement as the rigid configuration.

Data for these two conditions are plotted in Fig. 9. One would expect the data for the starburst condition to be consistent with d' additivity because the dots move in independent directions. As shown in Fig. 9, this is roughly true for the data of observer PV. However, the data for this condition for observer SPM fall short of d' additivity. The data for the rigid configuration seem to be slightly better than the d' additivity prediction for both observers. These results make several points. First, observers are better able to detect motion signals in a rigid configuration than one with independently moving dots. Second, observers do not always combine the independent motion signals in the starburst condition as efficiently as d' additivity. Finally, while the rigid configuration is almost as detectable as the perpendicular configuration, it is much less detectable than the parallel configuration. This is true despite the fact that both the perpendicular and the parallel configurations are special cases of the general rigid configuration. This result provides further support for the existence of interconnections between motion units along the direction of the trajectory.

5. GENERAL DISCUSSION

Our results show that a signal triplet aligned parallel to the direction of motion is much more detectable than a triplet arranged perpendicular to the direction of motion. The temporal summation experiment indicates that contrast summation within units responding to a single location is not adequate to explain the detectability of the parallel trajectory. Finally, a comparison with the d' additivity prediction indicates that the parallel triplet is more detectable than even the predicted improvement from the summation of three independent signals across space. Other studies on motion flow suggest that there is physiological integration of motion signals over very large areas[32] and for long durations.[33] Our results show preferential combination along the direction of motion, rather than areal summation over extended regions of visual space.

As we noted in the Introduction, numerous psychophysical studies have determined the spatial dimensions of the primary human motion detectors.[7,15,16,23] There is some evidence that the aspect ratio of these detectors is not symmetric, being elongated parallel to the motion direction that produces an optimal response from the detectors.[15] However, no one claims that a single primary motion unit, responsive to 12 deg/sec, is summing signals over the distances ($5°$) and times (>200 ms) associated with the spacing of our parallel triplet. Nor are

we. Rather, our results support the hypothesis that a network enhances motion signals that lie along the same motion path.

Geisler[34] has noted that the motion streaks that follow in the wake of any moving target could be used by the static orientation system to detect motion. Watamaniuk *et al.*[12] explicitly tested whether the signal trajectory was detected on the basis of orientation cues alone. They showed that when a dot hops randomly among the positions that define a motion trajectory, it is poorly detected in noise. In this case, the dot positions create a robust orientation signal, but, because they are not presented in sequential order, they produce a poor motion signal. Watamaniuk *et al.*[12] also showed that the moving signal dot was easily detected if it moved opposite to the direction of a noise flow field but that it was almost undetectable if it moved in the same direction as the noise. An oriented static detector would not distinguish motions in opposite directions. Thus the orientation signal created by the moving dot is not sufficient to explain the trajectory detection.

Geisler's model,[34] however, proposes that the output of a static orientation detector is combined with a perpendicularly oriented direction-selective motion detector, so that the combined detector codes both the orientation and the direction of motion of a motion streak. This model cannot explain why the parallel trajectory with three collinear motion streaks is more detectable than the perpendicular trajectory with three streaks marching abreast. One might suggest that the three parallel streaks define a contour that is detected by contour integrating mechanisms. While that is plausible, we suggest rather that trajectory is the motion-equivalent of the static contour system and that it is likely coded by a combination of signals from the primary motion units stimulated along the direction of motion.

At every level of motion processing, there appear to be mechanisms that enhance the predicted direction of motion. For example, the effect of contrast normalization on the primary motion units biases the response so that it tends to lead the actual position of the signal[35]—an effect that may account for the flash-lag effect.[36] The elongated shape of motion units also enhances motion along the trajectory rather than perpendicular to it.[15] Yet another specialization is the aforementioned coupling between motion and static orientation signals. Why this preference for motion parallel to the trajectory?

Under natural circumstances, the observer's self-motion can create a flow field of textures that stimulates primary motion detectors tuned to all directions and orientations. We speculate that by identifying the signals that are moving in consistent directions, the visual system can more easily bind together the motion signals associated with a given point on a surface or contour. Our results comparing the parallel triplet to a rigid configuration of three dots, suggest that signals along a trajectory are enhanced relative to signals generated by a translating rigid body. We conclude that the visual system has strong expectations about the probable ways in which motion signals are arranged, and these "priors" enhance the chances of finding the parallel triplet in our experimental paradigm. Our trajectory network is yet another ex-

ample of how the visual system combines local signals to predict future motion paths.

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The corresponding author, P. Verghese, can be reached at the address on the title page or by e-mail at preeti @ski.org.

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26. Since the trajectory passes so close to the fixation point, it is detected almost perfectly if we set the number of possible directions to two, as in Fredericksen *et al.* (Ref. 15). This is true even at the highest noise density that we used. Setting the number of directions to eight considerably increases the uncertainty of the signal trajectory.
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31. The d' additivity equation assumes an underlying Gaussian probability distribution, which is not unreasonable. Alternatively, one could calculate probability summation using a high-threshold model, $P_3 = 1 - (1 - P_1)^3$, where P_3 and P_1 are the true probabilities of detecting three- and one-dot trajectories, respectively. The high-threshold model yields slightly higher predictions for probability summation, but the error bars on our data roughly span this difference, so it is hard to differentiate between the high-threshold and the d' additivity versions of probability summation.
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