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A Target in Real Motion Appears Blurred in the Absence of Other Proximal Moving Targets*

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For exposure durations longer than about 40 msec, a field of dots in sampled motion has been reported to appear less smeared than predicted from the visual persistence of static displays. This reduction of perceived smear has been attributed to a motion "deblurring" mechanism. However, it has been long recognized that an isolated target moving continuously in a dark field appears to be extensively smeared. To reconcile these apparently contradictory observations, we investigated the effect of dot density on the extent of perceived smear for a single moving dot and for fields of dots with densities ranging from 0.75 to 7.5 dots/deg^2. Bright targets were presented in continuous motion against a photopically illuminated background field. The results reconcile previous conflicting observations by showing that the length of perceived smear decreases systematically with dot density for exposure durations longer than about 50 msec. In three additional experiments, we arranged the spatial configuration of the targets to evaluate whether motion deblurring results primarily from a motion compensation mechanism (such as integration within the spatiotemporally oriented receptive fields of putative motion mechanisms) or from inhibition exerted by spatiotemporally adjacent targets. The results show that the activation of motion mechanisms is not a sufficient condition for motion deblurring and that the reduction of perceived smear requires the presence of spatiotemporally adjacent targets. Taken together, these findings suggest that motion deblurring results primarily from masking exerted by spatiotemporally proximal targets.

Visual persistence Motion blur Deblurring Masking

INTRODUCTION

Several studies have shown that the visual persistence of stationary targets is approx. 120 msec under daylight viewing conditions (e.g. Haber & Standing, 1970; see also Coltheart, 1980). Based on this duration of visual persistence, we would expect that objects should appear smeared when moving, even at a moderate speed. However under normal viewing conditions, objects in motion usually look sharp and clear, even if the moving object is physically blurred to some degree (Ramachandran, Rao, & Vidyasagar, 1974; Bex, Edgar, & Smith, 1994). To quantify the perception of smear for moving targets, Burr (1980) and Hogben and Di Lollo (1985) had observers match the apparent extent of smear produced by a field of moving dots with a stationary line of variable length. The maximum extent of perceived smear occurred when the moving targets were exposed for a duration of only about 40 msec; for longer durations (but still too brief for pursuit eye movements to reduce the retinal image motion), the length of perceived smear was much less than predicted from the persistence of static displays. This reduction of perceived smear when the targets are exposed in motion for longer than about 40 msec has been called motion "deblurring".

Contrary to the reports of motion deblurring, it has been long known that isolated targets in real motion exhibit extensive smear, within which lighter and darker regions ("Charpentier's bands") can often be identified (Bidwell, 1899; McDougall, 1904). The phenomenon was described by McDougall (1904) as follows (text in brackets added):

> "A radial slit 2° in width and 7 cm. in length, its mid point 15 cm. from the centre of the disc, rotating at the rate of 1 rev. per 3″ before the glass lit by four burners, appears as a fanlike bundle of narrow bright rays of diminishing brightness from before backwards. Four such rays can usually be distinguished with certainty at this speed [ca. 9 deg/sec]. They are not separated by distinct dark intervals but appear to overlap one another, and together they fill a sector about 12° in width [equivalent to a duration of 100 msec]."

These early observations of extensive smear were made for high contrast stimuli that moved against a dark field. However, in pilot experiments we failed to find deblurring for a single bright or dark spot that moved against

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a photopically illuminated background (see also Lubimov & Logvinenko, 1993). Isolated targets in sampled motion also exhibit prolonged persistence, particularly when the spatial separation between successively presented targets is greater than about 10 min arc (Dixon & Hammond, 1972; Farrell, 1984; Di Lollo & Hogben, 1985; Farrell, Pavel, & Sperling, 1990; Castet, 1994).

One aim of our experiments was to reconcile the apparent contradiction between evidence for motion deblurring and the extensive smear observed for isolated moving targets. Previous studies assessed perceived smear either for a single moving dot or line (e.g. McDougall, 1904), or for a field of dots of only a single density (e.g. Burr, 1980; Hogben & Di Lollo, 1985). In addition, the studies of motion deblurring employed stimuli in sampled motion rather than real continuous motion (Burr, 1980; Hogben & Di Lollo, 1985; Watamaniuk, 1992). Whether these results apply to the perception of targets in real motion depends on the extent to which real and sampled motion share the same underlying mechanisms (Frisby, 1972; Kolers, 1972; Morgan, 1980; Burr, Ross, & Morrone, 1986b; Watson, Ahumada, & Farrell, 1986). The chief purpose of Expt 1 was to systematically investigate the effect of dot density on the perception of smear for moving targets. A second purpose of Expt 1 was to determine whether the outcome of previous motion deblurring studies can be generalized to stimuli in continuous, real motion. The results of Expt 1 offer a reconciliation of the apparent contradiction by showing that perceived smear decreases dramatically (i.e. motion deblurring increases) as the density of dots in a moving stimulus is increased and confirm the validity of motion deblurring for real motion.

Another aim of our study, addressed by Expts 2, 3, and 4 was to investigate the mechanisms that underlie the motion deblurring phenomenon. Although several models have been suggested to account for motion deblurring (e.g. Burr, 1980; Di Lollo & Hogben, 1985; Anderson & van Essen, 1987; Martin & Marshall, 1993; Öğmen, 1993; Francis, Grossberg, & Mingolla, 1994; Pääkkönen & Morgan, 1994) most of them can be categorized according to two fundamental hypotheses. One hypothesis is that motion deblurring results from stimulation of motion detectors, which have receptive fields that are oriented in the space–time domain and therefore summate signals effectively along the path of motion (Burr, 1980; Burr, Ross, & Morone, 1986a). An implicit assumption of this hypothesis is that the smear produced in visual channels sensitive to stationary form is suppressed or, equivalently, that motion channels are responsible not only for the perception of motion but also for the perception of the form of moving objects. An alternative hypothesis is that motion deblurring results from the active inhibition or suppression of a target's visible persistence when the same target or a different target is presented soon afterward in close spatial proximity (McDougall, 1904; Dixon & Hammond, 1972; Di Lollo & Hogben, 1985, 1987; Castet, 1994). Hogben and Di Lollo (1985) found that the perceived extent of smear increases with target velocity and decreases with background luminance, and concluded that these findings support the hypothesis that motion deblurring results from inhibition rather than from the summation of motion signals. Results of Expt 1 do not allow us to distinguish between these two hypotheses. In Expts 2 and 3, the spatial configuration of targets was arranged to generate distinct predictions from these hypotheses. The results favor spatio-temporal inhibition over motion summation as the primary mechanism for the deblurring phenomenon.

GENERAL METHODS

Visual display

The stimuli consisted of single or multiple dots, each with a diameter of 1 min arc, produced on 2 × 2 in. slides and displayed through a Maxwellian view optical system (Fig. 1). Homogeneous background illumination was provided by a backlighted diffusing plate viewed from a 30% reflection, 70% transmission plate beam splitter. The background field subtended an area of 8.25 deg horizontally × 12.1 deg vertically and, after reflection, had a luminance of 200 cd/m^2 as measured with a

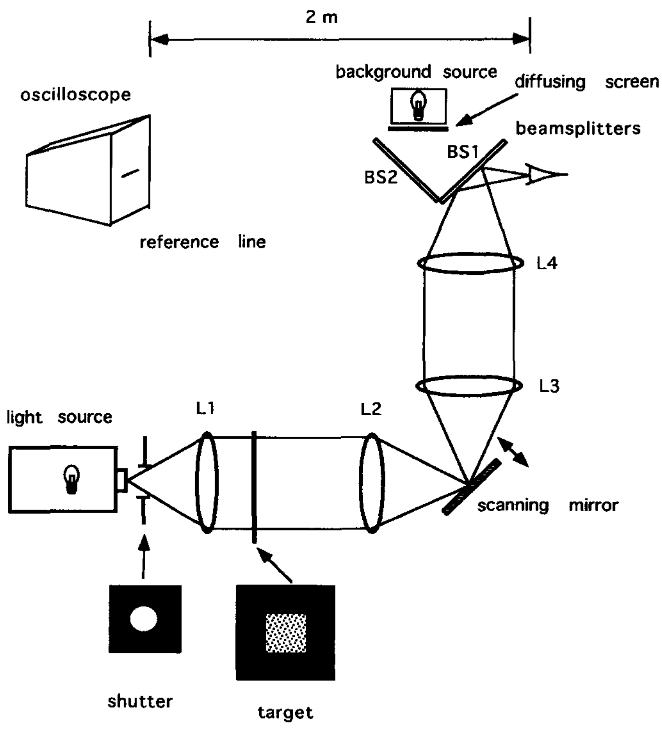

FIGURE 1. Diagram of the experimental setup (not to scale). A two-part Maxwellian view system was used. The first part (lenses L1 and L2) focused a point source (a light source and a pinhole) at the rotation axis of a galvanometer-mounted mirror. An electronic shutter controlled the exposure duration. Lenses L3 and L4, and the beam splitter BS1 formed the second part of the system, the exit pupil of which was aligned with the pupil of the subject's eye. The stimuli were printed on slides and placed between lenses L1 and L2 to produce a virtual image at 2 m from the subject. Rotating the galvanometer-mounted mirror about its vertical axis produced horizontal motion of the stimuli without shifting the exit pupil of the Maxwellian view system. A backlighted diffusing plate provided background illumination through beam splitters BS2 and BS1. An oscilloscope at 2 m from the eye displayed the horizontal comparison line.

Minolta model LS-100 photometer. In all experiments, the luminance of the dot stimuli was adjusted to 2 log units above the detection threshold against the homogeneous background. Horizontal motion of the dots was produced by rotating a galvanometer-mounted mirror (General Scanning model G330) in the Maxwellian view optical system about a vertical axis. Output to the mirror was a voltage ramp generated from a PC 386 computer using a 12-bit Scientific Solutions DADIO board; each voltage increment corresponded to a nominal rotation of the mirror of 7.1 sec arc. Velocity was calibrated by measuring the amplitude and duration of mirror movement separately. The exposure duration of the moving targets was controlled by a Uniblitz model VS14 electronic shutter, with a response time of 4 msec. To ensure that the dot motion produced by mirror rotation was smooth, the mirror began moving 20 msec before the shutter opened and continued to move for another 20 msec after the shutter closed. The perceived length of the smear produced by the moving dots was estimated by comparison to a stationary horizontal line, presented at the center of a HP 1311B oscilloscope after each trial. Pixel to pixel separation on the oscilloscope screen was nominally 4 sec arc both horizontally and vertically, at the viewing distance of 2 m. To ensure that the detectability of the stationary line was comparable to that of the moving dots, the luminance of the line was also adjusted to 2 log units above its detection threshold. A gelatin filter approximating the green color of the oscilloscope's P31 phosphor was placed in the path of the optical system so that the moving dots and the stationary line were similar in color. All experiments were conducted in a dimly lit room.

Observers

The three authors served as observers. All had normal or corrected-to-normal vision. Observers SC and HB used the left eye and HO used the right eye.

Procedure

The observer viewed the display monocularly, while the non-viewing eye was occluded with a black patch. Head position was restrained using chin- and head-rests. During experiments, each observer repeatedly checked that his pupil remained in correct alignment with the exit pupil of the Maxwellian view system by opening the electronic shutter between trials. Trials were initiated by pressing the button of a joystick. After a sound signal alerted the observer, the moving dots were presented, followed by the stationary line after a delay of 775 msec. There was no fixation target or stationary presentation of the dots between trials. The observer's task was to indicate, using a joystick, whether the length of the stationary line was shorter or longer than the perceived smear produced by the moving dots. The observer had the option of initiating a new trial without making a judgment if he did not properly attend to the stimulus or made an eye movement. In fact, the observers were encouraged to establish their criterion by viewing several trials at the start of a run before making judgments of smear length.

When the observer responded with judgments about smear length, the length of the stationary line varied from trial to trial according to a staircase procedure. Initially, line length was incremented or decremented by 24% if the observer judged the line to be shorter or longer, respectively, than the smear. After each staircase reversal, the step size was halved until a minimum step size of 6% was reached. Six reversals at the minimum step size ended the staircase; the average of these six reversals provided an estimate of smear length. Observers were instructed to report the *entire* length of any detectable smear, even if the smear appeared to be spatially discontinuous. This instruction was adopted because all subjects reported that a single moving dot was followed directly by a bright trail and, after an intercalated darker region containing little or no visible smear, an additional dimmer trail (Bidwell, 1899; McDougall, 1904). Criterion was stabilized during several practice sessions, the results of which were discarded.

Two velocities (5 and 10 deg/sec) and eight durations of motion (20, 30, 40, 50, 70, 100, 120, 150 msec) were tested in all experiments. To minimize anticipatory eye-movements, the direction of motion (left or right) was chosen randomly on each trial, with the initial position of the target offset so that the target's excursion was symmetrical about the center of the background field. Each set of trials tested a single velocity and duration of motion. Sixteen sets of trials, comprising one session, were required to estimate the perceived smear for the two velocities and eight durations of motion. Testing order was randomized within each session. The plotted data represent the mean of either two or three estimates of perceived smear length, collected on different days.

EXPERIMENT 1: DOT DENSITY

Methods

The length of perceived smear was determined for the motion of a single bright dot and for fields of random dots of four different densities. The densities used were 0.75, 1.5, 5, and 7.5 dots/deg^2, which include close approximations to the dot densities used in both Burr's (1980) and Hogben's and Di Lollo's (1985) experiments (5.1 and 1.56 dots/deg^2 respectively). The single dot was presented at the center of the field; random-dot stimuli covered an area of 7.27×7.27 deg^2. Hogben and Di Lollo (1985) reported that the length of perceived smear decreased as the luminance of the background field increased. Therefore, to provide an optimal situation for motion deblurring, we used a background luminance of 200 cd/m^2, which is substantially brighter than the background used in either Burr's (30 cd/m^2) or Hogben's and Di Lollo's experiments (0.3–30 cd/m^2).

Results

Following the convention of Hogben and Di Lollo (1985), the perceived length of smear was converted to an equivalent duration of perceived smear (duration of perceived smear = perceived length/speed of the target). The conversion of smear length to an equivalent duration allows perceived smear to be expressed in terms of visual persistence and permits the results for different velocities to be readily compared. Figures 2 and 3 show, separately for each of the three subjects, the duration (left ordinate) and the length (right ordinate) of perceived smear as a function of exposure duration, for target velocities of 5 and 10 deg/sec. Dot density is the parameter in each plot. For comparison, each panel contains a dashed line with a slope of 1, indicating where the duration of perceived smear is equal to the exposure duration (i.e. the duration of visual persistence is equal to or longer than the exposure duration). For exposure durations up to approx. 50 msec, the duration of perceived smear closely follows the dashed line for all dot densities. However, a pronounced effect of dot density is observed for exposure durations longer than 50 msec. In the case of a single dot, the duration of perceived smear increases up to a value around 100 msec, comparable to the duration of persistence reported for static targets. For the highest dot density, the duration of perceived

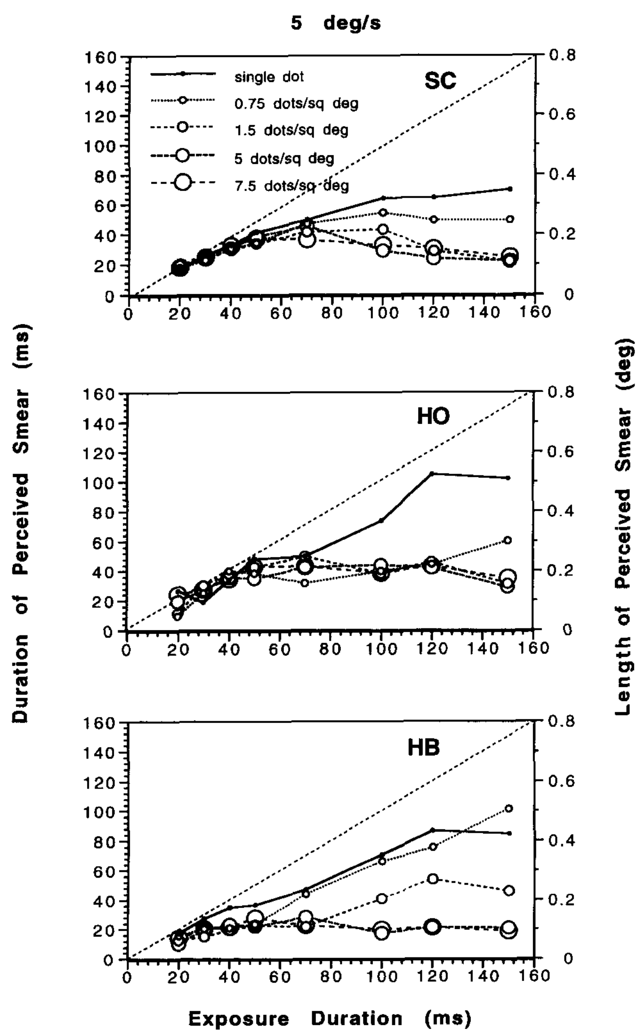

FIGURE 2. The duration (left ordinate) and length (right ordinate) of perceived smear as a function of motion exposure duration for a single dot and a field random dots with four different densities. Target velocity was 5 deg/sec. The diagonal dashed line indicates where the duration of perceived smear equals the exposure duration. Across subjects, standard deviations (not shown to prevent clutter) average 19% of the perceived length of smear.

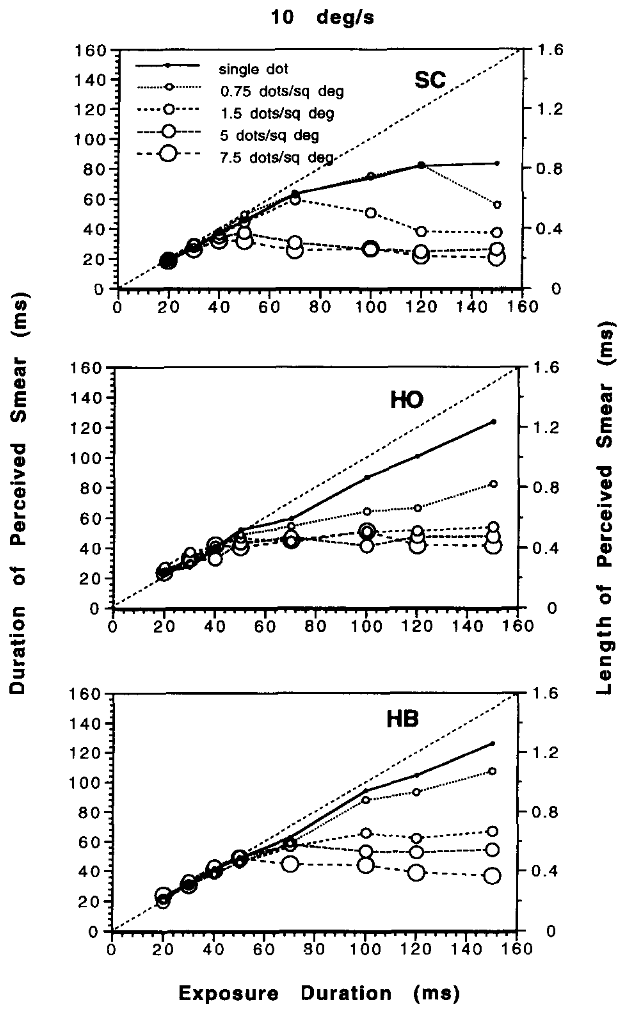

FIGURE 3. Same as Fig. 2 for a target velocity of 10 deg/sec. Standard deviations average 13% of the perceived length of smear.

smear either reaches an asymptote or decreases at exposure durations longer than 50 msec.

Comparison of the results in Figs 2 and 3 shows that the data depart from the dashed line at approximately the same exposure duration, indicating that the duration of perceived smear changes in a qualitatively similar way for velocities of 5 and 10 deg/sec. The main difference is quantitative: for exposure durations greater than approx. 50 msec, the duration of perceived smear is, in general, longer for targets moving at a speed of 10 than at 5 deg/sec.

Comparison with other studies

Our results show that the extensive smear observed by McDougall (1904) and Bidwell (1899) for a bright moving slit in a dark field occurs also for a single dot moving against a background of 200 cd/m^2. Qualitatively similar results were reported recently by Lubimov and Logvinenko (1993), who measured motion smear for a bright spot that moved in a circular trajectory on an oscilloscope screen with a background luminance of 30 cd/m^2. Lubimov and Logvinenko reported that the moving spot had a blurred tail, the length of which increased up to an exposure duration of 50–60 msec, and then remained constant. The quantitative discrepancies between our results and theirs may be attributed to differences in either (i) characteristics of the experimental stimuli; and/or (ii) the subjects' criteria for estimating the extent of motion smear (see below).

For high-density displays, our findings agree qualitatively with those of Burr (1980) and Hogben and Di Lollo (1985). Quantitatively, our results indicate that maximum smear of the moving dots occurs at an exposure duration around 50 msec, which is longer than the value of 30 msec reported by Burr, but close to the duration of 40 msec obtained by Hogben and Di Lollo. For longer exposure durations, we found a slightly greater duration of perceived smear than either Burr (1980) or Hogben and Di Lollo (1985), despite the higher background luminance in our study. In particular, an inverse relationship is known to exist between background luminance and the duration of perceived persistence (review Breitmeyer, 1984), which has also been shown to be valid for stimuli in sampled motion (Hogben & Di Lollo, 1985; Castet, Lorenceau, & Bonnet, 1993). However, our observers were instructed explicitly to judge the full extent of perceived smear, and to disregard any inhomogeneity or nonmonotonicity of the perceived brightness profile. We believe that these instructions account for the relatively greater extent of perceived smear in our study.

Previous studies of motion deblurring presented stimuli in sampled motion. The results of our study demonstrate that motion deblurring occurs also for stimuli that move continuously. Our results also validate the conclusion of Hogben and Di Lollo (1985) that the duration of perceived smear increases with target velocity (however, see also Bex *et al.*, 1994). In the study by Hogben and Di Lollo, stimuli were presented in sampled motion with a fixed interstimulus interval, so that the spatial separation between successively presented dots was confounded with the target velocity. This confound does not exist for our stimuli.

Relation to hypotheses for motion deblurring mechanisms

An important result of Expt 1 is that the extent of perceived smear for a continuously moving stimulus (exposed for longer than about 50 msec) depends critically on the density of the stimulus elements. This finding provides a means to reconcile previous observations that an isolated moving target appears to be followed by extensive smear (e.g. Bidwell, 1899; McDougall, 1904) with findings of very little smear in an array of moving random dots (e.g. Burr, 1980; Hogben & Di Lollo, 1985). However, the inverse relation between dot density and the perceived extent of smear found in Expt 1 does not distinguish between the spatio-temporal inhibition and the motion-summation hypotheses for motion deblurring.

Higher dot densities correspond to smaller spatial separations between the moving targets. Because the duration of visual persistence is related inversely to spatial proximity for static targets (Di Lollo & Hogben, 1987), as well as for targets in sampled motion (Farrell, 1984; Di Lollo & Hogben, 1985; Farrell *et al.*, 1990; Castet *et al.*, 1993; Castet, 1994), the spatio-temporal inhibition hypothesis predicts more deblurring for higher density displays. On the other hand, motion mechanisms are known to summate across space (Richards, 1971; Nakayama & Tyler, 1981; van Doorn & Koenderink, 1984; van de Grind, Koenderink, & van Doorn, 1986; Anderson & Blurr, 1991). Higher dot densities should cause stronger stimulation of the motion mechanisms and, according to the motion-summation hypothesis, greater deblurring. Although recent psychophysical estimates (van Doorn & Koenderink, 1984; van de Grind *et al.*, 1986; Anderson & Burr, 1991; Anderson, Burr, & Morrone, 1991) for the region of spatial summation in motion receptive fields are generally too small to generate a significant effect for the dot densities used in Expt 1, the inverse relationship we found between persistence and dot density may result from a more extensive summation at a neural site not revealed by these previous psychophysical paradigms (e.g. Felleman & Kaas, 1984; Tanaka, Hikosaka, Saito, Yukie, Fukada, & Iwai, 1986). In Expt 2, we arranged the spatial configuration of the stimuli so that these two hypotheses for motion deblurring generated different predictions.

EXPERIMENT 2: HORIZONTAL VS VERTICAL ARRAYS OF DOTS

Methods

The methods and procedure were the same as in Expt 1 except that the stimuli in this experiment were horizontally moving arrays of regularly spaced horizontal or vertical dots. Anderson and Burr (1991) compared the extent of spatial summation parallel and orthogonal to the direction of moving gratings and concluded that human motion detectors were equal in length and width (see also Anderson *et al.*, 1991). Motion mechanisms with this geometry should be stimulated equally by horizontal and vertical arrays of dots and, according to the motion-summation hypothesis for deblurring, both of these stimuli should be perceived as producing equivalent amounts of smear. However, as illustrated in Fig. 4, the distance between each moving dot and the smear resulting from other moving dots differs for horizontal and vertical dot arrays. In a vertical array, the dot-to-smear distance is never smaller than the dot-to-dot distance but, in a horizontal array, horizontal motion decreases the distance between moving dots and the smear from other, nearby dots. According to the spatio-temporal inhibition hypothesis, deblurring is more effective when the dot-to-smear distance is small, and less smear should be perceived for a horizontally oriented array of dots.

For both the vertical and horizontal arrays, the spacing between adjacent dots was 0.86, 1.22, 2.24, or 2.74 dots/deg corresponding, respectively, to the random dot densities of 0.75, 1.5, 5, and 7.5 dots/deg^2 examined in Expt 1. The overall height or width of the dot array corresponded to 7.27 deg when viewed through the Maxwellian view optical system and fixation was directed to the center of the display. Each observer noted

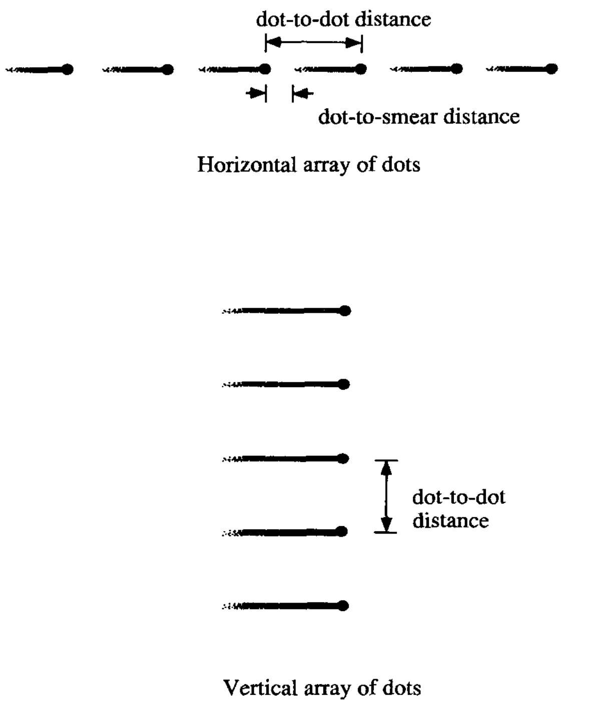

FIGURE 4. The spatial relationship between dots and the smear from adjacent dots for a horizontal and a vertical array of dots moving to the right. In both cases, the dot-to-dot distances are fixed by the density of the dots in the array. For the vertical array, the dot-to-smear distance is never less than the dot-to-dot distance. However, for the horizontal array, the minimum dot-to-smear distance is smaller than dot-to-dot distance.

that the length of perceived smear for the dots in the vertical array was clearly non-uniform with eccentricity. Specifically, dots located near the edges of the array (i.e. further peripherally) were perceived to be less smeared than dots located at the center of the array. Consequently, the observers were instructed to compare the length of the perceived smear for dots at the center of the array to the subsequently presented stationary line. In one session, a horizontal or vertical array of dots was tested for exposure durations ranging from 20 to 150 msec, and for velocities of 5 and 10 deg/sec. The different dot-to-dot spacings and array orientations (vertical vs horizontal) were randomized among sessions.

Results

The results for vertical and horizontal arrays of dots are presented, respectively, in the right and left columns of Figs 5, 6 and 7. To allow these results to be compared readily with those from Expt 1, perceived length of smear (right ordinate) is again converted to smear duration (left ordinate), and the spacing between dots in the vertical and horizontal arrays is expressed in units of dot density.

The main result of Expt 2 is the dissimilar effect of dot density for the vertical and horizontal dot arrays on the duration of perceived smear. The differences between the duration of perceived smear for vertical and horizontal arrays is clearest in the results of subject SC (Fig. 5), but the other two subjects show similar results. In particular, the duration of perceived smear is influenced very little by dot density for vertical arrays. Indeed, with the exception of the highest dot density at long exposure durations, the results for vertical arrays of all dot-to-dot spacings are comparable to those obtained in Expt 1 with a single moving dot. On the other hand, for horizontal arrays of dots, the duration of perceived smear decreases systematically with increasing dot density when the exposure duration is longer than about 50 msec. This result is qualitatively similar to that found for random-dot fields of increasing density in Expt 1.

Discussion

Di Lollo and Hogben (1985) assessed the persistence of targets presented with various spatial separations around the circumference of a circle, with eccentricities of 0.4–1.6 deg. Their results indicate that the suppression of persistence by spatially adjacent targets increases with retinal eccentricity. This result is consistent with our observation that the peripherally imaged dots in a horizontally moving vertical array have noticeably less perceived smear than the dots that move across the fovea. The implication of this observation is that motion deblurring is stronger in the periphery than in the fovea. This finding agrees with the spatio-temporal inhibition hypothesis, as metacontrast masking (a form of spatio-temporal inhibition) is known to be stronger in the periphery than the fovea (Bridgeman & Leff, 1979; Lyon, Matteson, & Maras, 1981).

An important assumption for interpreting the results of Expt 2 is that horizontal and vertical arrays of dots stimulate motion detectors equally. In part, this assumption is based on the results of a recent psychophysical summation experiment which indicated that the width and length of motion detectors are virtually identical (Anderson & Burr, 1991). Anderson *et al.* (1991) reached the same conclusion based on the calculation of two-dimensional receptive-field profiles of motion detectors from masking data. On the other hand, the minimum thresholds for detecting sampled motion in a dynamic random-dot display have been reported to occur when the coherently moving portion of the stimulus is several times longer than it is wide (van Doorn & Koenderink, 1984; van de Grind *et al.*, 1986).

Regardless of whether horizontal motion detectors summate equally across horizontal and vertical dot arrays, the assumption that the dot density effect observed in Expt 1 results from a more effective stimulation of motion mechanisms implies that these mechanisms should be stimulated more by a vertical array than by a single moving dot. Consequently, the motion-summation hypothesis for deblurring predicts that the extent of perceived smear should be greater for a single dot than for a vertical array of dots, especially when dot-to-dot separations are small. Comparison of the results of Expts 1 and 2 does not support this predictions as, with few exceptions, the duration of perceived smear changes similarly with exposure duration for a single dot (Fig. 2) and for vertical dot arrays (Figs 5, 6 and 7). Specifically, the duration of perceived smear for a single dot and for vertical arrays of dots show no significant difference when the velocity is 10 deg/sec; i.e. when the moving

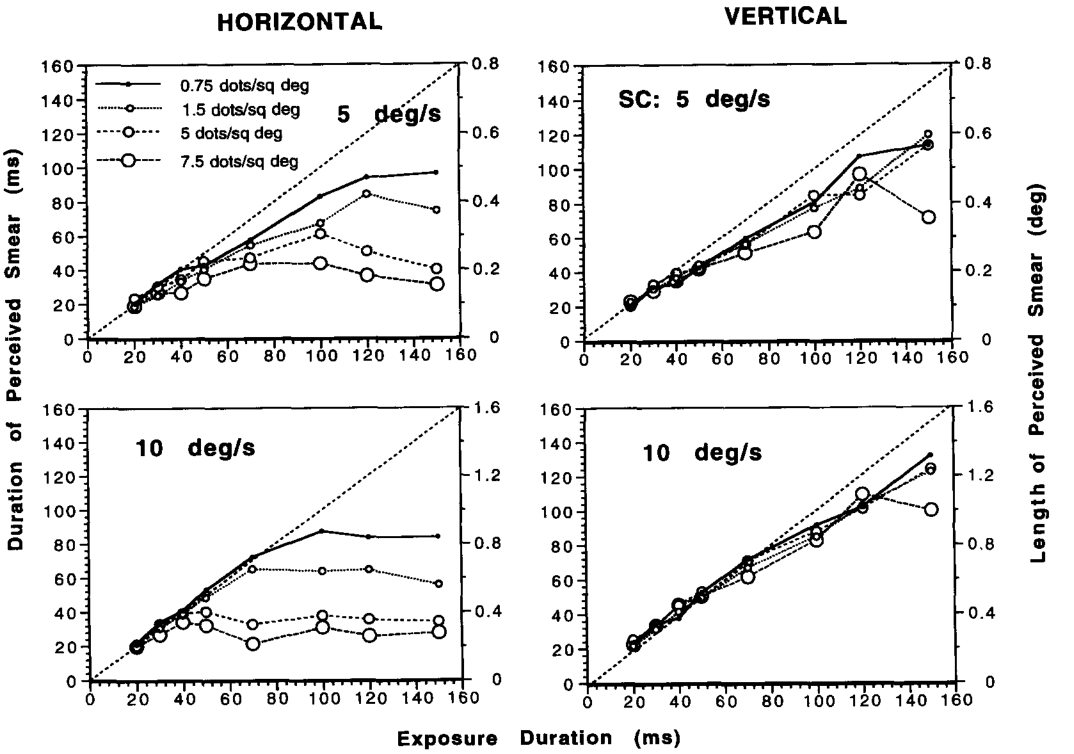

FIGURE 5. The duration (left ordinate) and length (right ordinate) of perceived smear as a function of motion exposure duration for subject SC at four dot-to-dot separations. For comparison with Expt 1, dot-to-dot separations are expressed in units of equivalent densities. The upper panels show the results for a velocity of 5 deg/sec, and the lower panels for 10 deg/sec. The left side shows results for the horizontal array of dots, and the right side for the vertical array.

stimuli would be expected to activate larger receptive fields (Burr *et al.*, 1986a; Anderson *et al.*, 1991).

Taken together, the results of Expts 1 and 2 suggest that the effect of dot density on the extent of perceived smear is not attributable to spatial summation, but rather to a decrease in the dot-to-dot separation as suggested by the spatio-temporal inhibition hypothesis. In Expt 3, we simplified the stimulus

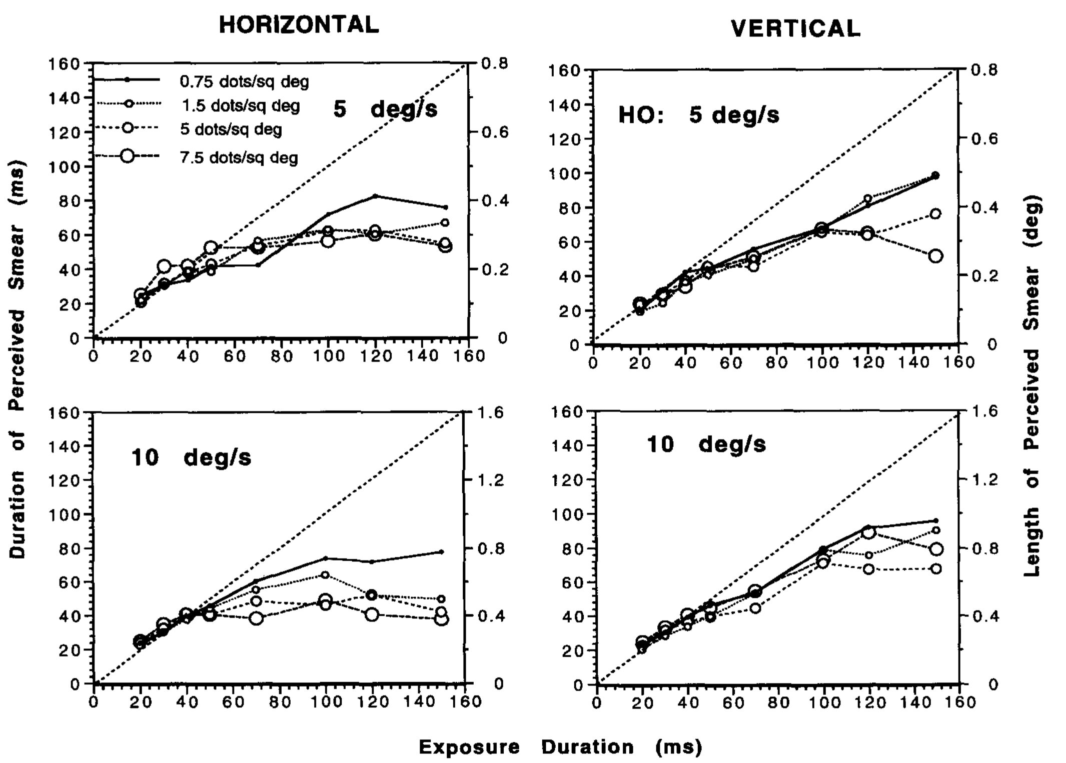

FIGURE 6. Same as Fig. 5 for subject HO.

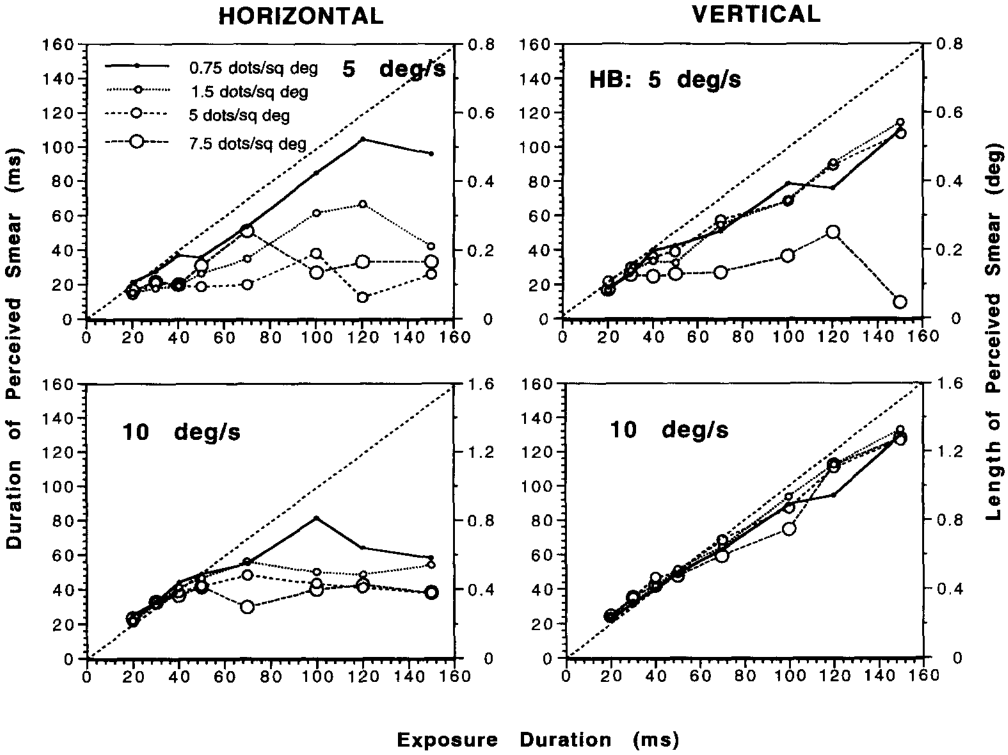

FIGURE 7. Same as Fig. 5 for subject HB.

to test the spatio-temporal inhibition hypothesis more directly.

EXPERIMENT 3: TWO DOTS

Methods

The methods and procedures were identical to Expt 2 except that the stimulus consisted of two horizontally separated dots. Because each dot should stimulate motion detectors approximately equally, the motion-summation hypothesis predicts equivalent deblurring; therefore, both dots should appear to be equally smeared. In contrast, the spatio-temporal inhibition hypothesis predicts greater deblurring (less perceived smear) for the first dot of the pair, provided that the second dot is close enough to the motion-produced smear left by the leading dot to engender inhibition. As there is no spatially proximal dot to inhibit the smear of the trailing dot, the extent of its perceived smear should be comparable to that of a single moving dot.

The four dot-to-dot separations tested were 0.86, 1.22, 2.24, and 2.74 dots/deg which correspond, respectively, to the random dot densities of 0.75, 1.5, 5, and 7.5 dots/deg^2 in Expt 1. The dot pair always moved in tandem, randomly to the right or left from trial to trial. Observers were required to match the perceived length of smear of the leading dot in one session, and to match the perceived length of smear of the trailing dot in another. The order of responding to the leading or the trailing dot was randomized among sessions.

Results and discussion

In Figs 8, 9 and 10, the length (right ordinate) and the duration (left ordinate) of perceived smear are shown for the leading dot in the left column and for the trailing dot in the right column. Dot-to-dot distances are expressed in units of dot density, for comparison with the results of the previous experiments. A clear difference exists between the duration of perceived smear for the leading and the trailing dots. Specifically, the perceived smear of the leading dot decreases systematically as the dot-to-dot separation ("density") is reduced, whereas perceived smear is essentially independent of density for the trailing dot. Each subject's pattern of results for the leading dot is very similar to that exhibited in Expt 1 for two-dimensional dot displays of comparable density. For the trailing dot, the pattern of results is comparable to that obtained in Expt 1 for a single moving dot.

The dramatic differences found between the perceived smear for the leading and trailing dots in a moving pair augment the evidence accumulated in Expt 2 against the motion-summation hypothesis. In particular, in interpreting the results of Expt 3, no assumptions are required concerning the shape or size of the receptive field of motion-detecting mechanisms.

It could be argued that the duration of perceived smear of the leading dot is short simply because the trailing dot traverses the same path and limits the maximum smear to the dot-to-dot separation. This possibility is not supported by the data for 5 deg/sec because perceived smear for the leading dot deviates from the dashed line at the same exposure duration for all dot-to-dot separations. Furthermore, these data also show that the asymptotic values for the duration of perceived smear are smaller than expected from various dot-to-dot separations. However, because these generalizations are not as clearly supported by the data for 10 deg/sec, we conducted a control experiment to

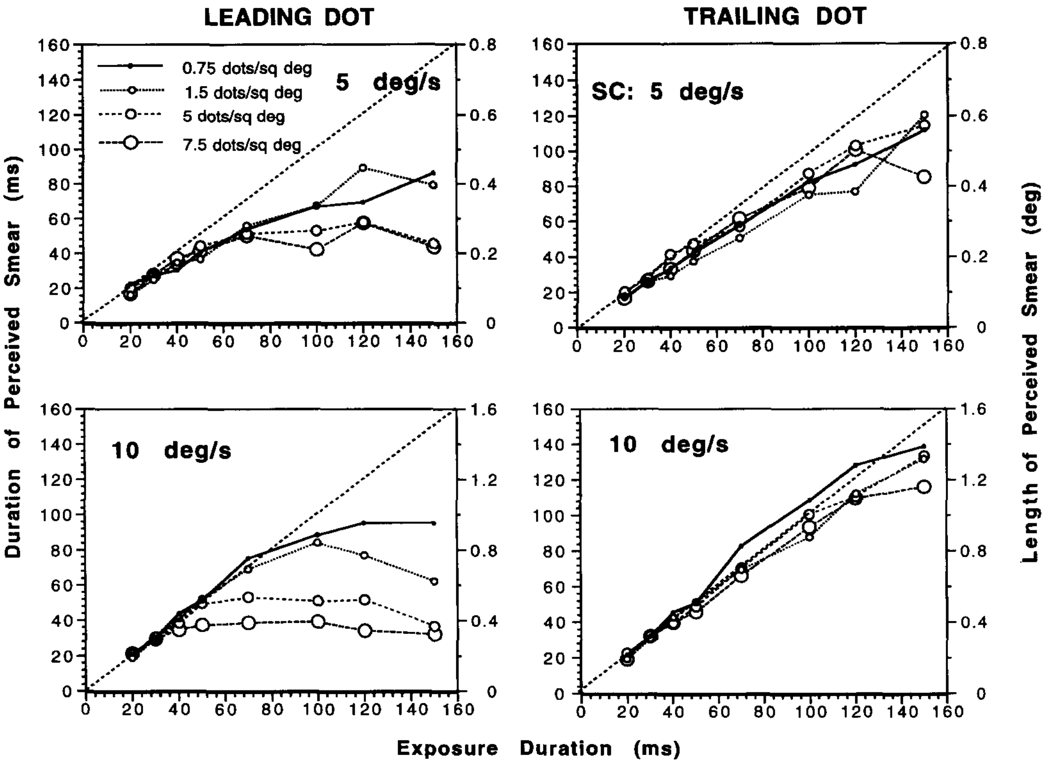

FIGURE 8. The duration (left ordinate) and length (right ordinate) of perceived smear as a function of motion exposure duration for subject SC at four separations between the leading and the trailing dot. Dot-to-dot separations are expressed in units of equivalent densities. The upper panels show the results for a velocity of 5 deg/sec, and the lower panels for 10 deg/sec. Left and right columns show the data for matches to the perceived smear of the leading and the trailing dot respectively.

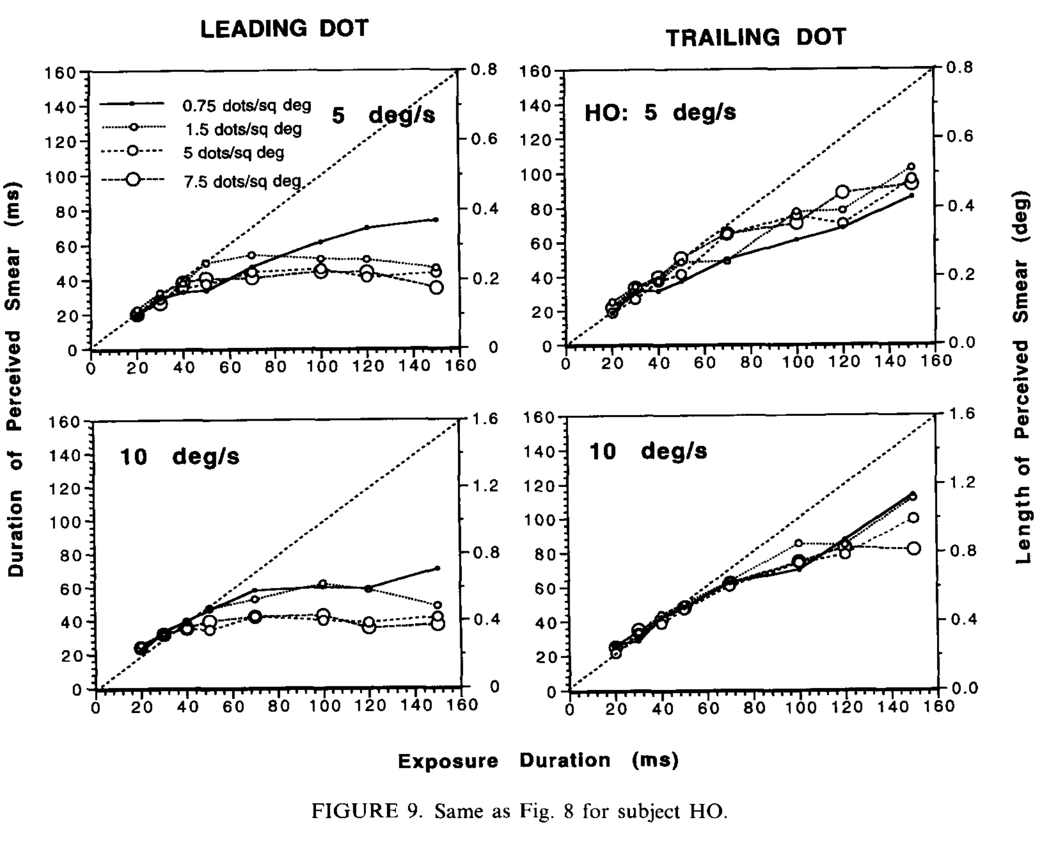

FIGURE 9. Same as Fig. 8 for subject HO.

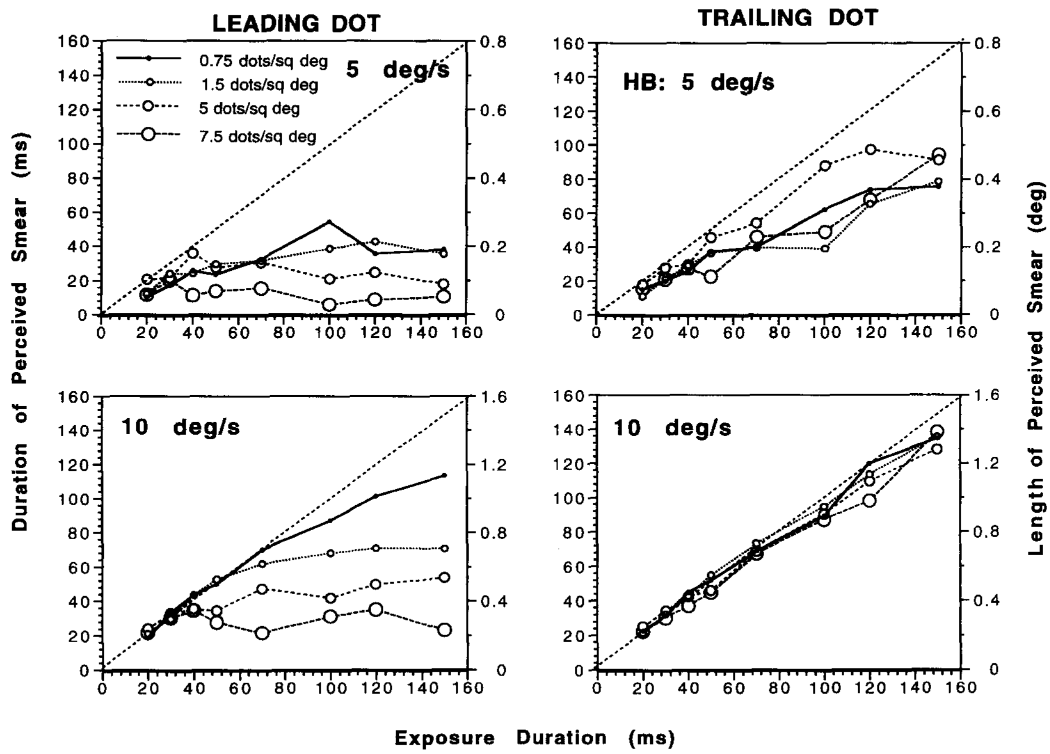

FIGURE 10. Same as Fig. 8 for subject HB.

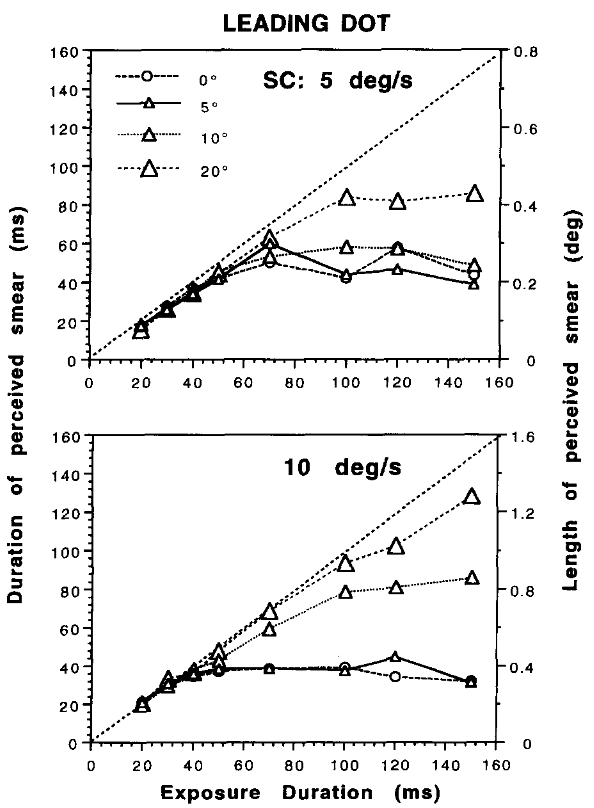

FIGURE 11. The duration (left ordinate) and length (right ordinate) of perceived smear of the leading dot of a horizontally moving pair as a function of motion exposure duration for subject SC. The dot-to-dot separation (density) was 0.37 deg (7.5 dots/deg^2). The dots were rotated by 5, 10, or 20 deg. Data for horizontally separated dots (rotation angle = 0) are replotted from Fig. 8 for comparison. The upper panel shows the results for a velocity of 5 deg/sec, and the lower panel for 10 deg/sec.

preclude the possibility that overlap by the trailing dot is necessary to limit the extent of the leading dot's perceived smear.

EXPERIMENT 4: TWO DOTS WITH NON-OVERLAPPING TRAJECTORIES

Methods

The methods and procedures were identical to those of Expt 3 except that only the perceived smear of the *leading* dot was estimated. The stimulus consisted of the slide containing two dots with the smallest separation (0.37 deg) used in Expt 3. The dots were rotated counterclockwise by 5, 10, and 20 deg so that their trajectories did not overlap during horizontal motion. Only subject SC was run in this experiment.

Results and discussion

Figure 11 shows the duration (left ordinate) and the length (right ordinate) of perceived smear of the leading dot for rotation angles of 5, 10, and 20 deg. The data for horizontally separated dots (rotation angle = 0) is included from Expt 3 for comparison. The upper and lower panels show the results for velocities of 5 and 10 deg/sec respectively. When the rotation angle is small (up to at least 10 and 5 deg for velocities of 5 and 10 deg/sec, respectively) the duration of perceived smear is very similar to that obtained for horizontally separated dots. Because the effect of the slight rotation is to prevent the overlap of trailing and leading dots without significantly increasing the dot-to-smear distance (cf. Fig. 4), we conclude that overlap is not required to limit the perceived smear. For larger angles of rotation, the duration of perceived smear increases. This is consistent with the results of Expt 2 and the hypothesis that dot-to-smear distance is an important parameter determining the extent of perceived blur.

In conjunction with the results of Expt 3, the results of this experiment provide additional support for the hypothesis that motion deblurring can be attributed primarily to the inhibition of perceived smear by spatially and temporally adjacent targets.

GENERAL DISCUSSION

In order to explain the difference between the visual persistence for static and dynamic targets, various models have posited mechanisms for motion "compensation," some of which take into account the motion of targets and prevent the persistence of static objects from carrying over to moving ones. According to Burr (1980), motion compensation occurs because receptive fields tuned to moving stimuli are oriented in the space–time domain and can therefore integrate stimulation along the motion path. Martin and Marshall (1993) proposed bidirectional inhibition combined with excitation propagated along the path of motion to reduce persistence in a network of sequentially stimulated cells. Anderson and van Essen (1987) proposed a "shifter circuit" model in which motion compensation occurs by a shifting pattern of inhibition on the afferent connections of successively excited precortical neurons, thereby maintaining convergence of inputs at the same cortical locus. Pääkkönen and Morgan (1994) postulated that the difference between static and dynamic persistence occurs because of two stages of visual integration. The first stage consists of a retinotopic integration mechanism which produces blurring of moving targets and the second stage integrates the responses to targets in a translation-invariant manner. Accordingly, only the retinotopic component and not the full extent of static persistence would apply to targets in translational motion. However, no specific mechanism was proposed to carry out translation-invariant integration.

All of these models predict that motion deblurring should be greater for coherently moving targets than for targets that move in independent random directions. The results of a recent study showed that the duration of visual persistence was less when the sampled motion of dog targets was along fixed trajectories, than when the dots were presented with the same spatial and temporal displacements, but in random directions from frame to frame (Watamaniuk, 1992; see also Braddick, Smith, & Scase, 1994). The reduction of persistence for targets in motion along fixed trajectories is consistent with the hypothesis that deblurring occurs when directionally tuned motion mechanisms are activated. However, this reduction occurred in Watamaniuk's study only when the spatial separation between the successive dots in sampled motion was between about 0.2 and 0.6 deg. When the separation between successive dots was 0.1 deg (i.e. the condition most closely approximating *real* motion) persistence was comparably brief for both fixed- and random-trajectories of motion.

The models outlined above also predict that an isolated moving target should not produce smear provided that it sufficiently stimulates the motion compensation mechanism. This prediction is in sharp contradiction with the extensive smear observed for an isolated target moving in an otherwise dark field (e.g. Bidwell, 1899; McDougall, 1904). Our results (single dot in Expt 1, vertical array in Expt 2, and the trailing dot in Expt 3) demonstrate that extensive smear occurs in the absence of spatio-temporally adjacent targets even in the presence of a bright photopic background. These findings provide strong evidence against a motion compensation mechanism as the primary factor for motion deblurring.

One striking aspect of motion deblurring is the similarity it bears to metacontrast masking in the way it depends on the luminance, spatial, and temporal separations of the targets. For example, several studies using stimuli in sampled motion showed that the duration of visual persistence decreases as the spatial separation between successively presented targets is reduced (Di Lollo & Hogben, 1985; Farrell, 1984; Castet *et al.*, 1993). Similarly, the reduction of visibility for a briefly presented target, produced by a masking stimulus that follows closely in time, increases as the spatial separation between the target and mask decreases (Alpern, 1953; Lefton, 1973). When the target and mask have similar energy, optimal metacontrast masking occurs when the mask follows the target by 50–100 msec, depending on the luminances of the background and the stimuli (review Breitmeyer, 1984). Breitmeyer and Horman (1981) showed that for high-contrast stimuli in sampled motion, optimal metacontrast occurred at a stimulus onset asynchrony of about 65–100 msec, depending on the spatial separation of the targets. In a more recent study, Castet (1994) explored the effect of interstimulus intervals ranging from 1 to 15 msec and reported that the visual persistence of stimuli in sampled motion decreases with the interstimulus interval within this range. All these findings suggest that similar mechanisms govern motion deblurring and metacontrast masking.

The inhibition-summation dichotomy, discussed in the context of deblurring models (cf. Introduction), has also been prevalent among the various neurophysiologically based models of metacontrast. One class of models explains metacontrast by a "fusion" or summation process (e.g. Burr, 1984). A second class of models proposes inhibitory interactions to account for the reduced perceptual qualities of the target (e.g. Landahl, 1967; Bridgeman, 1971; Weisstein, Ozog, & Szoc, 1975; Breitmeyer & Ganz, 1976; Oğmen, 1993). Some experimental support for the summation hypothesis came from a study that reported sub-threshold summation of target and mask stimuli in a forced-choice detection experiment (Burr, 1984). This sub-threshold summation and the strength of metacontrast masking, measured under similar conditions, were found to depend in a very similar fashion on stimulus onset asynchrony. However, in a series of experiments, Vrolijk and van der Wildt reported that when the stimulus onset asynchrony was such that an interaction occurred between the target and mask stimuli, this interaction always produced a *reduction* in the visibility (measured by the probability of detection) of the target–mask pair (van der Wildt & Vrolijk, 1981; Vrolijk & van der Wildt, 1982, 1985a, b). This reduction in visibility indicates the operation of an *inhibitory* mechanism. For other stimulus onset asynchronies, the probability of detection was equal to that predicted by probability summation (van der Wildt & Vrolijk, 1981). They also demonstrated that the pattern of results they obtained for threshold stimuli applied to suprathreshold foveal targets (Vrolijk & van der Wildt, 1985a). Since the stimuli used by Vrolijk and van der Wildt (small foveal or peripheral dots) give a good approximation to our stimuli, we propose that similar inhibitory interactions occur for continuously moving dots.

If inhibitory metacontrast mechanisms reduce the visual persistence of continuously moving targets then, at the optimal interstimulus interval, a moving dot should exert maximum masking on its *own* smear at a distance between 0.25–0.50 deg (for a speed of 5 deg/sec) or 0.5–1 deg (for a speed of 10 deg/sec). However, inhibition from nearby targets reduces visual persistence effectively only when the spatial separation between targets is less than about 0.25 deg (Dixon & Hammond, 1972; Farrell, 1984; Di Lollo & Hogben, 1985; Farrell *et al.*, 1990). These considerations indicate why multiple targets are necessary for deblurring and why a single moving dot is not effective in masking its own smear, at least for the velocities used in this study. Moreover, they reveal that the long duration of visual persistence that we measured for an isolated dot in continuous motion is consistent with the persistence measured when the targets are in sampled motion. Specifically, our results

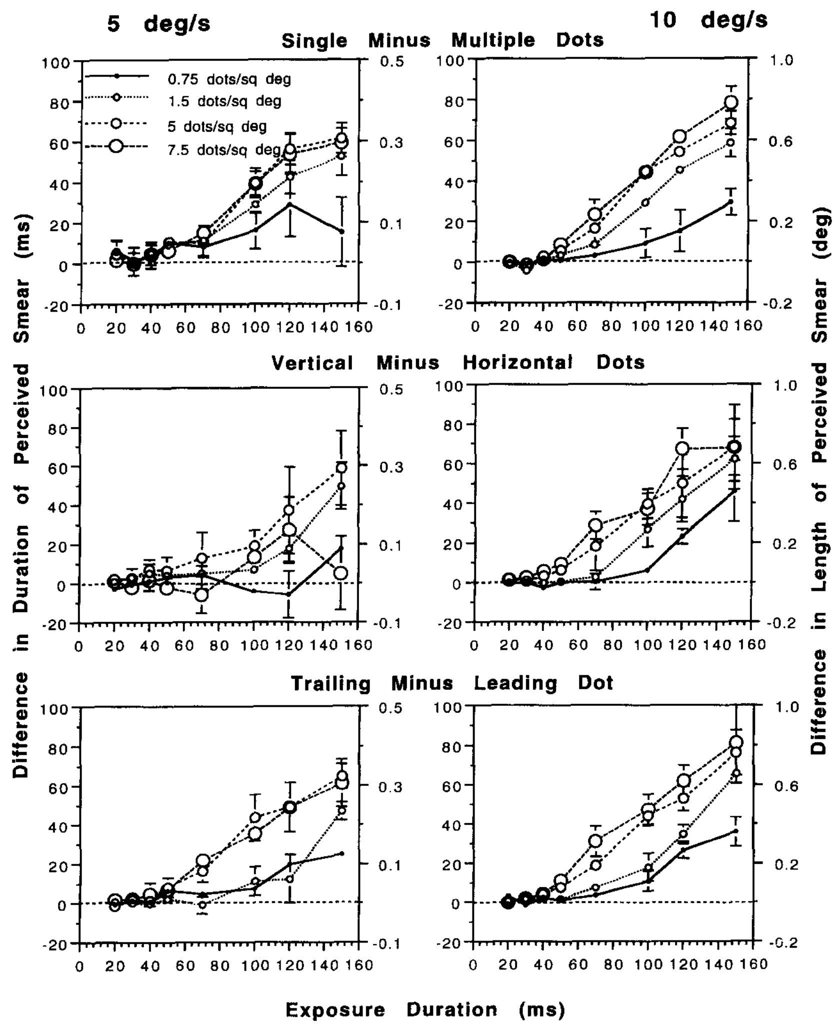

FIGURE 12. Summary of data from Expts 1–3 (averaged across the three subjects) showing the reduction of perceived smear as a function of exposure duration and dot density. The top panels shows the average differences between the duration (left ordinate) and length (right ordinate) of perceived smear for a single dot and multiple dots (Expt 1). The middle and bottom panels show the average differences between the duration and length of smear for vertical and horizontal dot arrays (from Expt 2) and between the trailing and leading dots of a pair (from Expt 3) respectively. As in previous figures, the separations between dots in Expts 2 and 3 are expressed in terms of the corresponding dot densities, from Expt 1. A positive difference indicates a reduction in perceived smear for multiple dots, horizontal arrays, and the leading of the two dots. The horizontal dashed line at 0 indicates no reduction in perceived smear. Error bars represent ± 1 SE.

for a dot in continuous motion at 5 deg/sec indicate a persistence duration of 70–100 msec. In a study of Di Lollo and Hogben (1987) using stimuli in sampled motion, the largest spatial separation between successive targets was 0.27 deg; for a temporal delay of 55 msec (corresponding to a velocity of 4.9 deg/sec), the duration of visible persistence (against their dimmer background) was 110–165 msec. It is noteworthy that a moving target would be expected to mask its own smear more effectively at lower velocities, because the separation between the target and its earlier position at the optimal temporal interval for metacontrast would be smaller. Perhaps this is the explanation for the increase in the duration of persistence with target velocity (Hogben & Di Lollo, 1985; Castet, 1994; see also Results), a finding that is difficult to reconcile with motion compensation.

We can draw two general conclusions from our findings. First, the activation of motion mechanisms (as implied by the summation models) is not a sufficient condition for motion deblurring. Second, our results strongly suggest that inhibition resulting from the spatiotemporal proximity between the target and smear, as illustrated in Fig. 4, is the key parameter that controls the reduction of perceived blur. Figure 12 illustrates our results in summary form. In the upper panels of the figure, the differences between the duration of perceived smear for a single dot and multiple dots (from Expt 1) are shown as an average across the three subjects. For comparison, the average differences are shown between the duration of smear for vertical and horizontal dot arrays (from Expt 2) and for the trailing and leading dots (from Expt 3) in the middle and lower panels of this figure respectively. Positive differences for exposure durations longer than about 50 msec indicate that the duration of perceived smear is reduced for multiple dots, horizontal arrays, and the leading of the two dots; larger reductions are seen as the target-to-smear separation decreases. As in the previous figures, the separations between dots in Expts 2 and 3 are expressed in terms of the corresponding dot densities, from Expt 1. For target motion at 5 deg/sec, the reduction of perceived smear is similar in Expts 1 and 3, except for a density of 1.5 dots/deg^2, which shows a smaller difference between trailing and leading dots than expected from the difference between the field of dots of comparable density and a single dot in Expt 1. The average difference in the duration of smear for horizontal and vertical dot arrays is also less than expected from comparable dot densities in Expt 1. This is because of the small difference between vertical and horizontal arrays exhibited by one of the subjects (HO) and the reduced duration of perceived smear, shown by all three subjects, for the vertical dot array of highest density at the longest exposure. Thus, the duration of perceived smear is less for the vertical dot arrays than for a single moving dot when the vertical separation between (slowly moving) targets is sufficiently small. For motion at 10 deg/sec, the reduction in the duration of perceived smear with dot density is very similar in all three experiments. Overall, the marked similarity of the difference plots from the three experiments, despite the different configurations of the stimuli, support spatio-temporal inhibition and, specifically, metacontrast masking as the primary (but not necessarily the only) mechanism involved in motion deblurring.

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