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Optical Blur and the Perception of Global Coherent Motion in Random Dot Cinematograms

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We evaluated the effect of +3.25 dioptres of optical blur on the discrimination of motion direction in random dot cinematograms. Dot displacement between frames varied from 2.1 to 63′ of visual angle while the temporal interval was held constant. Optical blur worsened discrimination in three normal subjects at displacements below 16′, but improved discrimination at displacements of 21′ or more. In a second experiment, two subjects viewed equivalent velocity stimuli constructed with different combinations of temporal interval and spatial displacement. Results showed that the effect of blur was specific to displacement and not velocity. Furthermore, varying the dot density of the display showed that the effect of blur correlated with dot displacement and not the probability of dot mismatches. Since optical blur attenuates high spatial frequencies, this suggests that high spatial frequencies are important for motion perception when dot displacements are less than 16′ to 21′, but reduce motion perception at larger dot displacements. The use of random dot cinematograms in populations must take into account stimulus displacement and optical causes of reduced spatial acuity. Copyright © 1996 Elsevier Science Ltd.

Motion Random dot cinematogram Blur Directional discrimination

INTRODUCTION

Current concepts of parallel visual processing suggest that motion processing occurs primarily in channels relatively insensitive to high spatial frequencies. The transient channel (Kulikowski & Tolhurst, 1973) responds best to stimuli of low spatial frequency and high temporal frequency (Green, 1981): this channel is not sensitive to hue, and under isoluminant conditions motion perception is only weakly perceived (Livingstone & Hubel, 1987). The magnocellular stream is more sensitive to high temporal frequencies whereas the parvocellular stream is more sensitive to high spatial frequencies (Schiller & Logothetis, 1990): ablations of the magnocellular layers of the lateral geniculate nucleus profoundly affect performance on motion detection tasks (Schiller *et al.*, 1990).

Other evidence also suggests that low spatial frequencies play a dominant role in motion perception (Ramachandran *et al.*, 1983). The maximum displacement of dots at which motion is still perceived, $d_{\max}$, is larger in peripheral vision, where high spatial frequencies are not well perceived (Baker & Braddick, 1985; Foster *et al.*, 1989) and is greater with stimuli that contain primarily low spatial frequencies (Chang & Julesz, 1983, 1985; Cleary & Braddick, 1990a, b; Bischof & Di Lollo, 1990, 1991; Boulton & Baker, 1991). Furthermore, high spatial frequencies may even degrade rather than contribute to the motion signal in low spatial frequencies (Chang & Julesz, 1983; Cleary & Braddick, 1990b). However, other studies indicate that motion might be perceived through multiple channels (Kulikowski, 1978; Anstis, 1980; Bonnet, 1984; Boulton, 1987) and that high spatial frequencies contribute to motion perception when exposure durations are long (Ohtani *et al.*, 1991).

Random dot cinematograms (RDCs) contain a wide range of spatial frequencies. The contribution of different spatial frequencies to motion perception in RDCs has been studied with two-frame random binary luminance patterns that measure response as a function of dot displacement (Chang & Julesz, 1983, 1985; Cleary & Braddick, 1990a; Bischof & Di Lollo, 1990, 1991). Other types of RDC vary the ratio of signal dots to randomly moving noise dots, requiring a global integration of spatially separate motion signals into a coherent motion percept (Williams & Sekuler, 1984; Buffington *et al.*, 1987). The effect of removing high spatial frequencies from these RDCs has not been studied previously.

We used optical blur to examine the role of high and low spatial frequencies in direction discrimination in such "coherent motion" RDCs. Defocusing vision with

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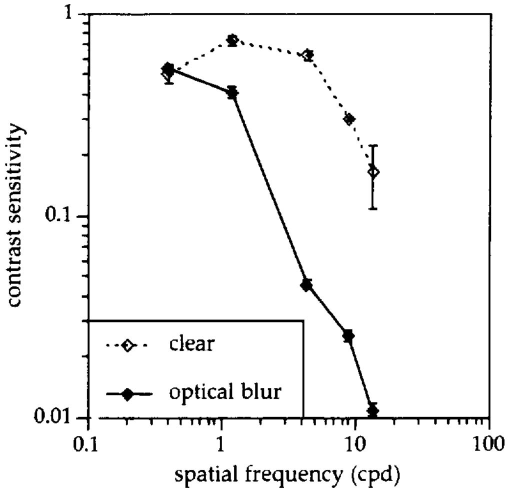

FIGURE 1. Contrast sensitivity vs spatial frequency for subject JB, comparing normal clear vision to vision blurred with +3.25 dioptre lenses.

positive dioptre lenses degrades high spatial frequencies more than low spatial frequencies (Westheimer & McKee, 1980), acting much like an isotropic low-pass filter (i.e. attenuating higher spatial frequencies in all orientations equally). If motion perception is supported primarily by channels insensitive to high spatial frequencies, optical blur should not affect performance. Furthermore, blur may actually improve motion perception if high spatial frequencies have a masking effect (Chang & Julesz, 1983; Cleary & Braddick, 1990b). The results of this study have clinical relevance since RDCs have been used in patients with optic neuropathy (Barton & Rizzo, 1994), primary open-angle glaucoma (Silverman *et al.*, 1990) and dementia (Trick & Silverman, 1991). As the latter two conditions affect mainly the elderly, testing in these populations may be confounded by the filtering effects of media opacities and refractive errors (Hess & Woo, 1978).

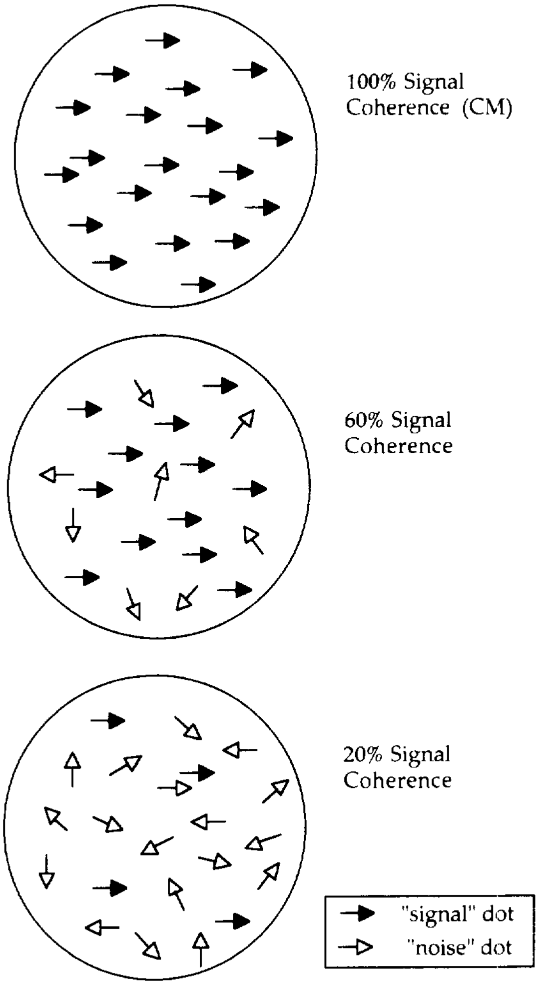

FIGURE 2. The principle of the random dot cinematograms. Black arrows symbolize the motion of signal dots. Clear arrows symbolize the random motion of noise dots, chosen from a flat distribution of other directions and with net global flow of zero. Three different degrees of signal coherence (%CM) are shown. See Methods section of Experiment 1 for details.

EXPERIMENT 1

Methods

Subjects. One of the authors and two naïve observers served as subjects. All had 20/20 Snellen visual acuity. Subject AN was emmetropic, while PM and JB were mildly myopic. Lenses during defocused conditions were selected to give each subject an additional +3.25 dioptres at the viewing distance employed. In all experiments, subjects viewed the display with natural pupils using the right eye alone.

Effect of blur on contrast sensitivity. First we determined the effects of +3.25 dioptres of optical blur on contrast sensitivity for one subject (JB). Horizontal sinusoidal gratings ranging from 0.4 to 13.5 c/deg, were displayed in a circular 3.6 deg patch, with mean luminance spatially modulated by a derivative of Gaussian function. Brackets surrounded the stimulus area, and the subject viewed the gratings from either 57, 114 or 161 cm away. A cosine function modulated the gratings temporally over 530 msec. The method of adjustment was used, adjusting at all times from low to high contrast to avoid problems with stimulus persistence or adaptation. At least three readings were taken at each spatial frequency tested, with random sorting of trials with and without optical blur.

The results are shown in Fig. 1. There was little effect at the lowest spatial frequency (0.4 c/deg), whereas blur rendered the 13.5 c/deg grating nearly invisible even at high contrast.

Motion apparatus and stimulus. Random dot cinematograms as described by Buffington *et al.* (1987) were generated by a Macintosh II x computer and displayed on a video monitor with a refresh rate of 67 Hz. The screen's background luminance was 21.13 cd/m^2. Each frame consisted of 200 black dots (luminance = 0.03 cd/m^2), each subtending 2.1 min angle, within a borderless square spanning 4.7 × 4.7 deg. Dot density was thus 9.0 dots/deg^2. The animation sequence consisted of 30 frames presented at the refresh rate of the monitor, and thus lasted 447 msec.

Apparent motion was created by displacing dots in successive frames (Fig. 2). While the size of the displacement of the dots from one frame to the next was kept constant within a given trial, the direction of the displacement of any given dot varied. A given percentage of the 200 dots (the "signal" dots) moved consistently from frame to frame in one of four directions (up, down, left, right). The remainder, the "noise" dots, chose a new displacement from a flat distribution of directions, such that their net motion flow as a group was nil. The dot population could be varied from 95% noise and 5% signal ("5% coherent motion") to 0% noise and 100% signal ("100% coherent motion"). It was impossible to determine direction of signal flow by following a single dot because the dots were small, spatially intermingled and were reassigned from frame to frame between the signal and noise groups, thus undergoing a "random walk" (Williams & Sekuler, 1984). Rather, detecting the global direction of flow required integration of the motion signal among the many elements of the display. The velocity of apparent motion for a set of trials could be varied by changing the size of dot displacement, ranging from 1 dot diameter (2.1′, or 2.3 deg/sec) to 30 dot diameters (63′, or 70.4 deg/sec).

Procedure. The subjects viewed the screen from 57 cm. Room lighting conditions were dim and kept constant for all testing. When blur was used, the viewing distance was increased to 71 cm to compensate for the magnification of the lens. Subjects fixated a cross-hair in the centre of the display area. They triggered presentation of the animation sequence of each trial and indicated which motion direction was displayed (right, left, up or down), guessing if necessary. A beep provided feedback when the answer was incorrect.

Each stimulus set consisted of 100 RDC trials of the same dot displacement, with the signal coherence and signal direction varying pseudo-randomly (method of constant stimuli). Each set contained five levels of coherent motion (CM), ranging from 5 to 25% CM in 5% steps, 10–50% CM in 10% steps, or 20–100% CM in 20% steps. For a given velocity, one of these three ranges of coherent motion was chosen so that the stimulus set spanned the region where the psychometric function was steepest, based on preliminary tests. At each %CM level, there were 20 RDC trials, five in each direction; thus each stimulus set contained 100 RDC trials. A stimulus set was performed first in the natural viewing state and then immediately afterwards with a defocusing lens. The dot displacement was varied between sets, using values of 2.1, 6.3, 10.5, 16.8, 21.0, 31.5 42 and 63′. A session consisted of 16 sets, one with and one without blur at each dot displacement, with dot displacement sets randomly interleaved. Sessions were repeated three times on separate days to avoid fatigue, for a total of 4800 trials for each subject. Thus, each data point represents the average of 60 trials. The midpoint of each psychometric function was estimated using logit analysis (Berkson, 1953). This midpoint estimates the %CM required for a subject to achieve a correct response rate of 62.5%, which we designated the %CM threshold. Since chance performance in a four-alternative design is 25%, this threshold value is set at half-way between perfect discrimination and chance.

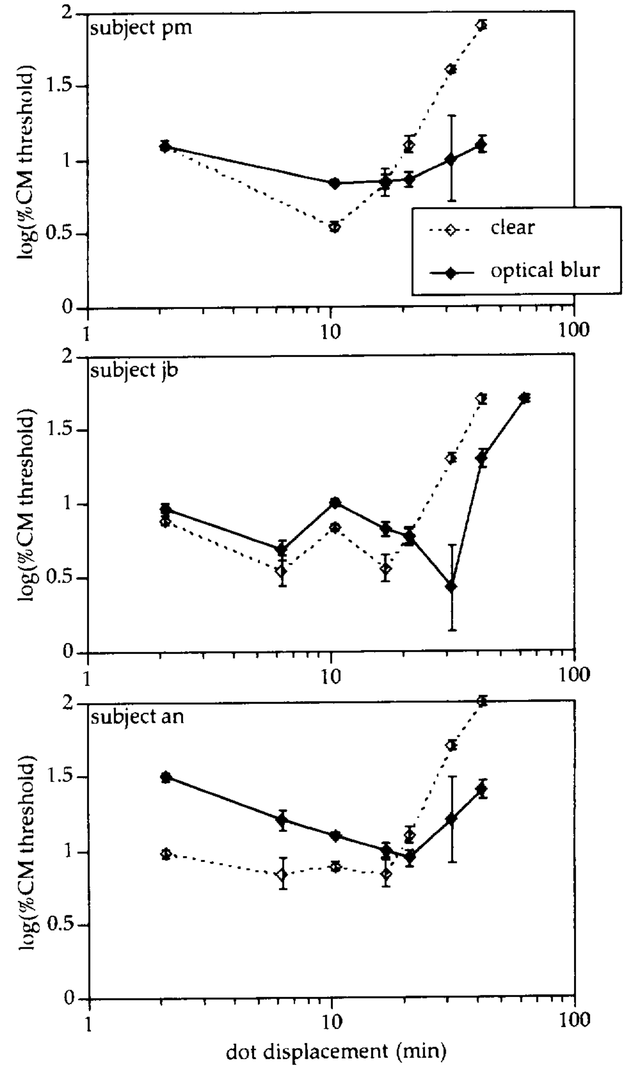

FIGURE 3. Per cent coherence motion thresholds (± 1 SE, ordinate) for three subjects as a function of the dot displacement (arc min, abscissa) of the random dot stimulus. Open diamonds with dotted lines are data with normal vision and solid diamonds with solid lines are data with +3.25 dioptres of blur. Note that in all three subjects the effect of blur on motion perception switches from worsening to improvement around 16–21 min arc.

Results

The %CM thresholds derived from logit analysis are shown in Fig. 3 for all three subjects both with and without blur. All three subjects showed impaired discrimination with blur at small displacements and improved performance at large displacements. The change from impairment to improvement with blur occurred between displacements of 16.8 and 21′ of

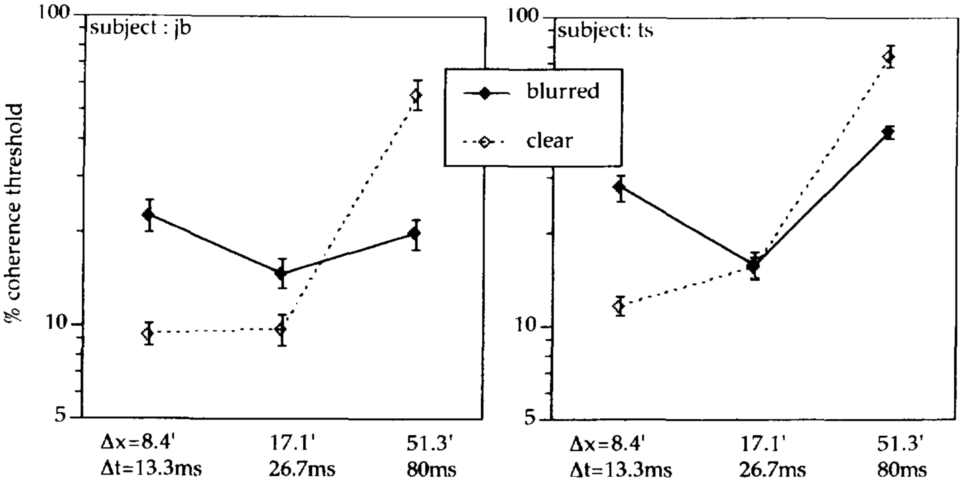

FIGURE 4. Per cent coherence motion thresholds (± 1 SE) with and without +3.25 dioptres of blur, for three different combinations of spatial and temporal interval but all with the same effective velocity of apparent motion (10.7 deg/sec). The effect of blur differs, worsening performance for the smaller displacement of 8.4′ but improving it for the larger displacement of 51.3′.

angle. Thus, the removal of high spatial frequencies by optical blur affects motion perception in RDCs as a function of dot spatial displacement. Motion perception is not mediated entirely by low spatial frequencies, since perception for small dot displacements is reduced by blur. However, blur improves motion perception at large dot displacements, consistent with previous suggestions that high spatial frequencies mask motion signals in low spatial frequencies (Chang & Julesz, 1983).

Since optical blur primarily alters the spatial characteristics of visual information, it might be expected that its effects are dependent on spatial displacement. However, in this first experiment, dot displacement co-varied with velocity, since the temporal rate of presentation was kept constant. Thus the effects of optical blur might be a function of either stimulus velocity or spatial displacement. To clarify which was the critical variable, we designed a second experiment to examine the effect of optical blur at a single velocity created by different combinations of spatial displacement and temporal interval. If the effect of blur depends on velocity, then the changes in threshold induced by blur should be the same in all the different combinations. On the other hand, if the effect depends on spatial displacement, then the effect of blur should vary.

EXPERIMENT 2

Method

Subjects. Two of the authors served as subjects: JB as above, and TS who was emmetropic. The same strength of plus dioptre lens was used for defocusing.

Apparatus and stimulus. The RDCs were produced with different custom software that used a staircase rather than the previous constant stimuli method, but followed the same principle for generating signal and noise dots as in the first experiment. However, these RDCs contained 134 white dots (luminance 37.5 cd/m^2) within a borderless 4 × 4 deg square of the black background (luminance 0.25 cd/m^2), rather than black dots on a white background. Reversing contrast allowed us to verify that the blur effect was independent of luminance polarity. Dot density was 8.4 dots/deg^2. Each RDC stimulus consisted of five frames without an inter-stimulus interval. The duration of each frame and the dot displacement could both be varied. The RDCs were generated on a MacIntosh IIfx computer and displayed in black and white on a Supermac 19″ monitor with a resolution of 72 dpi and a vertical refresh rate of 75 Hz.

Procedure. Viewing distances were the same as for Experiment 1. The room was dark. No fixation target or feedback was provided. An automated staircase procedure varied the %CM, starting at 100% CM (only signal dots). Subjects again guessed the direction of motion, left, right up or down. After a correct response the %CM was decreased by a step amount in the next trial; after an incorrect response %CM was increased by a step of the same size. The staircase step was a fraction of the %CM of the preceding RDC trial. Step size began as one-half of the preceding %CM but was reduced to one-eighth by the fifth trial. The staircase continued until 11 response reversals ("correct to incorrect" or vice versa) had occurred. The mean of the last six reversals was designated the %CM threshold, which determined the %CM at which the subject's responses were correct 50% of the time. The staircase algorithm determined %CM thresholds for each of the four signal directions separately and concurrently. The %CM thresholds of the four directions were then averaged to give an overall %CM threshold for the stimulus set.

Three combinations of dot spatial displacement and temporal interval were used. These were: (a) 8.4′ and 13 msec; (b) 17.1′ and 27 msec; (c) 51.3′ and 80 msec. All three combinations give an effective dot velocity of 10.7

deg/sec. Although keeping the number of frames constant at five meant that the durations of the RDCs varied from a very brief 67 msec for (a) to 400 msec for (c), this would not alter the nature of the comparison between normal viewing and dioptric blur for a given combination. Each of the three combinations were viewed with and without dioptric blur, for a total of six stimulus sets. These were ordered randomly for testing and all were repeated three times. Thus, final thresholds for each viewing condition of a particular combination of displacement and temporal interval are the mean and SD of 12 %CM threshold values, each in turn derived from the mean of six response reversals.

Results

Despite the fact that all three combinations of spatial displacement and temporal interval create the same effective dot velocity, blur did not have the same effect in all three (Fig. 4). At a large dot displacement of 51.3′, thresholds were high with normal vision and decreased significantly with optical blur. At a small displacement of 8.4′, the effect reversed, with low thresholds for normal vision (despite the short presentation time) that worsened with blur. At an intermediate displacement of 17.1′, the worsening with blur was less in subject JB (the most practised observer), while in subject TS there was no difference between normal and blurred viewing. Thus, despite the different technique, both the first and second experiments indicate a crossover point around 16–21′ of displacement, between displacements where blur worsens and displacements where blur improves motion perception.

The results of this second experiment show that the effect of blur is determined by dot displacement rather than dot velocity. However, another consideration is that with increasing displacement there is increasing probability of mismatches between dots, assuming the matching of dots between frames is based on a preference for the nearest dot in the next frame (Williams & Sekuler, 1984). With increasing dot displacement, there is increasing chance for a given dot that the nearest dot in the second frame will not be the one programmed by the random walk, but a different one. The probability that the nearest dot in the next frame is less than the dot displacement equals $1 - \exp(-\pi d \Delta x^2)$, where d is dot density (dot/deg^2) and Δx is dot displacement (deg) (Williams & Sekuler, 1984). The probability of mismatch thus increases as either dot density or displacement increases. It is possible to dissociate the effects of dot displacement and the probability of mismatches by manipulating either dot density or displacement separately. In the next experiment, we investigated whether the effect of blur is related to the probability of mismatches rather than dot displacement. Since, by definition, mismatches involve smaller displacements than true matches, the improvement with blur at larger dot displacements might be due to reduced perception of mismatches.

TABLE 1. Probability of mismatch $P(m)$: probability that the distance from a given dot in a frame to the nearest dot in the next frame is less than the size of dot displacement, indicated by values within the box for a given dot displacement and density

Number of dots	134	34
Dot density (dots/deg^2)	8.4	2.1
Step size (min)	*P(m)*	*P(m)*
8.4′	0.40	
17.1′	0.88	0.41
34.2′	1.00	0.88
51.3′	1.00	

$P(m) = 1 - \exp(-\pi d \Delta x^2)$, where d is dot density (dot/deg^2) and Δx is dot displacement (deg). For the two conditions with $P(m) = 1.00$, there is always another dot nearer than the dot displacement; however, the true probability of mismatch might continue to increase as the probability of *several* dots being nearer will continue to rise.

EXPERIMENT 3

Method

Subject, apparatus and procedure. Subjects JB and TS were tested monocularly, using the same apparatus and procedure as for Experiment 2, but with different values of dot displacement, temporal interval and dot density. Dot density was changed by decreasing the number of dots displayed from 134 (density = 8.4 dots/deg^2) to 34 (density = 2.1 dots/deg^2), while keeping stimulus area constant. The following combinations of dot displacement, temporal interval and dot density were used: (a) 17.1′, 27 msec and 2.1 dots/deg^2; (b) 34.2′, 54 msec and 2.1 dots/deg^2; (c) 34.2′, 54 msec and 8.4 dots/deg^2. Again, the spatial and temporal intervals were chosen to give the same effective velocity of 10.7 deg/sec. These results were compared to those obtained in Experiment 2 with dot densities of 8.4 dots/deg^2. These parameters were chosen so that a nearly identical probability of mismatch existed between one stimulus with a smaller displacement and the higher density and the stimulus with the next larger displacement and the lower density (Table 1).

We wished to compare whether thresholds with and without blurring were more similar between conditions that shared a common dot displacement or between conditions that shared a common probability of mismatch. At each combination of displacement and density, we calculated the "blur effect", which we defined as the difference between log(%CM thresholds) for blurred and clear viewing conditions. We then matched conditions and calculated the paired difference in blur effects, first pairing conditions with similar displacements, then pairing conditions with similar probability of mismatches. We used t-tests to examine whether the paired difference for conditions with similar displacement were significantly different from zero, and likewise for pairings based on similar probability of mismatch.

Results

Figure 5 shows the %CM thresholds with and without blur for all five conditions with the same effective

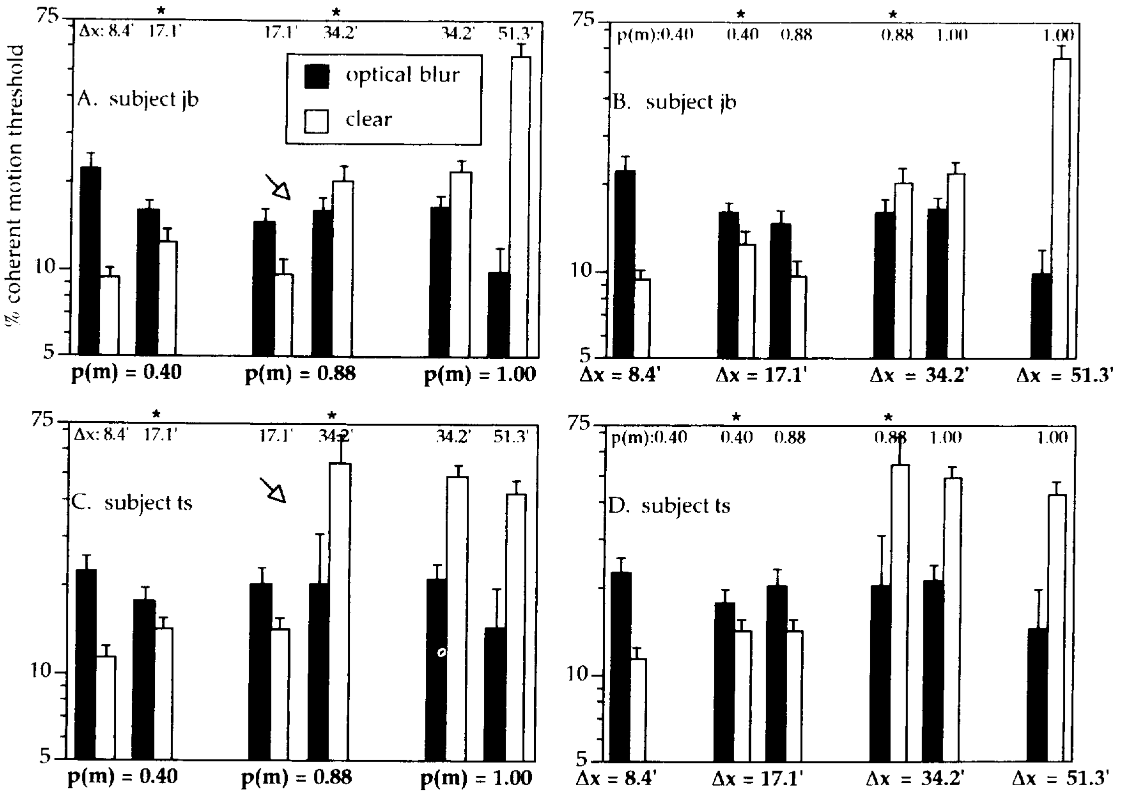

FIGURE 5. Per cent coherence motion thresholds (+1SE) for two subjects using stimuli with effective dot speeds of 10.7 deg/sec, but with dot displacements (Δ x) of varying size and different probabilities of mismatch [$P(m)$] created by manipulating dot density as well as displacement (see text). Trials with the reduced dot density of 2.1 dots/deg^2 are indicated by an asterisk. White bars indicate thresholds with normal corrected vision ("clear") and black bars indicate thresholds with +3.25 dioptres of blur. Results are shown twice, arranged differently. On the graphs on the left-hand side, (A) and (C), results with common probabilities of mismatch (but different dot displacements) are grouped together. On the right-hand side graphs, (B) and (D), results with common dot displacements (but different probabilities of mismatch) are grouped together. It is evident that performance and the effect of blur on thresholds are more similar between trials with common dot displacements than trials with common probabilities of mismatch. This is especially notable for the trials with $P(m) = 0.88$ (arrows), where blur worsens performance for the displacement of 17.1′, but improves it for the displacement of 34.2′.

velocity. Two effects are evident. Firstly, the thresholds are more similar between conditions that share the same dot displacement than between conditions that share the same probability of mismatch. This is true for both blurred and normal conditions. Secondly, the position of the blurred vision threshold relative to the normal vision threshold is more similar between conditions that share a common dot displacement. This is most apparent for the condition with 34.2′ displacement and 2.1 dots/deg^2 density, displayed as the right-hand set of thick-lined bars. Blurred vision gave a lower threshold than normal vision, the same result obtained with the same dot displacement but higher density of 8.4 dots/deg^2. In contrast, the result was opposite to that for the condition of 17.1′ displacement and 8.4 dots/deg^2 density, which has the same probability of mismatch of 0.88. The *t*-tests confirmed that, when conditions with similar probability of mismatch were paired, the mean paired difference in blur effect was 0.35 (SD = 0.21), which was significantly different from zero ($P < 0.01$). On the other hand, when conditions with similar dot displacement were paired, the mean paired difference was −0.04 (SD = 0.04), which was not significantly different from zero. Thus, the blur effect varied between conditions with similar probability of mismatch but not between conditions with similar displacements.

This experiment showed that the varying effect of optical blur correlates with dot displacement rather than with probability of mismatches. In particular, the improvement with blur with dot displacement of 34.2′ remains even when the probability of mismatch is reduced to the same level as in another condition where blur had the reverse effect. Furthermore, reducing the probability of mismatch by reducing dot density did not improve performance with either the 17.1′ or 34.2′ displacement; in fact, for the 17.1′ displacement, thresholds both with and without blur were slightly worse for JB, probably from the reduced signal when only 33 dots are displayed. This lack of effect of the probability of mismatch is in agreement with the previous findings of Baker and Braddick (1982) that dot density has little effect on $d_{\max}$ in two-frame RDCs.

DISCUSSION

Four points emerge from the results of our study. Firstly, we found that the discrimination of motion direction in RDCs that contain a wide range of spatial frequencies is affected by optical blur, which eliminates high spatial frequencies in the visual image. Secondly, this effect of optical blur varies non-monotonically with dot displacement. For small displacements, blur degrades motion perception whereas, for large displacements, it enhances motion perception. In addition, around displacements of 16–21′, the amount of blur employed has no effect on motion discrimination. Thirdly, this effect of blur depends on dot displacement, not dot velocity. Fourthly, the effects of blur are not due to a reduction in the perception of mismatches under blurred viewing conditions.

Motion signals in high spatial frequencies

We found that blurring did degrade motion perception at small displacements. This suggests that high spatial frequencies participate in motion perception under these conditions. Other studies provide support for a contribution of high spatial frequencies to motion perception. Kulikowski (1978) proposed that a separate "sustained channel" detected slow motion of high spatial frequencies. Under conditions thought to favour this sustained channel, such as long inter-stimulus intervals or long exposure times, motion perception is degraded by blur (von Grünau, 1978) or is stronger in high spatial frequencies (Ohtani *et al.*, 1991). Direct support for the role of high spatial frequencies in motion perception also has been provided recently. Smith *et al.* (1994) found no impairment of direction or speed discrimination when spatial frequencies below 12 c/deg were removed from RDCs with a high-pass filter. The spatial displacements of 5.4–16.2′ they employed fall within the range where we found degraded motion perception when optical blur removed spatial frequencies *above* 13 c/deg (Fig. 2).

Our study shows that high spatial frequencies enhance motion perception, but only when spatial displacements are less than 16–21′. This limitation of high spatial frequency motion detection to small displacements is supported by studies of $d_{\max}$ in high-pass filtered two-frame RDCs (Chang & Julesz, 1983). Interestingly, the position of the cross-over point at about 16–21′ coincides approximately with the original estimate of 15′ for $d_{\max}$ in unfiltered two-frame random binary luminance patterns viewed foveally (Braddick, 1974). This suggests that, despite differences in stimulus configuration and independent variables, both types of RDCs share the same spatially dependent process which determines the limits of performance.

Multiple-channel models and cross-channel inhibition

Several reports in the literature suggest that motion perception may involve more than one process. Braddick (1974) proposed a short-range process operating over small displacements and short time intervals, which was dependent on low-level mechanisms, and a long-range process mediating larger displacements and longer intervals. Chubb and Sperling (1988) have distinguished between first- and second-order motion. In first-order motion, changes in luminance give rise to a directional signal in the spatio-temporal Fourier power spectrum: detection of such motion is modelled adequately with early linear spatial filters. In second-order motion, the motion signal is not evident as a change in luminance, but by changes in space and time of other stimulus attributes, such as texture, disparity, or relative motion (Petersik, 1995). First- and second-order processing also have been equated with quasi-linear and non-linear mechanisms (Boulton & Baker, 1993a, b). Under conditions of high density and short time intervals, $d_{\max}$ depends on spatial frequency and performance is predicted by the stimulus" Fourier power spectrum, compatible with a linear or quasi-linear process. With low density or long time intervals, $d_{\max}$ varies with the number of stimuli, but not with spatial frequency or element size, and performance is independent of the Fourier power spectrum, suggesting a non-linear mechanism.

Do our results involve these proposed dichotomies? While the initial estimate of $d_{\max}$ for the short-range process was 15′ (Braddick, 1974), subsequent experiments showed an inverse relation of $d_{\max}$ with the spatial frequencies of the stimulus (Chang & Julesz, 1983). Thus the motion at displacements larger than 15′ in our blurred RDCs are still short-range, given the elimination of higher spatial frequencies and the resulting reduction in centre spatial frequency. Similarly, the moving luminant dots in all our RDCs are a first-order stimulus, and our use of stimuli with relatively high density and short frame durations without inter-stimulus intervals is consistent with the conditions favouring the quasi-linear mechanism (Boulton & Baker, 1993a, b). The dependence of performance on the spatial frequency content of the RDCs across the range of temporal and spatial conditions used also suggests this (Boulton & Baker, 1991, 1993a). Thus, all our stimuli can be categorized as short-range and first-order (quasi-linear) motion.

While differences between short- and long-range and first- and second-order motion may not be involved in our findings, it remains possible that within these processes there are multiple independent processing channels, which may be selective for spatial frequency, and that interactions between such channels can explain some of our results. The improvement in motion perception with blur at dot displacements greater than 16–21′ can be interpreted as masking of motion in low spatial frequencies by high spatial frequencies in the RDC. Chang and Julesz (1983, 1985), using spatially filtered RDC images, found that high spatial frequencies inhibit the perception of motion information in low spatial frequencies. Similarly, Cleary and Braddick (1990b) showed that $d_{\max}$ varied inversely with the upper cut-off frequency in spatially low-pass filtered RDCs, which they interpreted as a masking effect. These results were considered analogous to the "Abraham Lincoln" effect noted for edge perception in static pictures (Harmon &

Julesz, 1973). Other motion studies have also found evidence of "sustained-on-transient inhibition" (i.e. masking of transient, low spatial frequency channels by sustained, high spatial frequency channels). Banta and Breitmeyer (1985) showed that flanking stationary bars, supposedly processed by the sustained channel, inhibited the perception of motion between two sequentially flashed vertical bars. von Grünau (1978) found that blur improved perception of apparent motion in sequentially flashed light squares. Increases of $d_{\min}$ for sine-wave gratings with increased contrast was interpreted as sustained-on-transient inhibition (Boulton & Hess, 1990).

Masking hypotheses assume activity of multiple independent channels during motion perception, with inhibitory actions from those operating at high spatial frequencies upon those operating at low spatial frequencies. Proposals for at least two parallel motion mechanisms have been made by other investigators (Kulikowski, 1978; Bonnet, 1984; Boulton, 1987). Masking would explain our results at large displacements by assuming that the $d_{\max}$ of the high spatial frequency channel is around 16–21′, and that above this limit the information in this channel serves to inhibit rather than enhance motion perception in the low-frequency channel. At smaller displacements within the spatial range of this high-frequency channel, its motion signal must add to that of the low-frequency channel, since performance is better without blur. It may be also that there is a lower limit to the displacement detectable by the low-frequency channel, below which motion perception is supported primarily by high spatial frequencies. On the other hand, beyond the $d_{\max}$ of the low-frequency channel blur would have no effect, since there would be no motion signal to mask.

Summation in a unitary motion system

Although masking between parallel motion systems can explain our findings, our results do not necessarily provide evidence for such systems. Studies with spatially band-pass filtered RDCs (Bischof & Di Lollo, 1990; 1991) showed that $d_{\max}$ increased as the lower cut-off frequency of the band increased, as spatial frequency bandwidth increased, or as orientation bandwidth decreased. These findings were interpreted in terms of a single motion-detecting system receiving multiple inputs from parallel orientation- and frequency-selective channels in two dimensions. Their model proposed a linear summation of these inputs with inverse scaling of $d_{\max}$ with the mean spatial frequency parallel to the direction of motion. This proposal is not unlike the conclusion of Cleary and Braddick (1990a) that $d_{\max}$ scales with the centre frequency of a band-pass filtered image. Since this mean frequency would be reduced by low-pass filtering, masking is not required to explain the increase in $d_{\max}$ caused by such filtering in Cleary and Braddick's study (1990b). Similarly, the improved motion perception with blur at large displacements we found could be explained by inverse scaling of $d_{\max}$ with the mean spatial frequency of the stimulus. The better performance with unfiltered vision at small displacements represents the effects of summation of inputs. Furthermore, since $d_{\min}$ (the minimum dot displacement at which motion is discerned) also scales inversely with the centre frequency (Cleary & Braddick, 1990a) and increases with blur (Mather, 1987), unfiltered vision would have a distinct advantage at very small displacements.

Similar conclusions about a single common motion processor operating on input from multiple channels have been reached in experiments with random binary luminance patterns using varying element size (Morgan, 1992) or low-pass filtering of one or both frames in a two-frame sequence (Morgan & Mather, 1994). These studies suggested a dependence of $d_{\max}$ on element spacing, but that motion input was treated first by a spatial frequency filter with a space constant of about 20′. The authors further suggested that this value corresponded approximately to the receptive field size of magnocellular neurons. Furthermore, sequence effects in one-frame filtering (Morgan & Mather, 1994) showed slower processing of high spatial frequencies, possibly through the slower conducting parvocellular channel. Morgan's estimate of the size of the spatial pre-filter is very similar to the value of 16–21′ we found for the point at which the effect of blur changes from degradation to enhancement of motion perception. The implied interpretation of our data is that motion perception with the unfiltered (broad-band) RDCs deteriorates when the displacement between small, high spatial frequency elements exceeds the size of the physiologic pre-filter.

Thus, our results can be interpreted with models of either multiple motion-detecting channels (Kulikowski, 1978; Bonnet, 1984; Ohtani *et al.*, 1991) or a single motion-sensitive mechanism with broad spatial frequency inputs (Bischof & Di Lollo, 1990, 1991) and with a spatial pre-filter (Morgan, 1992; Morgan & Mather, 1994). If processing through multiple channels lies behind our findings, then it appears that displacement is a more critical encoded feature than velocity. Our study did not address the possible effects of different temporal intervals independent of changes in spatial displacement, however.

On a practical level, studies of populations of varying age and visual status must exclude optical conditions that reduce visual acuity before concluding that raised motion thresholds with RDCs of displacements below 16′ represent a specific motion perceptual defect. On the other hand, a normal threshold for larger displacements might actually be a defective result in someone with optically reduced acuity. It might be possible to select a dot displacement (≈16–21′) that minimizes the effect of blur, although we do not know whether this value applies for all degrees of blur or is specific for the amount of blur we tested.

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