Global motion processing is not tuned for binocular disparity

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Abstract

An important goal of the visual system is the segmentation of image features into objects and their backgrounds. A primary cue for this is motion: when a region shares the same pattern of motion it is segregated from its surround. Three experiments were carried out to investigate whether the segmentation of image features on the basis of motion information is facilitated by the addition of binocular disparity. Coherence thresholds were measured for the discrimination of the global direction of motion of random dot kinematograms (RDKs) in which the relative disparity of the signal and noise dots was manipulated. When the signal dots were embedded in a three dimensional cloud of noise dots, coherence thresholds were similar to those measured when signal and noise dots were both presented with zero disparity. However, when the signal dots were separated from the noise dots in depth, global motion processing was strongly facilitated. These results were considered in terms of two models, one in which global motion is processed by disparity tuned mechanisms, the other in which the discrimination of the direction of motion is mediated by an attention-based system. It was concluded that global motion processing is not tuned for binocular disparity and that the facilitation of the discrimination of direction provided by binocular disparity in certain circumstances reflects the rôle of an attention-based system. © 1998 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The motion of an observer through the natural environment and the motions of objects within this environment, generate complex patterns of optic flow on the retinae. These flow fields represent an important source of information for the visual system, which can support a variety of different behaviours (Gibson, 1950; Lee, 1980). For example, optic flow can be used to compute ego-motion and to control balance, in addition to the recovery of three dimensional scene structure (Wallach & O'Connell, 1953; Ullman, 1979; Lee, 1980).

Motion also provides a useful cue for image segmentation, i.e. where the image is divided into different regions corresponding to physical objects and their backgrounds. To do this, the visual system appears to exploit the fact that the world is not comprised of disjointed, randomly moving elements, but of rigid objects, moving coherently through the environment. Regions of the image which share a common pattern of

motion, therefore, tend to be grouped together and segmented from the background. A prime example of this process is the random dot kinematogram (RDK) demonstrations described by Julesz (1971), in which a perfectly camouflaged static region of dots becomes immediately apparent when it is moved relative to background dots. The segmentation of the visual image is an important goal of early visual processing and can be accomplished on the basis of a range of different visual cues (e.g. orientation, colour or disparity), in addition to motion (Julesz, 1981; Treisman, 1985).

In order to exploit motion information for these purposes, a comparison of velocity estimates from different spatial locations is required. It is often assumed that this analysis occurs in two stages (Braddick, 1993). First, local estimates of velocity are obtained within small areas of the image and these, in turn, are combined in a second stage to compute global aspects of the optic flow within larger regions of the image.

This two-stage view is supported by evidence from physiological studies which suggest that the local and global stages are computed in different regions of the cortex. Many cells in area V1 are sensitive to the

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direction of retinal motion (Poggio & Fischer, 1977; Poggio & Talbot, 1981). These cells have small receptive fields and respond to a moving stimulus in their preferred direction only. Many cells in V5/MT and MST, on the other hand, have large receptive fields and respond to complex motions, such as rotations and dilations, which contain different directions of motion centred in their receptive fields (Lagae, Maes, Raiguel, Xiao & Orban, 1994). The receptive fields of cells in MT and MST may be constructed by pooling the responses of the directionally selective V1 cells from different locations of the retina (Newsome & Paré, 1988; Tanaka, Fukada & Saito, 1989). Psychophysical evidence suggests that the human visual system is also sensitive to different optic flow components (Regan & Beverley, 1978; Beverley & Regan, 1979) and that local estimates of velocity provide the initial stages in their computation in a similar scheme to that described above (Braddick & Holliday, 1991).

The integration of elements within an image on the basis of their common motions, leading to their segmentation from the background, is not confined to those situations in which the different velocities are present in distinct regions of the image. For example, observers can integrate the motion of elements moving with a common velocity when presented within a field of randomly moving elements (Williams & Sekuler, 1984). This has been studied using RDKs in which the majority of the dots in a sequence of images are replaced in random positions between frames (noise dots) while the remainder are moved according to the same velocity (signal dots). When the proportion of the signal dots is sufficiently large, their global motion is apparent and observers can indicate the direction of motion of the signal dots. Stimuli of this type have proved valuable analytical tools in the study of global motion perception because the motion of any single dot does not specify the global motion since there is no way of knowing, at a local level, which dots are signal and which dots are noise. Rather, to recover the global motion, information must be integrated over the entire display.

The perception of motion in these stimuli may reflect the two-stage scheme, based on the responses of single cells, introduced above. The response of a V1 neuron to the presence of motion in its preferred direction is not greatly affected by the presence of motion in other directions. Conversely, the response of an MT cell to motion in its preferred direction is greatly reduced by the presence of motion in the opposite direction (Snowden, Treue, Erickson & Andersen, 1991). As a result, V1 cells will still respond strongly to a RDK which contains local motions in many directions, whereas cells in MT or MST will not respond as they are selective for global motions in a particular direction only. This property allows cells later in the cortical pathway to respond selectively to a particular global motion in stimuli which contain elements moving in many different directions (Williams & Sekuler, 1984; Newsome & Paré, 1988).

It is interesting in this regard, that if other sources of visual information are available to indicate which dots are signal and which dots are noise the discrimination of global motion may be greatly facilitated. For example, Croner and Albright (1994, 1997), demonstrated that, when all the signal dots in a RDK were indicated by the colour green and all the noise dots were indicated by the colour red, thresholds to discriminate the direction of motion were greatly decreased. Croner and Albright (1997), presented similar results for signal and noise dots that were segmented on the grounds of contrast polarity and weaker effects for dots that were segmented by luminance amplitude. In these situations, however, observers may have based their decisions on the motion of a single dot, since colour, contrast or luminance provides the necessary information to specify which of the dots are signal and which are noise. Facilitation, therefore could be attributable to an attention based system which mediates performance by allowing a particular signal dot to be scrutinised or tracked (Cavanagh, 1992; Edwards & Badcock, 1996).

In the present paper we investigate whether binocular disparity can contribute to or facilitate the perception of global motion. The fact that many MT and MST cells, which are tuned for binocular disparity, are also tuned to the direction of motion lends strong support to this idea (Maunsell & Van Essen, 1983; Komatsu, Roy & Wurtz, 1988; Bradley, Qian & Andersen, 1995). If global motion processing is disparity tuned, then the extent to which noise dots mask a coherent motion signal should depend on the difference in disparity between the signal and noise dots. However, care must be taken in the design of the experiments to distinguish between attentional based facilitation (Cavanagh, 1992) and actual disparity tuning of the mechanisms involved in global motion processing.

The paradigm we used here employed two frame RDKs which comprised a number of randomly positioned dots. Between frames, a proportion of the dots, 'the signal dots', were moved in the same direction and the remainder, 'the noise dots', were repositioned randomly. The ability to discriminate the global direction of motion in RDKs depends on the coherence of the stimulus, i.e. the number of signal dots relative to the number of noise dots. As the number of noise dots increases, the number of signal dots required to determine the global direction of motion also increases (Watamaniuk, 1993; Scase, Braddick & Raymond, 1996). If global motion processing is disparity tuned, therefore, noise dots which are separated from signal dots by virtue of disparity should have relatively little effect on the detectability of the motion signal.

A second purpose of the study was to establish the extent of motion integration in three dimensional space. It has been shown that, as the size of a RDK is increased, motion discrimination improves, as predicted by an ideal observer model (Watamaniuk, 1993). This improvement is observed for stimuli with an area of up to 25 deg^2 (Downing & Movshon, 1989), suggesting that motion is integrated spatially over this relatively large area. Similarly, it may be predicted that motion is integrated in depth. Therefore, we examined whether a link exists between the integration of motion across the two dimensional area of stimuli and through depth (defined by disparity).

A final purpose of the current study was to compare performance for horizontal and vertical motion. This was motivated by two considerations. First, Raymond (1994) reported that, for monocularly viewed stimuli, coherence thresholds were lower for global horizontal motion than for global vertical motion. We were interested in establishing whether a similar anisotropy would be evident for the three-dimensional, binocularly viewed stimuli used here. Second, Morgan and Tyler (1995) suggested that channels tuned jointly to disparity and motion respond selectively to horizontal components of motion. A similar link between binocular disparity and horizontal components of motion is implicit in the Qian and Andersen (1997) model of stereo-motion integration, in which sensitivity to disparity and temporal frequency are confounded. We therefore investigated whether coherence thresholds for global horizontal motions are affected by binocular disparity to a greater extent than thresholds for vertical global motions.

In summary, we report three experiments which investigate whether the mechanisms which compute global motion are tuned for binocular disparity. We also address whether there is similar summation in 3D as has been observed in 2D and whether there is any advantage for horizontal versus vertical motions.

2. Experiment one

This experiment was designed to establish whether the visual system is able to use binocular disparity to segregate signal from noise in the processing of global motion. To do this, stereoscopically viewed RDKs were used, in which the dots were distributed in depth. Dots were assigned as either noise or signal dots. Noise dots were presented on 11 planes, separated in depth by binocular disparity. It is important to note that, monocularly, these stimuli are identical to those in which all dots are presented at zero disparity. When viewed binocularly, each stimulus appeared as a cloud of dots, contained within a cuboid volume of space. Each of the 11 disparity planes within this space contained only 1/11 of the total number of noise dots. Signal dots were

presented on a subset of the planes occupied by the noise dots, ranging from the single plane lying in the centre of the distribution of noise, to the full 11 planes. Fig. 1 illustrates the stimulus. In Fig. 1A, the 11 planes of dots are shown. An aerial view is given in Fig. 1B, which shows the signal presented on: (i) one plane; (ii) five planes; and (iii) all 11 planes. A stereogram is given in Fig. 1C, to illustrate how the stimulus appeared perceptually.

By confining the signal dots to a single plane, the signal to noise ratio for that plane could be increased, without affecting this ratio for the stimulus overall. If global motion processing is tuned for disparity, this should result in a decrease in the number of signal dots required to discriminate the direction of motion. If we assume that global motion is processed by channels narrowly tuned for disparity, which depend only on the motions of dots on a single plane and that an observer has access to the output of such channels, then the number of signal dots required in order to discriminate the direction of motion should be related to the number of noise dots on a single plane. If the mechanism processing global motion shows broader tuning, then its response should also be affected by the presence of noise dots on other planes. This would increase the total number of noise dots contributing to the mechanism's response and lead to an increase in the number of signal dots required to discriminate the direction of motion. If global motion is processed by a mechanism that is not disparity tuned, or that is very broadly tuned for disparity, then all the dots present in the stimulus should contribute to its response and coherence thresholds would be the same as if all the noise dots had been presented in a single plane. The composition of this stimulus deliberately excludes the possibility that an attention based system could mediate a reduction in motion coherence thresholds, since the signal and noise dots were intermingled in depth. Therefore, any effect found can be attributed to disparity tuning of the global motion mechanism.

2.1. Method

2.1.1. Stimuli

Two frame RDKs were used. Each frame was presented for 150 ms, with no inter-stimulus interval. All stimuli had a dot density of 12.5 dots deg^{-2}. Dots were presented in a 2, 4 or 6 deg^2 window. Stimuli were surrounded by an 8 deg^2 of static random dots, also with a density of 12.5 dots deg^{-2}. Individual dots were formed from Gaussian blobs with a spatial S.D. of 2.5 arc min, positioned with sub-pixel accuracy using a standard grey-level interpolation algorithm. The Gaussian blobs had a maximum luminance of 73.0 cd m^{-2}. The background luminance of the screen was 0.4 cd m^{-2}.
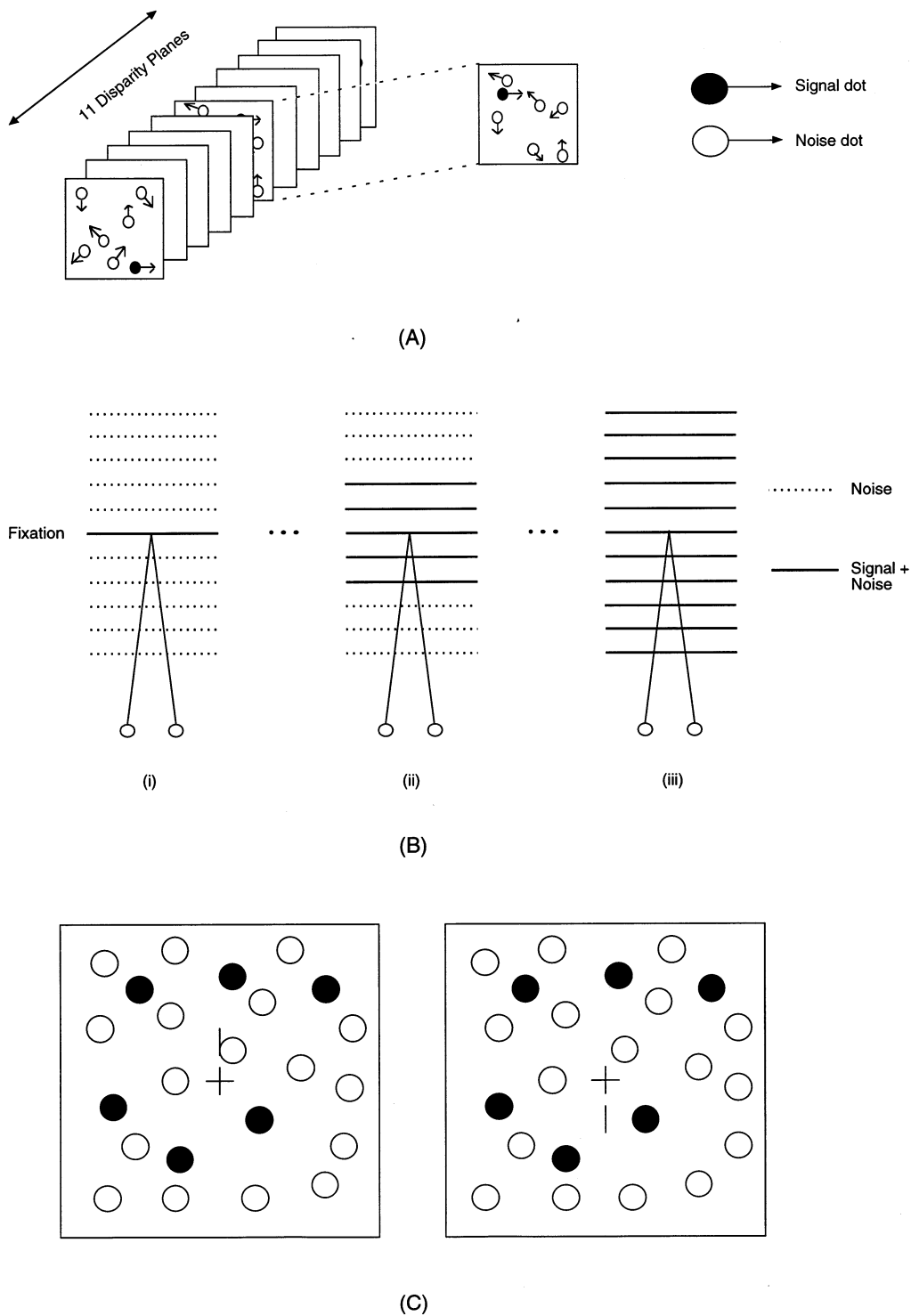
(A)

(B)

(C)

Fig. 1. Stimulus used in Experiment 1. (A) The 11 planes occupied by the dots. (B) Signal dots were presented on 1, 3,..., 11 of these planes. (C) Schematic random dot stereogram to illustrate the appearance of the stimuli. Cross eyed fusion should reveal a cloud of dots, distributed in depth. Signal dots are indicated by ● and noise dots are indicated by ○. Here, all signal dots are in the fixation plane.

For each trial, a proportion of the dots were assigned randomly as signal dots. All signal dots were moved 8 arc min in the same direction between frames. In separate experimental sessions, the directions of motion to be discriminated were either horizontal (leftward vs rightward) or vertical (upward vs downward). The remaining dots, the noise dots, were each replaced 8 arc min from their original position, in a random direction. For each noise dot, this direction was chosen from a rectangular distribution, covering the full 360° of possi-

ble directions. Under the classification scheme proposed by Scase et al. (1996), this may be described as 'random direction' or 'random walk' noise[1].

Noise dots were evenly distributed in depth across 11 planes, defined by binocular disparity. Adjacent planes were separated by 2 arc min, with a total disparity range of ± 10 arc min. The stimuli appeared as a three dimensional cloud of dots; the individual depth planes were not perceptually salient. Between blocks of trials, the number of planes occupied by the signal dots was varied between 1 (the fixation plane) and 11 (the 11 planes occupied by the noise dots). Signal dots were presented on 1, 3, 5, 7, 9 or 11 of these planes; three representative examples are shown in Fig. 1B. In addition, we also used stimuli in which all of the signal and noise dots were presented in the fixation plane.

2.1.2. Apparatus

Stimuli were presented on two Apple 12 inch monochrome monitors, driven by a Macintosh 7500 and arranged in a standard Wheatstone stereoscope configuration. The monitors were viewed through two first-surface mirrors set at $\pm 45°$ to the median plane. The viewing distance was 114 cm, at which each pixel subtended 1 arc min. The refresh rate of the monitors was 67 Hz.

2.1.3. Observers

Two of the co-authors served as observers. Both observers had good stereopsis and had normal or corrected to normal vision.

2.1.4. Procedure

Observers were asked to discriminate the direction of motion in the RDKs, using a binary forced choice procedure. Observers were presented with a nonius fixation marker at the beginning of each block of trials. When this marker was fused, observers pressed a key to start the trials. The nonius marker remained visible throughout the block of trials. Each trial was initiated when the nonius lines in the fixation marker were aligned. For each trial, a two frame RDK was presented. Observers decided whether the direction of motion was to the left or to the right, for horizontal motion, or up or down, for vertical motion. This decision was recorded by pressing one of two keys on a keypad.

Coherence thresholds for the discrimination of direction were measured using the method of constant stimuli. Psychometric functions were obtained on the basis of 40 observations at each of eight motion coherence levels. The range was selected on the basis of pilot studies. Motion coherence thresholds were obtained by

fitting a Weibull function to each psychometric function.

2.2. Results and discussion

Fig. 2 shows coherence thresholds plotted against the spread, in disparity, of signal dots. Thresholds represent the 81.6% correct point of the fitted function; error bars represent the S.E. of the parameter estimates. Graphs are plotted separately for the horizontal and vertical directions of motion. The arrows to the left of each graph represent coherence thresholds when signal and noise were presented on a single plane. Thresholds were no lower when the noise was spread through a volume, than when both signal and noise were presented on a single plane. Further, thresholds did not increase as the signal too was spread in depth. Disparity had no apparent effect for any size of stimulus studied, for either horizontal or vertical motion, despite the fact that the parameters of the stimulus had been optimised to provide a strong disparity cue.

Fig. 3 summarises the effects of stimulus size and motion direction for the two observers. Mean thresholds were obtained across the range of signal disparities, for each condition. Each bar thus represents the mean of all data points for a single line in Fig. 2. Thresholds decreased with increasing stimulus area, as found previously for two dimensional stimuli (Downing & Movshon, 1989). Disparity did not affect motion coherence thresholds for any of the stimulus sizes tested. We therefore found no relationship between the two dimensional extent of the stimuli and the extent to which motion information is integrated through depth.

It is also evident in Fig. 3 that no significant difference was found between thresholds for horizontal and vertical motion. This contrasts with the findings of Raymond (1994), that sensitivity to global horizontal motion is greater than sensitivity to global vertical motion. However, there are a number of important differences between the stimuli used here and those used by Raymond (1994). The most obvious difference is that the stimuli were viewed binocularly in the current study, whereas Raymond's experiments were concerned with monocularly viewed stimuli. Further, Raymond used four frame stimuli, with 'random position' noise, in contrast to the two frame, 'random walk/random direction' noise stimuli used here.

The present results suggest that binocular global motion perception cannot take advantage of disparity when a motion signal is spread through depth. We found no obvious relationship between horizontal motion and horizontal disparity, as might be predicted on the basis of the results of Morgan and Tyler (1995) and the model of Qian and Andersen (1997). Therefore, global motion perception would appear not to be tuned for binocular disparity, as a similar pattern of results

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[1] For two-frame RDKs, the two are synonymous.
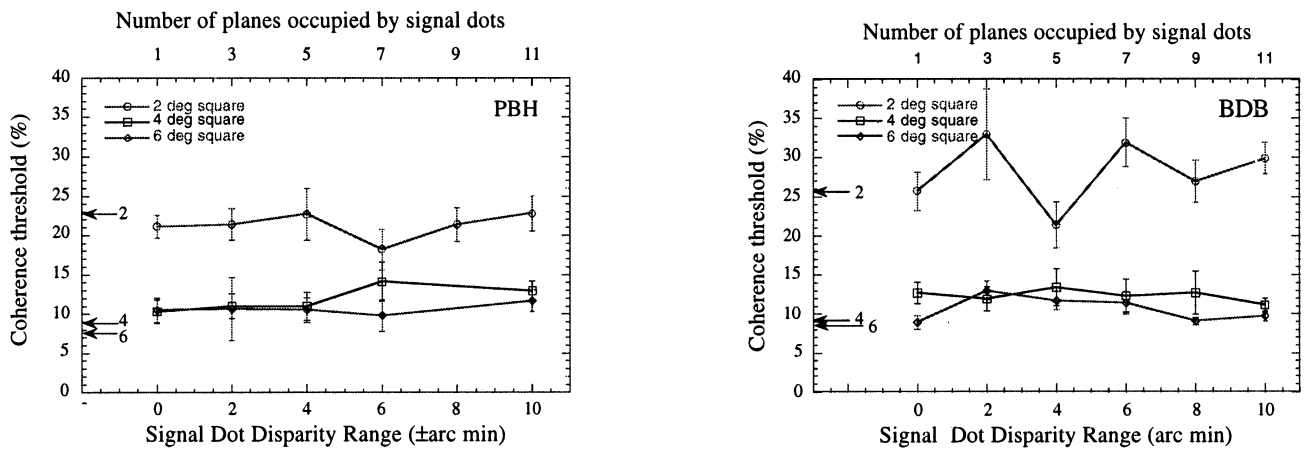
HORIZONTAL MOTION
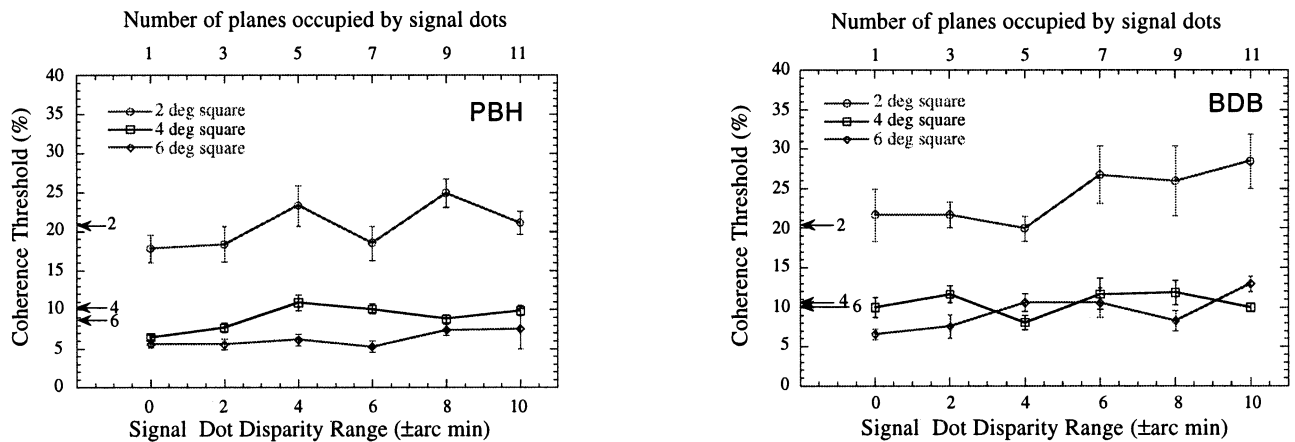
VERTICAL MOTION

Fig. 2. Thresholds for the detection of coherent motion in noise that is distributed in depth as a function of the distribution of signal dots. Results are plotted separately for horizontal and vertical motion. Error bars represent ± 1 S.E. The arrows to the left of each graph show thresholds for the single plane condition, for each of the three stimulus sizes.

would have been obtained had the stimuli been viewed monocularly.

However, before we make this conclusion, we must also consider the possibility that observers were unable to make use of the binocular disparities in the stimuli due to some aspect of our design. For example, disparity averaging may have acted to reduce the apparent disparity of the stimuli. Andersen (1992) reported strong disparity averaging for dynamic random dot stereograms in which dots were presented with random positions in three dimensional space. If similar disparity averaging occurred in the current study, it would have reduced the effective range of disparities presented and thus would diminish any effects which may be attributed to disparity tuning. This possibility can be rejected on several grounds. First, observers reported seeing the appropriate magnitude of depth in the three dimensional clouds of dots presented. To determine this

a comparison stimulus was used in which dots with the same total disparity as the noise volume were presented on two spatially separated planes. The experimental stimulus and the comparison stimulus appeared to have the same magnitude of depth. Second, the results we report here were replicated with stimuli with lower dot densities, of 6.3 dots deg^{-2} and 3.1 dots deg^{-2}, in which the potential for disparity averaging is reduced. Finally, the experiment presented above was repeated, for the single condition in which all the signal dots were presented on the fixation plane, but the noise dots were again presented on 11 planes, separated in depth by disparity. This is the condition for which disparity would be expected to provide the greatest facilitation. The separation between adjacent noise planes was varied. Separations of 0.5, 1, 2, 4 and 8 arc min were used; the total disparity range occupied by the noise dots therefore varied between ± 2.5 and ± 40 arc min.
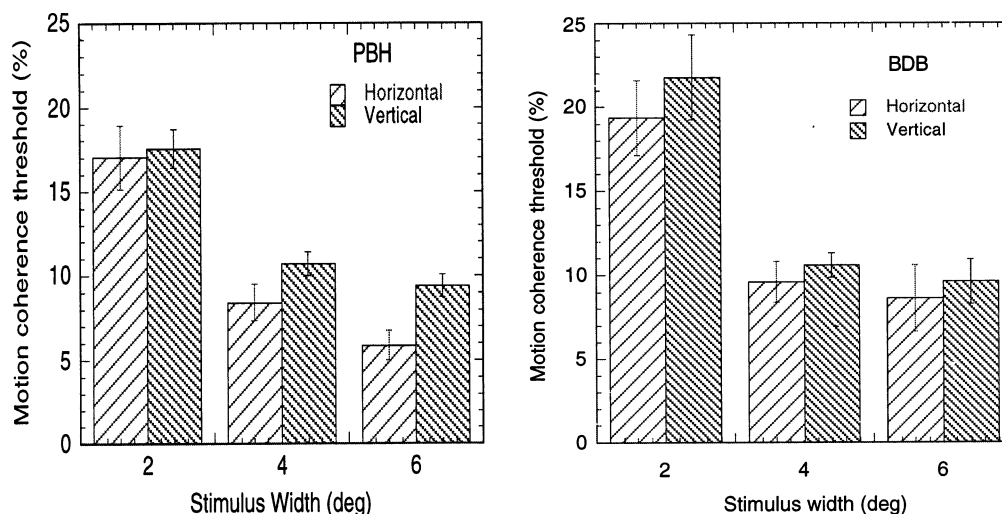
Fig. 3. Summary of results for Experiment 1. Each bar represents the mean coherence threshold, taken across the different distributions of signal disparities, for one size of stimulus and direction of motion.

Coherence thresholds were measured for a 4 deg^2 stimulus, for both horizontal and vertical motion. The results are shown in Fig. 4. No improvement in coherence thresholds was observed for any of the disparities used, for either horizontal or vertical motion. It is unlikely therefore that the results obtained were due to the disparities chosen, since similar results were obtained over a wide range of disparities.

Another possible problem in the design of the stimuli in the present experiment is that the presentation time of 300 ms may have been too brief to allow disparities to be registered. However, similar results were found in a series of pilot studies in which stimuli with increased presentation times and increased numbers of frames were used. Moreover, the remaining two experiments, described below, demonstrate that facilitation of global motion perception can occur using the same stimulus parameters (two frame stimuli with the same duration, velocity, dot density and distribution of noise dots) as used in this experiment. Therefore, our conclusion that global motion processing is not tuned for binocular disparity seems justified.

3. Experiment two

As introduced above, the possible effect of disparity on global motion perception may be compared to that of colour. Croner and Albright (1994, 1997) found that introducing colour to RDKs could greatly improve the discrimination of global motion. However, Edwards and Badcock (1996) found no decrease in global motion detection thresholds in stimuli in which half the noise dots were the same colour as the signal dots. They argued that the facilitation observed by Croner and Albright may have resulted from an attention-based

system which identified and tracked particular signal dots. This would not have been possible in their experiment since, at threshold levels of coherence, the majority of dots of each colour would have been noise dots. The stimuli used in our first experiment may be compared to those used in the latter study. In our experiment, signal dots were presented on a number of planes, lying within the volume of space occupied by the noise dots. In all cases, therefore, a proportion of the noise dots had the same disparity as each of the signal dots. If disparity affects global motion processing in the same way as colour, we would not expect any decrease in motion discrimination thresholds in these stimuli. In the second experiment, we investigated stimuli in which the signal and noise dots were presented on two separate planes. These stimuli may be compared to those used by Croner and Albright, for which strong facilitation of global motion processing was observed.

3.1. Method

3.1.1. Stimuli

Stimuli consisted of two frame RDKs, similar to those used in the first experiment (see Section 2.1.1). RDKs again had a density of 12.5 dots deg^{-2}. Dots were presented in a 4 deg central square, surrounded by an 8 deg^2 border of static, randomly positioned dots. All dots were moved 8 arc min between frames; signal dots were all moved in the same horizontal direction, while noise dots were moved in random directions. For each noise dot, this direction was chosen from a rectangular distribution, covering the full 360° of possible directions.

In all cases, signal dots were presented with zero disparity. Noise dots were presented with a crossed or uncrossed disparity, which was varied between blocks
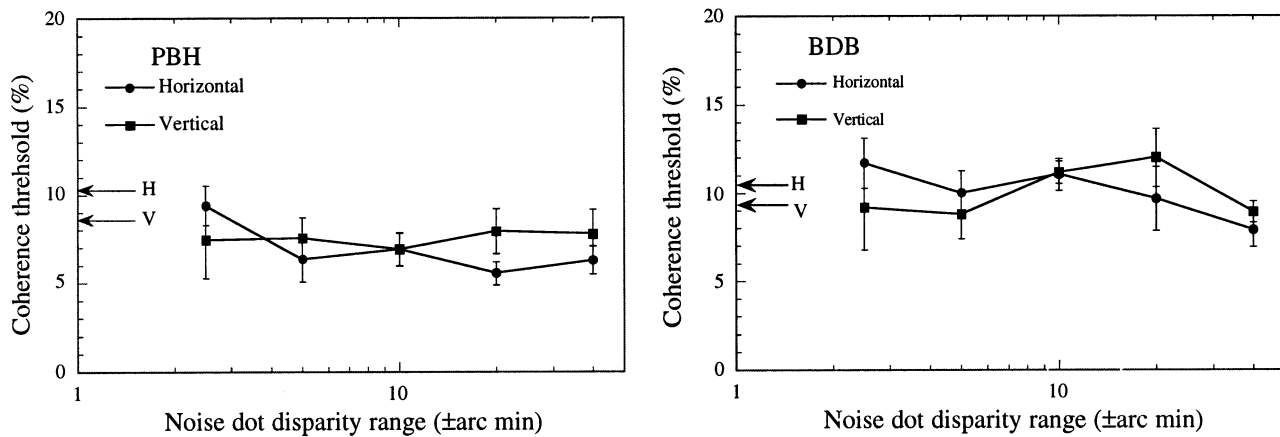
Fig. 4. Thresholds for the detection of coherent motion in noise that is distributed in depth, as a function of the disparity distribution of the noise. In all cases, all signal dots were presented in the fixation plane. Error bars represent ± 1 S.E.

of trials. Signal and noise dots thus appeared on two separate planes in depth. The noise dots appeared either in front of (crossed disparity) or behind (uncrossed disparity) the signal dots (Fig. 5). Crossed and uncrossed disparities of 1, 5, 10, 20 and 40 arc min were used.

3.1.2. Apparatus

The apparatus used was identical to that used in the first experiment (see Section 2.1.2).

3.1.3. Observers

The three co-authors and one naïve observer participated in the study. All observers had good stereopsis and had normal or corrected to normal vision.
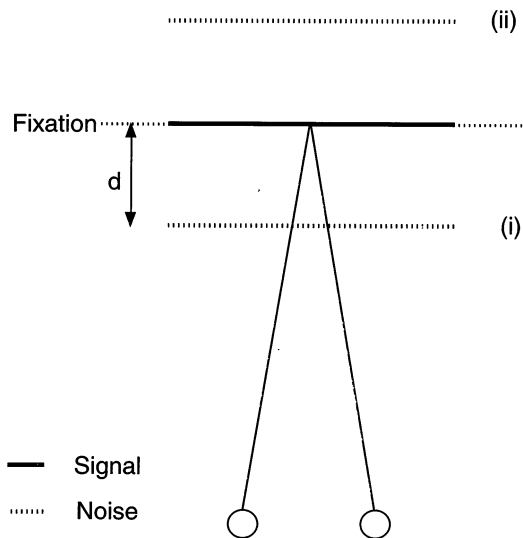

Fig. 5. Stimuli used in the second experiment. Signal dots were always presented in the fixation plane. Noise dots were presented with: (i) a crossed disparity of d arc min; or (ii) an uncrossed disparity of d arc min.

3.1.4. Procedure

The procedure was identical to that used in the first experiment (see Section 2.1.4). Observers were asked to discriminate the direction of motion of the two frame RDKs, using a binary forced choice procedure. For each trial, observers decided whether the direction of motion was to the left or to the right. Again, coherence thresholds for the discrimination of direction were measured using the method of constant stimuli. Psychometric functions were obtained on the basis of 40 observations, at each of eight motion coherence levels.

3.2. Results and discussion

As Fig. 6 shows, thresholds decreased when the signal dots were presented with zero disparity and the noise dots with an uncrossed disparity. These results showed clear disparity tuning, the lowest coherence thresholds occurring when signal and noise were separated by a disparity of 10 arc min. Here, thresholds were on average a factor of 22 lower than those measured when signal and noise dots were both presented with zero disparity. Probit analysis was used to compare the thresholds for the zero disparity and 10 arc min^{-1} uncrossed disparity conditions on the basis of the fiducial limits on the difference between the thresholds of the two data sets (Finney, 1971, p. 101). For all observers, thresholds were significantly lower when the noise dots were presented with a disparity of 10 arc min than when they were presented with zero disparity ($P < 0.05$). For larger disparities, distinct signal and noise planes could not be discriminated and coherence thresholds rose to a level comparable to those obtained when the signal and noise dots were presented on a single plane.

When the signal dots were presented with zero disparity and the noise dots with a crossed disparity, a different pattern of results was found for two of the four observers. PBH and MFB again showed clear
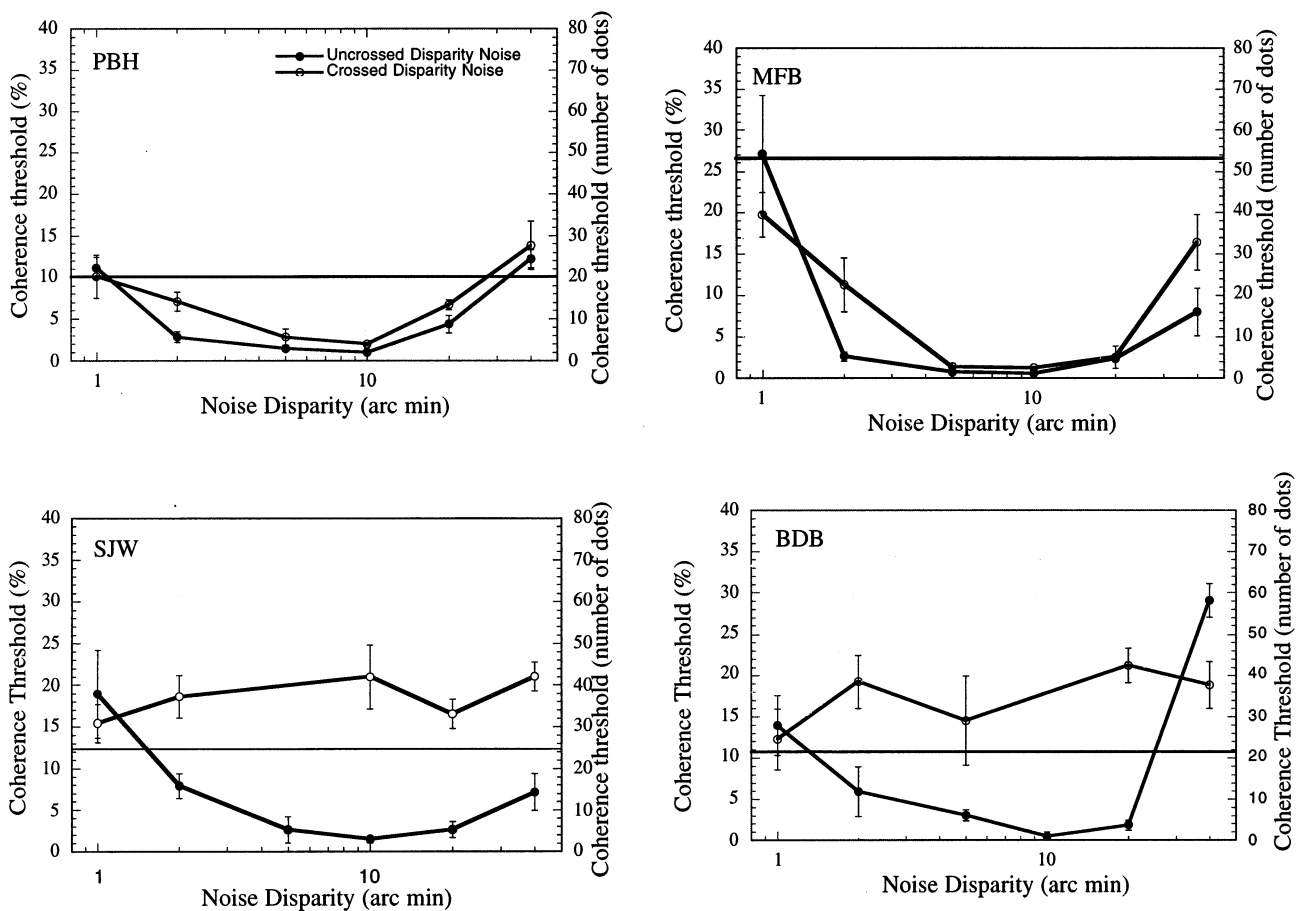
Fig. 6. Coherence thresholds plotted as a function of the disparity difference between signal and noise dots. Error bars show ± 1 S.E.

disparity tuning, whereas BDB and SJW did not. Again, thresholds were lowest for the first two observers when the noise dots were presented with a disparity of 10 arc min. In this case, thresholds were a factor of 13 lower than thresholds measured when signal and noise were both presented with zero disparity. This reduction in thresholds was again found to be significant ($P < 0.05$). Coherence thresholds were actually higher for observers BDB and SJW when the noise dots appeared in front of the signal dots than when all signal and noise dots were presented with zero disparity.

For two of the four subjects, facilitation only occurred when the noise dots were presented with uncrossed disparities, suggesting they were only able to identify signal dots if they appeared in front of the noise dots. This asymmetry in preference may be related to the 'front effect' (Lehmkuhle & Fox, 1980; Fox & Patterson, 1981). This is the finding that visual masking effects may decline as the disparity difference between the mask and target pattern increases if the target is presented in front of the mask. If, however, the mask is presented in front of the target pattern, then masking effects may actually increase. Other related asymmetric effects of disparity have been reported. For example, O'Toole and Walker (1997) found that search for features defined by binocular

disparity may be parallel when the targets are presented in front of the distracters, but serial when the targets are presented behind the distracters. In addition, Landers and Cormack (1997) found shorter reaction times and lower error rates, for the detection of targets with crossed disparities than for the detection of targets with uncrossed disparities.

The tuning curves obtained in this experiment are similar to those presented by McKee, Watamaniuk, Harris, Smallman and Taylor (1997) for the detection of the trajectory of a single dot, which suggests that similar mechanisms may underpin performance in both studies. McKee et al. considered their results to demonstrate disparity tuning of local motion mechanisms. However, it is also possible that observers in their study could have tracked the motion of the perceptually salient signal dot, in a similar manner to that proposed by Edwards and Badcock (1996). If disparity is used to distinguish signal from noise dots then our results too can be considered in this way. Because of the disparity signal, a single signal dot is sufficient to perform the task. In fact, under certain conditions, performance was above chance levels when the signal was carried by a single dot.

The results of Experiment two are markedly different to those obtained in the first experiment and show clearly

an effect of binocular disparity on global motion perception. The facilitation observed is consistent with disparity tuning of global motion processing. However, when considered in the light of the results of Experiment one, it is more likely that they reflect the effects of an attention-based mechanism. Cavanagh (1992) suggested that motion could be discriminated by tracking perceptually salient image features, a strategy which might not rely on low-level motion mechanisms. Likewise, Edwards and Badcock (1996) suggested that the facilitation of global motion provided by colour might rely on a similar strategy. This is consistent with the fact that they only observed facilitation when all the noise dots were presented in a different colour to the signal dots. When half of the noise dots were presented in the same colour as the signal dots, observers would have been unable to completely segregate signal from noise on the basis of colour. A similar explanation may be appropriate for the results obtained here. In the first experiment, the ranges of disparities of the signal dots and noise dots always overlapped and no facilitation was found. When this was not the case, in the second experiment, binocular disparity strongly facilitated global motion discrimination. In the latter case, observers may have been able to use disparity to distinguish between the signal and noise dots and to encode the motion of the signal dots preferentially. However, a further difference between the experiments was the use of a 'noise volume' in Experiment one. The possible consequences of this are addressed in a third and final experiment.

4. Experiment three

An important difference between the two experiments reported above is that, whereas in the first experiment the signal was embedded in a three dimensional volume of noise, there was a complete separation in depth between signal and noise in the second experiment. The results of Edwards and Badcock (1996) suggest that the separation in depth might be the important difference between the two experiments. Therefore, this final experiment was carried out to resolve this issue. Its design allowed us to assess whether the significant difference between the stimuli used in Experiments one and two was the separation in depth between signal and noise dots or whether it was the fact that the dots were presented in a three dimensional volume in Experiment one as opposed to on two distinct planes in Experiment two.

4.1. Method

4.1.1. Stimuli

As in the first two experiments, stimuli consisted of two frame RDKs with a density of 12.5 dots deg^{-2}.

Dots were presented in a 4 deg central square, surrounded by an 8 deg^2 border of static, randomly positioned dots. Again, all dots were moved 8 arc min between frames. All the signal dots were moved in the same horizontal direction, while the noise dots were moved in random directions. For each noise dot, this direction was chosen from a rectangular distribution, covering the full 360° of possible directions.

Noise dots were evenly distributed in depth across 11 planes. Adjacent planes were separated by 1.2 arc min, giving a total disparity range of ± 6 arc min. The signal dots were presented on a single plane, as illustrated in Fig. 7, with a disparity of ± 8 arc min (i and v), ± 6 arc min (ii and iv), or 0 arc min (iii). The signal dots were thus presented on a plane 2 arc min in front of or behind the noise dots, on the front or back face of the volume containing the noise dots, or in the centre of the noise dots. Thus, while the overall range of disparities in the stimuli was almost identical to that used in the first experiment, the stimuli differed in terms of the distribution of signal and noise dots within this range.

4.1.2. Apparatus

The apparatus used was identical to that used in the first two experiments (see Section 2.1.2).

4.1.3. Observers

One of the co-authors and one naïve observer participated in the experiment. The observers were selected as they showed different effects of disparity in Experiment two. Both observers had good stereopsis and had normal or corrected to normal vision.
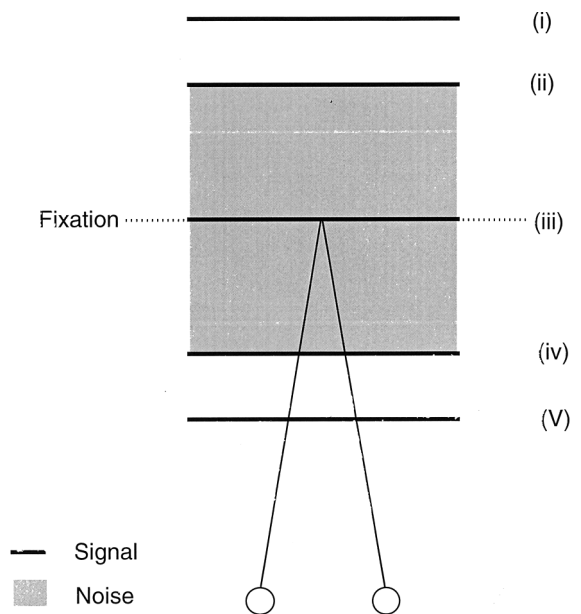

Fig. 7. The design of the stimuli used in the third experiment. Noise dots were presented on 11 planes, with a total disparity range of ± 6 arc min. Signal dots were presented with a disparity of 0, ± 6 or ± 8 arc min, represented by the dark horizontal lines.
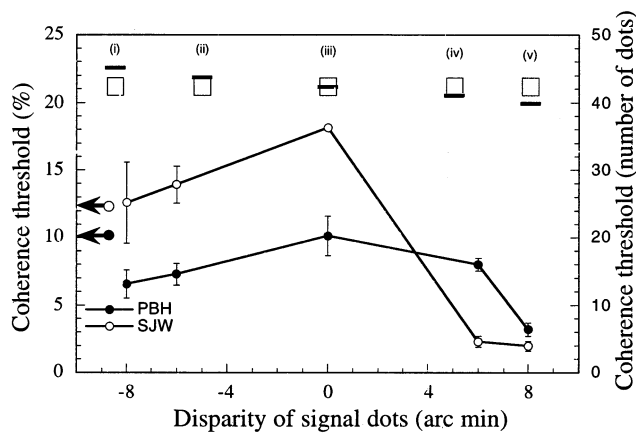
Fig. 8. Results for Experiment three. Coherence thresholds are plotted as a function of the disparity of the signal dots. Pictograms are provided for comparison with Fig. 7. Error bars represent ± 1 S.E. The arrows to the left of the graph show thresholds for the single plane condition, for each observer.

4.1.4. Procedure

Again, observers were asked to discriminate the direction of motion of the two frame RDKs, using a binary forced choice procedure identical to that used in the two previous experiments. Observers decided whether each RDK contained motion to the left or to the right. Coherence thresholds for the discrimination of direction of motion were measured using the method of constant stimuli. Psychometric functions were obtained on the basis of 40 observations, at each of eight motion coherence levels.

4.2. Results and discussion

Coherence thresholds are plotted against the disparity of the signal dots in Fig. 8; the pictograms on each graph show the relationship between the signal and noise dots for each case. When the signal was embedded in the noise (condition (iii)) thresholds were comparable to those for the single plane condition (shown by the horizontal arrows to the left of the graph), which concurred with the results of the first experiment. When the signal dots were presented in front of the noise dots (conditions (iv) and (v)), thresholds were significantly lower than in the zero disparity condition for both observers ($P < 0.05$). This was true both when the signal dots were presented on a separate plane and when they were presented on the front plane of the volume containing the noise. When the signal dots were presented behind the noise dots (conditions (i) and (ii)), thresholds were not significantly lower than the zero disparity condition. These results thus demonstrate a marked asymmetry between crossed and uncrossed disparities. Thresholds were lower when the signal was presented in front of the noise than when it was presented behind the noise. This difference reflects a similar pattern of results

observed in the previous experiment, where disparity was found not to facilitate motion processing when the signal dots were presented behind the noise dots for two of the four observers.

In conclusion, it is clear from this experiment that the facilitation of global motion processing provided by disparity is primarily related to the separation in depth between signal and noise and that the difference between the results of our first two experiments cannot be accounted for merely in terms of the use of a volume of noise rather than two distinct planes of dots.

5. General discussion

Three experiments were performed to address the role of disparity in the perception of global motion in binocularly viewed RDKs. In the first experiment we measured coherence thresholds for the discrimination of the direction of motion in RDKs in which the signal dots were embedded in a three dimensional cloud of noise dots. Coherence thresholds were measured for three sizes of stimuli and separately for vertical and horizontal directions of motion. We investigated: (i) whether a link exists between the two dimensional size of stimuli and the extent to which motion information is integrated through depth; and (ii) whether any facilitation provided by binocular disparity was influenced by the direction of motion. In all cases, coherence thresholds were indistinguishable from those obtained when both signal and noise were presented with zero disparity, despite the fact that the majority of noise dots had a disparity that was different to that of the signal dots. These results provide no evidence for disparity tuning in the process of global motion perception for the stimulus sizes or directions of motion tested.

In the second experiment we measured coherence thresholds for stimuli in which signal and noise dots were presented on two separate planes. In this case, the lowest coherence thresholds were observed when signal and noise dots were separated by a disparity of 10 arc min. When the separation was increased or decreased from this value, thresholds rose significantly. The fall off in performance, when disparity was decreased below 10 arc min, may be explained by a simple model of disparity tuning. Disparity tuned cells have been found in areas V1 and V2 (Poggio & Fischer, 1977; Freeman & Ohzawa, 1990) and in areas MT and MST (Maunsell & Van Essen, 1983; Roy, Komatsu & Wurtz, 1992) of the awake macaque. Maunsell and Van Essen (1983) reported disparity tuned MT cells that were also tuned for the direction of motion. If global motion processing is mediated by cells of this type, it should show similar disparity tuning. In our stimuli, signal dots presented in the fixation plane would stimulate directionally selective, disparity tuned cells with tuning functions centred on the

fixation plane and selective to the direction of the signal dots. Noise dots, which were also presented with zero disparity, but which moved in other directions, would be expected to inhibit the response of such cells. As the disparity of the noise dots is increased, the extent of this inhibition would be expected to decrease. Thus, increasing the disparity of the noise dots should decrease the level of motion coherence required to discriminate the direction of motion. This would account for the decrease in motion coherence thresholds observed as the disparity was increased from 0 to 10 arc min. Note that while small errors in fixation may have altered the sign of the disparities of some of the dots, the discussion presented here relates only to the relative magnitudes of disparities, which are not affected by changes in fixation. For disparities beyond 10 arc min the fall off may be explained differently. In the extreme, diplopia was evident and the signal and noise dots did not appear to lie on two separate planes in depth. Here, global motion processing would presumably rely on monocularly driven mechanisms. This would then explain why, as the disparity of the noise dots was increased beyond 10 arc min, thresholds rose to a level comparable to, or greater than thresholds obtained for stimuli in which signal and noise were presented on a single plane.

An alternative explanation however must also be considered. The decrease in thresholds observed for disparities ≈ 10 arc min may reflect the involvement of an attention-based system, as the unique attribute of disparity could be used to distinguish signal from noise. This argument has also been raised in relation to those studies in which signal and noise dots could be distinguished on the basis of other attributes, such as colour, contrast or luminance, which also facilitate performance (Edwards & Badcock, 1996). This is not possible in stimuli in which signal and noise share common attributes, as in Experiment one. Croner and Albright (1997) similarly suggest that attention may be an important factor in the facilitation of motion detection by segmentation cues. They explained their results using a model in which dots are first segmented on the grounds of colour before global motion is analysed. However, this model would predict facilitation even when some of the noise dots were presented in the same colour as the signal dots, in contrast with the findings reported by Edwards and Badcock. Croner and Albright rejected the alternative model, similar to that tested here in terms of disparity, in which the motion detectors themselves are tuned for colour. This was primarily on the grounds that no differences have been observed in the responses of MT cells to segmented and non-segmented displays (Croner & Albright, 1995, 1996). Increased activation of a subset of MT neurons, they argued, would be expected in response to segmented stimuli, for which increased sensitivity was observed psychophysically. It should be noted however, that neither of the models proposed by Croner and Albright

can explain why colour facilitates motion in the former but not in the latter condition.

In the current study, the separation in depth between signal and noise would allow observers to base their responses on the motions of dots with the appropriate disparity, in a similar manner to that suggested by Cavanagh (1992), Croner and Albright (1997) and Edwards and Badcock (1996). This explanation does not assume any joint tuning of global motion mechanisms to disparity and direction of motion. Rather, it assumes that the visual system is able to determine the direction of motion of individual dots which are salient as a result of their disparity. This possibility, of course, did not exist in Experiment one, when the signal and noise were intermingled in depth. Disparity tuning would also be expected under this explanation, since increasing the disparity separation between signal and noise dots will increase the salience of the signal dots, up to the magnitude at which diplopia becomes evident.

To explore this further, a third experiment was carried out. In this, we investigated whether coherence thresholds were affected when signal dots were presented on a single plane in front of, behind, or within a three dimensional cloud of noise. Thresholds were lower when the signal dots were presented on a plane in front of the noise volume, than when they were embedded within the noise.

Again, these results may be considered in terms of a simple disparity tuning model. When signal dots were presented with crossed disparities, they would stimulate cells tuned to crossed disparities of the correct magnitude and to the direction of motion of the signal dots. Noise dots with similar disparities, moving in other directions, would be expected to inhibit this response. However, as the majority of noise dots would have disparities different to that of the signal dots and would not therefore be expected to inhibit the responses of cells to the signal dots, coherence thresholds would be expected to be lower than when signal and noise were presented with zero disparity. Similar predictions can be made for when the signal dots were presented with uncrossed disparities, or with zero disparity. This was not observed. A simple model of disparity tuning cannot therefore explain the differences in discriminability of global motion in these stimuli.

These results can again be explained, however, in terms of the attention-based system referred to above. When the signal dots were presented in front of the noise dots, it would have been possible for observers to segment the signal from the noise and thus to attend to the signal dots. These results showed a marked asymmetry with respect to disparity, suggesting that it was easier to perceive the motion of signal dots which were in front of the cloud of noise dots, than those which were behind the noise dots. This type of asymmetry in performance for stimuli of this nature has been noted before. For example, Lehmkuhle and Fox (1980) reported that masking effects may decrease when a target is presented in front of a mask, but not when it is presented behind

the mask (the 'front effect'). Other researchers have also found that stimuli presented closer to an observer may be processed more readily than similar stimuli presented further away (Fox & Patterson, 1981).

The lack of disparity-motion tuning found in the current study seems surprising in light of the physiological work that motivated our investigation. However, other psychophysical studies have found similar results. For example, Hiris and Blake (1996) found that direction repulsion effects occurred regardless of whether two motion signals were presented with the same or different disparities. They concluded that the process responsible for direction repulsion occurs prior to selectivity for binocular disparity. McKee et al. (1997) reported that the trajectory of a dot in three dimensions through a three-dimensional random dot pattern was no better than the detectability of the trajectory of a dot in a two-dimensional plane, despite the lower density of dots in three dimensions in the former case.

The most likely anatomical site for the detection of global motion in RDKs is area MT (Newsome & Paré, 1988). Single cell recordings in this area have revealed cells that are tuned both to the direction of motion and to the sign of binocular disparity (Maunsell & Van Essen, 1983). Further, it has been observed that the inhibition of the response of an MT cell to motion in its preferred direction, presented at its preferred disparity, is strongly reduced for motions in other directions if they are presented at a different disparity (Bradley et al., 1995). This latter result leads to the prediction that the effect of noise on global motion processing would depend on the relationship between the disparities of the signal and noise stimuli. This was not found when the signal was presented amongst noise with a distribution of disparities. However, the disparity tuning found by Bradley et al. has been observed psychophysically in studies using transparent motion stimuli. Qian, Andersen and Adelson (1994) showed that the perception of transparent motion may be enhanced if opposite directions of motion are presented at different disparities. Similarly, Hibbard and Bradshaw (1998) showed that the detectability of transparent motion is enhanced if two opposite directions of motion are presented with different disparities and that this facilitation exhibits disparity tuning. Therefore, the functional significance of the disparity motion tuning found in cells in the dorsal visual pathway may reflect mechanisms which detect transparency or depth boundaries.

Certainly there is now an extensive body of psychophysical evidence from a range of paradigms which shows links between the processing of motion and binocular disparity. Anstis and Harris (1974) for example, demonstrated directional motion after effects which were contingent on disparity and depth/disparity after effects which were contingent on the direction of motion (Smith, 1976; Verstraten, Verlinde, Fredrickson & van de Grind, 1994; Patterson, Bowd, Phinney, Fox & Lehmkuhle, 1996).

Bradshaw and Rogers (1996) have shown cross modality adaptation and subthreshold interaction, between depth from disparity and from motion parallax (see also Graham and Rogers, 1982a,b). Bradshaw and Cumming (1997) demonstrated that the direction of motion can help solve the stereoscopic correspondence problem. Finally, in a depth judgement task, Johnston, Cumming and Landy (1994) demonstrated that the visual system can exploit the simultaneous presence of disparity and motion cues to recover perceived shape accurately, whereas shape judgements based on either cue in isolation are subject to systematic distortions.

In conclusion, we report the results of three experiments in which the effects of binocular disparity on the discrimination of the global direction of motion in RDKs was investigated. In the first experiment, we found no facilitation of global motion discrimination for a signal which was embedded in a three-dimensional cloud of dots. In the second experiment, signal and noise dots were presented on two planes, separated in depth. Here, clear disparity tuning was observed and the lowest thresholds were observed when the signal and noise dots were separated by a disparity of 10 arc min. In the third experiment, the noise dots were again presented in a three-dimensional volume. When the signal dots lay on a plane in front of this noise, lower coherence thresholds were observed than when the signal dots lay on a plane embedded within the noise. Two possible explanations of these effects were contrasted: that global motion processing is tuned for binocular disparity, or that facilitation is provided indirectly via an attention-based mechanism which identifies and tracks signal dots that are salient as a result of their disparity. When the results of all three experiments are taken into account, the attention-based account provides the more consistent explanation.

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