

Interocular velocity difference contributes to stereomotion speed perception

Kevin R. Brooks

Experimental Psychology, University of Sussex, Brighton, UK



Two experiments are presented assessing the contributions of the rate of change of disparity (CD) and interocular velocity difference (IOVD) cues to stereomotion speed perception. Using a two-interval forced-choice paradigm, the perceived speed of directly approaching and receding stereomotion and of monocular lateral motion in random dot stereogram (RDS) targets was measured. Prior adaptation using dysjunctively moving random dot stimuli induced a velocity aftereffect (VAE). The degree of interocular correlation in the adapting images was manipulated to assess the effectiveness of each cue. While correlated adaptation involved a conventional RDS stimulus, containing both IOVD and CD cues, uncorrelated adaptation featured an independent dot array in each monocular half-image, and hence lacked a coherent disparity signal. Adaptation produced a larger VAE for stereomotion than for monocular lateral motion, implying effects at neural sites beyond that of binocular combination. For motion passing through the horopter, correlated and uncorrelated adaptation stimuli produced equivalent stereomotion VAEs. The possibility that these results were due to the adaptation of a CD mechanism through random matches in the uncorrelated stimulus was discounted in a control experiment. Here both simultaneous and sequential adaptation of left and right eyes produced similar stereomotion VAEs. Motion at uncrossed disparities was also affected by both correlated and uncorrelated adaptation stimuli, but showed a significantly greater VAE in response to the former. These results show that (1) there are two separate, specialised mechanisms for encoding stereomotion: one through IOVD, the other through CD; (2) the IOVD cue dominates the perception of stereomotion speed for stimuli passing through the horopter; and (3) at a disparity pedestal both the IOVD and the CD cues have a significant influence.

Keywords: binocular vision, motion adaptation, motion in depth, speed discrimination, velocity aftereffect

Introduction

When an object directly approaches an observer (or vice versa) both monocular and binocular visual cues to motion are available. It has long been known that binocular cues alone are capable of providing a convincing motion in depth (MID) percept (Wheatstone, 1852), and it has also been shown that for small, rapidly moving objects, monocular cues (e.g., image expansion/contraction) should be relatively ineffective compared to binocular cues (Regan & Beverley, 1979). Two distinct binocular correlates of MID, or “stereomotion,” exist: the changing disparity (CD) and the interocular velocity difference (IOVD) cues. As an object's distance from the observer changes, so does its disparity (relative to other binocularly visible static features). The rate of change of disparity over time gives a cue to stimulus speed, which will henceforth be referred to as the CD cue. This system is represented in Figure 1a. It should be noted that in this system a motion signal is not derived until after the stage of binocular combination, presumably at or beyond V1.

Simultaneously, each monocular retinal image moves at a different velocity. Specifically, for an object approaching the binocular along the midline, monocular speeds will be the same, albeit in opposite directions. The magnitude of these opposing monocular motion signals will give the IOVD cue to stereomotion speed. This

system is represented in Figure 1b. Here two independent motion signals must be derived before binocular combination, possibly in V1, and compared in the higher visual areas. This study intends to determine the relative potency of the two cues using a velocity aftereffect (VAE) paradigm.

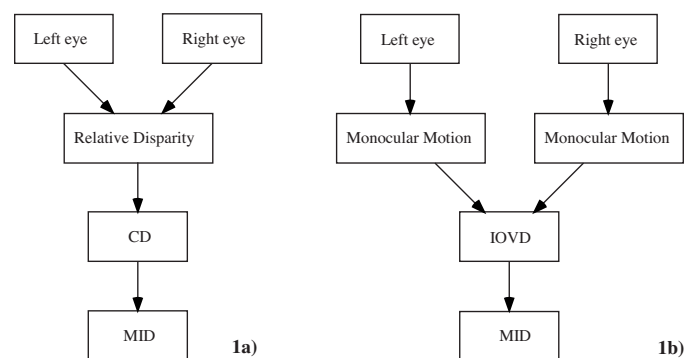


Figure 1. Hypothetical mechanisms for the perception of stereomotion processing: a. Changing disparity. b. Interocular velocity difference.

In natural examples of MID, the IOVD and CD cues correspond perfectly; therefore, their relative contributions to the processing of stereomotion have long remained obscure. More recently, psychophysicists have attempted to parse the two with the use of stimuli that

selectively omit one cue or the other. Stereomotion can be simulated in a random dot stereogram (RDS) by moving the central stimulus patch in opposite directions, and hence changing its disparity relative to other binocularly visible features. However, it is possible to create a stimulus that lacks IOVD cues if a new random array of dots is created in each frame, correlated between the two eyes to give the correct disparity for that moment in time. Though each eye sees a featureless field of dynamic random noise, and hence no coherent monocular motion, the central patch does contain a consistent rate of change of disparity. This stimulus is known as a dynamic random dot stereogram (DRDS). Similarly, the RDS can be adapted to provide a stimulus with IOVD, but no coherent CD cues, by generating each monocular random dot image independently, and therefore, removing any consistent disparity information. This stimulus will be referred to as an uncorrelated random dot stereogram (URDS).

In the context of stereomotion detection, several studies have indicated the superiority of the CD cue since RDS detection thresholds were no lower than those for DRDS stimuli (Cumming & Parker, 1994; Gray & Regan, 1996). Data supporting the use of the CD cue in stereomotion detection have been presented by Harris and colleagues (Harris, McKee, & Watamaniuk, 1998; Harris & Sumnall, 2000), who report that during a visual search task, the detection of a pure stereomotion stimulus is more drastically affected by disparity noise dots than is monocular (lateral) motion. More recently, demonstrations of MID perception from URDS stimuli have suggested that IOVD does have a role to play (Howard, Allison, & Howard, 1998; Shioiri, Saisho, & Yaguchi, 2000; Allison, Howard & Howard, 1998). However, concerns have been voiced that these results are due to detection of the changing disparity of randomly matched dots (Howard et al., 1998; Allison et al., 1998).

The situation for the encoding of stereomotion speed may be different. The finding that for an RDS stimulus, stereomotion speed discrimination thresholds were lower than those for DRDS has suggested that IOVD plays a pivotal role in the encoding of stereomotion speed (Harris & Watamaniuk, 1995). However, Portfors-Yeomans & Regan (1996) find equivalent performance for “cyclopean” (DRDS) and “monocularly visible” stimuli (see also Portfors & Regan, 1997).

Here adaptation is used to elucidate the mechanisms involved in 3D speed perception. Adaptation effects on perceived speed, in the case of lateral motion, have been established for many years (e.g., Wohlgenuth, 1911; Gibson, 1937; Thompson, 1981). After adaptation to a moving stimulus, a subsequently seen stimulus travelling in the same direction is seen as travelling at a reduced rate (compared to its unadapted perceived velocity). This is known as a velocity aftereffect (VAE). The experiments presented here intend to test for just such a phenomenon in the stereomotion domain.

Effects of adaptation on stereomotion perception have been described previously. Beverley and Regan (1973a,b) and Regan and Beverley (1973) showed evidence of detection threshold elevation after prolonged exposure to a stereomotion stimulus that oscillated toward and away from the observer. A motion aftereffect has been demonstrated for stimuli that rotated in depth by Smith (1976) and by Webster, Panthradil, and Conway (1998). However, these experiments do not allow us to distinguish between the possible cues to stereomotion, since the adapting and test stimuli all featured both CD and IOVD cues. Here, comparisons will be made between stereomotion stimuli presented before and after substantial adaptation to either RDS stimuli (containing both IOVD and CD cues) or URDS stimuli (containing only the IOVD cue). It is intended that the relative contributions of CD and IOVD cues can be estimated from the ability of these types of adaptation stimuli to cause a VAE.

Experiment 1

The goal of this experiment is to establish a VAE from prolonged adaptation to unidirectional stereomotion in a conventional, binocularly correlated RDS. Demonstration of such an effect would be indicative of a specialised stereomotion speed mechanism. Also, by attempting to induce a VAE using interocularly uncorrelated stimuli (lacking coherent disparity information), the importance of differential monocular motion signals in stereomotion speed perception can be assessed. If IOVD has no role to play, then such uncorrelated adaptation should be entirely ineffective. However, if IOVD is the sole salient cue, then this uncorrelated adaptation should be as effective as the correlated adaptation. The effect of both binocular adaptation conditions on the perceived speed of monocular/lateral motion was also assessed to ensure that both adaptation stimuli are equally effective in this respect.

However, a stereomotion adaptation effect from uncorrelated stimuli may not, by itself, be sufficient to convincingly demonstrate an influence of IOVD in the perception of MID, since it is possible that subjects were (consciously or otherwise) attending to one monocular image alone. However, there is a possibility that our adaptation could adapt the IOVD unit, which would manifest itself in a more profound adaptation for the stereomotion condition, compared with monocular speed discrimination. For this reason, statistical tests compare the size of the adaptation in the uncorrelated monocular and stereomotion conditions. Any such difference would indicate the existence of a specific IOVD mechanism, discounting the possibility that observers based their responses solely on the properties of monocular half-images.

Control tests were also performed to assess the possibility that stereomotion phenomena from uncorrelated stimuli in this and other studies are due to CD cues through random dot matching (Howard et al., 1998; Allison et al., 1998). Though our uncorrelated binocular stimulus contained no coherent disparity information, this does not prevent disparities arising in the stimulus through random correspondences of individual monocular features, such as dots or edges. Despite the fact that the mean disparity of these troublesome random correlations at any instant is zero, the opposite motions of each dot pattern could produce a consistent CD signal. Each randomly correlated feature will have the same speed and trajectory in 3D as specified by its CD cue. The control experiment assessed the relative effectiveness of adaptation using stimuli either with or without the possibility of random correspondences between monocular features. To achieve this, interocularly uncorrelated stimuli that were only monocularly visible for half of the total adaptation period were used. In one condition, adaptation was simultaneous (with both eyes receiving stimulation simultaneously for 2.4 s, then neither one receiving any stimulation), whilst in the other, adaptation was sequential (L eye adapts for 2.4 s whilst R eye is not stimulated, then R eye adapts for 2.4 s whilst L eye is not stimulated). Both stimuli should provide equivalent monocular adaptation, but only the simultaneous condition could possibly give rise to any random correspondences. If IOVD per se is a genuine force in MID perception, then the degree of VAE produced should be comparable for these two control conditions. If, instead, the observed adaptation in uncorrelated RDS is merely due to random correspondences, then there should be no sign of adaptation in the sequential condition.

Methods

Apparatus and Stimuli

A PC-compatible computer equipped with a super-VGA display card was used to generate the left and right halves of each stereo image side by side on a NEC Multisync Plus colour monitor running at 60 Hz. Subjects viewed the two images through a mirror stereoscope (adjusted to give convergence appropriate for the viewing distance of 1.8 m, whilst maintaining the line of sight perpendicular to the display surface, to avoid unwanted vertical disparities). A partition was placed in the median plane between the stereoscope and the screen to ensure that each eye saw only the appropriate monocular image. The mean luminance of the screen was 50 cd/m^2 , and all tests took place in a darkened room. Responses were

recorded from a two-button response box connected to the computer's game port.

The stimuli used for this experiment were all RDSs in which all motion was displayed within a fixed aperture, as shown in Figure 2. This stimulus allowed us to avoid the possibility that observed adaptation was due to a change in the disparity of features other than those defined by luminance boundaries (e.g., Ramachandran, Rao, Sriram, & Vidyasagar, 1973; Rogers, 1987; Halpern, 1991). Such features, it has been shown, can produce an MID percept (Lee, 1970; Prazdny, 1984).

In each stereo half-image, the background pattern, which filled the 8.89×5.81 deg (visual angle) screen, comprised interocularly correlated 50% density bright/dark dots at a Michelson contrast of 80%, each subtending 4.2×3.6 min arc (an 8×8 pixel square). It featured two rectangular apertures, displayed at screen mean luminance, each subtending 2.24×1.93 deg. These were immediately above and below a small high-contrast fixation cross located in a rectangle also at mean luminance. All of these features were in identical positions in each stereo half-image, and hence were located binocularly in the fixation plane. Nonius lines were also provided on each side of the cross as a fixation aid and a vergence control. Target dot patterns were presented either in the upper or lower aperture, had the same dot size, density, and contrast as the background, and left no visible gap between themselves and the background pattern.

Standard and adaptation stimuli were presented immediately above the fixation point, while test stimuli appeared immediately below the fixation point. Adaptation sequences were identical for both monocular and stereomotion speed discrimination tasks. Adaptation consisted of smooth unidirectional motion in each eye for 800 ms, following which the stimulus instantaneously returned to its original position and repeated the sequence. Both retinal images of the adaptation stimulus drifted in a temporal direction, simulating approaching motion, as did standard and test stimuli. Initial adaptation lasted 60 s (75 repetitions), while top-up adaptation (presented before every trial except the first) lasted for 8 s (10 repetitions). An adaptation speed of 0.525 deg/s (higher than any test speed) was chosen in view of the fact that adaptation stimuli slower than test speeds can produce a VAE of increased speed under some circumstances (Rappoport, 1964; Clymer, 1973; Thompson, 1981). Though some observers reported a degree of diplopia at the start and end of each sequence at this adaptation speed, this stimulus provided a convincing impression of MID. An interval of 200 ms, during which subjects saw the blank aperture at screen mean luminance, distinguished the adaptation phase from the standard/test pair.

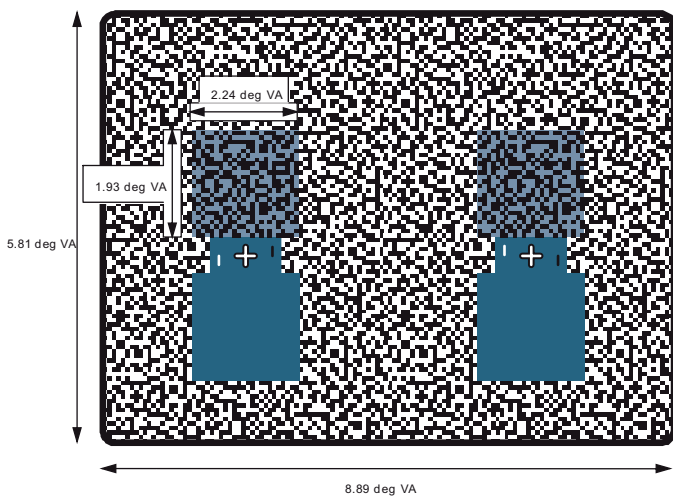


Figure 2. General screen arrangement. Here stimuli are presented in low contrast for identification purposes only. Figure not to scale.

Subjects

Four subjects contributed data in this experiment, after screening for stereoanomalous observers (see Brooks & Mather, 2000). There were two women and two men between the ages of 20 and 30 years. All had normal or corrected to normal vision, and although they were experienced in psychophysical speed discrimination experiments, they were naïve as to the purposes of the experiment. Payment for participation was given on an hourly rate.

Design and Procedure

A two-factor repeated measures design was used, employing the method of constant stimuli. It is assumed that the subjects make comparisons between test and standard stimuli within each trial independently. The two factors were adaptation condition (Baseline, Correlated, and Uncorrelated), and x-axis speed (5 speeds, see below), or stereomotion speed. In the Correlated condition, the adaptation sequence featured an RDS whose elements were matched in each eye, whilst in the Uncorrelated condition, the adaptation stimulus consisted of two entirely independent dot arrays in the stereo half-images. Baseline measures were performed without adaptation stimuli. All three adaptation conditions generated separate psychometric functions for each of the two different tasks: monocular speed discrimination and stereomotion speed discrimination.

Stereomotion speed discrimination

The 5 levels of x-axis speed, determined by previous investigations (see Brooks & Mather, 2000), were 0.105, 0.175, 0.263, 0.350 and 0.394 deg/s. The 5 levels of stereomotion speed to which these monocular speeds correspond were 0.18, 0.3, 0.46, 0.61, and 0.69 m/s at the viewing distance used. The initial and final positions

of all stimuli were equidistant from the fixation plane, and as such, the mean disparity was zero. A two-interval forced-choice procedure was used. On each trial, two binocularly correlated stereo targets were presented, one with both images moving at 0.263 deg/s (the standard) and the other with both images moving at one of the 5 speeds shown above (the test). In each case, the stimulus simulated MID with a trajectory directly along the midline. The test could appear either first or second in the sequence with equal probability on each trial. The subject was asked to indicate with the response box which stimulus appeared to travel faster. Retinal images always moved in a temporal direction. Stimulus duration was constant for all standard and test stimuli at 800 ms with an inter-stimulus interval (ISI) of 200 ms. The next trial was initiated after the subject's response, following an inter-trial interval of at least 1000 ms. In the baseline condition, speed discriminations were completed in 2 blocks of 100 trials. Each block lasted approximately 5 minutes, and one was performed prior to each set of adaptation tasks. In the Correlated and Uncorrelated conditions, tests were performed in 4 blocks of 50 trials. Each block lasted approximately 12 minutes, and a set 1-minute interval was given before the next block commenced. Tests from each of these conditions were performed on separate days to avoid the possible effects of long-term adaptation that have been noted in the stereomotion literature (Beverly & Regan, 1973b). The order of Correlated/Uncorrelated adaptation sessions was randomised between subjects.

Tests were also performed on one subject (T.B.) in which all adaptation, standard, and test stimuli moved nasally, simulating receding motion. All other methodological details remained unchanged.

Monocular speed discrimination

Adaptation stimuli for the monocular speed discrimination trials were identical to those described above for stereomotion speed discrimination. The target stimuli, however, were similar to the stereo images in the stereomotion speed discrimination trials, except that in each trial only one eye was ever stimulated. This was the same eye throughout the entire experiment. Meanwhile, the other eye viewed the background pattern and blank aperture at mean luminance. In all other respects, the procedure was identical to the stereomotion speed discrimination task.

Control for random correlations

Details for these tests are the same as above, except for the following points. Only 3 observers were used, each of whom had contributed data in the previous tests. There were 3 adaptation conditions labelled Baseline, Simultaneous, and Sequential. While the Baseline condition was the same as above, the Simultaneous and Sequential conditions differed in their temporal details. Stimuli from both of these adaptation conditions could

be described as uncorrelated (as defined above) since they both comprised two monocular images with independent random dot arrays. In addition, both presented moving adaptation stimuli for 2.4 s (3 cycles of stimulus motion), followed by no stimulation for 2.4 s (i.e., period = 4.8 s). However, while in the Simultaneous condition, stimulation of both eyes occurred concurrently, in the Sequential condition only one eye was stimulated at any one time. Durations were 96 s for the initial adaptation, and 9.6 s for top-up adaptation. All patterns drifted nasally. In this experiment, the standard and adaptation stimuli appeared in the lower aperture, while test presentations took place above the fixation point. Though extensive monocular data were not collected from the 3 subjects, preliminary tests ensured that both simultaneous and sequential adaptation conditions produced a similar degree of monocular adaptation.

Data analysis

For each subject, the point of subjective equality, or PSE (where responding is at chance levels), was determined after cumulative Gaussian curves had been fitted to the psychometric functions using probit analysis (Finney, 1971). These were then analysed separately for each observer.

Results

Adaptation Effects on Speed Discrimination

Psychometric functions for the discrimination of stereomotion speed can be seen in Figure 3, for all 4 subjects. This shows a shift in the function to the left for both adaptation conditions with respect to the Baseline unadapted results, indicating a reduction in perceived speed.

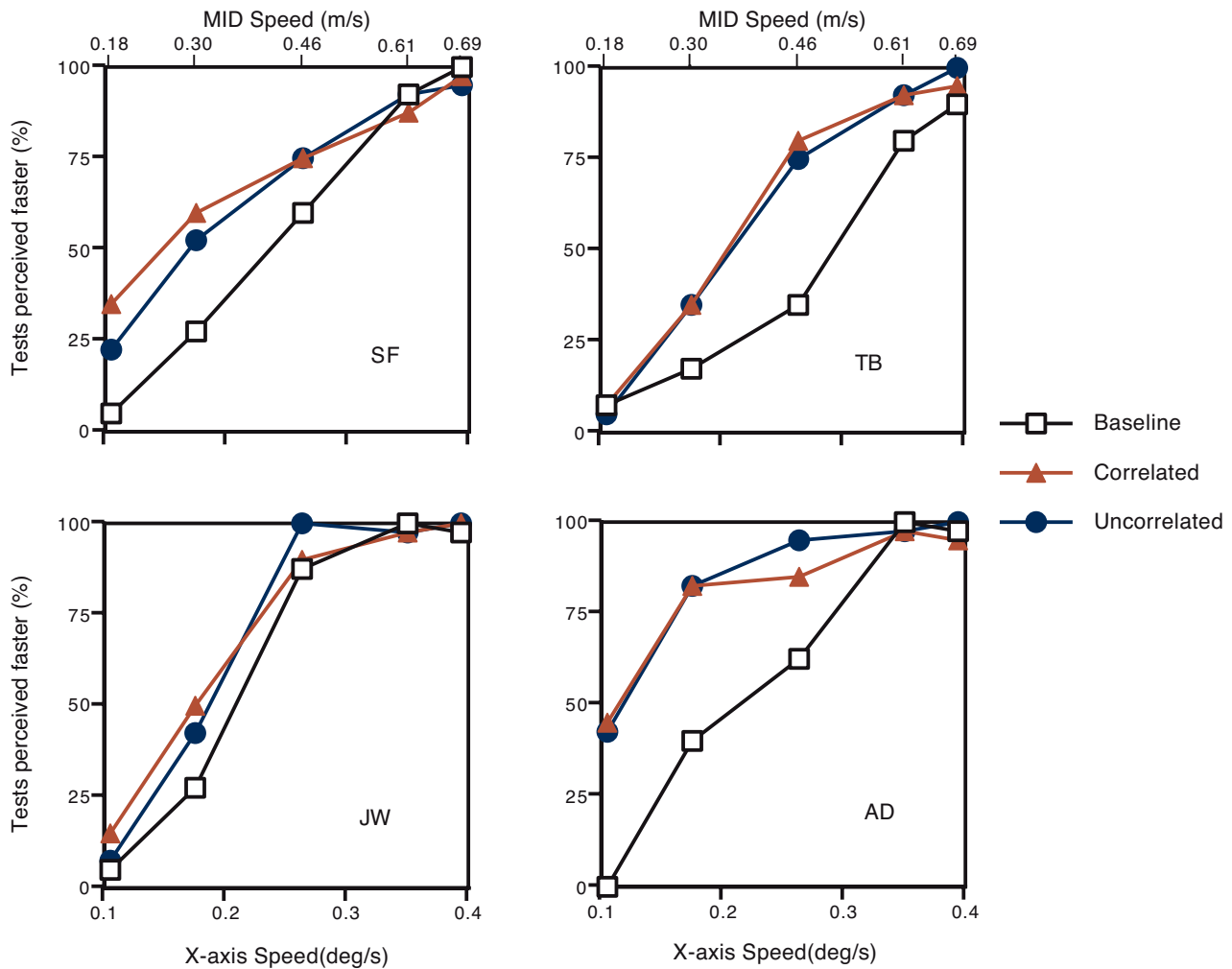


Figure 3. Raw data for stereomotion speed discrimination without adaptation (open squares) or following correlated (red triangles) or uncorrelated (blue circles) adaptation. Psychometric functions are plotted versus x-axis speed of the monocular components of the test stimulus. Speed of motion in depth is indicated above.

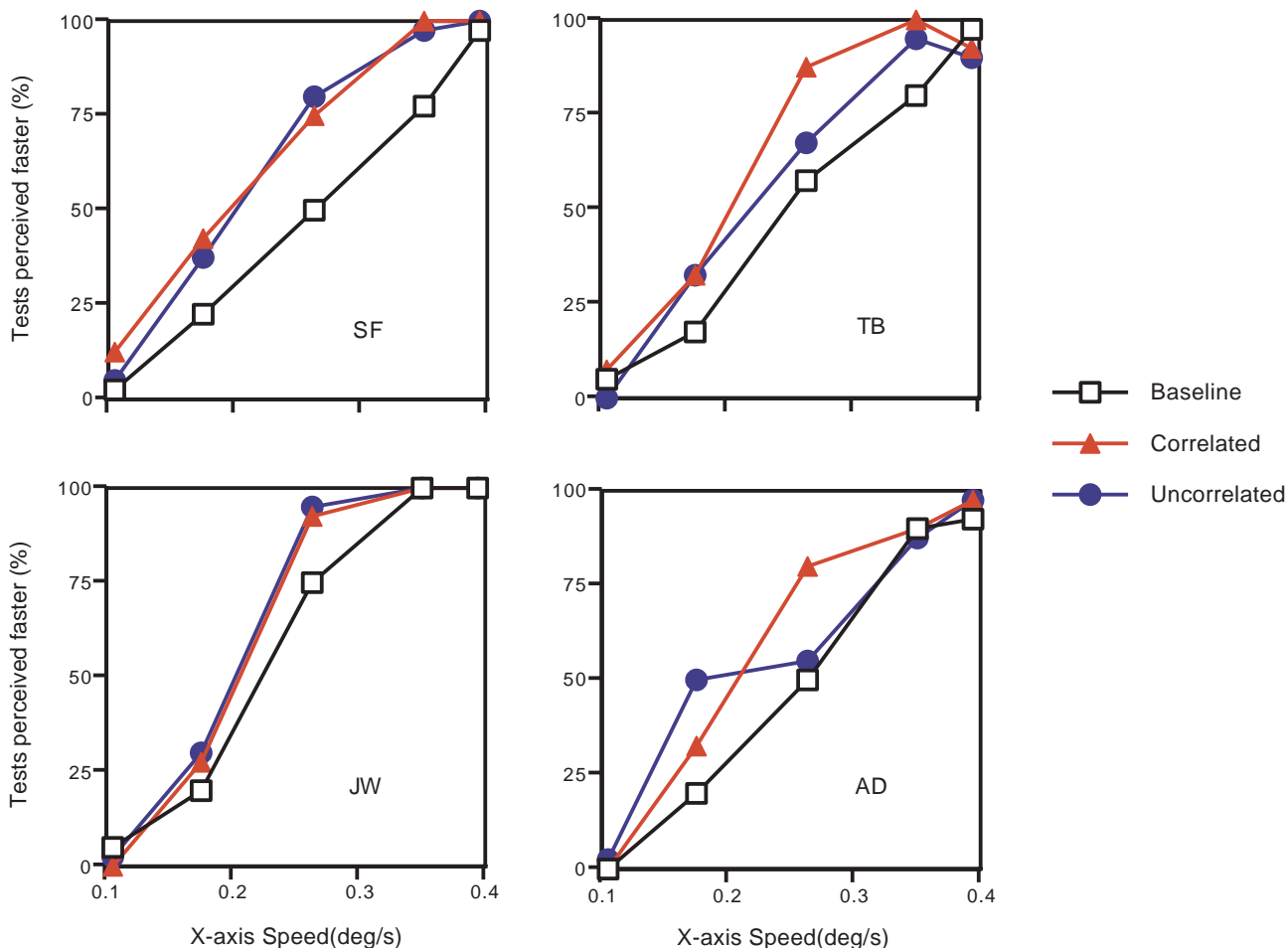


Figure 4. Raw data for monocular speed discrimination without adaptation (open squares) or following correlated (red triangles) or uncorrelated (blue circles) adaptation. Psychometric functions are plotted versus x-axis speed of the test stimulus.

Results from monocular speed discrimination tasks yielded psychometric functions that can be seen in Figure 4. Adaptation had a similar effect to that described above for stereomotion stimuli in that functions for the two adaptation conditions are shifted to the left, compared with the Baseline condition.

For stereomotion speed discrimination, mean PSEs for Baseline, Correlated, and Uncorrelated conditions are 0.233 ± 0.015 (1 SEM), 0.159 ± 0.019 (a 32% reduction), and 0.172 ± 0.019 deg/s (a 26% reduction), respectively. In the monocular conditions, mean PSEs for Baseline, Correlated and Uncorrelated conditions are 0.249 ± 0.009 , 0.206 ± 0.005 (an 17% reduction), and 0.213 ± 0.008 deg/s (a 14% reduction), respectively. These are represented graphically in Figure 5. The data clearly show a similar degree of adaptation when comparing Correlated versus Uncorrelated conditions (regardless of motion type), but a small difference in the size of the adaptation effect across motion type (regardless of the degree of correlation in the adapting stimulus). To test for a significant increase in the VAE across motion type, the results for Uncorrelated conditions were analysed independently for each subject using a one-tailed within

subjects *t* test. These showed statistically significantly higher stereomotion VAEs for all subjects (S.F.: $p = 0.041$; T.B.: $p = 0.048$; J.W.: $p = 0.016$; A.D.: $p < 0.0005$; $df=6$).

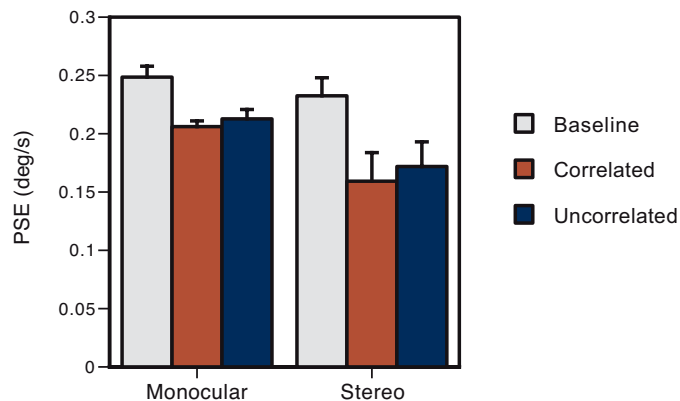


Figure 5. PSE data for all adaptation conditions in stereomotion and monocular speed discrimination tasks. PSEs are represented in deg/s of the monocular components. Vertical error bars mark ± 1 SEM.

Receding Motion: Subject T.B.

Additional tests were also conducted on subject T.B., whose original data can be seen in Figures 3 and 4. In the supplementary stereomotion speed discrimination tests, the conditions were identical to those performed earlier except that now all stimuli (adaptation, test and standard) moved away from the observer. Results of these tests can be seen in Figure 6.

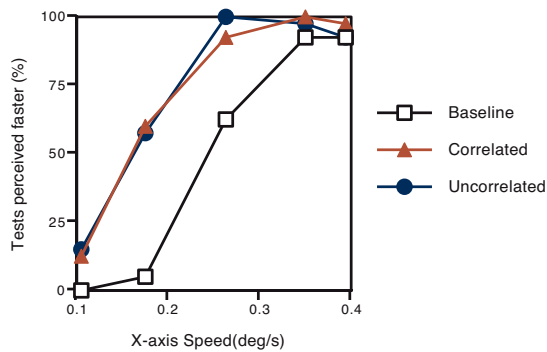


Figure 6. Raw speed discrimination data for subject T.B.: (receding motion) without adaptation (open squares) or following correlated (red triangles) or uncorrelated (blue circles) adaptation. Psychometric functions are plotted versus x-axis speed of the monocular components of the test stimulus.

Informal inspection shows a slightly steeper psychometric function for receding motion compared with the data from Figure 3. Such asymmetries have previously been documented, both in the context of

stereomotion (Beverley & Regan, 1974) and of expansion/optic flow (Perrone, 1986; Edwards & Badcock, 1993). However, the pattern of results is very similar to that shown above for approaching motion. Again, a similar degree of adaptation can be seen, irrespective of the degree of interocular correlation. There is no reason to believe that the processing of receding stereomotion differs from that for approaching motion.

Control for Random Correspondences

Psychometric functions for the discrimination of stereomotion speed can be seen in Figure 7. The curves for the two adaptation conditions are shifted to the left, compared to baseline data, for all 3 subjects. Mean PSEs for the Baseline, Sequential, and Simultaneous conditions were 0.279 ± 0.011 , 0.227 ± 0.005 (a 19% decrease), and 0.204 ± 0.016 deg/s (a 27% decrease) respectively, calculated as before. The PSEs were analysed in a one-way ANOVA for each subject, which showed a statistically significant effect of adaptation condition for each subject (S.F.: $F(2,9)=24.44$, $p < 0.0005$; J.W.: $F(2,9)=133.86$, $p < 0.0005$; A.D.: $F(2,9)=64.59$, $p < 0.0005$). Neuman-Keuls post hoc tests showed that for S.F., the pair-wise comparison of Sequential and Simultaneous data failed to reach statistical significance, while for J.W. and A.D., all 3 comparisons showed significant differences.

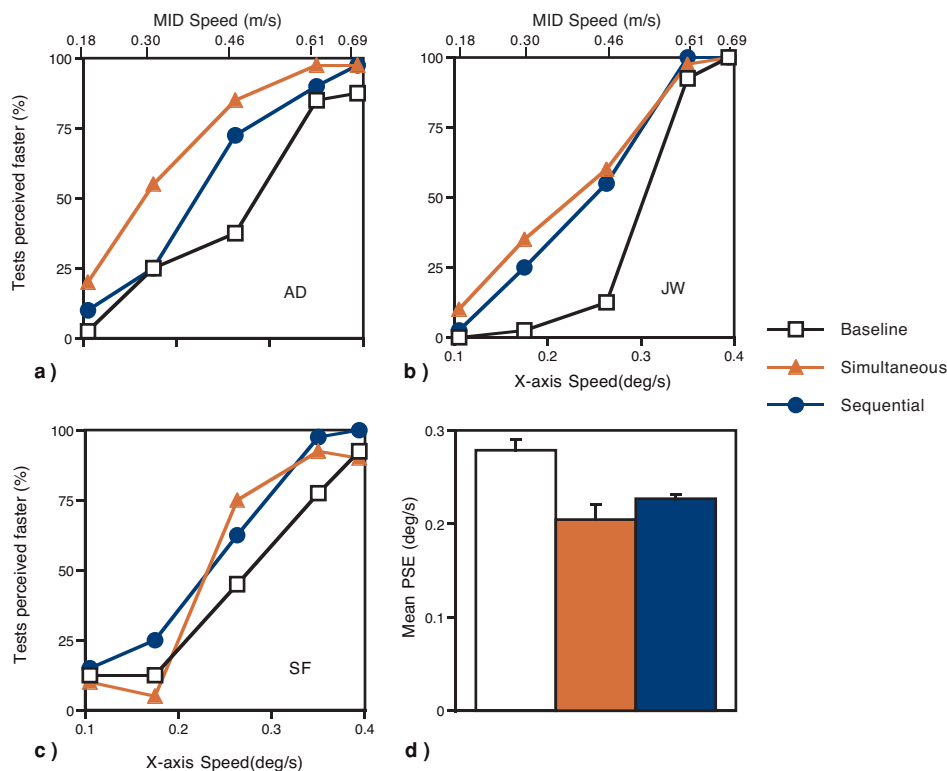


Figure 7. Control experiment data in the form of raw psychometric functions for individuals J.W., A.D., and S.F., and mean PSEs, either without adaptation (open squares) or following Simultaneous (red triangles) or Sequential (red circles) adaptation.

Discussion

Adaptation Effects on Perceived Speed

The data show that binocularly correlated or uncorrelated stimuli are equally effective in causing a VAE in stereomotion stimuli. Adaptation of a CD mechanism is, therefore, not necessary to explain the data. This is clear evidence for the existence of a mechanism that is affected by prolonged exposure to a stimulus that contains IOVD information. The two adaptation conditions are also equally effective in causing a monocular VAE. Though the magnitude of this effect was only assessed in one eye, it is expected that there is a similar monocular effect in each eye simultaneously, irrespective of the effects at other levels at and beyond that of binocular combination. The size of the shift in perceived speed of laterally moving monocular patterns is remarkably similar for each type of adaptation, which is crucial for the generation of the aforementioned hypotheses. Any difference in the effectiveness of these stimuli would have complicated the interpretation of the results of adaptation on stereomotion perception.

Adaptation of CD Mechanisms

The effects of adaptation using either stimulus type on monocular motion perception are entirely equal. The fact that there was no additional effect for the stimulus containing a changing disparity signal could have several interpretations. Firstly, it is possible that the perception of stereomotion speed is based entirely on IOVD, with no contribution from CD units. A second possibility is that though monocular motion mechanisms are easily adapted, CD units require prolonged stimulation. Previous studies that have claimed adaptation of stereomotion units have usually provided adaptation stimuli with a duration far longer than that used in the present study (e.g., [Beverley & Regan, 1973a](#): 15 minutes; [Beverley & Regan 1973b](#): 10 minutes) even though their stimuli contained both IOVD and CD cues. The only study known to this author that attempted to adapt CD mechanisms selectively was [Regan, Portfors, and Hong \(1997](#); see also [Regan, Gray, Portfors, Hamstra, Vincent, Hong, Kohly, & Beverley, 1998](#)), who did not present details of the adaptation duration. If a longer duration is necessary in order to adapt CD mechanisms, then it is not surprising that there was equivalent performance in each case. It must be concluded that both stimuli affected IOVD units to the same degree. The lack of any additional VAE could reflect either an ineffectiveness of this stimulus to cause adaptation to CD units or a lack of influence of CD mechanisms under these conditions.

Adaptation of IOVD Mechanisms

Though the effect of a reduced PSE following adaptation to uncorrelated dot patterns is an entirely novel phenomenon that reinforces the influence of an IOVD system, it could be explained by the adaptation of monocular motion units alone, without the need to appeal to the adaptation of any IOVD mechanism. Consider the hypothetical stereomotion system depicted in [Figure 1b](#). Following adaptation, the responses of monocular motion units will be reduced, presumably due to neural fatigue. When these responses are fed into the IOVD stage, a lower speed of stereomotion will be calculated even if the IOVD unit has not been affected by prolonged stimulation. If this were the case, the MID signal from an IOVD mechanism would be expected to show the same degree of error as that in the monocular signal. If we accept that no adaptation of CD units has taken place, then during test presentations the MID signal from this source alone would be veridical. Overall, we might expect both signals to combine to reach a compromise: a misperception of MID speed less severe than in the monocular case. However, it is interesting to note that the adaptation effect in the 3D case is in fact significantly larger than that for the monocular stimuli. In order to explain this difference between the size of VAE for the two types of motion, we have to consider effects post binocular combination, and in particular, adaptation of the IOVD units themselves. Though adaptation sequences for monocular and stereomotion tasks were identical and should have produced equivalent neural effects, an adapted IOVD unit would not have been consulted when the monocular speed discrimination responses were made. The significantly larger stereomotion VAE can be explained by an additional contribution from an adapted IOVD unit. Furthermore, the significant difference in monocular-stereo VAEs here prevents any possible interpretation of the results in terms of subjects attending and responding purely to monocular velocities.

It has been suggested that an increased VAE in the stereomotion condition might be a result of the adaptation of two independent monocular motion units, followed by a nonlinearity at the site of binocular combination. If this were indeed the case, it would still imply the existence of an IOVD unit comparing two monocular speed measurements, though there would be no need to appeal to any adaptation of this unit. However, previously published data show no significant difference in the degree of misperception of monocular motion and stereomotion speed in response to peripheral presentation when compared across subjects ([Brooks & Mather, 2000](#)), or in response to a contrast reduction when compared within each subject ([Brooks, 2001](#)). Such a non-linearity appears highly unlikely.

Random Correspondences

The control experiment was designed to investigate the possibility that random correspondences between monocular features in our Uncorrelated adaptation stimuli could be responsible for the adaptation effect found in the data discussed above. If such artifacts were responsible for the effect, we would expect the degree of adaptation to vary with the degree of interocular correlation (i.e., a larger effect for 100% correlated stimuli, a smaller effect for randomly correlated stimuli). The fact that no such difference was observed already argues strongly against such an artifact.

In addition, the presence of an adaptation effect for the sequential condition, which prevented any possible random correspondences, strongly supports the claim that a specific IOVD mechanism does exist. Effects of adaptation in this condition could not be explained as artifacts of CD signals from randomly paired dots, since this stimulus precludes any such matching. However, the results can be explained as the result of the reduction (through adaptation) of two separate monocular motion signals, that are then compared binocularly in an IOVD unit, that in turn signals a lower perceived speed of stereomotion.

There is a small but consistent difference between sequential versus simultaneous conditions for 2 subjects (A.D. and J.W.), and, indeed, this did reach statistical significance. This could feasibly be evidence for a small effect of adaptation of CD units in these subjects, which could only be affected by simultaneous stimulation, though in the light of previous data from Experiment 1, it seems unlikely that any such adaptation would have taken place. More likely is the possibility that the simultaneous adaptation stimulus has more opportunity for adaptation since it can stimulate both left and right monocular neurons, and the IOVD neurons for which we saw evidence of adaptation earlier. The sequential adaptation stimulus is unlikely to cause any adaptation to such neurons. In either case, the fact that adaptation is successful without any possible disparity signal shows that adaptation of the IOVD pathway is without doubt the dominant factor in this experiment.

Relationship to Previous Studies

The experiments presented so far prove that monocular motion signals are important in the processing of stereomotion speed information, and hence support the existence of a specific IOVD system. The collective results shown above cannot be accounted for by a CD mechanism.

Previous studies on stereomotion speed discrimination (Harris & Watamaniuk, 1995; Portfors-Yeomans & Regan, 1996; Portfors & Regan, 1997; Brooks and Mather, 2000) have employed methods differing slightly from those used here. Each of these

studies has attempted to ensure that subjects respond to the speed of stereomotion stimuli per se, not to their disparity excursion, by varying stimulus duration. Though, unlike these studies, our stimuli were presented for a constant duration in order to standardise the effect of adaptation, it has been repeatedly demonstrated that for RDS stimuli, subjects ignore changes in stimulus duration and total excursion, and respond on the basis of stimulus speed alone. For this reason, it is valid to compare the results of this study to those previously conducted.

As mentioned earlier, Harris and Watamaniuk (1995) have presented other evidence to support the existence of the use of IOVD in stereomotion speed perception for stimuli with a mean relative disparity of zero. In their study, superior speed discrimination performance was shown for RDS stimuli compared to equivalent DRDS stimuli. However, this study has been criticised on the grounds that the DRDS stimuli lacked visibility for a brief period as they crossed the fixation plane, and their relative disparity was near zero. This difference in visibility, say Portfors-Yeomans and Regan, (1996; see also Portfors & Regan, 1997), is the genuine reason for the performance difference. Portfors-Yeomans & Regan conducted tests away from the horopter where all stimuli were constantly visible and found equivalent performance for “cyclopean” (DRDS) and “monocularly visible” stimuli. For these authors, this was evidence for the importance of the CD cue alone once good visibility was ensured for both stimuli. Recently, Brooks and Mather (2000) have produced evidence of the influence of IOVD on stereomotion speed perception under some circumstances. For a constantly visible RDS with a mean disparity of zero, the perceived speed of stereomotion for peripheral targets was reduced in line with the reduced apparent speed of monocular images, while perceived static disparity remained unaffected. Similar results have been reported when the apparent speed of images, both monocular and stereomotion, was attenuated due to low contrast (Brooks, 2001). Rather than simply eliminating the IOVD cue to changing depth, the experiment presented here sets the two cues in internal conflict to assess their relative contributions. Unlike stimuli from Harris and Watamaniuk (1995), our stimuli remained constantly visible as they passed through zero relative disparity. The effect of visibility cannot account for the discrepancies between this study and those by Portfors-Yeomans and Regan, (1996) and Portfors and Regan (1997).

There is an alternative explanation. Since the Portfors-Yeomans and Regan study manipulated the mean disparity of the stimulus in order to improve visibility, it may be that the cause of the discrepancy between studies is in the range of disparities used, rather than visibility per se. It is possible that the depth region surrounding the zero relative disparity point is an area

over which the CD cue is ineffective. Over this range, IOVD—the only available cue—takes over.

We may be able to reconcile all available results using the idea that only when a stimulus passes through zero relative disparity does the IOVD cue influence stereomotion speed perception. It allows us to accept the continued good discrimination ability shown in RDS stimuli (compared with their temporally uncorrelated DRDS counterparts) even when passing through zero relative disparity as the work of an IOVD mechanism. It can also accommodate the fact that when similar comparisons are performed at disparity pedestals, the difference in performance is much smaller (Portfors-Yeomans & Regan, 1996; Portfors & Regan, 1997) and the phenomenon of apparent slowing of stereomotion due to low contrast images or peripheral presentation (Brooks & Mather, 2000; Brooks, 2001). It is possible that for a short duration the disparities in our stimuli from Experiment 1 were below static disparity detection threshold. Hence inputs to a CD mechanism were impoverished, leading to a reliance on a contribution from the (usually defunct) IOVD source. If this were the case, we should regard the results of the experiments above as reflecting a special case of stereomotion speed processing rather than being generally applicable to all examples of stereomotion.

Experiment 2

In this experiment, the hypothesis that the IOVD cue is used only when the stimulus passes through zero relative disparity is examined, by repeating tests from Experiment 1 using stimuli that do not pass through the fixation plane.

Methods

The details of this experiment are identical to those in Experiment 1 except for the following points. The 3 subjects, J.W., A.D., and S.F., were experienced psychophysical observers, but remained naïve to the purposes of the experiment. All stimuli, with the exception of the uncorrelated adaptation stimulus, were presented with an uncrossed disparity and remained behind the fixation plane for the entirety of their duration. It should be noted that the concept of a disparity pedestal is meaningless in the case of the uncorrelated adaptation stimulus. Though random correspondences again have a mean disparity of zero, the control experiment showed these to be irrelevant to our adaptation. This is the appropriate comparison condition since it contains monocular motion cues identical to those in the correlated case, whilst lacking coherent disparity cues. The mean uncrossed disparity of all stimuli was 12 arc min. In order to prevent diplopia, the stimulus duration was reduced to 400 ms, as was the duration of

one cycle of the adaptation stimulus. In addition, it was decided that the motion should be away from the horopter (receding) in order to make use of the hysteresis of Panum's fusional area (Fender & Julesz, 1967). Initial adaptation for subjects A.D. and J.W. lasted 60 s (150 cycles), and top up adaptation lasted for 8 s (20 cycles). For subject S.F., initial adaptation duration was 120 s, and top up period was 10 s.

Results

Though all subjects showed similar patterns of responding in this experiment, slight differences in stimulus parameters led us to analyse results individually. Data for subject J.W. can be seen in Figure 8. This shows a clear change in the perceived speed of receding patterns following adaptation to uncorrelated stimuli, but an even larger change following correlated adaptation. For the baseline condition, the PSE was 0.217 ± 0.009 deg/s, whilst the PSEs for correlated and uncorrelated adaptation were 0.106 ± 0.015 and 0.149 ± 0.010 deg/s, respectively. A one-way ANOVA showed these results to be significantly different ($F(2,9) = 24.14$, $p < 0.0005$). A Newman-Keuls post hoc test confirmed that all pairwise comparisons showed significant differences. Results for subject S.F. are also shown in Figure 8. The general pattern of results appears very similar to that for J.W., with PSEs for correlated and uncorrelated adaptation at 0.145 ± 0.0130 and 0.182 ± 0.010 deg/s, respectively. The baseline condition showed a PSE of 0.236 ± 0.010 deg/s. Again, a one-way ANOVA found that these results show significant differences ($F(2,9) = 17.53$, $p < 0.0005$). A Newman-Keuls post hoc test confirmed that all pairwise differences between means were statistically significant. For subject A.D., there is a similar, though more exaggerated, pattern of results. A reduction of perceived speed following adaptation is shown, which is very much larger for correlated adaptation than for uncorrelated. In order for probit analysis to find a reasonable fit for the data in the correlated condition, which showed only one data point at less than 100%, the slope of the fit line had to be constrained. It was decided that the curve fit should be forced to have a slope as steep as any in this experiment, in order to produce a PSE that was as high as possible. If anything, this produces an underestimation of the bias in this condition. The PSE for correlated and uncorrelated adaptation is 0.034 ± 0.030 and 0.136 ± 0.010 deg/s, respectively. The baseline PSE was 0.160 ± 0.013 deg/s. A one-way ANOVA indicated a statistically significant effect in these results ($F(2,9) = 11.31$, $p = 0.004$). A Newman-Keuls post hoc test showed that though the difference between Baseline and Uncorrelated conditions did not reach significance, there was a significant difference both between Correlated and Baseline conditions, and between Correlated and Uncorrelated conditions.

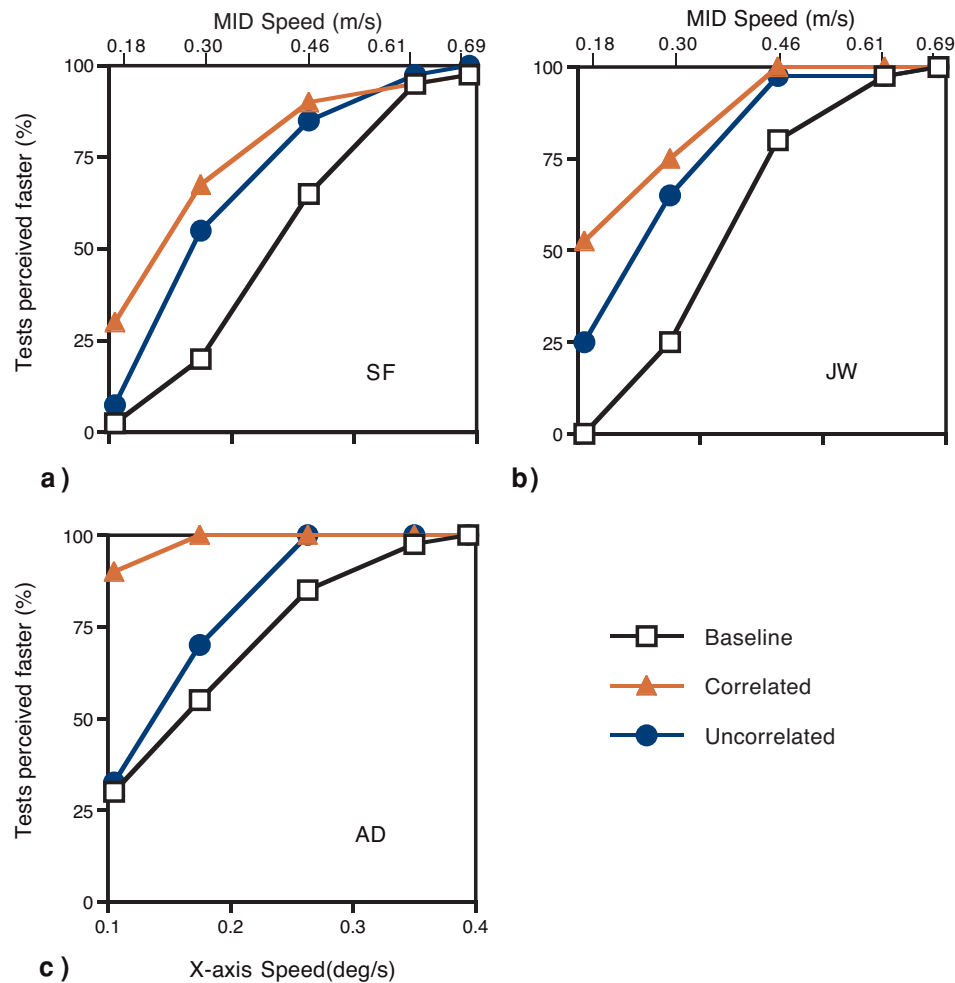


Figure 8. Psychometric functions from Experiment 2 for subject J.W. (a), subject S.F. (b), and subject A.D. (c). Data represent stereomotion speed discrimination performance for stimuli at an uncrossed disparity pedestal without adaptation (open squares) or following correlated (red triangles) or uncorrelated (blue circles) adaptation.

Discussion

It is clear that for stereomotion occurring at entirely uncrossed disparities, uncorrelated adaptation stimuli can cause a VAE, but correlated stimuli are far more effective in this respect. Adaptation of CD units is still not necessary to produce a VAE, since stimuli with no coherent disparity information are effective. By extension, stereomotion speed perception does involve IOVD mechanisms even for motion that remains on one side of the horopter, and does not cross zero relative disparity. However, it is also clear that correlation between stereo half-images can increase the observed adaptation effect. This can only be explained by the additional adaptation of a CD mechanism. Such a mechanism must also make a substantial contribution toward the computation of stereomotion speed for motion at a depth pedestal.

Though subject A.D. fails to show a statistically significant effect for Uncorrelated adaptation in this experiment, there is a clear difference in the two psychometric functions in the predicted direction.

Though one possible conclusion could be that IOVD mechanisms have no effect over this disparity range for this subject, the failure to observe a significant effect does not allow us to conclude that no such effect exists. In view of the pattern of results in Figure 8, it is likely that more extensive testing would allow a significant difference to emerge.

In addition, these results serve to dispel further any concerns about the true binocular nature of the data presented in this paper. The difference in results for the two conditions in Experiment 2 can only be explained by a binocular interaction of some kind, since the concept of degree of interocular correlation (and hence presence of disparity) has no relevance if stimuli are being discriminated purely on the basis of their monocular characteristics.

General Discussion

Experiment 1 showed that IOVD has a significant influence on stereomotion processing for stimuli that

traverse the zero relative disparity point, and that the contributions of CD mechanisms could not be assessed due to a lack of observed adaptation. In Experiment 2, the evidence of adaptation of CD channels throws new light on data from Experiment 1. Though there are slight differences in stimulus parameters, the adaptation durations for Experiments 1 and 2 are similar, which may lead us to believe that it was not the duration but the depth range used that prevented any adaptation from occurring. This supports the theory that CD has little or no influence on stereomotion speed perception for motion passing through zero relative disparity. In contrast, when stereomotion occurs without passing through this area, CD has a substantial influence.

These conclusions have implications for the interpretation of previous studies on stereomotion speed perception mentioned earlier. It would seem that the work of [Harris and Watamaniuk \(1995\)](#) can be seen as appropriate for motion passing through zero relative disparity, despite worries about stimulus visibility. In addition, we can reconcile this with the finding of [Portfors-Yeomans and Regan \(1996\)](#) and of [Portfors and Regan \(1997\)](#), that the CD cue is potent in the processing of stereomotion speed at disparity pedestals. However, the lack of any sign of a contribution of the IOVD mechanism in these studies remains puzzling. It is possible that, though this cue contributes to the speed signal at suprathreshold levels, it has a higher threshold (in terms of detection and of speed difference limens) and hence its contribution is obscured in studies purely taking these measures. Alternatively, the reason for the discrepancy may be a lack of stimulus equivalence in the aforementioned studies. Rather than being strictly RDS targets, the “monocularly visible” stimuli in the latter experiments were DRDS targets presented on either a blank or a static noise background. Though the entire dynamic central patch could be seen monocularly to move across the display, individual dots in this patch did not carry IOVD information; rather, the target patch as a whole carried either a reduced contrast first order monocular motion signal, or a second order motion signal only. At this time, we do not know whether the IOVD system requires first order motion. With an RDS carrying such a monocular signal, speed discrimination performance may have been superior. Based on results reported here, it seems possible that if stimuli were properly balanced, stereomotion speed discrimination thresholds may be slightly lower for RDS compared to DRDS stimuli.

[Brooks and Mather \(2000\)](#) have presented work similar to this study, in that peripheral stimulus presentation caused a similar speed bias for stereomotion speed and for monocular/lateral motion speed. However, the only way to assess the effects on the CD system in their study was to show that an identical manipulation had no effect on perceived depth in static stereo images. As such, this left open the possibility that the CD system

could have been responsible for the effects on stereomotion speed if the inputs to this system were units other than those used to discriminate static disparities. If separate disparity sensitive units with different spatiotemporal parameters were inputs to a CD system, it is possible that the stereomotion bias could have an entirely independent route from the monocular/lateral motion bias in that study, and that an IOVD system was not truly responsible. In a similar study, [Brooks \(2001\)](#) showed that the perceived speeds of stereomotion and monocular motion are also affected in an almost identical fashion by contrast manipulations, but again, one cannot rule out the possible effects of contrast on the CD system. However, in the experiments presented here, this alternative explanation cannot hold. The method of distinguishing effects on IOVD and CD mechanisms by selective adaptation of one or both systems (in conjunction with the control for random correspondences) ensures that the evidence of IOVD influence in Experiment 1 cannot be the result of a CD system with either static or dynamic disparity inputs.

In the perception of motion in depth speed, the human visual system is clearly sensitive not only to the changing disparity (CD) cue but also to that of interocular velocity difference (IOVD). To be precise, we should realise that the latter cue is actually perceived IOVD, since though absolute monocular speeds remained the same, the adaptation altered the neural representation of these monocular velocities, which had effects on higher motion centres. An IOVD mechanism has been demonstrated for stereomotion passing through the fixation plane, for motion either approaching or receding from the observer, and for motion that has a relative disparity always greater than zero. For near-zero disparity stereomotion, the IOVD cue dominates, whilst at an uncrossed disparity pedestal, both the CD and the IOVD cues appear to play a role. Though it has yet to be confirmed experimentally, there seems to be no reason to assume that the case would be any different for motion at entirely crossed disparities.

Many neurophysiological studies have presented evidence of cells selective for stereomotion (in cat area 18: [Pettigrew, 1973](#); [Cynader & Regan, 1978](#); [Cynader & Regan, 1982](#); [Spileers, Orban, Gulyas, & Maes, 1990](#); in cat area Clare-Bishop: [Toyama & Kozasa, 1982](#); [Toyama, Komatsu, Kasai, Fuji, & Umetani, 1985](#); [Toyama, Fujii, & Umetani, 1990](#); and in monkey middle temporal area [MT/V5]: [Poggio & Talbot, 1981](#)). Most of these used noncyclopean stimuli, and hence contain both IOVD and changing disparity cues. As such, it is impossible to tell to which aspect of these stimuli the relevant cells are sensitive. However, [Zeki \(1974\)](#) has presented evidence that relates to this issue, identifying cells in monkey area MT that are selective for opposite directions of motion in each eye, but which do not require any disparity between monocular images (because they were stimulated non-simultaneously). Similar evidence from cells in cat cortical

area Claire-Bishop (Toyama, Komatsu, & Kozasa, 1986), and specifically in the posteromedial lateral suprasylvian cortex (Akase, Inokawa, & Toyama, 1998), has been presented, showing cells with opposite direction selectivity in each eye when tested simultaneously or sequentially. Though it is by no means certain that these cells form part of the IOVD mechanism identified psychophysically here, such a scheme is clearly biologically plausible.

Conclusions

For stimuli passing through the horopter, the IOVD cue dominates the perception of stereomotion speed. However, for stimuli at a disparity pedestal, both the IOVD and CD cues make a significant contribution.

Acknowledgments

The author would like to thank Drs. George Mather, Lee Stone, Brent Beutter, Anton Krukowski, and Stuart Smith for critical insights and frank discussions on earlier drafts. This work was supported by an MRC studentship.

References

- Akase, E., Inokawa, H., & Toyama, K. (1998). Neuronal responsiveness to three-dimensional motion in cat posteromedial lateral suprasylvian cortex. *Experimental Brain Research*, *122*, 214-226.
- Allison, R. S., Howard, I. P., & Howard, A. (1998). Motion in depth can be elicited by dichoptically uncorrelated textures. *Perception*, *27*(Suppl.), 46.
- Beverley, K. I., & Regan, D. (1973a). Selective adaptation in stereoscopic depth perception. *Journal of Physiology*, *232*, 40-41.
- Beverley, K. I., & Regan, D. (1973b). Evidence for the existence of neural mechanisms selectively sensitive to the direction of movement in space. *Journal of Physiology*, *235*, 17-29. [PubMed]
- Beverley, K. I., & Regan, D. (1974). Visual sensitivity to disparity pulses: Evidence for directional selectivity. *Vision Research*, *14*, 357-361. [PubMed]
- Brooks, K. (2001). Stereomotion speed perception is contrast dependent. *Perception*, *30*, 725-731. [PubMed]
- Brooks, K., & Mather, G., (2000). Perceived speed of motion in depth is reduced in the periphery. *Vision Research*, *40*, 3507-3516. [PubMed]
- Clymer, A. B. (1973). The effect of seen motion on the apparent speed of subsequent test velocities: Speed tuning of movement aftereffects. Doctoral dissertation, Columbia University, New York.
- Cumming, B. G., & Parker, A. J. (1994). Binocular mechanisms for detecting motion-in-depth. *Vision Research*, *34*, 483-496. [PubMed]
- Cynader, M., & Regan, D. (1978). Neurons in cat parastriate cortex sensitive to the direction of motion in three-dimensional space. *Journal of Physiology*, *274*, 549-569. [PubMed]
- Cynader, M., & Regan, D. (1982). Neurons in cat visual cortex tuned to the direction of motion in depth: Effect of positional disparity. *Vision Research*, *22*, 967-982. [PubMed]
- Edwards, M., & Badcock, D. R. (1993). Asymmetries in the sensitivity to motion in depth: A centripetal bias. *Perception*, *22*, 1013-1023. [PubMed]
- Fender, D., & Julesz, B. (1967). Extension of Panum's fusional area in binocularly stabilised vision. *Journal of the Optical Society of America A*, *57*, 819-830. [PubMed]
- Finney, D. J. (1971). *Probit analysis*. Cambridge, UK: Cambridge University Press.
- Gibson, J. J. (1937). Adaptation with negative aftereffect. *Psychological Review*, *44*, 222-244.
- Gray, R., & Regan, D. (1996). Cyclopean motion perception produced by oscillations of size, disparity and location. *Vision Research*, *36*, 655-665. [PubMed]
- Halpern, D. L. (1991). Stereopsis from motion defined contours. *Vision Research*, *31*, 1611-1617. [PubMed]
- Harris, J. M., McKee, S. P., & Watamaniuk, S. N. J. (1998). Visual search for motion in depth: Stereomotion does not 'pop-out' from disparity noise. *Nature Neuroscience*, *1*, 165-168. [PubMed]
- Harris, J. M., and Sumnall, J. H. (2000). Detecting 3D motion in static 3D noise: No effect of viewing distance. *Spatial Vision*, *14*, 11-19. [PubMed]
- Harris, J. M., & Watamaniuk, S. N. J. (1995). Speed discrimination of motion-in-depth using binocular cues. *Vision Research*, *35*, 885-896. [PubMed]
- Howard, I. P., Allison, R. S., & Howard, A. (1998). Depth from moving uncorrelated random dot displays. *Investigative Ophthalmology and Visual Science*, *31*(Suppl.), 669.

- Lee, D. N. (1970). Binocular stereopsis without spatial disparity. *Perception and Psychophysics*, 9, 216-218.
- Perrone, J. A. (1986). Anisotropic responses to motion towards and away from the eye. *Perception and Psychophysics*, 39, 1-8. [PubMed]
- Pettigrew, J. D. (1973). Binocular neurons which signal change of disparity in area 18 of cat visual cortex. *Nature New Biology*, 241, 123-124. [PubMed]
- Poggio, G. F., & Talbot, W. H. (1981). Mechanisms of static and dynamic stereopsis in foveal cortex of the rhesus monkey. *Journal of Physiology*, 315, 469-492. [PubMed]
- Portfors, C., & Regan, D. (1997). Just noticeable difference in the speed of cyclopean mid and the speed of cyclopean motion within a frontoparallel plane. *Journal of Experimental Psychology: Human Perception and Performance*, 23, 1074-1086. [PubMed]
- Portfors-Yeomans, C., & Regan, D. (1996). Cyclopean discrimination thresholds for the direction and speed of motion in depth. *Vision Research*, 36, 3265-3279. [PubMed]
- Prazdny, K. (1984). Stereopsis from kinetic and flicker edges. *Perception and Psychophysics*, 36, 490-492. [PubMed]
- Ramachandran, V. S., Rao, V. M., Sriram, S., & Vidyasagar, T. R. (1973). The role of colour perception and "pattern" recognition in stereopsis. *Vision Research*, 13, 503-509.
- Rapoport, J. (1964). Adaptation in the perception of rotary motion. *Journal of Experimental Psychology*, 67, 263-267.
- Regan, D., & Beverley, K. I. (1973). Disparity detectors in human depth perception: Evidence for directional selectivity. *Science*, 181, 877-879. [PubMed]
- Regan, D., & Beverley, K. I. (1979). Binocular and monocular stimuli for motion in depth: Changing-disparity and changing-size feed the same motion-in-depth stage. *Vision Research*, 19, 1331-1342. [PubMed]
- Regan, D., Gray, R., Portfors, C. V., Hamstra, S. J., Vincent, A., Hong, X. H., Kohly, R., & Beverley, K. (1998). Catching, hitting and collision avoidance. In L. Harris & M. Jenkin (Eds.), *Vision and action*. Cambridge, UK: Cambridge University Press.
- Regan, D., Portfors, C., & Hong, X. (1997). Cyclopean mechanisms for the direction of MID. *Investigative Ophthalmology and Visual Science*, 38(Suppl.), 1168.
- Rogers, B. J. (1987). Motion disparity and structure from motion disparity. *Investigative Ophthalmology and Visual Science*, 20(Suppl.), 233.
- Shioiri, S., Saisho, H., & Yaguchi, H. (2000). Motion in depth based on inter-ocular velocity differences. *Vision Research*, 40, 2565-2572. [PubMed]
- Smith, R. A. (1976). The motion disparity aftereffect: A preliminary study. *Vision Research*, 16, 1507-1509. [PubMed]
- Spileers, W., Orban, G. A., Gulyas, B., & Maes, H. (1990). Selectivity of cat area 18 neurons for direction and speed. *Journal of Neurophysiology*, 63, 936-953. [PubMed]
- Thompson, P. (1981). Velocity aftereffects: The effects of adaptation to moving stimuli on the perception of subsequently seen moving stimuli. *Vision Research*, 21, 337-345. [PubMed]
- Toyama, K., Komatsu, Y., Kasai, H., Fuji, K., & Umetani, K. (1985). Responsiveness of Clare-Bishop neurons to visual cues associated with the motion of a visual stimulus in three-dimensional space. *Vision Research*, 25, 407-414. [PubMed]
- Toyama, K., Komatsu, Y., & Kozasa, T. (1986). The responsiveness of Clare-Bishop neurons to motion cues for motion stereopsis. *Neuroscience Research*, 4, 83-109.
- Toyama, K., & Kozasa, T. (1982). Responses of Clare-Bishop neurons to three dimensional movement of a light stimulus. *Vision Research*, 22, 571-574.
- Toyama, K., Fujii, K., & Umetani, K. (1990). Functional differentiation between the anterior and posterior Clare-Bishop cortex of the cat. *Experimental Brain Research*, 81, 221-233.
- Webster, W. R., Panthradil, J. T., & Conway, D. M. (1998). A rotational stereoscopic 3-dimensional movement aftereffect. *Vision Research*, 38, 1745-1752. [PubMed]
- Wheatstone, C. (1852). Contributions to the physiology of vision. II. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 142, 1-18.
- Wohlgemuth, A. (1911). On the aftereffect of seen movement. *British Journal of Psychology Monograph Supplement*, 1, 1-117.
- Zeki, S. M. (1974). Cells responding to changing image size and disparity in the cortex of the rhesus monkey. *Journal of Physiology*, 242, 827-841. [PubMed]