



Direction-selective Coding of Stereoscopic (Cyclopean) Motion

RAYMOND E. PHINNEY,* CHRISTOPHER BOWD,† ROBERT PATTERSON‡

Received 21 April 1995; in revised form 7 November 1995; in final form 21 August 1996

This study employed a selective adaptation paradigm and investigated thresholds for direction discrimination of translational stereoscopic motion (moving binocular disparity information). The stimuli were moving arrays of randomly positioned stereoscopic discs created from disparity embedded in dynamic random-element stereograms. When discrimination thresholds were measured across a range of base directions following adaptation in a fixed direction, discrimination thresholds were maximally elevated 20–30 deg away from adaptation and reduced in the same direction as adaptation. These results are consistent with a distributed-channel model of direction coding and indicate that the direction of stereoscopic motion is encoded by adaptable direction-selective mechanisms similar to those proposed for luminance-defined motion. © 1997 Elsevier Science Ltd. All rights reserved.

Motion perception Direction discrimination Stereoscopic Cyclopean

INTRODUCTION

It is now recognized that motion may be sensed by the displacement of stimulus boundaries defined by differences in binocular disparity (stereoscopic depth), as well as differences in luminance or texture (Cavanagh and Mather, 1989; Patterson *et al.*, 1992). The perception of motion from moving (i.e., translational) binocular disparity information is called *stereoscopic motion*. The perception of stereoscopic motion involves cyclopean information arising centrally at binocular integration levels of vision (Julesz, 1971), the existence of which suggests a central site for motion processing in so far as motion is computed subsequent to disparity (Sekuler, 1975).

The present paper reports the results of a study investigating direction discrimination of stereoscopic motion. We employed motion adaptation as a tool to investigate the degree of selectivity, and the level of processing, of the mechanisms which code for perceived direction of stereoscopic motion. The motivation for this study was similar to the motivation for studies examining direction coding of luminance-domain motion.

One framework for the neural basis of direction coding is a distributed-channel model, in which perceived direction of moving stimuli is coded in the distribution of activity among a population of direction-selective

mechanisms (Levinson and Sekuler, 1976; Marshak and Sekuler, 1979; Mather and Moulden, 1980). In such a framework, detection of motion is based on the activity of the most excited (peak) mechanism (the mechanism whose preferred direction matches the direction of the stimulus), whereas discrimination of differences in the direction of motion is based on the change in activity of neighboring off-peak mechanisms. This is because tuning functions have a steep slope some distance away from their peak and a zero slope at their peak. Small changes in direction will produce large changes in response magnitude from off-peak mechanisms but little or no change from peak mechanisms (Regan and Beverley, 1983, 1985; Wilson and Gelb, 1984).

Evidence for a distributed-channel model comes from adaptation and its effects on discrimination (Regan and Beverley, 1983, 1985). Applying this model to the motion domain, decreasing the responsiveness of mechanisms through adaptation should degrade discrimination some angular distance away from the direction of adaptation (and not in the direction of adaptation). This is because the adapted mechanisms are off-peak mechanisms for directions away from adaptation. The adapted state of the off-peak mechanisms should compromise their ability to differentially respond to two directions of motion, resulting in poor discrimination some distance away from adaptation. Regan & Beverley (1983, 1985) reported such results for spatial frequency discrimination and orientation discrimination.

To test this prediction in the stereoscopic motion domain, this experiment investigated direction discrimination of stereoscopic motion with and without motion adaptation. Discrimination was measured for patterns

*Center for Molecular and Behavioral Neuroscience, Rutgers University, Newark, NJ 07102, U.S.A.

†Department of Psychology, Washington State University, Pullman, WA 99164-4820, U.S.A.

‡To whom all correspondence should be addressed [Email rpatter@mail.wsu.edu].

composed of randomly positioned stereoscopic discs, which moved in a single direction in the X/Y plane. Specifically, direction discrimination was measured from various base directions following adaptation to motion in a fixed direction. The question of interest was whether adaptation would degrade discrimination performance some angular distance away from the direction of adaptation (and not in the direction of adaptation), as predicted by a distributed-channel model.

METHODS

Observers

Three individuals (RP, AW, CB) served as observers. The observers possessed normal or corrected-to-normal acuity (tested by a Bausch and Lomb Ortho-Rater) and good stereopsis (tested by viewing static random-element stereograms in Julesz, 1971). AW and CB were naïve with respect to the purpose of the study, yet they were highly trained psychophysical observers.

Stimuli

Direction discrimination was measured using arrays of randomly positioned stereoscopic discs whose diameter was 0.75 arcdeg, moving in a single direction at 6.11 deg/sec. Approximately 15 discs were visible through a circular aperture at any one time. The stereoscopic discs were displayed with 11.4 arcmin of crossed disparity relative to the display monitor.

Apparatus

A random-element stereogram generation system (Shetty *et al.*, 1979) was used to create the stereoscopic stimuli. Observers viewed a 19-inch color display monitor (Sharp model XM 1900), masked to create the

circular viewing aperture whose diameter was 10 arcdeg, from a viewing distance of 1.5 m. Pixel size (and size of each element of the random-element stereogram) was 5.7 arcmin. The red and green guns of the monitor were electronically controlled by a stereogram generator to produce red and green random-element matrices of 50% density (approx. 5000 elements in each matrix). Stereoscopic viewing was accomplished by placing red and green filters in front of the observer's eyes (anaglyph method). The average luminance of the red half-image (luminance of red elements measured through the red filter) was 3.1 cd/m^2 , while the average luminance of the green half-image (luminance of green elements measured through the green filter) was 7.5 cd/m^2 .^{*} Overall luminance of the stereogram display (without filters) was 25.2 cd/m^2 .

The stereogram generator produced random elements and created disparity, resulting in the production of stereoscopic discs (background elements correlated between eyes). All elements were replaced dynamically with positions assigned randomly at 60 Hz, which allowed for the stereoscopic discs to be moved without monocular cues (Julesz and Payne, 1968). Pairs of modified black and white video cameras, whose scan rate was synchronized to that of the stereogram generator and monitor, scanned two-dimensional arrays of randomly positioned white discs on a black background, moving on a conveyor belt controlled by a d.c. motor. The voltage output from the cameras specified where disparity was inserted in the stereogram. Timing and duration of stimulus presentation were controlled by timers in the stereogram generator. Timing was phase-locked to the start of each raster and was measured in integer multiples of raster frame duration.

Control trials were performed to rule out the existence of monocular cues in our display. Observers wore either red or green filters over both eyes and attempted forced-choice discrimination of the direction of stereoscopic patterns of varying configurations (e.g. squares, arrays of discs, etcetera) that moved either rightward or leftward on each trial. Observers never perceived the patterns and discrimination performance was always at chance level. Such results indicated that monocular cues were not present in our display.[†]

We also examined direction discrimination with luminance-defined stimuli. To generate the luminance stimuli, the stereogram generator was set to luminance mode, in which black discs on a red background were displayed. These stimuli were defined by both luminance and color contrast. The luminance of the black areas was 0.09 cd/m^2 and that of the red areas was 4.7 cd/m^2 , yielding a space-averaged luminance of 4.3 cd/m^2 . The luminance stimuli were 100% detectable to all observers (as were the stereoscopic stimuli).

Procedure

Two kinds of trials were performed, adaptation and non-adaptation trials. On each adaptation trial, the observer viewed three sequentially presented moving

^{*}A control experiment showed that this difference in interocular brightness did not affect discrimination performance. Observers CB and MD were tested under two conditions: when luminance of the red and green half-images was 3.1 and 7.5 cd/m^2 , respectively, as in the main experiment, and when luminance of the red and green half-images was 3.1 and 3.3 cd/m^2 , respectively, which was achieved by placing a 0.35 neutral density filter over the eye receiving the green half-image (observers stated that this value equated the red and green half-images for brightness). Discrimination thresholds were essentially the same with and without the neutral density filter (5.4 and 5.5 deg under the no-filter and filter conditions, respectively, for CB and 3.0 deg under both conditions for MD).

[†]On a related idea, one might argue that adaptation to cyclopean motion produces illusory movement of the luminance elements of the stereogram which somehow affects the direction judgments of the stereoscopic discs. To test this idea, one observer (CB) adapted to stereoscopic motion using procedures similar to those in the main experiment (i.e., 5 min of initial adaptation followed by 1 min of top-up adaptation between trials; six trials performed per condition) and tested for a motion aftereffect by viewing the display either with or without a stationary cyclopean test pattern (when the cyclopean test pattern was absent, the observer viewed only the luminance elements of the display). The duration of the aftereffect was 10.9 sec (SE = 0.3) with the cyclopean test pattern, and 1.1 sec (SE = 0.1) without the test pattern, indicating that adaptation to cyclopean motion produces very little illusory movement of the luminance elements of the stereogram.

random-disc arrays: the adapting array, standard array, and comparison array. First, the observer adapted to the adapting array for an initial period of 5 min with the adapting direction set at 0 deg (rightward toward 3 o'clock). Following this initial adaptation period, discrimination trials (see below) were interspersed with top-up adaptation periods of 10 sec duration (a 500 msec interstimulus interval occurred between adaptation and the beginning and ending of each trial). Following adaptation, the observer viewed two other sequentially presented arrays (standard and comparison arrays, respectively) of the same size, average disc density, and speed moving in similar or different directions and attempted to discriminate their directional difference. The observer's task was to indicate whether the direction of the comparison was clockwise or counterclockwise relative to the direction of the standard. Duration of standard and comparison was 500 msec with a 500 msec interstimulus interval. On each non-adaptation trial, the observer viewed the standard and comparison arrays and attempted to discriminate differences in their direction without prior adaptation. Direction discrimination was measured both with and without adaptation for base directions of 0, 10, 20, 30, and 40 deg clockwise, away from the direction of adaptation.

Owing to the large number of thresholds that had to be collected each session, an abbreviated staircase, developed by Regan and Beverley (1983), was used to track a 79.4% threshold (Weatherill and Levitt, 1965). Each staircase began with a 30 deg angle between standard and comparison with step size equal to 1 deg. After each single correct response, the angular difference between standard and comparison was decreased. After the first incorrect response, the difference between standard and comparison was increased and the staircase was then governed by the following rule: after an incorrect response, the angular difference between directions of motion of standard and comparison was increased; following three consecutive correct responses, the angular difference between standard and comparison was decreased. Four reversals were obtained, with the fourth reversal being taken as the estimate of threshold (see Regan and Beverley, 1983, 1985).

For each session, the order of conditions was randomly determined for each observer. Extensive practice was undertaken by all observers before the start of the experiment so that performance was at asymptotic levels.

Control for orientation cues

Before direction discrimination could be measured, we had to rule out the possibility that pattern orientation cues were used to make the discrimination. If any oriented features were present in the random-disc patterns, observers could have used changes in such features to make the discrimination because the orientation of the array would have changed with direction of motion.

To document the lack of such cues, we performed a control experiment with observers RP and AW. On each trial, the observer was presented with the standard array

followed by the comparison array. In the *motion condition*, the observer was presented with moving arrays and he/she indicated whether the direction of the comparison was clockwise or counterclockwise relative to the direction of the standard (rightward). In the *orientation condition*, the observer was presented with stationary arrays, with the comparison array being a rotated version of the standard array, and he/she indicated whether the comparison was oriented in a clockwise or counterclockwise direction relative to the standard. Here, the standard stimulus was a stationary random-disc array whose orientation was defined arbitrarily as "horizontal" (the array had no oriented features and thus no true orientation) and the comparison was rotated a certain angular amount clockwise or counterclockwise from that orientation. (These stationary arrays were renewed before each stimulus exposure by moving the conveyor belt the same amount as occurs in the motion sequence so that the standard and comparison stimuli were different random-disc patterns.)

Each staircase began with a 45 deg angle between standard and comparison. Step size of the staircase was 5 deg. The staircase was terminated after 12 reversals or when the separation between standard and comparison reached 90 deg. If twelve reversals were achieved, the average of the last six reversals was taken as threshold, otherwise threshold was defined as 90 deg. Four thresholds were obtained under each condition for each observer.

All motion conditions yielded a full staircase of 12 reversals and thresholds of 3.18 deg for RP and 6.67 deg for AW for stereoscopic motion and 2.0 deg for each observer for luminance motion. All orientation conditions produced thresholds of 90 deg (chance performance) because no observer achieved 12 reversals before separation between standard and comparison reached 90 deg.

It is possible that observers might have achieved thresholds of 70% or less, given the opportunity to perform on a less rigorous staircase. To determine if this was possible, RP and AW performed motion vs orientation discrimination with the stereoscopic stimuli in a slightly different manner. The direction or orientation difference between standard and comparison was fixed at 30 deg and the observer performed the discrimination tasks as before (50 trials each of motion and orientation discrimination). Both observers performed perfectly (100%) at motion discrimination and at chance level (46% correct for AW and 44% correct for RP) at orientation discrimination. Finally, RP attempted orientation discrimination with the difference between standard and comparison fixed at 15 deg for the luminance stimuli; performance was at chance level.

This control experiment indicates that orientation cues were minimized or eliminated as a contributing factor to motion direction discrimination.

RESULTS

The four direction discrimination thresholds obtained

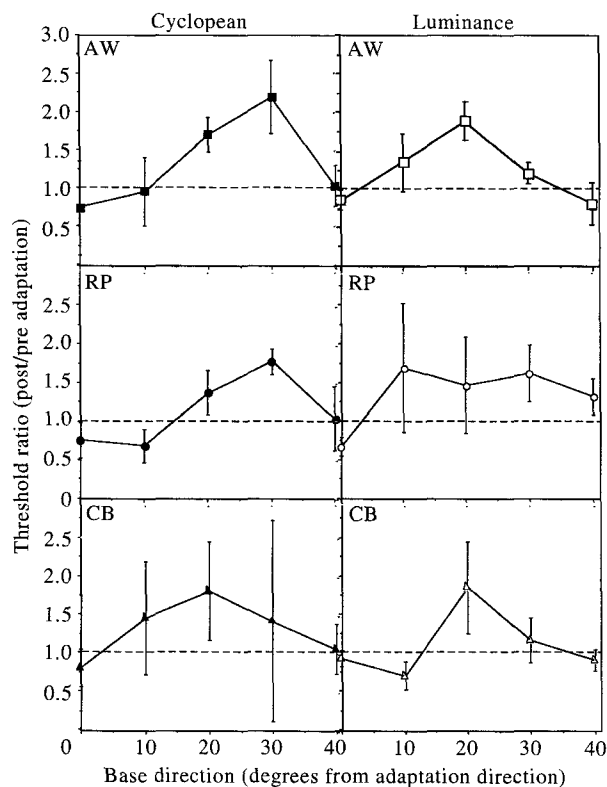


FIGURE 1. Ratio of post- to pre-adaptation thresholds for stereoscopic motion (left-hand panels labeled "cyclopean") and luminance motion (right-hand panels) as a function of angular distance between base direction (i.e., direction from which discrimination was measured) and direction of adapting motion, for three observers. Ratios below 1.0 indicate post-adaptation threshold decreases, while ratios greater than 1.0 indicate post-adaptation threshold increases (ratio of 1.0 indicates that post-adaptation threshold equaled pre-adaptation threshold). Each point represents the mean of four ratio estimates. Error bars equal 1 SEM. Error bars not shown are smaller than the symbol used to plot the point.

under each condition were averaged together for each observer and then across observers to provide an overall estimate of performance. For stereoscopic motion, mean post-adaptation thresholds were 1.7 deg lower than mean pre-adaptation thresholds (5.5 vs 7.2 deg) at the 0 deg base direction, 0.1 deg lower (8.1 vs 8.2 deg) at the 10 deg base direction, 4.2 deg higher (11.3 vs 7.1 deg) at the 20 deg base direction, 4.93 deg higher (11.6 vs 6.67 deg) at the 30 deg base direction, and 0.17 deg higher (10.1 vs 9.93 deg) at the 40 deg base direction. For luminance motion, mean post-adaptation thresholds were 0.59 deg lower than pre-adaptation thresholds (2.58 vs 3.17 deg) at the 0 deg base direction, 0.5 deg higher (4.33 vs 3.83 deg) at the 10 deg base direction, 2.75 deg higher (6.33 vs 3.58 deg) at the 20 deg base direction, 1.0 deg higher (5.42 vs 4.42 deg) at the 30 deg base direction, and

0.67 deg higher (6.5 vs 5.83 deg) at the 40 deg base direction.

To depict the effect of adaptation on threshold, the ratio of post-adaptation threshold to pre-adaptation threshold was computed for each observer and condition individually and displayed in Fig. 1. A ratio less than 1.0 indicates that threshold was lower following adaptation, while a ratio greater than 1.0 means that threshold was higher following adaptation (a ratio of 1.0 indicates that threshold was unchanged following adaptation). Figure 1 reveals that, for all three observers, the shapes of the adaptation tuning functions were similar for stereoscopic motion (left-hand panels labeled "cyclopean" in the figure) and luminance motion (right-hand panels in the figure): post-adaptation thresholds were lower than pre-adaptation thresholds at the 0 deg base direction and maximally higher at the 20 and 30 deg base directions. An analysis of variance supported this trend by revealing that post-adaptation thresholds were lower than pre-adaptation thresholds at the 0 deg base direction (approached significance with $P = 0.057$) and reliably higher at the 20 and 30 deg base directions ($P < 0.005$). There was no reliable difference in threshold ratio between the stereoscopic and luminance stimuli. Thus, the effects of adaptation are the same for the two stimulus types.

Previous work from our laboratory investigating the stereoscopic motion aftereffect in a large number of naïve observers (Patterson *et al.*, 1994) found large individual differences. The present results are quite consistent among observers which is probably due, in part, to extensive practice.

DISCUSSION

Adaptation to stereoscopic motion produces an increase in discrimination threshold when discrimination is measured 20–30 deg away from adaptation, similar to effects induced by luminance motion. As discussed in the Introduction, this is consistent with a distributed-channel model of direction coding. According to this model (e.g. Regan and Beverley, 1983, 1985), decreasing the responsiveness of mechanisms via adaptation should degrade discrimination some distance away from adaptation because the adapted mechanisms are off-peak mechanisms for directions away from adaptation, and it is the off-peak mechanisms which should mediate discrimination performance.

Adaptation to stereoscopic motion produces a decrease in discrimination threshold when discrimination is measured in the same direction as adaptation, also similar to effects induced by luminance motion. This may be explained in the following way. Decreasing the responsiveness of mechanisms via adaptation most likely leads to enhanced discrimination performance in the direction of adaptation owing to the existence of inhibitory interactions among the mechanisms. The most adapted mechanisms are peak mechanisms for that direction and their adapted state would disinhibit the off-peak mechanisms, leading to improved discrimination.*

*In their study of orientation discrimination, Regan and Beverley (1985) and Wilson and Regan (1984) interpreted this threshold depression as produced by improved signal-to-noise ratio rather than by disinhibition. We have no empirical data which would support or refute either of these alternative explanations; we adopt the suggestion of disinhibition here.

The effects of adaptation are direction contingent in this study in so far as adaptation produces an increase or decrease in discrimination threshold, depending upon the base direction from which discrimination is measured. Patterson and Becker (1996) also found evidence for direction-contingent adaptation by showing that perceived direction of stereoscopic motion appeared repulsed away from its true direction following adaptation in a similar direction (repulsion aftereffect). They also found that the perceived angle between two stereoscopic patterns moving in slightly different directions appeared exaggerated (simultaneous contrast effect). The adaptation and contrast effects were direction contingent because they occurred only when the difference between directions of motion was small.

The direction-contingent effects shown in this study and in the Patterson and Becker (1996) investigation suggest that the direction of stereoscopic motion is coded in the responses of adaptable directionally selective mechanisms in ways consistent with a distributed-channel model (Levinson and Sekuler, 1976; Marshak and Sekuler, 1979; Mather and Moulden, 1980).

REFERENCES

- Cavanagh, P. & Mather, G. (1989). Motion: the long and short of it. *Spatial Vision*, 4, 103–129.
- Julesz, B. (1971). *Foundations of cyclopean perception*, Chicago: University of Chicago Press.
- Julesz, B. & Payne, R. (1968). Difference between monocular and binocular stroboscopic movement perception. *Vision Research*, 8, 433–444.
- Levinson, E. & Sekuler, R. (1976). Adaptation alters perceived direction of motion. *Vision Research*, 16, 779–781.
- Marshak, W. & Sekuler, R. (1979). Mutual repulsion between moving visual targets. *Science*, 205(28), 1399–1401.
- Mather, G. & Moulden, B. (1980). A simultaneous shift in apparent direction: further evidence for a “distribution shift” model of direction coding. *Quarterly Journal of Experimental Psychology*, 32, 325–333.
- Patterson, R. & Becker, S. (1996). Direction-selective adaptation and simultaneous contrast induced by stereoscopic (cyclopean) motion. *Vision Research*, 36, 1773–1781.
- Patterson, R., Bowd, C., Phinney, R., Pohndorf, R., Barton-Howard, W. & Angilletta, M. (1994). Properties of stereoscopic motion aftereffects. *Vision Research*, 34, 1139–1147.
- Patterson, R., Ricker, C., McGary, J. & Rose, D. (1992). Properties of cyclopean motion perception. *Vision Research*, 32, 149–156.
- Regan, D. & Beverley, K. I. (1983). Spatial-frequency discrimination and detection: comparison of postadaptation thresholds. *Journal of the Optical Society of America*, 73, 1684–1690.
- Regan, D. & Beverley, K. I. (1985). Postadaptation orientation discrimination. *Journal of the Optical Society of America A*, 2, 147–155.
- Sekuler, R. (1975). Visual motion perception. In Carterette, E. C. and Friedman, M. P. (Eds), *Handbook of perception, Vol 5, Seeing* (pp. 387–430). New York: Academic Press.
- Shetty, S. S., Broderson, A. J. & Fox, R. (1979). System for generating dynamic random-element stereograms. *Behavioral Research Methods and Instrumentation*, 11, 485–490.
- Weatherill, G. B. & Levitt, H. (1965). Sequential estimation of points on a psychometric function. *British Journal of Mathematical and Statistical Psychology*, 18, 1–10.
- Wilson, H. R. & Gelb, D. J. (1984). Modified line-element theory of spatial-frequency and width discrimination. *Journal of the Optical Society of America A*, 1, 124–131.
- Wilson, H. R. & Regan, D. M. (1984). Spatial-frequency adaptation and grating discrimination: predictions of a line-element model. *Journal of the Optical Society of America A*, 1, 1091–1096.