



Behavioral Studies of Local Stereopsis and Disparity Vergence in Monkeys

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Received 27 April 1994; in revised form 19 September 1994

Investigations on macaque monkeys have provided much of our knowledge of the neural mechanisms of binocular vision, but there is little psychophysical data on the accuracy of vergence responses or the precision of stereoscopic depth perception in these primates. We have conducted comparative behavioral studies of binocular disparity processing in rhesus monkeys and humans via measurements of prism-induced fixation disparities (disparity vergence) and relative depth discrimination for spatially localized stimuli (local stereopsis). The results of these studies demonstrated a remarkable similarity in both the oculomotor and the sensory aspects of binocular vision in the two species when the stimulus dimensions were specified in visual angles, which were independent of interocular separation. The disparity vergence functions for the two species revealed fusion responses over the same range of prism-induced vergence and comparable vergence errors for stimuli near their fusional limits. Disparity vergence responses were independent of the spatial frequency of the binocular fusion stimulus. Stereothresholds as a function of the spatial frequency of the difference-of-Gaussian stimuli were of the same form, with equivalent stereoacuties, in monkey and human observers. The presence of substantial vergence errors had only a small effect on the precision of stereoscopic depth perception. We conclude that, after compensation for the differences in the lateral separation of their eyes, the operating characteristics of disparity vergence and stereoscopic vision are virtually identical in rhesus monkeys and humans and, consequently, the performance limits for these visual functions must be determined by anatomical and/or neural constraints that are similar in both species.

Monkey Psychophysics Binocular disparity Stereopsis Disparity vergence

INTRODUCTION

Normal, single binocular vision involves complex interactions between oculomotor and sensory processes to obtain fusion and stereopsis. Many of the physiological mechanisms of these processes have been studied in macaque monkey (e.g. Poggio, Gonzales & Krause, 1988; Zhang, Mays & Gamlin, 1992), but there have been surprisingly few reports on the psychophysical properties of normal binocular vision (stereopsis and disparity vergence) in monkeys. More importantly, even though such data would be influential in defining psychophysiological links for binocular vision, presently available data have not clearly established an equivalence of binocular vision in normal monkeys and humans. The comparison of psychophysical functions of binocular vision in monkeys and humans is especially important because the response properties of binocular vision are directly dependent upon the lateral separation of the eyes,

which is about two times larger in humans than macaque monkeys.

The paramount sensory function of binocular vision is stereopsis. Both local (Sarmiento, 1974) and global (Bough, 1970; Cowey, Parkinson & Warnick, 1975; Harwerth & Boltz, 1979a,b) stereopsis have been demonstrated in monkeys, but stereothresholds in a range that are typical of normal human observers (Westheimer, 1979a) have been reported in only one of these studies (Sarmiento, 1975). In that study, Sarmiento found thresholds for local stereopsis (Howard-Dolman test) that were similar to humans' thresholds for one of his five monkey subjects, while the other four were unable to perform the depth discrimination task well enough to obtain stereothresholds of small magnitude. The data from the one successful subject are important, but *in toto*, Sarmiento's experiments are equivocal with respect to the equivalence of stereopsis in monkeys and humans. Similarly, the equivalence of global stereopsis in monkeys and humans has not been determined. The reported investigations (Bough, 1970; Cowey *et al.*, 1975; Harwerth & Boltz, 1979a,b) have been mainly demonstrations of depth discrimination with random-dot stereograms and the small amount of comparison data

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that is available (Harwerth & Boltz, 1979b) show an apparent superiority of human performance over monkeys.

Convergence, to align the two eyes at the plane of fixation, is the key oculomotor component of binocular vision. The vergence response must be accurate to within the limits of Panum's fusional area to obtain haplopia and fine stereoscopic depth perception. It is generally considered that the total vergence response involves four components (Maddox, 1893), one of which, disparity (fusional) vergence, is driven by binocular, retinal image disparity. Disparity vergence is, therefore, the mechanism which normally eliminates residual vergence errors (Judge, 1991) to establish binocular registration of the retinal images. Behavioral investigations of disparity vergence in monkeys (Boltz & Harwerth, 1979; Boltz, Smith, Bennett & Harwerth, 1980) have demonstrated a similarity in the horizontal and vertical fusion ranges for monkey and human observers, but they have not addressed the accuracy of disparity vergence eye movements. Obviously, as in humans (Ogle, Martens & Dyer, 1967; Schor, 1983; Sheedy & Saladin, 1983), the determination of the accuracy of disparity vergence eye movements would be an important characterization of the normal binocular vision of monkeys.

Based on the previous research, it is quite likely that the motor and sensory components of binocular vision of monkeys and humans will have many common features, however, empirical confirmation from psychophysical measurements of the precision of stereoscopic depth perception and the accuracy of the vergence response is lacking. Because the homology of binocular vision in the two species is the foundation for extrapolating neurophysiological mechanisms to binocular vision functions of humans, we have compared the oculomotor and sensory components of binocular vision in normally reared monkeys and in humans with clinically defined, normal binocular vision. The two disparity processing systems were assessed behaviorally by measurements of prism-induced fixation disparities (disparity vergence) and the discrimination of relative depth for spatially localized stimuli (local stereopsis). In addition, because stereopsis in humans (Julesz & Miller, 1975; Schor & Wood, 1983; Schor, Wood & Ogawa, 1984a; Halpern & Blake, 1988; Legge & Gu, 1989; Wilson, Blake & Halpern, 1991) and possibly, the accuracy of disparity vergence (Frisby & Mayhew, 1980; Mowforth, Mayhew & Frisby, 1981; Schor, Wesson & Robertson, 1986) are dependent upon spatial scale, the spatial frequency dependent responses of these aspects of binocular disparity processing were also investigated. An abstract of the results of these experiments has been published (Harwerth, Smith, Crawford & von Noorden, 1993).

METHODS

Subjects

The animal subjects were four, normally reared, male rhesus monkeys (*Macaca mulatta*), 4–6 yr of age

(designated by subject codes NM-1, NM-2, NM-3, and NM-4). The refractive errors of all four of the monkeys were near emmetropia, as determined by retinoscopy under cycloplegia. Experimental and animal care procedures were in compliance with the NIH Guide for the Care and Use of Laboratory Animals (NIH Publication No. 85-23, 1985). Four humans (subjects NH-1, NH-2, NH-3, and NH-4) with normal binocular vision as defined by standard Snellen acuity, normal stereopsis on clinical tests, and normal heterophoria and fusional vergence measurements, also participated in the experiments. Informed consent was obtained from the subjects and approval from the institutional human experimentation committee was granted for use of human subjects.

Apparatus

During the experiments, the monkeys were placed in a primate chair inside a sound-attenuating chamber. The primate chair was fitted with a response lever on the waist plate and a drink spout on the neck plate. A lens holder and viewing mask were positioned on the chair so that the monkey's eyes were centered in the lens wells when his mouth was on the juice spout. A set of counter-rotating (Risley) prisms were attached to the front of the lens holder to control the vergence demand for binocular single vision. A liquid crystal shutter system was also mounted on the viewing mask device to obtain dichoptic or stereoscopic viewing.

The human subjects were positioned at the correct viewing distance by a table-mounted chin cup and wore goggles with the liquid crystal shutters mounted in the lens wells. Ophthalmic prisms and lenses to correct the subjects' refractive errors were placed in a trial frame inside the goggles.

The dichoptic and stereoscopic stimuli were presented by a stereoscopic video system (Stereographics Corporation 3Display, San Rafael, Calif.) which was effectively a phase haploscope. Alternate, interlaced video frames were presented to each of the eyes with the viewing eye controlled by the electro-optical shutter system mounted on the viewing mask. With the monitor frame rate of 120 Hz, each eye viewed alternate frames at 60 Hz. The stereoscopic and dichoptic stimuli were generated with a high-resolution (1280 × 1024 pixels) graphics board (Pepper board, Number Nine Corporation, Cambridge, Mass.) and presented on a video monitor with a white (P4) phosphor and mean luminance of 14 cd/m². The screen luminance was reduced by approx. 75% when viewed through the liquid crystal shutters. A "milk white" plastic frame was mounted to the monitor to limit the stimulus area to 12 deg horizontally and 9.5 deg vertically at the subject's 114 cm viewing distance.

The stimuli for fixation disparity measurements consisted of a set of dichoptic, square-wave nonius lines flanked by a binocular fusion lock. A diagram of the luminance profile of the binocular fusion lock and a photograph of the visual stimulus are presented in Fig. 1(a). The binocular fusion stimuli were high contrast

(83%), cosine gratings. The central 2 deg of the fusion lock grating was a single cycle of a 0.5 c/deg raised cosine grating on which the nonius targets were presented. The nonius stimuli were drawn into the central region as dark bars 5.5 min arc wide \times 55 min arc high. In order to eliminate extraneous stimulus clues, the position of the upper nonius line (reference stimulus) was varied randomly within the central 1 deg of the stimulus field and the relative contrast of each line was varied randomly by $\pm 30\%$ from trial to trial. The lower nonius line (test stimulus) could be offset to the left or right side of the reference stimulus in 1 pixel (0.56 min arc) increments.

The stimuli used to measure stereothresholds and monocular vernier alignment thresholds were high contrast (100%) spatial frequency filtered stimuli which were mathematically derived from the difference of two Gaussian functions (Schor & Wood, 1983). A diagram of the luminance profile and a photograph of these difference-of-Gaussian (DoG) stimuli are presented in Fig. 1(b). These stimuli are spatially localized with narrow band-pass properties [1.75 octaves at half-height for all spatial frequencies (Wilson & Bergen, 1979)]. The upper (reference) and lower (test) DoG stimuli were separated vertically by 9 min arc. In the stereopsis experiments, the upper (reference) stimulus was positioned laterally at the center of the video screen and the lower (test) stimulus was presented with crossed or uncrossed binocular disparity with respect to the reference. In order to minimize monocular offset cues, the mean position of the test stimulus also was offset randomly (left or right) by either 0.5 or 1.0 times the trial disparity magnitude. The binocular disparity of the stereoscopic stimuli could be positioned with sub-pixel resolution (0.056 min arc) using methods described by Krauskopf and Farell (1991).

For the determination of monocular spatial vision functions, the DoG stimuli were presented as vernier targets for the left or right eye independently. All of the other stimulus conditions were identical for the vernier and stereopsis measurements.

Procedures

The monkeys were trained on a single-response behavioral protocol commonly called a "go/no-go" discrimination paradigm. This task has the essential features of the traditional temporal-interval, two-alternative, forced-choice discrimination procedure often used with human observers, but it is better suited for monkey psychophysics because it requires only a single, trained response. Depending upon the visual function under investigation, the monkeys were required to discriminate either, the direction of offset for the lower test target with respect to the upper reference target (nonius alignment, vernier thresholds), or the relative depth of the lower test target with respect to the upper reference (stereoscopic depth). Each trial started with the onset of an 8 Hz auditory trial cue. Once the trial had started, the monkey's sustained lever press initiated a short orienting interval (1 sec) and, in the fixation disparity experiments, the fusion lock and reference

stimulus were presented. The end of the orienting interval and the beginning of an observation-response interval was signaled by the onset of a second auditory cue (200 Hz tone). At the onset of the observation-response interval, the discrimination stimuli were presented (i.e. the test stimulus in the fixation disparity experiments or both the test and reference stimuli in the stereopsis experiments). The stimulus duration was 250 msec in fixation disparity trials or 1000 msec for stereoscopic depth trials, while the response interval was 1 sec in all trials. At the end of the 1 sec interval, the tones were silenced and the stimulus field was blanked. Correct behavior during the observation-response interval was defined as: (1) a lever release (a "go" response), if the test stimulus was offset to the right-side or in crossed disparity with respect to the reference stimulus; or (2) a maintained lever press throughout the entire interval (a "no-go" response), if the test stimulus was one of the opposite types. Either of these correct behaviors was taken as evidence that the monkey had perceived the offset direction or relative distance of the test stimulus and he was rewarded by a conditioned reinforcer (a tone) and, randomly, with 0.5 ml of orange drink. The opposite pairings of stimuli and responses simply initiated new intertrial intervals, without reward or punishment. Because the monkeys quickly developed response biases if they had a 50-50 chance of reward for either response, a correction routine was included in the procedure. In the correction routine, the stimuli associated with incorrect responses were repeated in subsequent trials until the animal performed the correct operant response, but only the response to the first presentation was rewarded with orange juice or included in the data for psychometric functions.

The correction routine was used in all experiments except for the measurements of fixation disparities during the disparity vergence experiments. The correction routine was not used during these investigations because the determination of fixation disparity was based on the relative locations of dichoptic stimuli which appeared to have identical visual directions for each eye. It was, therefore, impossible to objectively reward these subjective responses because the relationship between perceived direction and physical offset was unknown, yet a consistent rate of reinforcement was necessary to maintain the operant behavior needed for the measurement. In the strategy adopted for these experiments the animals were initially trained to discriminate the direction of nonius offset under monoptic viewing. After they were under stimulus control with each eye, dichoptic nonius alignment trials were interleaved with the monoptic trials. In dichoptic trials, the first five trials at each offset value were reinforced randomly and, subsequently, rewards were based upon the probability the trial response correlated with the responses in previous trials at the same stimulus magnitude. In this way, as long as the animals were unable to differentiate between monoptic and dichoptic trials, the behavioral responses were reinforced without biasing the type of response. Several specific stimulus characteristics, e.g. jitter of the contrast and position of the nonius stimuli, a short viewing duration

(250 msec), and a relatively wide range of nonius offset values, were included to preclude the recognition of monoptic vs dichoptic trials.

Stimulus magnitudes (offset or disparity) were presented in accordance with the method of constant stimuli to generate psychometric functions for the discrimination of direction or depth. In the typical 2-hr daily sessions, the monkeys would run about 1000 trials with 30–35 trials for each of the stimulus magnitudes selected to establish two interleaved psychometric functions. The experimental data were fitted with a logistic function to determine the slope and position

parameters of the psychometric function (Berkson, 1953). The mean and SD of these parameters, across at least three sessions, were used to describe an subject's performance for each of the visual functions that was measured in these experiments.

RESULTS

Disparity vergence

The investigations of disparity vergence eye movements were accomplished by measuring the accuracy of the

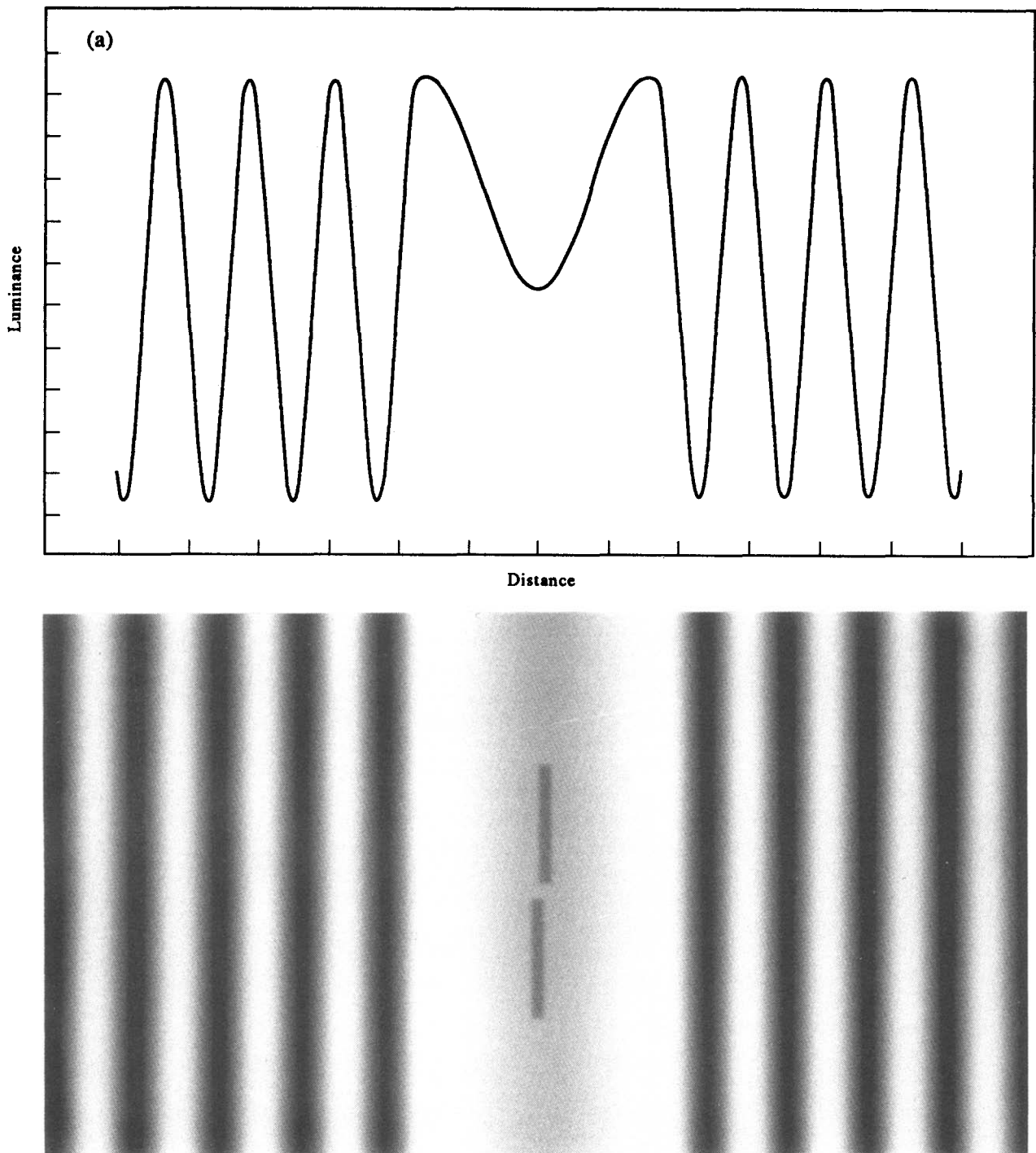


FIGURE 1(a). *Caption on facing page.*

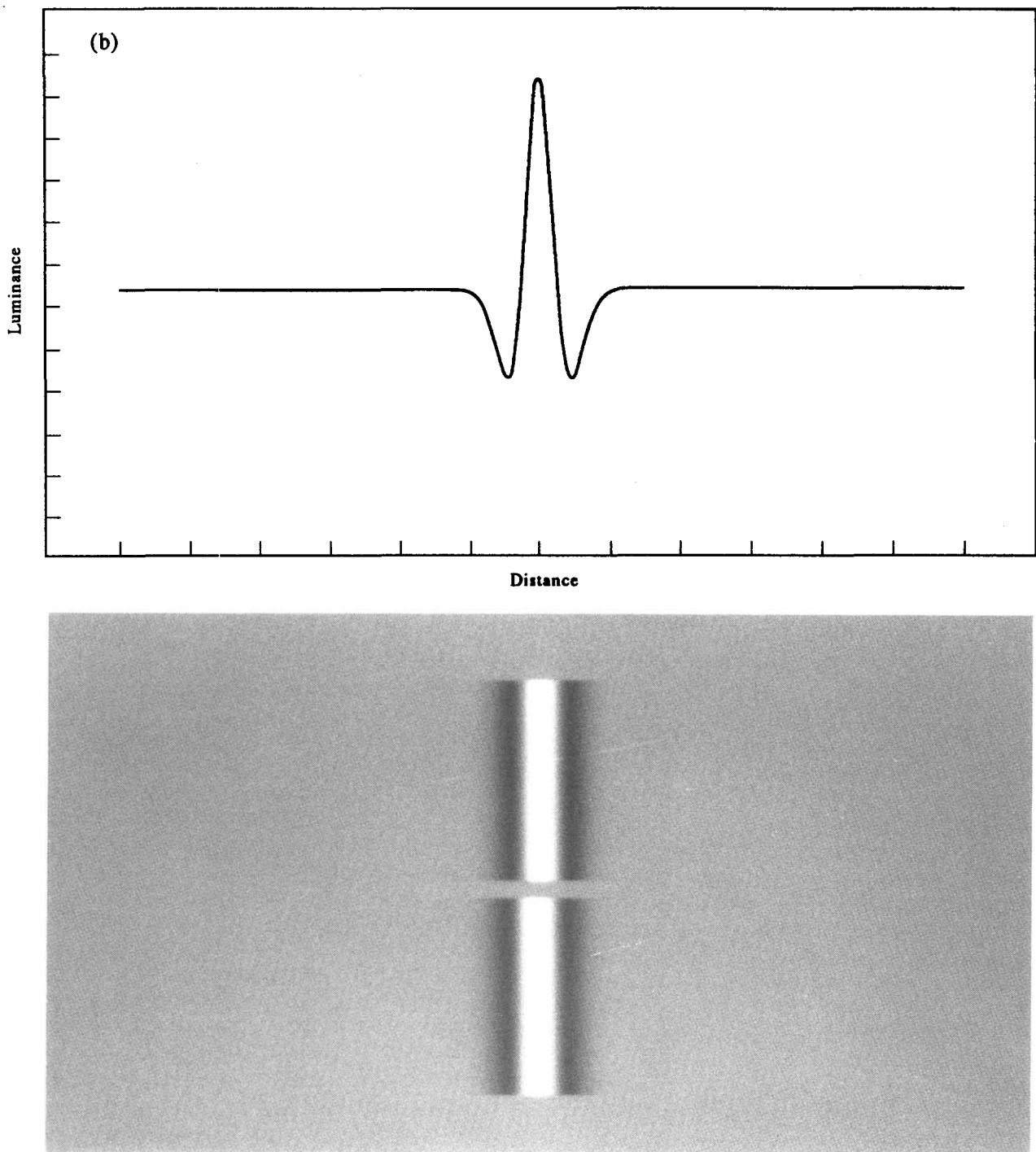


FIGURE 1. Illustrations of the stimulus configurations for measurements of fixation disparity (a) and stereopsis (b). (a) The luminance profile of the binocular grating (fusion) stimulus (upper panel) and a photograph of the binocular fusion stimulus with the dichoptic vernier stimuli for measurements of fixation disparity, superimposed on the central test area (lower panel). (b) The luminance profile (upper panel) and a photograph of the DoG stimuli used for measurements of stereothresholds and vernier thresholds.

fusional reflex induced by ophthalmic prisms. Prisms introduce a uniform binocular disparity by displacement of the retinal images onto non-corresponding retinal locations and, thereby, elicit the vergence eye movements that are necessary to re-establish single binocular vision. However, because of Panum's fusional areas, exact binocular fixation is not necessary for single binocular vision and, thus, the subject's vergence response may be incomplete. The residual binocular disparity associated

with a vergence error is called a fixation disparity (Ogle *et al.*, 1967) and its magnitude (the difference between the vergence stimulus and vergence response) is a measure of the accuracy of the vergence response. Psychophysically, vergence responses were measured by determining the point of intersection of the lines of sight of objects having common perceived visual directions for the two eyes, i.e. the location of objects falling on corresponding retinal points.

The subjects' fixation disparities were quantified by data from the dichoptic vernier alignment task, specifically, from their psychometric functions for perceived direction of the lower test target with respect to the upper reference target (see Fig. 1). The psychometric functions represent the relationship between the probability that a subject's response signaled that the test target was seen on the right side of the reference target, as a function of the magnitude of the vernier offset. For the purposes of data analysis, leftward offsets were considered as negative values, rightward offsets as positive values, and the behavioral data were fitted with a logistic function (Berkson, 1953).

The examples of the psychometric functions, presented in Fig. 2, illustrate the effects of vergence demand on the vergence response. These data from subject NM-3, were collected with a 0.5 c/deg binocular fusion stimulus for three vergence stimulus conditions, normal convergence for the 114 cm fixation distance (●), a 4 Δ D divergence stimulus (base-in prism, □), and a 16 Δ D convergence stimulus (base-out prism, ◇). It is obvious that the primary effect of the different vergence stimuli was to produce a shift in the position of the psychometric function, to the left with base-in prism (indicating a relative over-convergence or eso-fixation disparity) or to the right with base-out prism (indicating a relative under-convergence or exo-fixation disparity). In addition, the slopes of the psychometric functions were also affected by the vergence demand in some cases, indicating an effect

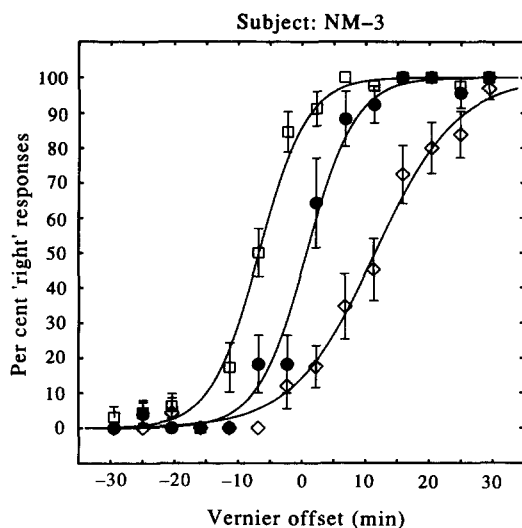


FIGURE 2. Examples of the psychometric functions for discrimination of relative direction in the dichoptic vernier experiments. The functions represent the percentage of trials in which the monkey's response indicated that the lower test stimulus appeared to be offset to the right side of the upper test stimulus. Leftward stimulus offsets are designated by negative abscissa values and rightward stimulus offsets are designated by positive abscissa values. The monkey's fixation disparity (the point of subjective alignment, 50% correct), and vernier alignment threshold (the semi-interquartile range) were derived from the best-fitting logistic functions (shown by the curves drawn through the data). Psychometric functions are illustrated for three vergence-stimulus conditions: ● zero prism, i.e. normal accommodation and convergence; □ 4 Δ D base-in, i.e. 4 Δ D of relative divergence; ◇ 16 Δ D base-out, i.e. 16 Δ D of relative convergence. All of the data were obtained with a binocular grating fusion stimulus of 0.5 c/deg. The error bars represent SEMs.

on the precision of vergence responses. For example, the flatter slope of the psychometric function for the data with 16 Δ D of base-out prism (◇, Fig. 2), compared to the function with normal viewing (●, Fig. 2), demonstrates a reduction in the precision of the monkey's vergence response, as well as the reduction in accuracy that is indicated by the displacement of the curves toward underconvergence. These two response measures assess independent characteristics of the disparity vergence system and, therefore, to obtain a relatively complete description of a subject's fusional abilities the individual psychometric functions were analyzed to determine both the fixation disparity (the point of subjective equality or 50% "right" point) and the alignment threshold (the semi-interquartile range or one-half of the offset range between 25% and 75% "right" responses). In accord with convention for the graphical representation of fixation disparity data (Ogle *et al.*, 1967), the data for over-convergence (eso-) fixation disparities were plotted as positive values and under-convergence (exo-) fixation disparities as negative values, while the alignment thresholds were plotted as unsigned values. The abscissa values, the disparity vergence stimuli (Δ D), were considered as positive values for convergent (base-out) or as negative values for divergent (base-in) stimuli.

The relationships between fixation disparities (lower panels) and alignment thresholds (upper panels) as a function of vergence stimuli are presented in Fig. 3 for human subjects, and Fig. 4 for monkey subjects. A comparison of the data these figures demonstrates several important properties of the disparity vergence response that are common across all subjects. (i) All subjects demonstrated disparity vergence (i.e. fusion reflex) over a range of prism-induced retinal disparities. The magnitude of the fixation disparity increased systematically with increasing vergence stimulus values, especially for convergence stimuli, but the slope of the functions are considerably more shallow than the slope of the function for simple prismatic image displacement (see Fig. 3). With the exception of subject NM-4, fixation disparities within the limits imposed by Panum's fusional areas were found for a range from approx. 4 Δ D base-in to 16 Δ D base-out. The slope of the functions, over the region from 0 to 8 Δ D base-out, were generally quite shallow. The reasonably accurate vergence responses may be considered as an indication of a vergence range of effective prism adaptation (Schor, 1979, 1983). (ii) The accuracy and precision of the vergence response worsened as the vergence stimulus varied from the normal accommodative-convergence demand of the fixation distance. A comparison of the data in the upper and lower panels for each subject indicates that alignment thresholds were usually the smallest with the stimulus value that resulted in the smallest vergence error. Toward either the convergence or divergence extreme, vergence errors were of greater magnitude, were more noisy within a measurement session, and were more variable across sessions. (iii) The forms of disparity vergence, stimulus-response functions were somewhat variable across observers, as has also been shown for clinical patients (e.g.

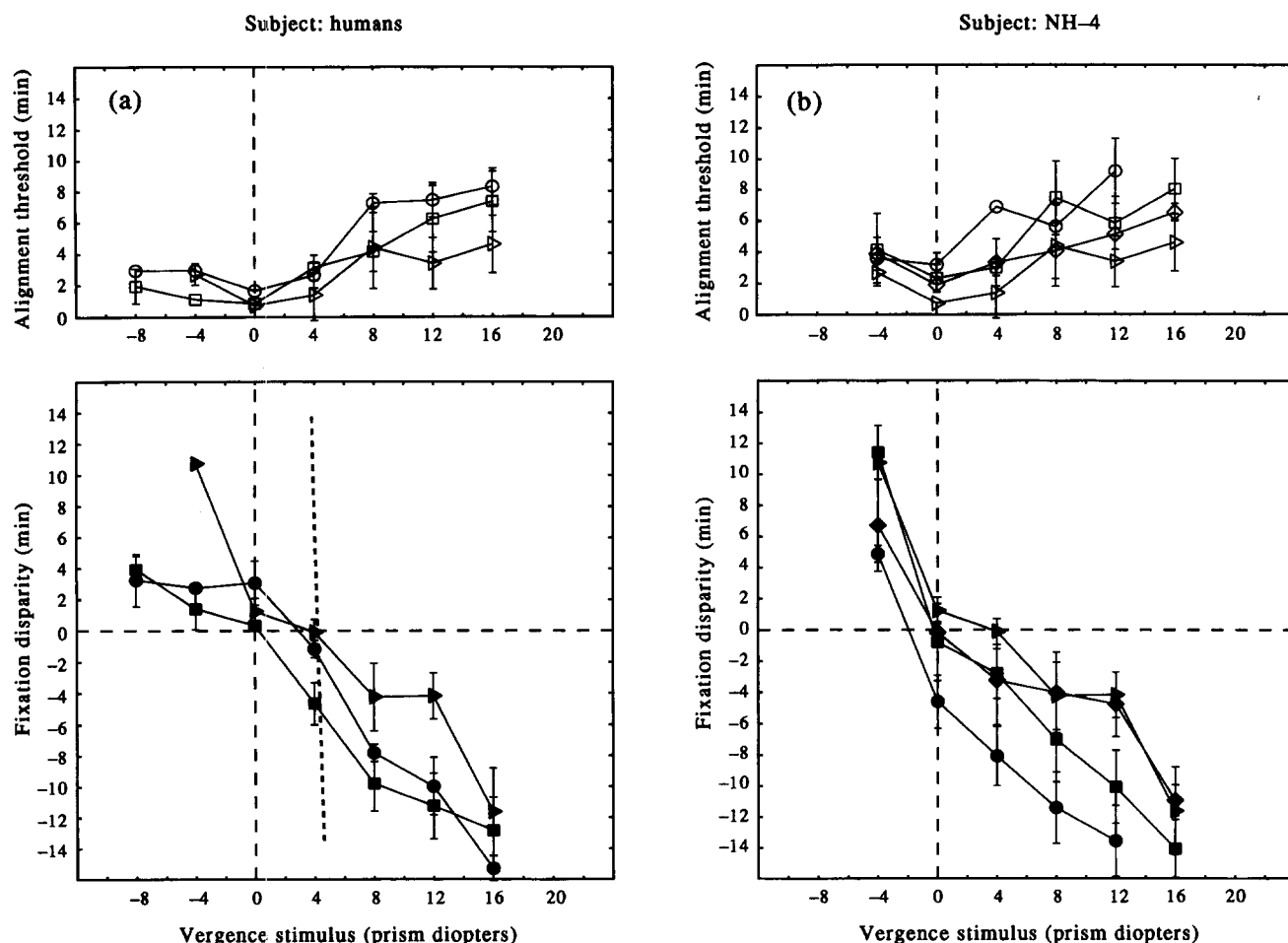


FIGURE 3. Dichoptic vernier alignment thresholds (upper panels) and fixation disparities (lower panels) as a function of prism-induced disparity vergence for human subjects. Eso-fixation disparities (over-convergence) are plotted as positive values and exo-fixation disparities (under-convergence) are plotted as negative values. Base-in prism (divergence) stimuli are designated as negative values and base-out (convergence) stimuli are designated as positive values on the abscissa. (a) Data for three observers (circles, NH-1; squares, NH-2; triangles, NH-4) with a 2 c/deg binocular grating fusion stimulus. The bold-dashed line constructed to pass through the dashed abscissa at 4 Δ D base-out represents the prismatic displacement of retinal images that would occur without disparity vergence eye movements. (b) Data for one observer (NH-4) with four binocular fusion stimulus conditions: a blank screen (circles), 0.5 c/deg (squares), 2 c/deg (triangles), and 8 c/deg (diamonds) binocular grating fusion stimuli. The error bars represent ± 1 SD for the mean of data from three sessions.

Ogle *et al.*, 1967; Sheedy & Saladin, 1983), but for a given observer they were consistent across all binocular fusion stimuli. The data for a human [Fig. 3(b)] and monkeys (Fig. 4) illustrate that neither the form or magnitude of the fixation disparities, nor the alignment thresholds varied systematically as a function of the spatial configuration of the binocular fusion lock (circles, blank screen; squares, 0.5 c/deg; triangles, 2 c/deg; diamonds, 8 c/deg). In fact, the functions were also similar whether or not the fusion stimulus was present. In the absence of the binocular grating, the nonius lines were presented on a homogeneous field and the nearest lateral binocular contours were 6 deg from the center of the stimulus field. The systematic stimulus-response relationship with only peripheral stimuli indicates that, for subjects with normal binocular vision, binocular mechanisms from peripheral vision are remarkably effective in eliciting a fusion reflex and, consequently, it is sensible that more centrally located contours would not produce large effects on disparity vergence responses.

Even given the substantial, normal inter-subject variability for these functions, the data for subject NM-4 (Fig. 3) seem to represent an extreme variation. As shown by the relatively large alignment thresholds (upper panel), the psychometric functions for these measurements were consistently more shallow than those for the other monkeys. In addition, the monkey's fixation disparity functions (lower panel) were quite steep and measurements could be made over only a limited range of disparity vergence stimuli. However, the functions evidently represent positive disparity vergence responses because their slopes are not as steep as predicted by image displacement caused by the prisms in the absence of convergence eye movements, which is shown by the nearly vertical line constructed to pass through the dashed abscissa at about 14 Δ D base-out. Even though the monkey's over-convergence cannot be explained by an uncorrected hyperopic refractive error, it is possible that he would have normal fusion with more distant fixation. The monkey's interpupillary distance was approx. 3 cm

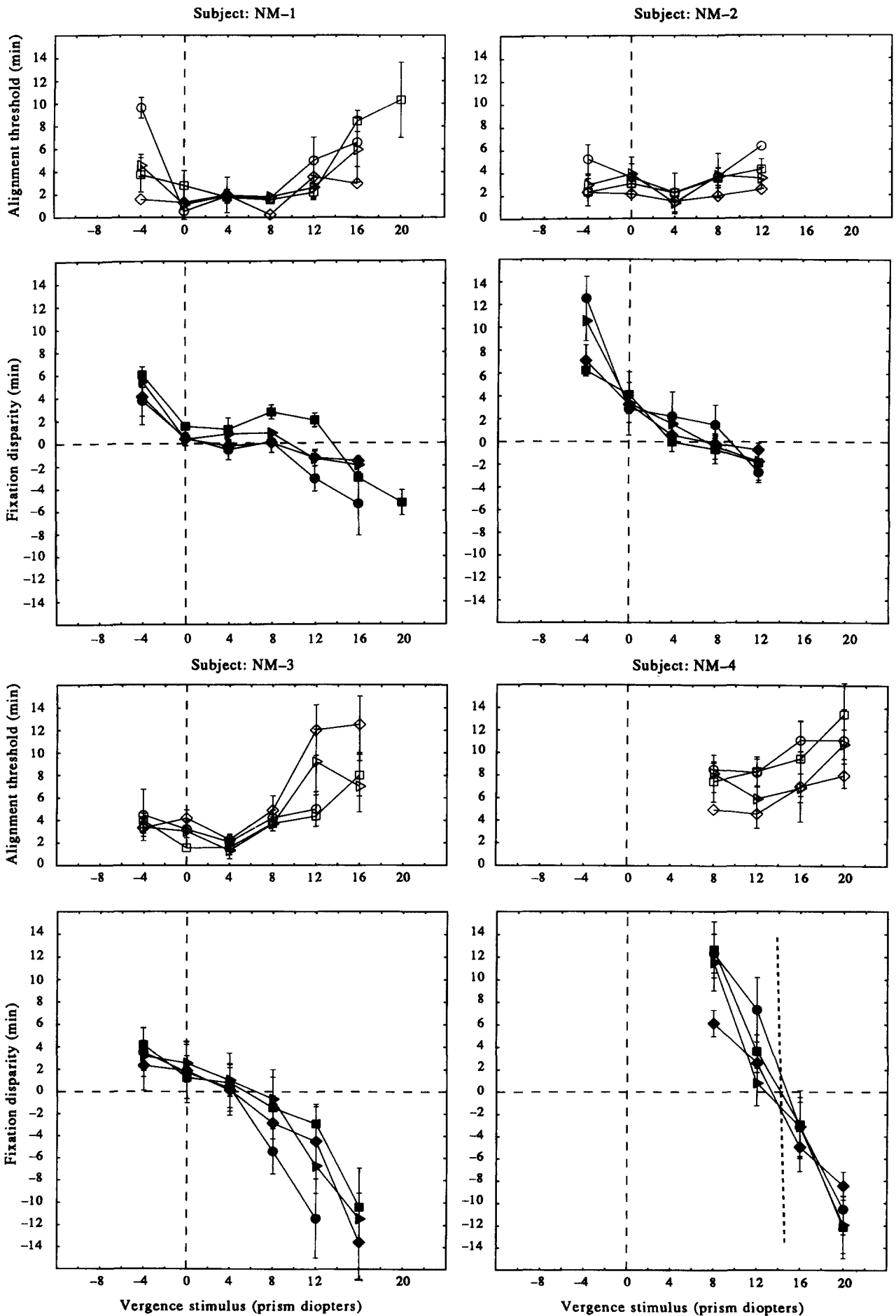


FIGURE 4. *Caption on facing page.*

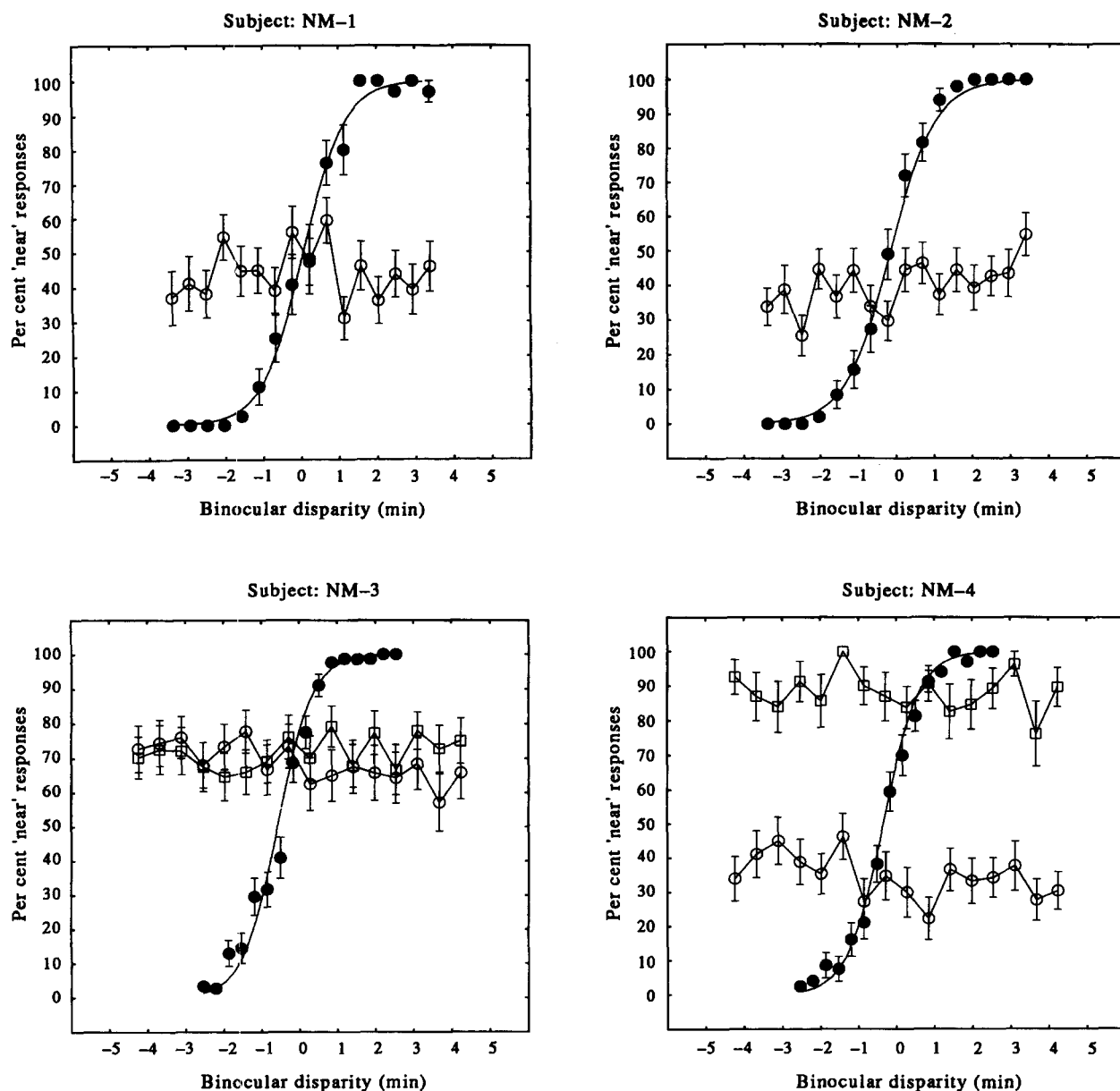


FIGURE 5. Examples of psychometric functions for depth discrimination for each of the monkey subjects. The functions represent the probability that the monkey's response indicated that the test stimulus was perceived as nearer than the reference stimulus as a function of the sign and magnitude of binocular disparity. Uncrossed binocular disparities are designated as negative values on the abscissa and crossed binocular disparities are designated as positive values. All of the data were collected with a 2 c/deg DoG stimulus. The solid symbols represent discrimination of relative distance with normal stereoscopic viewing. The monkeys' stereothresholds (the semi-interquartile range) and disparity biases (the point of subjective equality, 50% correct) were derived from the best-fitting logistic functions (shown by the curves drawn through the data). \circ Data from a control session with monocular viewing. \square For subjects NM-3 and NM-4, represent psychometric functions with disparity vergence stimuli that exceeded the monkeys' binocular fusional limits (8 Δ D base-in for NM-3 and zero prism for NM-4). The error bars represent SEMs.

and, therefore, the convergence demand for the 114 cm fixation distance was approx. 3 Δ D. The vergence function for a more distant fixation point would be displaced to the left by 3 Δ D, resulting in a residual eso-

fixation disparity of 20–22 min arc. While this fixation disparity is somewhat larger than the traditionally defined limits of Panum's fusional areas (Ogle, 1952), the monkey should have normal fusion for low spatial frequencies

FIGURE 4 (opposite). Dichoptic vernier alignment thresholds (upper panels) and fixation disparities (lower panels) as a function of prism-induced disparity vergence for four monkey subjects. Eso-fixation disparities (over-convergence) are plotted as positive values and exo-fixation disparities (under-convergence) are plotted as negative values on the ordinate. Base-in prism (divergence) stimuli are designated as negative values and base-out (convergence) stimuli are designated as positive values on the abscissa. For each monkey data are presented for four binocular fusion stimuli: a blank screen (circles), 0.5 c/deg (squares), 2 c/deg (triangles), and 8 c/deg (diamonds) binocular grating fusion stimuli. The bold-dashed line, in the plot for subject NM-4, constructed to pass through the dashed abscissa at 14 Δ D base-out represents the prismatic displacement of retinal images without disparity vergence eye movements. The error bars represent ± 1 SD of the mean of data from three experimental sessions.

(Schor, Wood & Ogawa, 1984b). In addition, this monkey must have had normal binocular vision during his sensitive period of development for binocular vision (Harwerth, Smith, Crawford & von Noorden, 1990) because he subsequently demonstrated normal stereopsis, even for high spatial frequency stimuli, when the measurements were made with appropriate prism power to aid convergence.

Stereopsis

The subjects' stereoscopic capabilities were assessed from their psychometric functions for depth discrimination. The probability of their psychophysical responses corresponding to the perception of "near" were plotted as a function of disparity magnitude, using negative values to indicate uncrossed ("far") disparities and positive values for crossed ("near") disparities. Examples of these psychometric functions with a 2 c/deg DoG stimulus for each of the monkeys are presented in Fig. 5 (●) to illustrate two aspects of the behavior expected of subjects with normal binocular vision. First, the psychophysical responses for "near" were tightly correlated with the direction (crossed or uncrossed) and magnitude of binocular disparity, ranging from zero for the largest uncrossed disparities to 100% for the largest crossed disparities with the slope of the psychometric function reflecting the sensitivity of the subject's depth perception (i.e. stereothreshold). Secondly, the functions were closely centered at zero disparity, indicating a balance in stereopsis for crossed and uncrossed disparities. Alternatively, a displacement of the function on the disparity axis (i.e. stereo-bias) would indicate an imbalance or asymmetry in the sensitivities of the mechanisms for detecting crossed and uncrossed disparities, as has been shown for global stereopsis in monkeys (Harwerth & Boltz, 1979b) and humans (Legge & Gu, 1989). Both aspects of stereoscopic vision (stereothreshold and stereo-bias) were evaluated by logistic regression (Berkson, 1953) on the psychometric data for each stimulus spatial frequency.

The analysis of depth discrimination functions presumes binocular vision, but does not completely eliminate the possibility that the data were contaminated by monocular cues. More compelling evidence that these psychometric functions represent stereoscopic vision was obtained from monocular-viewing, control sessions. Under these conditions, the discriminability of crossed vs uncrossed disparities was nearly flat across all disparity values, as is illustrated by the results from one monocular-viewing control session for each monkey in Fig. 5 (○). The obvious differences in the animals' performances with non-stereoscopic monocular cues and with binocular disparity cues provide solid evidence of stereoscopic depth perception.

The stereothresholds (lower panels, ●) and stereo-bias (upper panels) for the monkeys are presented in Fig. 6 for a range of nominal spatial frequencies of 0.25–16 c/deg for the DoG stimuli. It should be noted that the threshold data are plotted in log–log coordinates while the bias data are plotted in semi-log coordinates. In agreement with

previous investigations with human observers (Schor & Wood, 1983; Legge & Gu, 1989), stereothreshold vs spatial frequency functions for monkeys can be well-described by two linear segments; one segment for spatial frequencies below 2–4 c/deg with a negative slope close to 1.0 (–1.06 to –0.86 for these subjects), and another segment for higher spatial frequencies with a slope near zero. The negative-sloped portion of the function is consistent with a threshold disparity determined by a constant phase shift of approx. 4 deg (3.09 to 5.43 deg) between the DoG stimuli in the two stereo half-views, while the zero-sloped portion indicates a disparity threshold that was determined by a constant positional offset between the stereoscopic stimuli of approx. 20 sec arc (16–24 sec arc for the four monkeys). The flat line segment for mid to high spatial frequencies was only an approximation of the data. In fact, the stereothreshold function was not flat across spatial frequencies higher than 4 c/deg, but rather the thresholds became larger with increasing spatial frequency, probably because the effective contrast of the stimulus was lower at high spatial frequencies (Legge & Gu, 1989).

The disparity biases in depth discrimination (Fig. 6, upper panels) showed effects that were small, but consistent for individual subjects. For two subjects (NM-1 and NM-2) small depth biases, in opposite directions, were apparent for spatial frequencies lower than approx. 1 c/deg; subject NM-3 demonstrated a constant uncrossed disparity bias of approx. 24 sec arc across the entire range of spatial frequencies, while the bias for subject NM-4 was insignificant at any spatial frequency. Because the disparity bias rarely exceeded the subject's stereothreshold at any spatial frequency, it may be concluded that with normal stereopsis the mechanisms for the detection of crossed and uncrossed disparities are reasonably well-balanced and symmetrical, with respect to the horopter.

Although it is generally assumed that keen stereoscopic vision is dependent upon an accurate and precise alignment of the visual axes, the monkeys' stereothresholds were only minimally affected by induced vergence errors. The measurements of stereothresholds shown in Fig. 6 were made with the subjects viewing through prismatic lenses that minimized their fixation errors and alignment thresholds (zero prism for NM-1, 4 ΔD base-out for NM-2 and NM-3, 12 ΔD base-out for NM-4), but the fixation disparity vs forced vergence functions (Fig. 4) indicate that alterations of the prismatic lenses can systematically change the subjects' vergence errors and variability. Therefore, the effects of forced vergence on stereothresholds were investigated in two monkeys, NM-3 and NM-4, for DoG stimuli of 2 c/deg (Fig. 7, circles) and 8 c/deg (Fig. 7, squares). The results indicate that the presence of fixation disparities, either eso- or exo-fixation disparity, caused a small elevation of stereothresholds (lower panels), but did not affect the disparity biases (upper panels) of these subjects. Although the prism-induced fixation disparity and nonius alignment functions differed substantially for these two monkeys, their stereothresholds were similar and only

changed by about a factor of 2, without inducing a disparity bias, for disparity vergence values between the optimal vergence conditions and the fusion limits.

Subsequent control experiments indicated that the small threshold elevations were most likely caused by the extra-horopter location of the reference stimulus in the

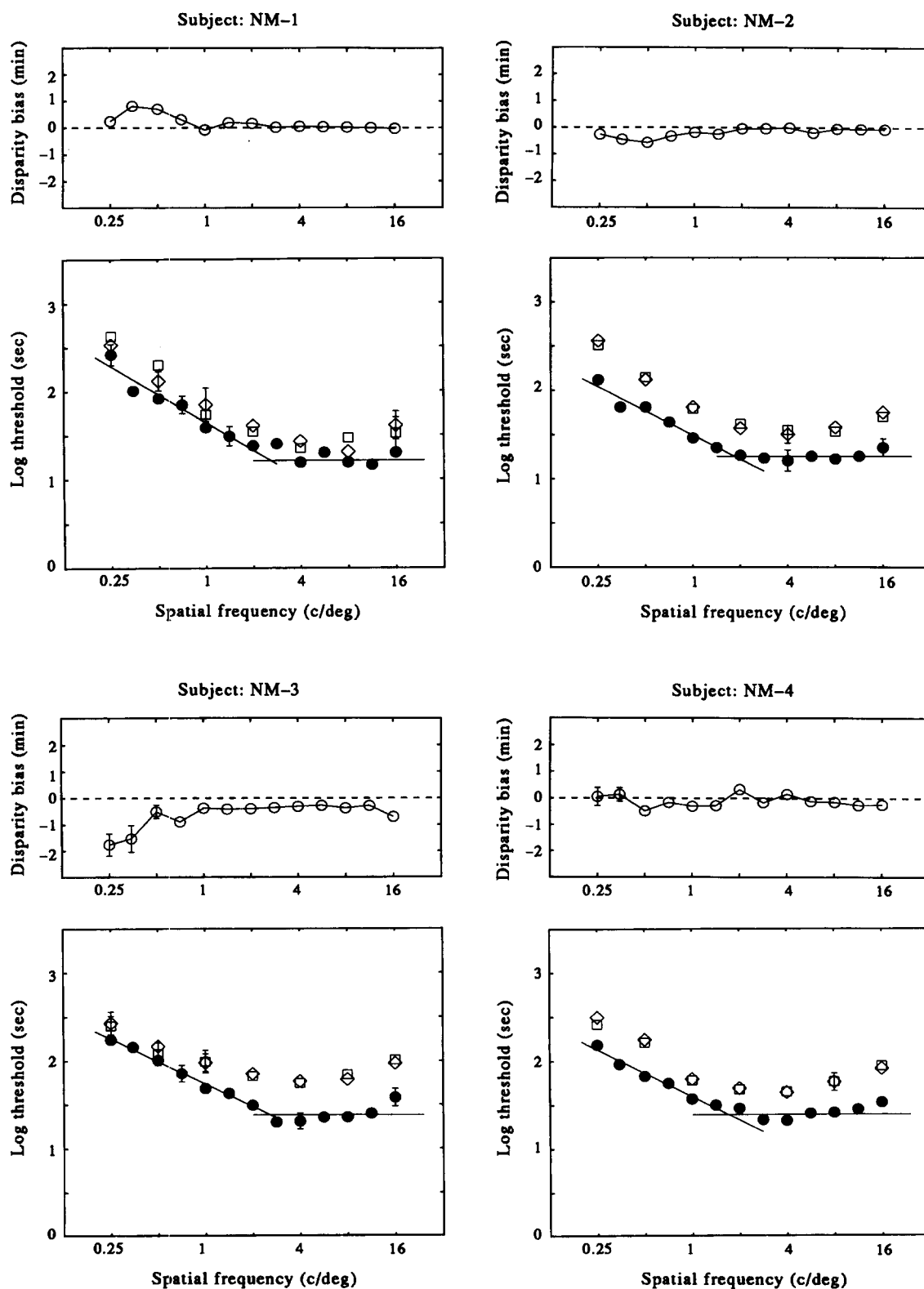


FIGURE 6. Disparity biases (upper panels) and vernier and binocular disparity thresholds (lower panels) as a function of the spatial frequency of the DoG stimuli, for each of the monkey subjects. Crossed disparity biases are designated as positive values and uncrossed disparity values are designated as negative values. The stereothreshold data (●) were fitted by two line segments, one segment with a negative slope for data from DoG spatial frequencies of 0.25–2.0 c/deg and another segment with zero slope for data from DoG spatial frequencies of 4.0–16.0 c/deg. Vernier alignment thresholds are presented for the subjects' right (□) and left (◇) eyes. Error bars, representing ± 1 SD, are shown if the SD exceeded the size of the symbol.

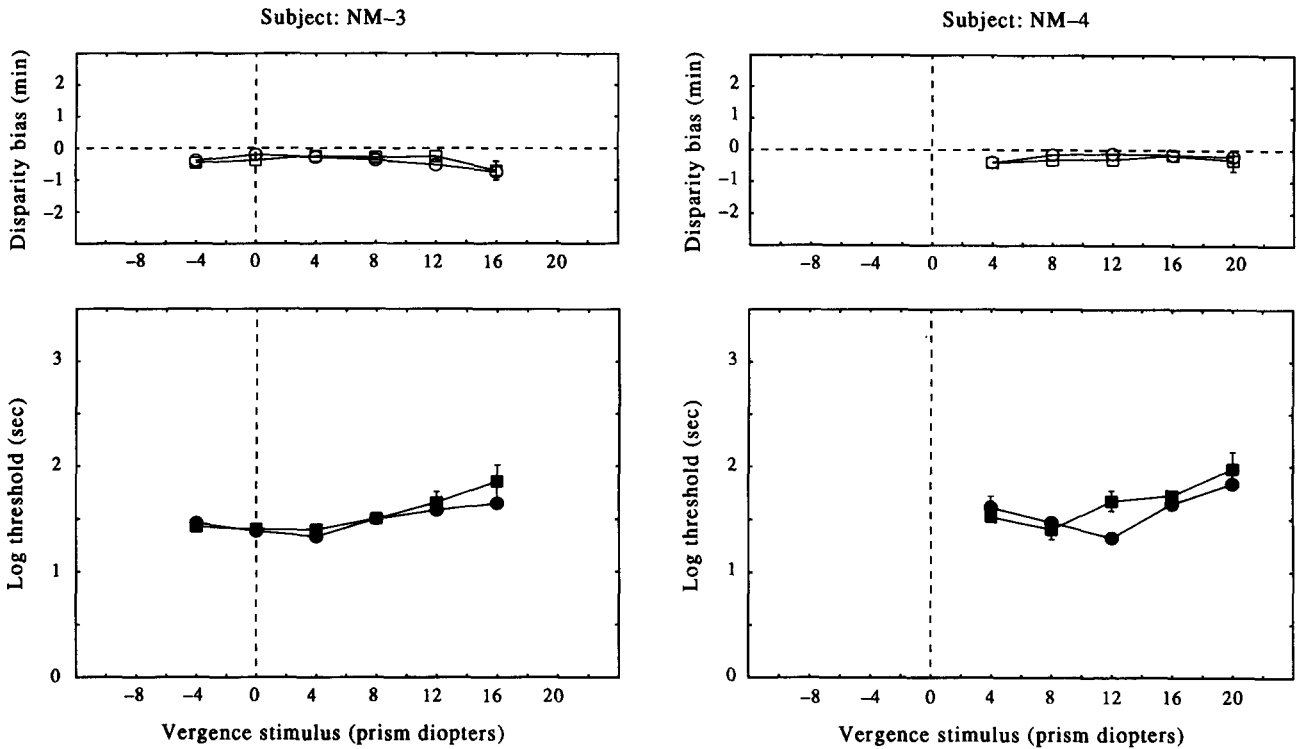


FIGURE 7. Disparity biases (upper panels) and binocular disparity thresholds (lower panels) as a function of prism-induced disparity vergence for subjects NM-3 and NM-4. Crossed disparity biases are designated as positive values and uncrossed disparity values are designated as negative values on the ordinate. Base-in prism (divergence) stimuli are designated as negative values and base-out (convergence) stimuli are designated as positive values on the abscissa. Disparity bias and disparity threshold data are presented for DoG stimuli of 2 c/deg (circles) and 8 c/deg (squares). Error bars, representing ± 1 SD, are shown if the SD exceeded the size of the symbol.

presence of a fixation disparity, rather than from elevated vergence noise near the monkeys' fusional limits. These control experiments showed that stereothresholds with pedestal disparities for the reference stimulus that approximated the largest vergence-induced fixation disparities were nearly equal to the stereothresholds with vergence-induced fixation disparities.

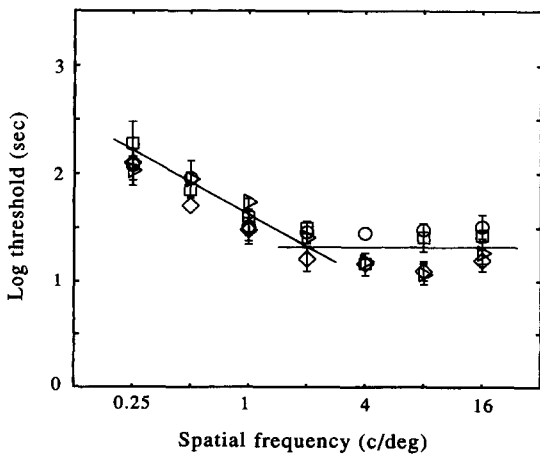


FIGURE 8. A comparison of stereothresholds for monkey and human observers. The symbols represent the stereothresholds of the human observers (\circ NH-1; \square NH-2; \triangle NH-3; \diamond NH-4). The stereothresholds of monkeys are represented by the two line segments fitted to the mean stereothresholds of the four monkey subjects (shown in Fig. 6). Error bars for the data of the human observers, representing ± 1 SD, are shown if the SD exceeded the size of the symbol.

It is also important to note that the stereothreshold data (Fig. 7) were very similar for both DoG spatial frequencies and, thus, independent of the specific spatial frequency channels (Schor *et al.*, 1984a) or the size of Panum's fusional areas (Schor & Tyler, 1981) involved in the binocular disparity processing. On the other hand, beyond the fusion limits stereopsis was eliminated and depth discrimination went to chance performance. This effect is illustrated by the psychometric data for these two subjects in Fig. 5 (\square) which were collected with disparity vergence stimuli of 8 Δ D base-in for subject NM-3 and zero prism for subject NM-4.

The stereothreshold functions for normally reared monkeys (Fig. 6) are virtually identical to those of humans with normal binocular vision. A comparison of data from the two species is presented in Fig. 8. The stereothresholds for four human subjects are represented by the symbols and the monkeys' data are represented by the two line segments obtained by linear regression to the mean data from the four monkeys. The agreement between the functions is remarkable and clearly demonstrates the similarities in the angular threshold disparities for local stereopsis in monkeys and humans.

It is also interesting to compare the monkeys' spatial resolution for monocular vernier offsets, using the DoG stimuli, to their binocular disparity offset resolution. The monocular vernier threshold data are presented in Fig. 6 (lower panels; right eye, \square ; left eye, \diamond), which also displays the stereothresholds for each of the monkeys.

Although the forms of the functions for vernier alignment thresholds vs spatial frequency and stereothresholds vs spatial frequency are quite similar, the stereothreshold values were consistently 0.2–0.3 log units lower than the vernier thresholds. However, the stimulus configuration, which included a 9 min arc vertical gap between the test and reference stimuli, was not optimal for vernier discrimination performance (McKee, Welch, Taylor & Bowne, 1990). Two of the monkeys (NM-1 and NM-2) tested on a monocular vernier acuity task which utilized DoG stimuli without a vertical separation, demonstrated vernier thresholds of <10 sec arc (Smith & Harwerth, 1993). Nevertheless, it is interesting that, under the stimulus conditions for the vernier and stereothreshold measurements, the total stimulus offset required for the discrimination of relative depth, which was divided between the two eyes in opposite directions, was roughly equal to the offset needed with either eye alone for the discrimination of relative direction.

DISCUSSION

The similarities in the characteristics of disparity vergence and stereoscopic vision of humans and macaque monkeys establishes a psychophysical homology for the processing of binocular disparities in the two species. The homology is interesting, and might not have been expected, because of the differences in the physiognomy of the two species. The properties of disparity vergence and stereopsis that we investigated were nearly equivalent for monkeys and humans in terms of angular stimulus dimensions. Such angular measures are independent of interocular separation, whereas binocular disparity specified in terms of physical distances in a natural environment are not independent of the subject's interocular separation. The interocular separation of humans is approximately twice that of monkeys and, accordingly, only one-half the physical distance is required to obtain a given binocular disparity for humans as for monkeys. Similarly, convergence is also dependent upon interocular separation and, in this case, monkeys need about one-half the convergence of humans for any given near fixation distance. These differences in the ordinary stimulus–response functions of binocular vision are substantial and might have predicated different evolutionary adaptations. Conversely, the similarity of angular stimulus dimensions for binocular vision mechanisms of monkeys and humans indicates that these processes are determined by anatomical and/or neural constraints that are similar in both species.

Current concepts of the neural processing of binocular disparities have been strongly influenced by investigations of the disparity tuning characteristics of cortical neurons in alert monkeys (Poggio & Fischer, 1977; Poggio & Talbot, 1981; Poggio *et al.*, 1988; Poggio, 1991). For example, neurons which are sensitive to specific ranges of either crossed or uncrossed positional disparities have been proposed as the neural substrates for fine, local stereopsis. The credibility of such psycho-physiological links has been strengthened by computational models of

the stereoscopic vision of human observers (Lehky & Sejnowski, 1990, 1991) which are based on disparity-tuned channels with response properties similar to disparity detectors of the monkey's striate cortex. The position disparity detector model has an attractive simplicity, but does not settle the issue because other neurophysiological models are equally viable. One recent alternative, based on receptive field data of cats, suggests that, rather than positional disparity tuning of individual neurons in the visual cortex, stereoscopic vision may be derived from differences in spatial phase between the right and left eyes' receptive fields (Ohzawa, DeAngelis & Freeman, 1990; Freeman & Ohzawa, 1990; DeAngelis, Ohzawa & Freeman, 1991). The threshold vs spatial frequency function for stereopsis (Freeman, DeAngelis & Ohzawa, 1992), of the form shown for humans (Schor & Wood, 1983) and monkeys (Fig. 6), is a natural outcome of this phase disparity model. The present experiments demonstrate that, whatever neural mechanisms are responsible for stereopsis, the macaque monkey is the most appropriate subject for investigations of neural, binocular depth mechanisms with disparity sensitivities equal to that of human vision.

The highest sensitivities for binocular disparity with spatially filtered stimuli (15–20 sec arc for nominal spatial frequencies of 2–8 c/deg for the DoG stimuli) are somewhat lower than has been reported for high contrast bar stimuli (Westheimer, 1979a,b). On the other hand, the stereothresholds of our subjects are similar to those of previous investigations of stereopsis using similar stimuli (Schor & Wood, 1983; Halpern & Blake, 1988; Legge & Gu, 1989). Therefore, we can conclude that the stereothreshold measurements were not affected by the particular video haploscope used in these experiments, but the lower thresholds were probably a consequence of the non-optimal spatial configuration of the test and reference stimuli (Westheimer, 1979b; Westheimer & McKee, 1979; McKee *et al.*, 1990) and the low mean luminance of the stereoscopic stimuli. The effective luminance of the video screen, about 4 cd/m², was considerably below that needed for optimal performance of stereoscopic discrimination (Berry, Riggs & Duncan, 1950; Lit, 1959).

The stereoscopic depth discrimination functions (Fig. 6) did not reveal the crossed–uncrossed disparity biases that have been demonstrated in other studies of stereopsis in humans (Richards, 1971; Legge & Gu, 1989) and monkeys (Harwerth & Boltz, 1979b). There are a couple of potential explanations for why disparity biases were not found in this study. First, the monkeys' rewards were based on the sign of the stereoscopic disparity and they may have adjusted their response criterion, although monkeys with anomalous stereopsis have maintained their disparity biases over long periods of testing (Harwerth *et al.*, 1993). A second possibility is that disparity biases appear to be more prominent in global stereopsis or coarse, local stereopsis than in fine, local stereopsis. The studies that have demonstrated depth bias have utilized grating stimuli (Legge & Gu, 1989) or random-dot stereograms (Harwerth & Boltz, 1979b), in

which the binocular correspondence problem is more salient, or have used coarse disparities (Richards, 1971) rather than local, fine disparities. The determination of whether disparity biases are a result of methodological or sensory factors must await further investigation.

In some respects, the results of the fixation disparity vs forced vergence experiments may also have been affected by the specific methodology used for the measurements. Most of the previous investigations of these relationships have employed specific procedures to minimize prism adaptation (Carter, 1965; Ogle *et al.*, 1967; Schor, 1979). Whereas the data from our investigations represent the upper limit of prism adaptation. A constant vergence stimulus was present throughout an entire experimental session, approx. 2 hr for the monkeys, and as a consequence, the fixation disparity vs forced vergence functions should represent the limit of the subjects' prism adaptability. The effect of prism adaptation should be seen as a relatively shallow slope of the fixation disparity vs forced vergence function over some range of prism stimuli (Schor, 1979). It is apparent that, with the exception of subject NM-4, relatively complete prism adaptation occurred over a range of approx. $8 \Delta D$, generally centered on base-out prism vergence. It is also important to observe that the range of most complete prism adaptation also represented the range of the highest precision for disparity vergence eye movements, as is indicated by the smallest dichoptic alignment thresholds. Therefore, although the experimental procedures deviated from the standard clinical methods of fixation disparity analysis, the premium of the data is that they provide important information about the monkeys' convergence responses under the conditions for stereoscopic discriminations. Equally important, the similarities in the characteristics of fusion reflexes of monkey and human subjects are critical data for the psycho-physiological linking of neural mechanisms for oculomotor responses (Judge, 1991).

The relationships between spatial frequency and vergence error (fixation disparity) and between vergence error and stereopsis are interesting. We found that the vergence errors as a function of the magnitude of the vergence stimuli did not vary with the spatial frequency of the parafoveal binocular fusion stimulus and, in fact, the vergence errors were essentially the same whether or not the parafoveal stimulus was present. Without the grating fusion stimulus, the binocular contours were 6 deg from central foveal vision. These findings are consistent with previous reports showing that disparity vergence responses were not dependent upon the spatial frequency composition of fusion stimuli (Frisby & Mayhew, 1980; Mowforth *et al.*, 1981) as well as reports that the magnitude of fixation disparity was not spatial frequency dependent (Schor *et al.*, 1986). However, rather than providing evidence against a special role for low spatial frequency mechanisms for the disparity vergence system, these studies may be interpreted as demonstrating that the frame of the stimulus field was relatively effective in

driving disparity vergence and, as a result, variations in the spatial frequency composition of more central binocular fusion stimuli do not cause large effects on the disparity vergence response. Furthermore, it seems incorrect, on the basis of this kind of data (Frisby & Mayhew, 1980; Mowforth *et al.*, 1981), to discount models of stereopsis which hypothesize a role of low spatial frequency mechanisms in initiating vergence eye movements in order to bring high spatial frequency mechanisms into binocular register (Marr & Poggio, 1979). Indeed, low spatial frequency mechanisms are probably very important in initiating disparity vergence movements because the disparity sensitivity of low spatial frequency mechanisms falls slowly in peripheral vision compared to high spatial frequency mechanisms (Schor & Badcock, 1985; Siderov & Harwerth, 1993a).

Our findings on the relationship between stereothresholds and fusional vergence (Fig. 7) have demonstrated that the monkey's fusion reflex was sufficiently strong to compensate for a broad range of vergence demands and allow the reliable extraction of depth information. The general effects of prism-induced fusional vergence on stereopsis are important because the fixation disparity functions (Fig. 4) demonstrated that the vergence response became less accurate and precise with increased stimulation of either convergence or divergence. With vergence errors, the binocular disparity of the test and reference stimuli are affected equally and it is well known that absolute stereothresholds are usually lower than increment disparity thresholds (Blakemore, 1970; Badcock & Schor, 1985; Siderov & Harwerth, 1993b).

Vergence-induced disparities cause similar extra-ocular effects and near the monkeys' fusional limits, the elevations of stereothresholds that were equivalent to the stereothreshold elevations associated with reference pedestal disparities that were equal to the fixation disparity. Consequently, it does not appear that the reduced precision of the vergence response substantially degraded stereopsis, nor did they introduce a stereoscopic depth bias, as might have been expected from vergence errors.

In conclusion, these investigations have demonstrated a remarkable similarity in the performance of binocular vision in macaque monkeys and humans. After compensation for the difference in the lateral separation of the eyes of the two species, the operating characteristics of their disparity vergence and stereoscopic vision were essentially identical. Consequently, binocular vision may be added to the long list for which a psychophysical homology has been established for visual functions of macaque monkeys and humans.

REFERENCES

- Badcock, D. R. & Schor, C. M. (1985). Depth-increment detection functions for individual spatial channels. *Journal of the Optical Society of America A*, 2, 1211-1215.
- Berkson, J. (1953). A statistically precise and relatively simple method of estimating the bioassay with quantal response, based on the logistic function. *Journal of the American Statistical Association*, 48, 565-599.

- Berry, R. N., Riggs, L. A. & Duncan, C. P. (1950). The relation of vernier and depth discriminations to field brightness. *Journal of Experimental Psychology*, *40*, 349–354.
- Blakemore, C. (1970). The range and scope of binocular depth discrimination in man. *Journal of Physiology, London*, *211*, 599–622.
- Boltz, R. L. & Harwerth, R. S. (1979). Fusional vergence ranges of the monkey: A behavioral study. *Experimental Brain Research*, *37*, 87–91.
- Boltz, R. L., Smith, E. L., Bennett, M. J. & Harwerth, R. S. (1980). Vertical fusional vergence ranges of the rhesus monkey. *Vision Research*, *20*, 83–85.
- Bough, E. W. (1970). Stereoscopic vision in the macaque monkey: A behavioral demonstration. *Nature*, *225*, 42–44.
- Carter, D. B. (1965). Fixation disparity and heterophoria following prolonged wearing of prisms. *American Journal of Optometry and Archives of the American Academy of Optometry*, *42*, 141–152.
- Cowey, A., Parkinson, A. M. & Warnick, L. (1975). Global stereopsis in rhesus monkeys. *Quarterly Journal of Experimental Psychology*, *27*, 93–109.
- DeAngelis, G. C., Ohzawa, I. & Freeman, R. D. (1991). Depth is encoded in the visual cortex by a specialized receptive field structure. *Nature*, *352*, 156–159.
- Freeman, R. D. & Ohzawa, I. (1990). On the neurophysiological organization of binocular vision. *Vision Research*, *30*, 1661–1676.
- Freeman, R. D., DeAngelis, G. C. & Ohzawa, I. (1992). Depth processing in the cat's visual cortex: Simple cells encode binocular disparity at multiple spatial scales. *Investigative Ophthalmology and Visual Sciences (Suppl.)*, *33*, 1021.
- Frisby, J. & Mayhew, J. (1980). The role of spatial frequency tuned channels in vergence control. *Vision Research*, *20*, 727–732.
- Halpern, D. L. & Blake, R. R. (1988). How contrast affects stereoacuity. *Perception*, *17*, 483–495.
- Harwerth, R. S. & Boltz, R. L. (1979a). Behavioral measures of stereopsis in monkeys using random dot stereograms. *Physiology and Behavior*, *22*, 229–234.
- Harwerth, R. S. & Boltz, R. L. (1979b). Stereopsis in monkeys using random dot stereograms: The effect of viewing duration. *Vision Research*, *19*, 985–991.
- Harwerth, R. S., Smith, E. L., Crawford, M. L. J. & von Noorden, G. K. (1990). Behavioral studies of the sensitive periods of development of visual functions in monkeys. *Behavioral Brain Research*, *41*, 179–198.
- Harwerth, R. S., Smith, E. L., Crawford, M. L. J. & von Noorden, G. K. (1993). Binocular disparity processing in monkeys with abnormal early vision. *Investigative Ophthalmology and Visual Science (Suppl.)*, *34*, 1188.
- Judge, S. J. (1991). Vergence. In Carpenter, R. H. S. (Ed.), *Vision and visual dysfunction, Vol. 8, eye movements* (pp. 157–172). Boca Raton, Fla: CRC Press.
- Julesz, B. & Miller, J. (1975). Independent spatial-frequency-tuned channels in binocular vision and rivalry. *Perception*, *4*, 125–143.
- Krauskopf, J. & Farell, B. (1991). Vernier acuity: Effects of chromatic content, blur and contrast. *Vision Research*, *31*, 735–749.
- Legge, G. E. & Gu, Y. (1989). Stereopsis and contrast. *Vision Research*, *29*, 989–1004.
- Lehky, S. R. & Sejnowski, T. J. (1990). Neural model of stereoacuity and depth interpolation based on a distributed representation of stereo disparity. *Journal of Neuroscience*, *10*, 2281–2299.
- Lehky, S. R. & Sejnowski, T. J. (1991). Neural model of stereoacuity based on a distributed representation of binocular disparity. In Kulikowski, J. J., Walsh, V. & Murray, I. J. (Eds), *Vision and visual dysfunction, Vol. 5, limits of vision* (pp. 133–146). Boca Raton, Fla: CRC Press.
- Lit, A. (1959). Depth-discrimination thresholds as a function of binocular differences in retinal illuminance at scotopic and photopic levels. *Journal of the Optical Society of America*, *49*, 476–481.
- Maddox, E. E. (1893). *The clinical use of prisms*. Bristol: Wright.
- Marr, D. & Poggio, T. (1979). A theory of human stereopsis. *Proceedings of the Royal Society of London B*, *204*, 301–328.
- McKee, S. P., Welch, L., Taylor, D. G. & Bowne, S. F. (1990). Finding the common bond: Stereoacuity and the other hyperacuties. *Vision Research*, *30*, 879–891.
- Mowforth, P., Mayhew, J. E. W. & Frisby, J. P. (1981). Vergence eye movements made in response to spatial-frequency-filtered random-dot stereograms. *Perception*, *10*, 299–304.
- Ogle, K. N. (1952). On the limits of stereoscopic vision. *Journal of Experimental Psychology*, *44*, 253–259.
- Ogle, K. N., Martens, T. G. & Dyer, J. A. (1967). *Oculomotor imbalance in binocular vision and fixation disparity*. Philadelphia, Pa: Lea & Febiger.
- Ohzawa, I., DeAngelis, G. C. & Freeman, R. D. (1990). Stereoscopic depth discrimination in the visual cortex: Neurons ideally suited as disparity detectors. *Science*, *249*, 1037–1041.
- Poggio, G. F. (1991). Physiological basis of stereoscopic vision. In Regan, D. (Ed.), *Vision and visual dysfunction, Vol. 9, binocular vision* (pp. 224–238). Boca Raton, Fla: CRC Press.
- Poggio, G. F. & Fischer, B. (1977). Binocular interaction and depth sensitivity in striate and prestriate cortex of behaving rhesus monkey. *Journal of Neurophysiology*, *40*, 1392–1407.
- Poggio, G. F. & Talbot, W. (1981). Mechanisms of static and dynamic stereopsis in the foveal cortex of the rhesus monkeys. *Journal of Physiology, London*, *315*, 469–492.
- Poggio, G. F., Gonzales, F. & Krause, F. (1988). Stereoscopic mechanisms in monkey visual cortex: Binocular correlation and disparity selectivity. *Journal of Neuroscience*, *8*, 4531–4550.
- Richards, W. (1971). Anomalous stereoscopic depth perception. *Journal of the Optical Society of America*, *61*, 410–414.
- Sarmiento, R. F. (1975). The stereoacuity of macaque monkeys. *Vision Research*, *15*, 493–498.
- Schor, C. M. (1979). The influence of rapid prism adaptation upon fixation disparity. *Vision Research*, *19*, 757–765.
- Schor, C. M. (1983). Fixation disparity and vergence adaptation. In Schor, C. M. & Ciuffreda, K. J. (Eds), *Vergence eye movements: Basic and clinical aspects* (pp. 465–516). London: Butterworths.
- Schor, C. M. & Badcock, D. R. (1985). A comparison of stereo and vernier acuity within spatial channels as a function of distance from fixation. *Vision Research*, *25*, 1113–1119.
- Schor, C. M. & Tyler, C. W. (1981). Spatio-temporal properties of Panum's fusional area. *Vision Research*, *21*, 683–692.
- Schor, C. M. & Wood, I. (1983). Disparity range for local stereopsis as a function of luminance spatial frequency. *Vision Research*, *23*, 1649–1654.
- Schor, C. M., Wesson, M. & Robertson, K. M. (1986). Combined effects of spatial frequency and retinal eccentricity upon fixation disparity. *American Journal of Optometry and Physiological Optics*, *63*, 619–626.
- Schor, C. M., Wood, I. C. & Ogawa, J. (1984a). Spatial tuning of static and dynamic local stereopsis. *Vision Research*, *24*, 573–578.
- Schor, C. M., Wood, I. C. & Ogawa, J. (1984b). Binocular sensory fusion is limited by spatial resolution. *Vision Research*, *24*, 661–665.
- Sheedy, J. E. & Saladin, J. J. (1983). Validity of diagnostic criteria and case analysis in binocular vision disorders. In Schor, C. M. & Ciuffreda, K. J. (Eds), *Vergence eye movements: Basic and clinical aspects* (pp. 517–540). London: Butterworths.
- Siderov, J. & Harwerth, R. S. (1993a). Stereopsis, spatial frequency and retinal eccentricity. *Investigative Ophthalmology and Visual Science (Suppl.)*, *34*, 1187.
- Siderov, J. & Harwerth, R. S. (1993b). Precision of stereoscopic depth perception from double images. *Vision Research*, *11*, 1553–1560.
- Smith, E. L. & Harwerth, R. S. (1993). Vernier discrimination thresholds in monkeys with anisometropic amblyopia. *Investigative Ophthalmology and Visual Science (Suppl.)*, *34*, 711.
- Westheimer, G. (1979a). The spatial sense of the eye. *Investigative Ophthalmology and Visual Science*, *18*, 893–912.
- Westheimer, G. (1979b). Cooperative neural processes involved in stereoscopic acuity. *Experimental Brain Research*, *36*, 585–597.

- Westheimer, G. & McKee, S. P. (1979). What prior unocular processing is necessary for stereopsis? *Investigative Ophthalmology and Visual Science*, *18*, 614–620.
- Wilson, H. R. & Bergen, J. R. (1979). A four mechanism model for threshold spatial vision. *Vision Research*, *19*, 19–32.
- Wilson, H. R., Blake, R. & Halpern, D. L. (1991). Coarse spatial scales constrain the range of binocular fusion on fine scales. *Journal of the Optical Society of America A*, *8*, 229–236.
- Zhang, Y., Mays, L. E. & Gamlin, P. D. R. (1992). Characteristics of near response cells projecting to the oculomotor nucleus. *Journal of Neurophysiology*, *67*, 944–960.

Acknowledgements—This work was supported by research grants EY 01139 and EY 03611, and core grant EY 07551, from the National Eye Institute, Bethesda, Md.