PROPERTIES OF BINOCULAR AND SPATIAL VISION OF THE RHESUS MONKEY

A Dissertation

Presented to the

Faculty of the Department of Physiological Optics

University of Houston

In Partial Fulfillment of the Requirement for the Degree Doctor of Philosophy

By:

Roger Lynn Boltz

August, 1978

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ABSTRACT

A series of experiments were undertaken to investigate, using psychophysical techniques, binocular and spatial resolution properties of the rhesus monkey. Using random dot stereogram stimuli to investigate both sensory and motor aspects of binocular vision, it was found that these properties are very much like those of man. Assessment of the monkey's stereothresholds revealed several important findings: 1) The stereothreshold of the monkey varies as a function of viewing duration in a way similar to man's, 2) Random dot stereogram stimuli appear to be detected by two types of stereopsis, patent stereopsis below 30 min of arc disparity and qualitative stereopsis above this value, 3) Several monkeys and most human subjects had better detection of crossed disparities than uncrossed disparities. Investigations into the monkey's fusional vergence ranges showed that man and monkey have approximately the same fusional vergence abilities.

The contrast sensitivities of monkey and man were studied through investigating the oblique effect. These studies revealed, for the first time, an animal other than man which possesses this phenomenon. Additionally it was found that the oblique effect exists at suprathreshold contrasts, a property not previously known.

The results of these experiments support the use of the monkey as a model of the human visual system for the processes of binocularity and spatial resolution.

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INTRODUCTION

The monkey has been used in vision research for a considerable period of time. Most of the studies of this animal's visual system have been neurophysiological or anatomical rather than psychophysical, resulting in the accumulation of relatively lesser amounts of knowledge about the behavioral aspects of the monkey's visual system. What psychophysical evidence we do have indicates that the monkey has a visual system similar to man's. For example, monkeys have been shown to possess trichromatic color vision (Sperling and Harwerth, 1971; De Valois, <u>et al.</u>, 1974), cone and rod sensitivities (Crawford, 1977), and spatial resolution properties (De Valois, Morgan, and Snodderly, 1974) which are close to those of humans.

Two of the areas currently under intensive physiological study in the monkey are binocular vision and two dimensionalspatial visual resolution (spatial vision). It becomes important, therefore, to obtain data on the behavioral aspects of these two areas so that comparisons may be made between the visual system of the monkey and man. The binocular vision system was studied on two levels; stereothresholds, a sensory process, and fusional vergence ranges, a motor process, while contrast sensitivity and orientation anisotropy were the two properties of spatial vision investigated. Data were obtained from man and monkey so that comparisons could be made between the visual functions of the two species.

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CHAPTER 1

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BINOCULAR VISION

INTRODUCTION

A. SENSORY ASPECTS

The neural mechanisms of binocular vision and stereopsis are beginning to be understood through electrophysiological experimentation with animals. While both cats (Barlow, Blakemore, and Pettigrew, 1967; Nikara, Pettigrew, and Bishop, 1968; Joshua and Bishop, 1970) and monkeys (Hubel and Weisel, 1970; Baker, Grigg, and von Noorden, 1974; Poggio and Fischer, 1977) have been used as subjects, the data from the monkey are more directly applicable to human binocular vision. Hubel and Weisel (1970) showed that about 43% of the single units found in area 18 of the monkey's cortex were sensitive to binocular disparity. Baker, et al (1974) also studied neurons in the prestriate cortex of the monkey and found that about 31% of these exhibited binocular facilitation or summation which was dependent on disparity. More recently, Poggio and Fischer (1977) further investigated these binocular depth cells, finding cells sensitive to disparity both in areas 17 and 18. They classified these neurons into four groups: (1) tuned excitatory, which gave responses over a narrow range about the fixation distance; (2) tuned inhibitory, which exhibited suppression of responses to stimuli at or close to the fixation plane; (3) near neurons, which responded to stimuli in front of the fixation plane, but were suppressed by stimuli behind it; (4) far neurons, the opposite of near neurons.

In addition to the electrophysiological data showing disparity detectors that may be the neural mechanism for stereopsis, there have been several behavioral

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demonstrations of stereopsis in monkeys reported. Bough (1970) presented a behavioral demonstration of stereopsis using random dot stereograms of the type developed by Julesz (1971). In this type of stereogram, all monocular cues to depth perception have been eliminated although binocular depth perception of a certain pattern or form in the stereogram can be obtained as the result of a displacement of a subset of dot elements. Cowey, et al. (1975) were unable to replicate Bough's results, but they did provide an adequate demonstration of stereopsis in monkeys using an anaglyph form of random dot stereograms containing disparities of 30-55 min of arc. However, the anaglyph form of random dot stereograms greatly complicates the measurement of stereothresholds. The depth discrimination behavior required in these studies was very difficult to develop and also required a considerable amount of time for training. Julesz, et al (1976) have reported a procedure using dynamic random dot stereograms which was more efficient, but they did not obtain psychophysical functions that could be compared to human data. Sarmiento (1975) investigated the stereoacuity of the macaque using a Howard-Dolman apparatus. He found the threshold disparity for the monkey was 2.4 sec of arc, while the threshold for humans tested on the same apparatus was 2.3 sec of arc.

A simple demonstration of binocular vision or stereopsis in the monkey is not sufficient to validate this species as a model for human binocular vision because similar demonstrations have been successful for such diverse species as the hawk (Fox, 1978) and the rabbit (Van Hof and Russell, 1977). Therefore, to provide unequivocal evidence, it must be shown that the binocular vision of the monkey is similar both qualitatively and quantitatively to that of humans. Therefore, in the present experiments a quantitative description of the binocular

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vision of the monkey has been made through the determination of stereothresholds for rhesus monkeys using a form discrimination paradigm. The form stimuli were created in the disparity areas of static random dot stereograms and could, therefore, be discriminated only if the retinal disparity creating the forms was above the stereothreshold for the subject. The functions relating the accuracy of form discrimination (hit rate) and retinal disparity provide psychophysical data that can be compared directly to similar data from human subjects.

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B. MOTOR ASPECTS

Humans possessing single binocular vision and stereopsis must make vergence eye movements as they change fixation distances if they are to maintain the object of regard on the foveae, a condition for fusion (Alpern, 1969). The behavioral studies of monkey binocular vision discussed above and the evidence to be presented in this work indicate that the sensory properties of binocular vision of the monkey make a good model for the human visual system. However, there are no behavioral data available in which the properties of the motor components of the monkey's binocular vision, vergence eye movements, have been investigated. The physiological characteristics of the vergence eye movements of the monkey, as well as saccadic and pursuit movements are not unlike those of humans, although the monkey's eye movements are generally of higher velocity (Keller and Robinson, 1972; Fuchs, 1967). The vergence eye movements measured by Keller and Robinson (1972) were accommodative vergence movements recorded on an occluded eye and thus not under conditions of fusion. In order to strengthen the use of the monkey as a model for the human visual system, it would be helpful to have comparable behavioral data on the fusional vergence ranges of the monkey and humans.

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The principle reason that behavioral data for the fusional ranges of the monkeys is unavailable is that stimulus control would be very difficult to obtain if the animal was required to discriminate between diplopic (double) and haplopic (single) vision, as is required of human clinical patients. These stimulus control problems can be overcome, however, by using a form discrimination task in which the forms are generated in the disparity areas of random dot stereograms. Reliable discrimination of these forms can occur only if the subject has fused the

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stereograms. Additionally in behavioral experiments with animals it is also necessary to define the response interval for the subject. Therefore, with animals, it is more appropriate to measure a reflex fusional amplitude with briefly presented stimuli rather than a pursuit fusional amplitude in which the presence of haplopia or diplopia must be reported for continuously viewed stimuli, as is done in clinical measurements. In the present study, the fusional vergence ranges of monkeys and humans have been investigated with a form discrimination paradigm and discrete viewing durations.

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METHODS

Six male rhesus monkeys (Macaca mullatta) were used in these experiments. Two of the monkeys were in adolescence at the time of data collection and the other four were pre-adolescent (2-3 years of age). All subjects were refracted by retinoscopy under cycloplegia prior to the experiments and lenses to correct any refractive error were placed in the stereoscope lens wells during the experimental sessions. One monkey (C-31) was a moderate compoundmyopic astigmat, but the refractive errors of the other five monkeys were not significant. The monkeys were fed a canned primate diet once a day and were water deprived for approximately 22 hours before each experimental session.

Fig. 1 is an illustration of the experimental apparatus. A standard primate chair, fitted on the waist plate with a three position lever with horizontal travel and a juice delivery system attached to the neck plates, was used to restrain the subjects during the experiments. The juice delivery system culminated in a metal spout that could be positioned to correctly align the animal with respect to the stereoscope optical system. The optical system, also attached directly to the primate chair, was an adaptation of a Brewster stereoscope. It consisted of a pair of 5.00 diopter convex lenses with a 65 mm separation, equal to the separation of the corresponding points in the two half-views of the stereograms. Remotely controlled motorized Risley prisms used for changing fusional vergence stimuli were placed in front of the lenses of the stereoscope. The visual stimuli were projected onto a rear projection screen located in the object plane of the stereoscope (20 cm from the lenses) by a random access slide projector (Kodak

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Diagrams of the apparatus used in the experiments.

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RA960) with an electronic shutter attached to the projector lens. A digital logic system (BRS/LVE) was programmed to control all of the experimental parameters, except the Risley prisms which were controlled by the experimenter. The data were recorded on a paper punch tape system, except the data from the vergence fusional ranges experiment which were recorded on a print-out counter.

The random dot stereograms were generated, according to the method described by Julesz (1971), at the Johnson Space Center on the Univac 1108 computer on 35 mm slides produced from the microfilm computer output. Examples of the random dot stereograms are shown in Fig. 2. The stereograms are 130 matrix elements wide by 90 matrix elements high. The matrix elements were rectangular in shape so the half-view of the stereogram was approximately square. Each element subtended a 6 min visual angle for the subject and the fused stereogram subtended a 13° visual angle. The retinal disparity stimuli were programmed in the stereograms by creating displacements of subsets of matrix elements in one half-view of the stereogram with respect to the other half-view. Disparity values of 0 to 54 min of arc, in 6 min steps, of either crossed disparity or uncrossed disparity were used in the experiments.

A technique of successive approximation was used in training the monkeys. The first discrimination task was between a red filter, for which the correct response was a lever press to the right and a green filter for which the correct response was a lever press to the left. Once discrimination for this task reached criterion (90% correct) these filters were then superimposed on the training stereograms seen in Fig. 2A, the red filter over the single rectangle stimulus and the green filter over the double rectangle stimulus. These color cues were faded each time the monkey's performance reached criterion until the behavioral

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paradigm consisted of only a form discrimination task between one rectangle or two rectangles. In order to develop the form discrimination behavior based only on disparity information, a stimulus cue fading technique was employed. Examples of the stereograms used for the form discrimination cue fading are shown in Fig. 2. The first stereograms of the series, Fig. 2A, contained obvious monocular form cues as well as a large binocular disparity, 48 min of arc. In each successive pair of stereograms the strength of the monocular cue was diminished, but the binocular cue remained constant for the entire series. In the final set of stereograms, Fig. 2D, the matrix element density in both the background and pattern area were equal so that the only stimulus cue for the form discrimination was the binocular disparity. Each time the monkey reached criterion performance (90% correct), stereograms with weaker monocular cues were used, until the monkey finally reached criterion with equal matrix element stereograms, i.e. Fig. 2D.

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A flow diagram of the final behavioral procedure used for the data collection for the stereothreshold experiments is shown in Fig. 3. The procedure involved a basic form discrimination task between single rectangle and double rectangle stimuli. Each experimental trial started with the onset of a "ready" stimulus in the form of an 8 Hz click tone. Concurrent with the ready stimulus, an interval (T_1) of 0.2 sec occurred to give the animal time to orient himself before the visual stimuli were presented. At the end of the interval T_1 , one of the stereograms was presented for a duration, T_2 . The stereograms with single and double rectangles-were presented with an equal random probability. The stimulus duration was varied between 4.0 and 0.015 sec from session to session.

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Examples of the random dot stereograms used to develop the form discrimination behavior. In A the stereograms contain both strong monocular and binocular cues. In the subsequent pairs of stereograms (B-D) the monocular form cue is faded while the binocular disparity cue is constant.



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Flow diagram of the behavioral procedure. See Text for details.



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The response interval was initiated concurrently with the presentation of the discrimination stimuli. Either a sustained lever press to the left, associated with S_1 , or a press to the right, associated with S_2 , was always reinforced by a conditioned reinforcer (1.4 KHz tone of 0.5 sec duration) and an unconditioned reinforcer (0.5 cc orange juice) on a 0.75 probability basis. Following each reinforced trial, there was a short intertrial period, TO1, before the next trial started. Any lever press in the intertrial period reset the timer so that there had to be a period of time equal to TO_1 without any responses before the next trial began. The incorrect responses, i.e., a right press associated with S_1 or a left press associated with S2, resulted in a mild punishment stimulus, TO2. The punishment was a longer intertrial period (16 sec) paired with an 80 Hz oscillating tone present for the entire intertrial period. In order to minimize position habits in the animal's response direction and to expedite stimulus control of their behavior, any stimulus which was followed by an incorrect response was re-presented (held) in subsequent trials until the correct response occurred. However only the response to the first presentation of any stimulus was considered in the data analysis.

With this behavioral procedure, the stereothresholds were assessed by using discrimination stimuli with varying amounts of retinal disparity values. A total of 320 different stereograms were used, divided into 4 trays of 80 slides. The trays were alternated daily. Each tray contained equal numbers of single and double forms with crossed and uncrossed retinal disparities. The disparity values were from 0 to 54 min of arc in 6 min increments. Normally, approximately 600 trials were run in each session.

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Human data were obtained on the same apparatus in the same manner but the unconditioned reinforcer, long time out (TO_2) and the hold condition for missed slides were eliminated. Additionally in most cases only 480 trials were run at each viewing duration.

The behavioral paradigm for the two monkeys used in obtaining vergence fusional ranges was the same as discussed above. The experimental protocol, however, was different. Random dot stereograms containing disparities of either 48 or 18 min or arc were shown for viewing durations of either 1.0 sec, 0.5 sec or 0.012 sec. The chamber containing the primate chair and stereoscope was darkened for this experiment so that no fusional cues were present except during the presentation of the random dot stereograms. During the interval following each correct response by the subject, the stereogram stimulus changed and the power of the Risley prisms in the stereoscope was changed symmetrically to alter the fusional vergence stimulus. The amount of prism was first increased in discrete amounts in a base-in direction from zero prism diopters (p.d.) to some maximal value which was determined in pilot studies. It was then decreased in the same number of steps back to zero. Following a number of trials at the zero prism condition, to eliminate after effects due to the vergence movements, the procedure-was repeated in the base-out direction. Data were collected for 6-8 trials at each prism setting during any one session. The response to each stimulus at each prism setting was recorded and from this, the percent correct responses for each value of prism was obtained.

Human data, on the same apparatus, were obtained in a similar manner using two subjects. Both have normal binocular vision by standard clinical criterion.

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RESULTS

A. SENSORY ASPECTS

An example of the form discrimination data for one of the subjects is shown in Fig. 4. The data for the single and double rectangle forms have been combined to present the mean form discrimination rate as a function of disparity for the crossed disparity stimuli (crosses) and the uncrossed disparity stimuli (circles) separately. The curves through the data points were fit by inspection. The data show a substantial difference between the discrimination of crossed and uncrossed disparities between 6 and 30 min of disparity. These data were collected during six sessions and each point is based on data from over 300 trials. Because of the large number of trials, the standard errors of the data are very small and, therefore, to show the variability of the data, the bars shown represent the total range of values for the six sessions. It can be seen that the difference between the discrimination rates for crossed and uncrossed disparities of less than one-half degree are quite reliable. However, with large disparities at this long viewing duration, the differences become smaller.

Fig. 5 shows the form discrimination data for one monkey, 7605, for several viewing durations. Data for the single and double rectangle forms have been again combined to present the mean form discrimination rate as a function of disparity for the crossed disparity stimuli (crosses) and the uncrossed disparity stimuli (circles). The squares in each graph represent the percent correct responses for stereogram stimuli containing no disparity information, and thus no discriminable form. In order to assure that the animals were under stimulus control, i.e. responding on the basis of disparity information rather than some

Example of form discrimination data as a function of disparity. Data, based on 300 trials per point, shown are the percent correct for stimuli with zero disparity (squares), crossed disparities (crosses), and uncrossed disparities (circles). The error bars shown are the entire range of discrimination rates for six sessions.



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Form discrimination curves for monkey 7605 as a function of disparity for viewing durations as indicated. Data are shown for stimuli with zerodisparity (squares), crossed disparity (crosses), and uncrossed disparity (circles), and for the monocular viewing control experiment (triangles).

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extraneous cue, during each experimental session, the same number of these zero disparity stimuli were presented as any other stimulus condition. The zero disparity stimuli were unsystematically assigned as containing the single or double rectangle forms for the purpose of requiring a specific response. Therefore, the percent correct value for the zero disparity stimuli represents the rate at which the monkey's response matched the stimulus code. The 50% or chance discrimination of form for the zero disparity value stimuli was based on retinal disparity information. As an additional control, several sessions were run under monocular viewing conditions. These results are shown in Fig. 5 as triangles. The discrimination rates for all disparities was near the chance rate as would be expected under monocular viewing.

The data in Fig. 5 show a significant difference between the discrimination of crossed and uncrossed disparities for all viewing durations used in the experiment. The effect of varying the viewing duration between 2.0 and 0.5 sec was very small for this subject. However, with shorter viewing durations, two changes occurred in the data. The slope of the ascending portion of the curve became more shallow and the asymptotic discrimination rate was reduced. The disparity range over which the discrimination rate improved as a function of disparity was always 30 min of arc or less, even with the shortest viewing duration. Two other subjects showed that crossed disparities were discriminated better than uncrossed disparities. The data for one of them, 7606, is shown in Fig. 6, and the data for the other, 7512, is shown in Fig. 7. These data are very similar to those of Fig. 5 and it can be seen that crossed disparities are

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Form discrimination curves for monkey 7606 as a function of disparity for viewing durations as indicated. Symbols are the same as in Fig. 5.

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DISPARITY (min)

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7606

Form discrimination curves for monkey 7512 as a function of disparity for viewing durations as indicated. Symbols are the same as in Fig. 5.

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discriminated consistently better than are uncrossed disparities.

Two other subjects showed approximately equal discrimination of crossed and uncrossed disparities. The individual discrimination functions for these animals are shown in Figs. 8 and 9. For these two animals the discrimination curves for crossed and uncrossed disparities could not be differentiated and they were curve fit as a single function.

The data for a sixth monkey showed still a different response pattern. The discrimination data for five viewing durations are shown in Fig. 10. For this subject, the discrimination data for the crossed and uncrossed disparities are the same for viewing durations of 1.0 and 0.5 sec, but for viewing durations of 0.25, 0.12 and 0.06 sec there is a higher discrimination rate for the crossed than the uncrossed disparities for the smaller disparity values, the curves then reach similar values for the large disparities.

The relationship between stereothreshold, i.e., the disparity value for a 75% correct discrimination rate, and the viewing duration for the data shown in Fig. 5 are shown in Fig. 11A. The thresholds for the four viewing durations from 0.5 sec to 0.06 sec are well described by the linear regression lines fitted through the data (r = 0.97 and 0.99 for the crossed and uncrossed disparity data, respectively) when plotted on logarithmic coordinates. The elevation of the stereothresholds occurs at approximately the same rate for both types of retinal disparity and the two linear regression lines are nearly parallel. Figs. 11B and 11C show the relationship between the log stereothreshold and log viewing duration for subjects 7512 and 7606 respectively. These data are similar to those of Fig. 11A except that the relationship is linear over the entire range of viewing

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Form discrimination curves for monkey C-48 as a function of disparity for different viewing durations as indicated. Symbols are the same as in Fig. 5.

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DISPARITY (min)

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Form discrimination curves for monkey C-31 as a function of disparity for viewing durations as indicated. Symbols are the same as in Fig. 5.

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Form discrimination curves for monkey 7508 as a function of disparity for viewing durations as indicated. Symbols are the same as in Fig. 5.

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DISPARITY (min)

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Log stereothreshold as a function of log viewing duration for all monkeys tested. Linear regression lines are fit to the data for crossed disparities (crosses) and uncrossed disparities (circles). The correlation coefficients for the lines fit to each direction of disparity are as follows: A) crossed r = -0.97; uncrossed r = -0.99, B) crossed r = -0.99; uncrossed r = -0.96, C) crossed r = -0.96; uncrossed r = -0.95, D) crossed and uncrossed fit by the same line r = -0.97, E) crossed and uncrossed fit by the same line r = -0.98, F) crossed r = -0.51; uncrossed r = -0.97.



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durations. Note that the linear regression lines fitted through the crossed and uncrossed disparity data are approximately parallel to each other. Figs. 11D and E show the stereothreshold viewing duration function of animals C-48 and C-31 respectively. Since a difference in discrimination of crossed and uncrossed disparities was not found for these two animals, the data were combined for this graph. Fig. 11F shows the data for subject 7508 who exhibited a crossed/uncrossed discrimination rate assymetry only for shorter viewing durations. This mixed response pattern results from a more rapid increase in the stereothreshold with decreasing viewing duration for uncrossed disparities than for crossed disparities. The slopes of the two linear regression lines fit to the data are substantially different from each other whereas they were similar for all of the other subjects.

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Four of the six animals showed a difference in the discriminability of crossed and uncrossed disparities. A similar difference has been found in six of eight human subjects tested on the same apparatus. The data for two of these subjects is presented in Fig. 12. Each data point represents the percent correct responses for 24 trials. Subject P.P., whose data are shown in Fig. 12A, shows no difference in the discrimination of crossed and uncrossed disparities for any of the viewing durations used. Subject R.M., whose data are shown in Fig. 12B, shows a difference between the discrimination of crossed and uncrossed and uncrossed disparities only for the two shorter viewing durations.

There are several possibilities for the difference in the discriminability of crossed and uncrossed disparities: 1) there may be a difference in the sensitivities of the neural disparity detector pools, 2) a small misalignment of the visual axes i.e., fixation disparity, may be present, or 3) there may be a figure-

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Form discrimination curves for two human observers as a function of disparity for viewing durations as indicated. Each data point is based on 24 trials. Symbols are the same as in Fig. 5.

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ground problem such that even though the depth of the stereograms is easily detected, it is more difficult to discriminate a pattern behind the background than in front of it. The latter two possibilities were eliminated by two additional experiments. Small amounts of prism, either base-out or base-in, were introduced before the monkey's eyes. This manipulation did not change the threshold for either type of disparity. The prism should have either eliminated or exaggerated the threshold differences if they were the result of a fixation disparity. The figure-ground problem is much harder to eliminate. However one way to improve the perception of forms made up of large matrix eliments is to filter the image through a high spatial frequency filter (Julesz, 1971). The matrix elements in the random dot stereograms were fairly large (6 min wide by 8.7 min high), and since an optical defocus of the retinal image from convex lenses, in excess of that needed to correct a refractive error, acts as a high spatial frequency filter (Green and Campbell, 1965; Campbell and Green, 1965; Levi and Harwerth, 1977) an additional experiment was carried out on two of the monkeys using 1, 2, 3 and 4 diopter plus lenses to defocus the retinal image. The results of one of these experiments is shown in Fig. 13A. The low power lenses improved the discriminability of both crossed and uncrossed disparities, but did not eliminate the difference between them. Additional lens power elevated the threshold for both disparity types, but the crossed disparities were more severely affected. With a 4 diopter optical blur the discrimination rates for all disparities were similar for both crossed and uncrossed disparities. Fig. 13B shows the relationship between the stereothreshold and power of the defocusing lens. The stereothresholds for both types of disparities pass through a minimum with one

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Effect of lens blur on form discrimination. A) Form discrimination curves as a function of disparity for amounts of plus lens blur as indicated. B) Effect of plus lens blur on stereothreshold. Symbols are the same as in Fig. 5.

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diopter of optical defocus, but the threshold for uncrossed disparities is still 0.2 log units higher than the threshold for crossed disparities.

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RESULTS

B. MOTOR ASPECTS

Fig. 14 shows the percent correct responses for one monkey, 7605, as a function of the amount and direction of the vergence stimulus in prism diopters (p.d.). Each point is the percent correct form discrimination for 50 trials and the standard error bars are shown. The curves have been fit by inspection. Curves A, B, and C, are data for stereograms with 48 min of arc of disparity presented for three viewing durations. Curve D is taken from data with stereograms of 18 min of arc disparity. As can be seen from the data in Fig. 14A, there is a range of prism power values on both sides of zero for which there is a high plateau of performance. As the amount of prism power is increased, the performance of the monkey begins to decrease until, at some value, the monkey's performance falls to chance (50%) for this task. The base-in (divergence) range is smaller than the base-out (convergence) range. A smaller divergence range than the convergence range was measured for both monkey and human subjects and is in agreement with data for human observers obtained using other methods (Weymouth, et al, 1925; Betts and Austin, 1941; Haines, 1941; Shepard, 1941). As the viewing duration decreases, the range of fusion becomes smaller. Taking the 75% correct level as the criterion for the limit of fusion, the range is 6 p.d. basein and 22 p.d. base-out for the 1.0 sec, viewing duration, 6 p.d. base-in and 14 p.d. base-out for the 0.5 sec viewing duration, and 1 p.d. base-in and 4 p.d. baseout for the 0.012 sec viewing duration. The range of fusion for the stereograms

Form discrimination as a function of prism vergence stimulus for monkey 7605. A) Stereograms containing 48 min of arc disparity, viewing duration 1.0 sec. B) Stereograms containing 48 min of arc disparity, viewing duration 0.5 sec. C) Stereograms containing 48 min of arc disparity, viewing duration 0.012 sec. D) Stereograms containing 18 min of arc disparity, viewing duration 0.5 sec. Each data point is the percent correct for 50 trials and standard error bars are shown.

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PRISM

containing 18 min of arc disparity is 4 p.d. base-in and 10 p.d. base-out.

Data obtained from another monkey, 7606, are shown in Fig. 15. The baseout ranges for this second monkey were too large to be measured completely with the apparatus at the longest viewing duration, but with a 0.5 sec viewing duration the base-out range was 26 p.d., considerably larger than that of the first monkey 7605. The base-in range at this 0.5 sec duration for 7606 was 4 p.d., about the same as the first monkey, 7605. The range for the 120 msec viewing duration was from 0 p.d. to 10 p.d. base-out. Using stereograms with 18 min of arc disparity, the range was from 4 p.d. base-in to 20 p.d. base-out.

Fig. 16A shows the data for a human subject, R.H., for 48 min of arc disparity stereograms for a viewing duration of 0.5 sec. Notice that the shape of the curve is very similar to Figs. 14B and 15B and the ranges are of about the same magnitude. Similar results were obtained from the other human subject, R.B., shown in Fig. 15B, except that his base-out range at this viewing duration range was larger than could be measured completely with this apparatus. Subject R.B. has a discrimination rate of chance when viewing stereograms with no prism power in place. However, this subject has normal binocular vision as measured clinically and given sufficient time, he was able to fuse the stereograms.

Fig. 17 shows data for both human subjects for 48 min of arc of disparity slides with a 120 msec viewing duration. The range for R.H., Fig. 17A, is considerably narrower than for this subject with a 0.5 sec viewing duration. There is a base-in range of 1 p.d., using the 75% correct criterion, and the base-out range is about 4 p.d., which is very similar to the monkey's data shown in Fig. 14C. It is interesting to note that the peak of the curve is around 1-2 p.d. of

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Form discrimination as a function of prism vergence stimulus for monkey 7606. A) Stereograms containing 48 min of arc disparity, viewing duration 1.0 sec. B) Stereograms containing 48 min of arc disparity, viewing duration 0.5 sec. C) Stereograms containing 48 min of arc disparity, viewing duration 0.012 sec. D) Stereograms containing 18 min of arc disparity, viewing duration 0.5 sec. Each data point is the percent correct for 50 trials and standard error bars are shown.



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Form discrimination as a function of prism vergence stimulus for human observers with 0.5 sec viewing duration. Data based on 50 trials per point is shown for A) R.H. and B) R.B. Standard error bars are shown. The stereograms contained 48 min of arc disparity.



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Form discrimination as a function of prism vergence stimulus for human observers with a 120 msec viewing duration. The data is based on 50 trials per point and standard error bars are shown. The stereograms contained 48 min of arc disparity. The arrows shown at the bottom of the graph for A) R.H. and B) R.B. indicate the magnitude of the alignment heterophoria.



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base-out prism. Because 120 msec is shorter than the latency for fusional eye movements, this peak should correspond to the subject's fusion free position or heterophoria position (Rashbass and Westheimer, 1961). A measurement of this subject's heterophoria was taken with a 120 msec viewing duration, using the same apparatus, and was found to be 2 p.d. of base-out prism which is indicated by the arrow at the bottom of the graph. The correspondence is good with the peak of the curve. The data for the other human subject, R.B., is shown in Fig. 17B. The range is somewhat broader and shifted to the right. There appears to be a peak around 13 p.d. base-out, which is the value of this subject's heterophoria (shown by the arrow).

DISCUSSION

A. SENSORY ASPECTS

The form discrimination paradigm appears to be an excellent method for evaluating the stereopsis of non-verbal primates. There is strong evidence that the monkeys were indeed using retinal disparity as the cue in the form discrimination task. 1) The discrimination of zero disparity stimuli was at the chance rate. 2) Under monocular viewing conditions the subjects could not perform the task at better than chance rate. 3) The shape of the discrimination curve as a function of disparity is similar to that expected of human subjects known to be under stimulus control. Also, the linear relationship between the logarithm of the stereothreshold and the logarithm of the viewing duration is the same as has been found for human observers (Harwerth and Rawlings, 1977). 4) The difference in the discriminability of form for crossed and uncrossed disparities shows that both the magnitude and the direction of the disparity are important parameters. Since all other binocular cues, such as retinal rivalry of the unfused dots, should be of equal strength for either type of disparity, the difference in the discrimination functions constitutes further evidence that the animals were using retinal disparity as the discrimination cue in these experiments. Therefore, as a demonstration of the stereopsis of monkeys, these experiments are in agreement with previous such demonstrations (Bough, 1970; Cowey, et al, 1975; Julesz, et al, 1976; Sarmiento, 1975).

Four of the six monkeys and six of eight human subjects showed a difference in form discrimination for forms produced by crossed and uncrossed

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disparities. Based on the data from experiments with prisms and defocusing lenses, it seems likely that this difference in discriminability results from a difference in the sensitivities of neural stereodetector pools such as Richards (1970, 1971) has proposed to explain the stereoanomalies of some of his subjects. Using a short (80 msec) flash and bar targets with disparities of 30 min to 4 deg of arc, he found three classes of stereodetectors; crossed disparity detectors, uncrossed disparity detectors, and zero disparity detectors, by discussions that some of his subjects lacked one or more of these classes of detectors. Richards and Regan (1973) have also shown evidence for separate processing of crossed and uncrossed disparities in subjects without stereoanomalies. Poggio and Fischer (1977) have provided neurophysiological evidence for stereodetectors in the macaque monkey. They classified the depth sensitive neurons in areas 17 and 18 of the monkey's cortex into four groups; tuned excitatory, tuned inhibitory, near neurons, and far neurons. Tuned excitatory neurons, they suggested, may be responsible for quantitative stereopsis with single vision. These cells appeared to be most responsive to disparities of $+0.2^{\circ}$. Tuned inhibitory neurons, exhibiting a disparity specificity of about +0.1°, may mediate double (or monocular vision) without depth. Poggio and Fischer (1977) also suggested that the qualitative sensation of depth which exists for large disparities when diplopia is present may be mediated by the near and far neurons and that these neurons may correspond to the classes of neural detectors postulated by Richards (1970, 1971). Several psychophysical studies of humans, including the data presented in these experiments, have shown that crossed stereodetectors have higher sensitivity that uncrossed stereodetectors (Regan and Beverly, 1973; Beverly and Regan,

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1974; Utial, Fitzgerald, and Eskin, 1975). The psychophysical data from the experiments presented in the present work shows the existence of separate neural channels for the detection of near and far depth in both monkey and man and shows that the crossed disparity detectors may be more sensitive than the uncrossed disparity detectors.

Ogle (1952) described two zones of stereopsis, patent and qualitative. Patent stereopsis is present for relatively small amounts of disparity and is characterized by a compelling sensation of depth which is proportional to the amount of disparity. Qualitative stereopsis is present for larger disparities and is characterized by a loss of the depth-disparity relationship but a maintenance of the ability to localize a target as being nearer or farther than the fixation point. The discrimination rate for all disparities above about 30 min of arc was nearly constant for each viewing duration for both monkeys and humans and the effect of reducing the viewing duration was to uniformly reduce the discrimination performance for all of the disparities above 30 min of arc. These data suggest that all disparities above a certain magnitude are detected by a different set of detectors than are the small disparities. Richards (1977) reported that the relative depth of patterns above a certain disparity cannot be correctly identified in briefly presented random dot stereograms. The equality of discriminability of disparities above about 30 min of arc and the inability to identify relative depth are the characteristics of qualitative stereopsis as described by Ogle (1952). Therefore, under the conditions of the present experiments the boundary between qualitative and patent stereopsis may be about 30 min of arc. However, qualitative stereopsis for random dot stereogram

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stimuli may be different from that discussed by Ogle (1952) since the random dot stereograms must be fused to be discriminated, while the stimuli of Ogle and others were seen diplopically.

The disparity discrimination functions were based on a form discrimination task rather than depth discrimination. Obviously, with a random dot stereogram, the depth of the form must be detected before the form itself can be perceived (Over and Long, 1973; Harwerth and Rawlings, 1975). However, the thresholds for form discrimination and depth discrimination have been shown to be highly correlated, with the threshold for form discrimination approximately twice the threshold for depth discrimination (Harwerth and Rawlings, 1977). Therefore, the data for form discrimination directly reflect the behavior that would be expected for a depth discrimination task and has an added advantage in animal psychophysics since an animal's bias could have resulted in erroneously high discrimination rate for the depth direction associated with his bias. However, since both discrimination stimuli were presented in crossed and uncrossed disparities, the presence of a response bias should be independent of the direction of the disparity.

The psychophysical assessment of the binocular vision of the rhesus monkey was successful in demonstrating a qualitative and quantitative similarity to that of humans tested on the same apparatus. The similarities between humans and monkeys for the relationship between stereothreshold and viewing duration, differential sensitivities of crossed and uncrossed stereodetectors, and the ranges of patent and qualitative stereopsis effectively support the use of the monkey as ` an animal model for the sensory aspects of binocular vision of humans.

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Therefore, the neurophysiological data on the normal binocular vision (e.g., Baker <u>et al.</u>, 1974; Poggio and Fisher, 1977) and abnormal binocular vision (e.g., Crawford, 1978; von Noorden, 1978) of monkeys can be confidently applied to humans.

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B. MOTOR ASPECTS

The results of these experiments also clearly indicate that the rhesus monkey is capable of fusional eye movements of approximately the same angular magnitude as humans. This finding is somewhat surprising because the small interpupillary distance of the monkey creates less of a demand on convergence than normally exists for man. One of the monkeys showed a fusional range of 6 prism diopters base-in and 22 prism diopters base-out for the longest viewing duration (1.0 sec) used. This is very similar to the previously published fusional ranges of 8 p.d. base-in and 22 p.d. base-out which were obtained by other methods (Weymouth, et all, 1925; Betts and Austin, 1941; Haines, 1941; Shepard, 1941). The results from the 0.5 sec viewing duration for the monkey and human also yield similar ranges.

The reduction in amplitude of the forced prism vergence as the viewing duration is reduced (c.f., Figs. 14A and 14B) is probably a result of the measuring procedure. In these experiments a reflex measure of fusion was obtained, i.e., the binocular stimulus was presented briefly and the subject had to make a vergence response and recognize the form in the stereogram. The lower fusional amplitude with the shorter viewing duration is most likely due to the inability to make a sufficiently large vergence movement during the exposure since other factors involved such as latency of eye movement and processing time for stereopsis are presumably constant. Most of the decrease in fusional range takes place on the base-out side probably because the base-in range is smaller and the small fusional eye movements can take place with even shorter viewing durations.

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When the viewing duration was shorter than the latency for vergence eye movements, which is on the order of 160-250 msec for both humans and monkeys, no vergence eye movements should occur during the stimulus presentation (Rashbass and Westheimer, 1961; Keller and Robinson, 1972). Thus the peaks of the graph for the data with the 120 msec viewing duration should represent the fusion free position of the eyes (i.e., lateral heterophoria position). The arrows shown in Figs. 17A and 17B are heterophoria measurements for human subjects taken on the apparatus with an alignment technique using a 120 msec viewing duration. There is good correlation between these heterophoria results and the peak of the curves in Fig. 17. From this it may be inferred that the monkey whose data is represented in Fig. 14C is approximately orthophoric. Data from the other monkey, shown in Fig. 15C, indicate it to be slightly (4 p.d.) esophoric. It is interesting to note that both the monkey and the human subject which showed esophoria at the 120 msec viewing duration showed extremely large baseout ranges with the longest viewing duration. The other monkey (7605) and human observer (R.H.) which showed approximately orthophoria, had smaller base-out ranges.

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Comparing Fig. 14B and 14D it can be seen that the fusional range decreases when stereograms containing relatively small disparities are used. Since the fusional movements required were the same in both conditions, it may be postulated that the processing time for stereopsis, once fusion was obtained, was longer for the smaller, weaker disparities. The data shown earlier indicate that for disparities of 18 min of arc to be detected at the same percent as. correct rate as those of 48 min of arc, longer viewing durations are required.

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Finally, Poggio and Fischer (1977) have reported neurons in areas 17 and 18 of the cortex of the monkey which are sensitive to large disparities, either crossed or uncrossed, but not both. These near/far neurons have been postulated to be responsible for vergence movements initiated by large amounts of disparity. The present study and the human data of others (Rashbass and Westheimer, 1967; Westheimer and Mitchell, 1969) have behaviorally demonstrated that monkeys and man make approximately equal vergence responses to large disparities which lie outside Panum's fusional areas. It may be, then, that vergence movements in man are initiated through these types of near/far neurons.

The data from these experiments show that the form discrimination paradigm with random dot stereograms provides a valid method for measurement of fusional ranges and that the rhesus monkey has fusional eye movements very similar to those of humans. These findings add strength to the validity of using the monkey as a model for the motor aspects of the binocular vision system of the human.

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CONCLUSIONS

Because of the many similarities between man and monkey found in the present study for both the sensory and motor aspects of binocular vision, much of the data which now exists for either species may be generalized to the other. For example, Poggio and Fischer (1977) have found neurons in areas 17 and 18 of the monkey's visual cortex which respond only to stimuli lying in front of or behind the plane of fixation. These near/far neurons, they postulated, may be associated with the crossed and uncrossed disparity pools of Richards (1970, Richards (1970, 1971) was led to hypothesize the existence of the 1971). disparity pools by studying subjects who could not detect disparities in one or more directions. The experiments of the present study also show, using random dot stereograms, evidence for the existence of disparity pools in the monkey as well as in man. From the data of the present study, it does not appear that any of the subjects, monkey or human, had a complete lack of one or more pools of detectors, but rather a decreased sensitivity of uncrossed detectors compared to This decreased sensitivity could be due either to lesser crossed detectors. sensitivity for the far neurons over the near neurons, or to a larger number of near neurons. Since this crossed/uncrossed detection assymetry has been found in other studies, (Beverly and Regan, 1973; Regan and Beverly, 1974; Uttal, et al, 1975) it may be a normal part of the organism and thus detectable in a study of near and far disparity detecting neurons. The sample of Poggio and Fischer, (1977) however, was not large enough to indicate which, if either, suggested neural basis for the assymetry is correct.

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The present study showed that disparities greater than 30 min of arc have properties of qualitative stereopsis while those of less than 30 min of arc have qualities of patent stereopsis, and that the crossed/uncrossed detection assymetry extends to these small disparities as well as existing for the larger disparities as found by Richards (1970, 1971) and Jones (1977). This would indicate that, at least for random dot stereogram stimuli, these near/far neuronal pools could extend into the range of the tuned excitatory cells found by Poggio and Fischer (1977). They postulated that these cells, which are sensitive to small disparities of ± 12 min of arc, may be involved in the perception of fine stereopsis. Their data however, does not indicate that these tuned excitatory cells have a near/far dichotomy. More research will have to be done in this area if we are to learn more about disparity pools.

Poggio and Fischer (1977) have hypothesized that the near/far neurons may also be responsible for the initiation of vergence movements since they respond to large disparities in only one direction. Jones (1977) found that many of his stereoanomalous observers did not make vergence movements to disparities in the direction of the anomaly, which is what would be expected if the near/far neurons mediated both processes. The monkeys in the fusional vergence range study do not appear to be stereoanomalous, they apparently have only a decreased sensitivity of the divergent disparity pool but were able to make fusional eye movements in the divergent direction.

In summary, the present experiments, by showing the similarities in the sensory and motor aspects of the binocular vision of man and monkey, have [•] strengthened the use of the monkey as a model for the human visual system.

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Based on this work, it is apparent that it is entirely appropriate to generalize physiological, anatomical, as well as psychophysical studies of monkey's vision to humans.

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CHAPTER 2 SPATIAL VISION INTRODUCTION

In addition to binocular vision, another area of major interests in vision research is spatial resolution. The present experiments were designed to investigate in monkey a particular property of spatial vision, the oblique effect, which has up to this time been found only in humans.

It is known that humans are able to resolve forms with vertical and horizontal orientations better than forms with oblique orientations. Generally investigated with line or grating stimuli, this orientation anisotropy or oblique effect was first studied by Higgens and Stultz (1948). Since then many studies have confirmed that there is a 7-20% difference between the acuity for stimuli oriented vertically or horizontally and those oriented obliquely (Ogilvie and Taylor, 1958; Taylor, 1963).

The oblique effect is resent only for central vision, and effect has many of the properties of meridional amblyopia (Berkley, Kitterle, and Watkins, 1975; Freeman, Mitchell, and Millodot, 1972; Mitchell, Freeman, Millodot, and Haegerstrom, 1973; Mitchell and Wilkinson, 1974; Freeman and Thibos, 1975), which is a decrease in acuity for stimuli oriented in the meridian of poorest focus caused by an uncorrected astigmatism which occurred early in life. This meridional amblyopia may be prevented if the astigmatism is corrected early in life (Mitchell, <u>etal.</u>, 1973; Gwiazda, Brill, and Held, 1976), but will persist even [•] after proper correction if this correction takes place too late. Both meridional

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amblyopia and the oblique effect are more pronounced for high than low spatial frequencies (Campbell, Kulikowski, and Levinson, 1966; Mitchell and Wilkinson, 1974; Freeman and Thibos, 1975a). Generally meridional amblyopia is present only for spatial frequencies of 0.5-1.5 cycles/degree and higher and the oblique effect is considered to be present for spatial frequencies above lcycle/degree. Because of the similarities between meridional amblyopia and the oblique effect, it has been postulated that the oblique effect may also result from environmental influences, chiefly a "carpentered world" predominated by horizontal and vertical contours. Annis and Frost (1973) reported finding no significant oblique effect in a group of Cree Indians whose world is not predominated by horizontal and vertical contours as is the world of most people in an urban society. Teller, Morse, Borton, and Regal (1974), using a perferential looking technique, showed no oblique effect in infant humans between the ages of one and six months, while Mayer (1977) showed that no oblique effect exists at age five years, but develops with time after this age. Leehey, Moskowitz-Cook, Brill, and Held (1975) on the other hand, also using a preferential looking technique, found orientation anisotropy in infants as young as six weeks of age, indicating that it may be innate.

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While the cause of the oblique effect is unknown at the present time, several studies have ruled out certain possibilities. This phenomenon is not mediated by the gravitational perception of horizontal and vertical. Rather it is the retinal orientation which is important (Lennie, 1975; Banks and Stolarz, 1975). Orientation anisotropy is not due to eye movements (Higgens and Stultz, -1950; Nachmias, 1960) or to optical factors such as astigmatism or aberrations,

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since it is present even if the optics of the eye are bypassed by forming laser interference fringes directly on the retina (Campbell, Kulikowski, and Levinson, 1966; Mitchell, Freeman, and Westheimer, 1967). These latter two studies have concluded that the oblique effect is of neural origin. Investigating this possibility further, Maffei and Campbell (1970) and Freeman and Thibos (1975b) have both measured an oblique effect using visual evoked potentials in man. Additionally, Maffei and Campbell (1970) could not find evidence for an oblique effect using the electroretinogram, leading them to conclude that the site of origin of this effect lies between the retina and the visual cortex. This neural theory of a basis for orientation anisotropy has led several investigators to look at single cortical units for evidence of this effect. Mansfield (1974) has reported finding a significant predominance of cortical cells with foveal receptive fields in the monkey which have a bias for horizontal and vertical stimuli. In the cat, Pettigrew, Nikara, and Bishop (1968) have found that a large proportion of cortical simple type cells with receptive fields close to the area centralis showed a preference for horizontal and vertical orientations. Hirsch and Leventhal (1978) have found in the cat a group of cells they describe as SAS cells (Small Area--Slow movement) which are concentrated in areas of the cortex subserving central vision. These SAS cells have small receptive fields, prefer slow moving stimuli, and the majority of them are biased toward stimuli oriented either horizontally or vertically. Other studies, notably Finlay, Schiller and Volman (1976) and Poggio, Doty and Talbot, (1977) have, however, found no predominance of the monkey's foveal cortical cells prefering horizontal or vertical stimuli.

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The conflicting physiological evidence from these animal studies is further compounded by the fact that an oblique effect has not been found behaviorally in animals, other than man, (Appell, 1972) even though two investigations of the cat's vision have looked into this area (Bisti and Maffei, 1974; Blake, 1978). It seems that the first question which must necessarily by answered before investigations into the neural mechanisms of the oblique effect become significant is: Do animals other than man behaviorally demonstrate an oblique effect? De Valois, Morgan, and Snodderly (1974) have shown that the contrast sensitivity function, for vertically oriented stimuli, of the monkey is very similar to that of man. Therefore, it would seem that this animal should be the most likely to possess an oblique effect. If the monkey possessed an oblique effect like that of man, the use of the monkey for a model of the human spatial vision system has added validity. The purpose of this study was to behaviorally test the monkey for an orientation anisotropy.

METHODS

Two pre-adolescent, colony born, cage reared, rhesus monkeys were used in this study. Each was refracted and correcting lenses were used during the experiments. The monkeys were water deprived for 20-22 hours before each session and received water or synthetic orange juice as a reward. The monkey sat in a standard primate chair placed in a darkened, sound attenuating chamber and was positioned so that the monkey could view an oscilloscope screen placed outside the chamber, 114 cm from the monkey's eyes. The monkey's head position was controlled by means of a spout, through which liquid reinforcement was dispensed, and side plates to prevent head rotation. The chair was also fitted, on the right hand side, with a two position lever, with downward travel from the level position.

Sinewave grating stimuli were generated in the usual manner (Campbell and Green, 1965) on a Tektronics 7603 oscilloscope with a high intensity phosphor. The oscilloscope screen was masked down to a 4° circular field and had a mean luminance of 67 cd/m² which remained constant for all contrast levels and spatial frequencies used. The oscilloscope was mounted in a cradle which allowed its rotation about the center of the circular screen. The window of the sound attenuating chamber reduced the mean luminance of the oscilloscope by 0.1 log units, so that when human subjects were used in this study, 0.1 neutral density filters were placed before their eyes.

BRS/LVE digital logic controlled the behavioral paradigm, provided timing for the experiments, and varied the contrast of the gratings. The monkey was

trained to press and hold the lever at the start of an 8 Hz auditory signal and to release the lever when the grating was flashed on the screen. This was accomplished through a seroes of successive approximations in which the monkey first learned to press the lever for reinforcement and was-later given reinforcement only upon lever release. Gradually the length of time required to hold the lever down was increased. Once this had been accomplished, lever release was paired with the onset of a grating so that any time after the grating appeared the lever could be released for reward. The oscilloscope screen was dark during the intertrial interval so that a luminance cue accompanied the grating onset. After the monkey was under control of this stimulus, the luminance cue was removed and the length of time in which the monkey could release the lever and still receive reinforcement was shortened. The final behavioral paradigm is shown in schematic form in Fig. 18. The lever press initiated a variable duration foreperiod during which the grating was presented for a 500 msec duration with a 0.02 probability at the end of any consecutive 100 msec period. Concurrent with the onset of the grating stimulus, a msec reaction time counter and an 700 msec limited-hold reinforcement period were started. If the monkey released the lever within the limited hold period, it was assumed that he had seen the stimulus, the reaction time was recorded and he was rewarded with a conditioned reinforcement (1.6 Khz tone) after each trial and water or juice on a 0.5 random probability basis. A 4 sec intertrial period followed each rewarded trial or trials for which the reaction time was longer than the limited-In order to discourage anticipatory responses, if the monkey' hold period. released the lever prior to the onset of the grating stimulus, a 14 sec intertrial

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Flow diagram of the behavioral procedure. See text for details.



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interval occurred. Data were collected by a descending method of limits. Each series started with a grating contrast of 70% which was reduced by a programmable attenuator in 0.1 log unit decrements following the rewarded trials. Reaction times were recorded for each contrast level for which a lever release occurred during the 700 msec hold period. If the monkey failed to release the lever within the limited hold period, it was assumed he had not seen On the next trial, the grating was presented with the same the stimulus. contrast level. A failure to release the lever within the hold period for each trial after the first hold-through had a probability of 0.5 of resetting the contrast of the grating to the maximum value. The contrast level for which the monkey failed to release the lever, at least twice, during the hold period, after which the contrast returned to maximum, was taken as the monkey's threshold. The 0.5 probability factor was employed to prevent the monkey from holding through the 700 msec period twice, as the grating became difficult to see, in order to reset the contrast to some higher level. During any one daily session, one grating orientation and spatial frequency were presented. Data on human subjects were obtained using the same paradigm and stimulus as for the monkey.

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RESULTS

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Fig. 19 shows the contrast sensitivity curves for the two monkeys tested as well as a human subject. Each data point for the monkeys is the mean of 12 threshold measurements taken with a descending method of limits design. The data points for the human observer are the means of six threshold measurements. Data for the human observer, Fig. 19C, and monkey 7512, Fig. 19A, were obtained binocularly while the data for monkey 7508, Fig. 19B, were obtained under monocular conditions with the left eye viewing. The curves were fit to the data by inspection and are similar for all three subjects. The functions for both the monkeys peak at about 3 cycles/degree while that for the human observer peaks around 4 cycles/degree. The decline in sensitivity for high spatial frequencies is about the same for all three observers although the low frequency roll-off is steeper for monkey 7512 than the other two subjects. Additionally. monkey 7508 appears to have slightly higher sensitivity than the other monkey subject for spatial frequencies lower than about 6 cycles/degree, but the sensitivity is about the same as the human observer. The data presented in this figure are quite similar to that found by De Valois, Morgan and Snodderly (1974) although the sensitivities of their monkeys and humans were slightly lower, probably because the gratings of their study had a mean luminance of about 17 cd/m^2 while those of the present study had a mean luminance of 67 cd/m^2 (Pantel, 1966).

The contrast sensitivity functions for four orientations of the gratings, 180° , 45° , 90° , 135° , for one monkey, 7512, are shown in Fig. 20 in which each

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Contrast sensitivity functions for monkey and human observers. The stimuli were oriented at 90° and were presented for a viewing duration of 500 msec with a limited hold time of 700 msec. The data for the monkeys A) 7512 and B) 7508 are the means of 12 trials per point while that for the human observer, C) R.B. is the mean of 6 trials per point.



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Contrast sensitivity function for monkey 7512 for four orientations. The stimuli were presented for 500 msec with a limited hold of 700 msec. Each data point is the mean of 30 threshold measurements. Orientations of 180° (squares), 45° (pluses), 90° (circles), and 135° (crosses) are shown.



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data point is the mean of thirty thresholds. The data for the horizontal and vertical gratings are well fit by a single curve as are the data for the two oblique orientations. As can be seen, the obliquely oriented gratings have a lower contrast sensitivity than do the horizontally and vertically oriented gratings for moderate to high spatial frequencies. The difference in the two functions is largest for the highest spatial frequency tested, 20 cycles/degree, decreases as the spatial frequency becomes lower, and disappears at about 1 cycle/degree; similar to the oblique effect as described by Campbell, Kulikowski, and Levinson (1966) for man.

These data may be represented in another way in which the oblique effect is more apparent. In Fig. 21 contrast sensitivity is plotted as a function of grating orientation for several spatial frequencies. Data from both monkeys, 7512, shown in solid lines, and 7508, shown in broken lines, both exhibit a W-type function characteristic of orientation anisotropy. The magnitude of the effect is largest, between 0.3 and 0.4 log units, for 20 cycles/degree and becomes smaller, systematically, as the spatial frequency decreases. Comparing the 16 cycle/degree data for both subjects, the magnitude of the effect is the same, although one subject, 7508, shows higher contrast sensitivity. For low spatial frequencies, the effect cannot be seen. The top of Fig. 21 (note that the graph is discontinuous) shows data for 7512 and 7508, for 1.0 cycles/degree and 0.5 cycles/degree gratings, respectively, are shown. While the lines are not absolutely flat, the symmetrical W-type function of the oblique effect is not seen at these low spatial frequencies, indicating that the effect is absent.

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Oblique effect at several spatial frequencies. Data is shown for monkey 7512 (solid lines, circles) and monkey 7508 (broken lines, squares). Each point is the mean of 30 trials for monkey 7512 and 12 trials for monkey 7508. Note that the upper part of the graph is discontinuous from the bottom part although the scale is the same.

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Fig. 22 shows the data for two human subjects as a function of orientation for two spatial frequencies. Each point is the mean of twelve threshold measurements. For a 16 cycles/degree grating, an orientation anisotropy of 0.2-0.3 log units is present. This is slightly smaller than that found for the monkeys (c.f., Fig. 21) but is within the range of values given by Camisa, Blake and Lema (1977), for human observers. In the upper portion of Fig. 22 (note the discontinuity in the graph) are the 0.5 cycle/degree data for both subjects. The contrast sensitivity for subject E.S. is nearly equal for all orientations of the grating, but there is some variation in sensitivity for subject R.H. These variations are unsystematic as a function of orientation, do not have the typical shape of the oblique effect, and are of small magnitude compared to this subjects orientation anisotropy. They are probably a result of the number of thresholds taken to derive this function.

The oblique effect is traditionally a phenomenon examined at threshold. The question thus arises; Does this effect exist for suprathreshold contrasts? In order to investigate the possibility of a suprathreshold oblique effect, reaction times were used as an index of stimulus strength. Reaction time is known to increase monotonically, without specific training, as a function of decreasing stimulus strength (Stebbins, 1966; Moody, 1970; Mansfield, 1973). Additionally, it is generally considered that reaction time is directly correlated to stimulus strength so that stimuli with equal reaction times should have equal perceptual values (Roufs, 1974; Manfield, 1973; Stebbins, 1966; Moody, 1970). Therefore, reaction times, in msec, were recorded for each contrast level as the monkey^{*} observed gratings of different orientations. From this data, the amount of

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Oblique effect for two spatial frequencies for two human observers. Data is shown for subject E.S. (squares, broken lines) and subject R.H.(circles, solid lines). Each point is the mean of 12 trials. Data for subject E.S. were obtained using a descending method of limits such as used with the monkeys. Data for subject R.H. were obtained using an ascending method of limits. Note that the upper part of the graph is discontinuous from the bottom part although the scale is the same.



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contrast for gratings of different orientations which produced equal criterion reaction times can be found as described below. The reciprocal of this contrast level, the contrast sensitivity, can then be plotted as a function of grating orientation in order to examine the obligue effect. The median reaction times for thirty stimulus presentations for each grating orientation and contrast level were plotted as a function of the log contrast of the grating. Median reaction times were used since the skewed nature of reaction time distributions requires a measure not so sensitive to extreme values as is the mean (Moody, 1970). An example of a reaction time vs. contrast function taken with a 16 cycle/degree grating oriented at 90°, is shown in Fig. 23. As can be seen, the reaction times for this subject increase monotonically as the contrast decreases. A power curve of the form $y=bx^{m}$ was fit to these data and had a correlation coefficient of -0.98. Similar functions were obtained for the other three orientations, 180° , 45° , and 135°, at this spatial frequency, all of which had the same form. The correlation coefficients for these curves were all -0.96 or better. From the power functions fit to the data for each orientation, contrast levels for several criterion reaction times were obtained. The reciprocal of these contrast levels was then plotted as a function of grating orientation for each of the criterion reaction times and can be seen in Fig. 24. The criterion reaction times used to determine each curve is indicated. It is clearly evident from this figure that the oblique effect is present for suprathreshold contrast levels and that its magnitude remains about the same over the entire range of suprathreshold contrast levels used in this experiment. The magnitude of the oblique effect is slightly larger, 0.05 log units, as determined from the suprathreshold data using a

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Reaction time as a function of contrast for monkey 7512. Data is shown for a 16 cycle/degree grating oriented vertically. The viewing duration was 500 msec and the limited hold was 700 msec. Each reaction time is the median of 30 trials. The data are fit by a power function which had a correlation coefficient of r = -0.98.



LOG CONTRAST

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Suprathreshold oblique effect for monkey 7512. The data are for a 16 cycle/degree grating viewed for a duration of 500 msec with a limited hold time of 700 msec. The criterion reaction time used to obtain each line is indicated.

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700 msec criterion reaction time, than as determined by the threshold data using a 700 msec limited hold time. At this criterion reaction time, the contrast sensitivity is also slightly, 0.1 log units, higher than that determined by the threshold data. Using a criterion reaction time of 700 msec implies that the monkey could see the grating, but a reaction time of 700 msec in a threshold trial implies that the monkey could not see the grating. Thus the suprathreshold oblique effect is slightly larger and shifted slightly higher on the contrast sensitivity scale for the 700 msec criterion reaction time. Comparing the data from Fig. 21 to the data of Fig. 24 for a criterion reaction time of 600 msec, a very good correspondence is found, which is expected since very few reaction times were greater than 600 msec but less than the limited hold time (700 msec). This property of the oblique effect has not been shown previously for either man or monkey and indicates that whatever mechanism is responsible for the effect operates at both threshold and suprathreshold contrast levels.

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A final experiment was performed on one monkey, 7512, to determine the effect of viewing duration of the oblique effect. Gratings of 16 cycles/degree were presented for 500 and 50 msec at orientations from 0° to 170° in 10° steps and at 45° and 135° . The results of this experiment are shown in Fig. 25. As can be seen, the effect of the shorter viewing duration was to lower the contrast sensitivity approximately 0.4 log units. However, the magnitude of the oblique effect remained unchanged. This was the effect expected since Nachmias (1966) showed that the effect, on the contrast sensitivity function, of reducing viewing duration is a nearly uniform lowering of the curve.

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Effect of two viewing durations on the oblique effect. The mean of twelve threshold measurements per data point were used to obtain these two functions for a 500 msec viewing duration (top) and a 50 msec viewing duration (bottom). The limited hold time was the same in both cases. Data were obtained for orientations from 0° to 170° in 10° steps with the inclusion of 45° and 135° .



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DISCUSSION

The contrast sensitivity functions of both the monkey and human subjects used in this study are remarkably similar and demonstrate again (De Valois, Morgan, and Snodderly, 1974) that the spatial resolution of monkey and man are very much the same. More interestingly, the data from these experiments also show that the monkey has an oblique effect, something which has not been previously demonstrated in any animal other than man. The magnitude of this effect is nearly equal for the two monkeys used in this study and is just slightly larger, 0.1 log units of contrast sensitivity, than the effect for the two human observers. Camisa, Blake, and Lema (1977) reported finding oblique effects of 0.2 to 0.5 log units of contrast sensitivity so that the effects for the observers of the present study fall within previously published ranges. As the spatial frequency of the grating decreases, the behavior of the effect is similar for man and monkey, i.e., it steadily decreases in magnitude until, at about 1.0 cycle/degree, it is no longer present (Campbell, Kulikowski, and Levinson, 1966; Mitchell and Wilkinson, 1974). The similarities between the monkey and human data are important in validating the monkey as a model for the human visual system's resolution properties since it shows that a relatively subtle effect, such as orientation anisotropy exists in both species.

The other important finding of this study is the behavioral evidence that the oblique effect exists at suprathreshold contrasts and has the same magnitude regardless of contrast. Suprathreshold contrasts have been used to elicit the ⁻ oblique effect with evoked potentials but the psychophysical evidence is

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important because it shows how an animal behaviorally processes information. This finding implies that the channels which process spatial information of the obliques are less sensitive at all contrast levels used, a finding which could not be implied from threshold data alone.

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While the data of the present experiment do not allow one to decide if the oblique effect is innate or environmentally influenced, or to discern its neurophysiological basis, the presence of an oblique effect in the monkey does make it possible to test some of the hypotheses which may be put forward. Current evidence from electrophysiological studies of the monkey is conflicting. Mansfield (1974) has described a significant bias for vertically and horizontally tuned receptive fields in the monkey while Finlay, et al (1974) and Poggio, et al (1977) have reported a homogeneous distribution of orientation tuned cells. Levinthal and Hirsch (1977) have, in the cat however, described a class of cells, SAS (Small Area-Slow movement), the majority of which respond best to stimuli with horizontal or vertical axes. These SAS cells have small receptive fields and respond only to relatively slow rates of stimulus motion compared to the other class of cells, LAF (Large Area-Fast movement) which had a more even distribution of orientation preferences. Hirsch and Levinthal (1978) have postulated that these SAS cells receive input from X-type (sustained) cells in the LGNd and possibly W-type cells. Psychophysical evidence for sustained and transient channels in man has been obtained by several studies (e.g., Kulikowski and Tolhurst, 1973; Tolhurst, 1975). Camisa, et al. (1976) used methods to isolate sustained and transient mechanisms and found that the oblique effect in man is a property of sustained channels. Evidence to further strengthen this hypothesis is

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that sustained cells, and SAS cells as well, in the cat are most prevalent in the area centralis and become fewer in the peripheral retina (Fukada, 1971; Ikeda and Wright, 1975b) and they are tuned to higher spatial frequencies than transient cells (Ikeda and Wright, 1975a). These properties are similar to those of the oblique effect since it is present only for central vision (Berkley, <u>et al.</u>, 1975) and is largest for high spatial frequencies (Campbell, <u>et al.</u>, 1966; Mitchell and Wilkinson, 1974; Freeman and Thibos, 1975). Although transient cells respond best to high temporal frequencies, the failure of decreasing the viewing duration from 500 to 50 msec to decrease the magnitude of the oblique effect is to be expected because a 16 cycle/degree grating should be detected by sustained channels (Tolhurst, 1975).

The monkey, because its resolving power is close to that of man and because the present study clearly demonstrates an oblique effect in monkeys, should be the animal of choice for electrophysiological experiments. Those experiments which have been done have not analyzed orientation bias in terms of various categories of cells, such as SAS and LAF. An analysis of orientation selectivity in terms of simple and complex cells in the cat showed no marked difference in the percent of each type tuned to horizontal or vertical lines, nor was there a great percentage (63%) of any one type tuned to horizontal or vertical lines. However, 86% of the SAS cells of the same sample were tuned to horizontal or vertical lines while only 57% of the LAF cells were so tuned (Hirsch and Levinthal, 1978). Perhaps equivalent types of cells exist in the monkey's cortex and are responsible for this effect. An investigation of cortical cells with-small receptive fields, lying near the fovea, tuned to high spatial frequencies may reveal an orientation bias which could be responsible for the oblique effect.

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If the oblique effect is mediated by SAS type cells, some inferences into whether the oblique effect is innate or environmentally influenced may be made. Levinthal and Hirsch (1977) found that nearly all the orientation selective cells in the visual cortex of cats raised deprived of form vision had characteristics of SAS cells, including the bias for horizontal and vertical lines. It would appear that these cells do not require visual experience to develop this bias, indicating that the bias is innate. It must be remembered, however, that the cat does not exhibit an oblique effect behaviorally (Bisti and Maffei, 1975; Blake, 1977) and than an orientation bias of cells in the cortex of an animal, even the monkey, is not necessarily responsible for the oblique effect. On the other hand, the reason that the cat fails to show an oblique effect may be because its visual resolution is so poor (Bisti and Maffei, 1975; Blake, Cool, and Crawford, 1975; Jacobson, Franklin, and McDonald, 1976) compared to man's. Even man shows only a very small oblique effect at spatial frequencies near the limit of resolution of the cat.

The question of whether orientation anisotropy is innate or environmentally influenced remains open. Although much of the electrophysiological evidence points to innate factors, much psychophysical evidence cited earlier supports a "carpentered world" hypothesis. This question might be best answered through special rearing techniques with monkeys to avoid predominating their environment with horizontal and vertical contours and then testing them both electrophysiologically and psychophysically. Since the monkeys used in this experiment were colony born and cage reared, they were exposed to the same "carpentered world" as man. Therefore, these experiments cannot be used to " predict the causes of the oblique effect.

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Another possible basis for the oblique effect also needs mention although no data appears to exist to support or refute it. It is possible that cells preferring horizontal or vertical stimuli may have maximal sensitivity to higher spatial frequencies and/or have a higher high spatial frequency seut-off that do cells which prefer oblique orientations. This hypothesis can also be tested in the monkey.

In summary, the monkey has an oblique effect similar to man's in magnitude. This effect is present for suprathreshold as well as threshold contrasts. This finding further strengthens the use of the monkey as a model for the human visual system and will allow further testing to find the basis of orientation anisotropy.

CONCLUSIONS

It is clearly evident from these experiments, and those of others, that the monkey has a visual system very similar to our own. This is an important finding for we can now begin to extrapolate data which exists only for the monkey, e.g. deprivation studies and other invasive types of experiments, to the human with a great amount of confidence. Additionally, using operant conditioning techniques, it is now possible to conduct experiments on a behaving animal which may be too time consuming or potentially hazardous for the use of human subjects. From the information we now possess about the monkey's color vision, binocular vision, spatial vision, etc. it is reasonable to assume that what data we generate using the monkey can be generalized to humans without having to obtain human companion data. In short, the behavior of the monkey's visual system should behave like that of the human, and vice versa.

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