BINOCULAR RIVALRY IN MACAQUE MONKEYS AND HUMANS: A COMPARATIVE STUDY IN PERCEPTION

JOEL MYERSON

Department of Psychology, University of California, Riverside, CA 92521, U.S.A.

FRANCIS MIEZIN and JOHN ALLMAN

Division of Biology, California Institute of Technology, Pasadena, CA 91125, U.S.A.

ABSTRACT

Macaque monkeys were trained to report the direction of movement of bar gratings. The monkeys were then exposed to rivalrous stimuli (gratings moving in opposite directions for each eye). The rate of perceived alternation in direction of movement as reported by the monkeys and by human subjects tested with the same procedure was an increasing function of the velocity of the gratings. For both monkeys and humans, gamma functions described the distributions of rivalry phase durations. and the form of the distributions changed systematically with the grating velocity and perceived rate of alternation. These results demonstrate the similarity of binocular rivalry in macaque and human subjects.

Key words: binocular rivalry; perception in animals; macaque.

When the two eyes receive dissimilar stimulation, human subjects often report abrupt alternations in perception; subjects report seeing alternately the stimulus viewed by one eye and then the stimulus viewed by the other eye (e.g., Lack, 1978; Levelt, 1965). This phenomenon is termed binocular rivalry. For example, when one eye views bars moving in one direction and the other eye views bars moving in the opposite direction, human subjects report seeing bars that periodically reverse their direction of movement (Fox, Todd and Bettinger, 1975). It would be extremely useful if animals could be trained to report their perceptions in such situations. This would make possible comparative studies of binocular rivalry and also provide a

behavioral preparation in which to study the underlying neural mechanisms.

Perceptual phenomena such as binocular rivalry pose a special challenge for animal research. Accurate reporting of perceptions cannot be achieved simply by reinforcing correct responses and not reinforcing incorrect responses because in such situations there is no correct response defined by external criteria (Malott and Malott, 1970). Instead, animals must be initially trained to discriminate between stimuli which, it is hypothesized, give rise to perceptions similar to those which will occur in the experimental situation (Scott and Milligan, 1970). We hypothesized that when exposed to gratings moving in opposite directions for each eye, monkeys like humans would perceive moving gratings that periodically reversed their direction. Therefore in the present experiment, macaque monkeys were trained to discriminate the direction of moving bar gratings. Subsequently, monkeys did report changes in perceived direction of movement induced by rivalrous stimuli. Quantitative aspects of their performance were compared with those of humans tested with the same procedure.

METHOD

Subjects

Two experimentally naive monkeys, one male (DJ) and one female (TH) juvenile *Macaca fasicularis*, served as subjects. A third monkey was trained but did not report binocular rivalry. Fluid intake was restricted to the fruit juice earned as reinforcements during experimental sessions and the water consumed during 30 min free access after experimental sessions. Dry food was always available in the home cage. One female and two male adult humans with corrected-to-normal vision also served. One human considered as a possible subject was unable to fuse the rivalrous stimuli and did not report rivalry.

Apparatus

As shown schematically in Figure 1, human and macaque subjects gazed into a haploscope so that each eye viewed a separate oscilloscope screen. The length of the optical path from eye to screen was 57 cm. The haploscope consisted of two front-surface mirrors (81 × 100 mm) mounted at an angle to each other. For the macaques this angle was set at 90°. Because the interpupillary distance for the macaques was quite small, with this mirror angle their convergence when fixating the screens would be appropriate for a binocular stimulus at 57 cm. For humans the mirror angle was adjusted by individual subjects to achieve optimal fusion of binocular images. Between the mirror and the oscilloscope screen the field of view was restricted by a 6.35-cm internal diameter lucite tube inserted in a lucite plate located near the mirror end of the tube. The plates and tubes were painted flat black. Subjects viewed the display through a 4° aperture positioned at the oscilloscope end of the tubes.
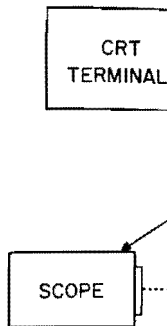
CRT
TERMINAL

SCOPE

Figure 1. Appara:

Under gene
procedures, ea
Caulk Co., M:
position durin;
positions.

Moving squ
programmable
were displayec
oscilloscopes
presentation o
also stored da
fitting using a

Human subj
standard teleg
specially const
was dispensec
haploscope.

Procedure

Macaques w

chanisms.
ıl challenge for
ieved simply by
ıses because in
ria (Malott and
minate between
hose which will
·pothesized that
e, monkeys like
their direction.
to discriminate
port changes in
ıtitative aspects
with the same

e (TH) juvenile
ed but did not
uice earned as
I during 30 min
ıle in the home
mal vision also
se the rivalrous

s gazed into a
e length of the
d of two front-
ther. For the
stance for the
when fixating
or humans the
mal fusion of
e field of view
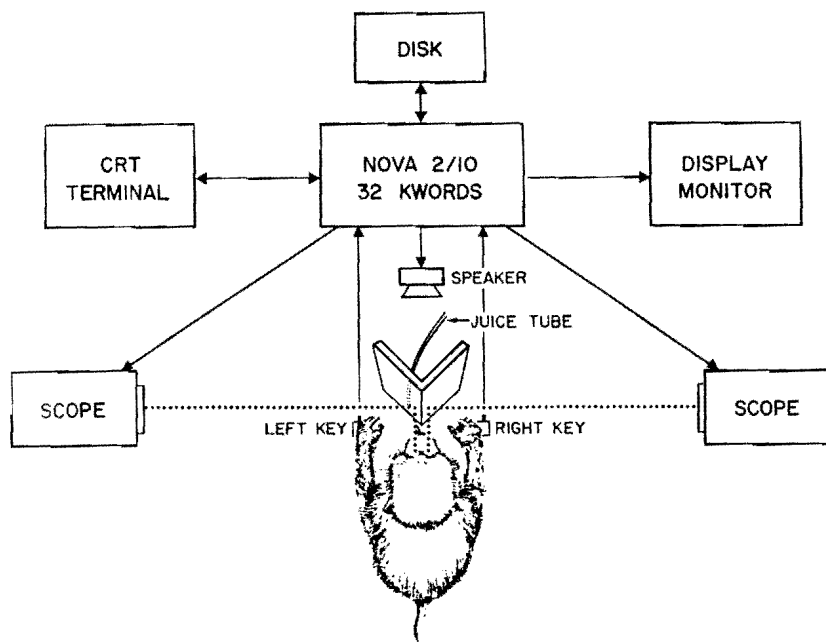a lucite plate
e painted flat
tioned at the

Figure 1. Apparatus for the study of binocular rivalry.

Under general anesthesia (Ketamine-HCl, 20 mg/kg/hr) and using aseptic procedures, each macaque had a bolt attached to its skull with Grip cement (L.D. Caulk Co., Milford, Del.). This bolt was used to hold the animal's head in a fixed position during experimental sessions. Humans used a bite bar to stabilize their head positions.

Moving square-wave gratings were generated by a set of special-purpose programmable counters controlled by a Data General Nova 2/10 computer and were displayed on a pair of Tektronix 606 oscilloscopes. The gratings on the oscilloscopes were refreshed 200 times per second. The computer controlled the presentation of all experimental stimuli, collected and analyzed data on-line, and also stored data for later, more extensive, off-line analysis which included curve-fitting using a nonlinear, least squares procedure (Curry, 1975).

Human subjects signaled the perceived direction of grating movement by tapping standard telegraph keys placed 81 cm apart, center to center; macaques used specially constructed stainless-steel keys placed 21.5 cm apart. Juice for macaques was dispensed from a stainless-steel lick tube mounted directly below the haploscope.

Procedure

Macaques were trained to seat themselves in a chair and accustomed to head

restraint. Their initial operant training was on a simple discrimination. Reinforcement (0.12 ml of fruit juice accompanied by a short tone) was contingent upon tapping a key when bars were displayed on the oscilloscope screens; following reinforcement there was an intertrial interval during which the screens were blank and responses were not reinforced. A second discrimination was then introduced such that in the presence of bars of one orientation, responses on the right key produced juice; when the bars were of a second orientation, left key responses were reinforced. A response on the key inappropriate to the displayed bar orientation resulted in the screen going blank and initiation of the intertrial interval. Responses on either key during the latter part of the intertrial interval postponed stimulus presentation. Self-administration of test stimuli by animal subjects often produces better stimulus control over behavior than response-independent stimulus presentation (Blough, 1966). Therefore an 'observing response' requirement was introduced such that after a minimum intertrial interval had elapsed, macaque subjects could initiate stimulus presentation by making contact with the lick tube.

Control over response latency was acquired through the addition of a limited-hold contingency (Moody, 1970), i.e., stimulus presentation initiated a brief limited-hold period during which the first correct response produced reinforcement; the display was terminated without reinforcement if either an incorrect response occurred or the limited-hold period elapsed without occurrence of a correct response. When reaction times had stabilized, reinforcement was made contingent upon the correct reporting of from 1 to 15 consecutive orientation changes; late or incorrect responses caused the display to terminate without reinforcement and the initiation of the intertrial period. A 'constant probability' schedule (Fleshler and Hoffman, 1962) with a mean of 2.0 sec and minimum and maximum intervals of 0.5 and 6.5 sec, respectively, determined the time between stimulus changes and the number of changes for each trial was determined by a pseudorandom procedure.

After subjects began to respond both rapidly and accurately to sequences of changes in grating orientation, vertically oriented moving gratings were substituted for the static gratings, and subjects were required to report the direction of movement whenever it changed. Movement to the right was reported by tapping the right key and movement to the left by tapping the left key. Because human subjects reported that rivalry began with a brief period during which neither eye was suppressed, a brief (500-msec) period of rivalrous stimulation was presented at the beginning of discrimination training trials to increase their similarity to rivalry trials.

When subjects consistently attained better than 95% accuracy with a mean latency of less than 400 msec, they were judged ready for the binocular rivalry stage of the experiment. Rivalry-inducing stimuli consisted of vertically oriented gratings moving in opposite directions for each eye. Rivalry trials varied randomly in duration from 0.5 to 30 sec with a mean of 15 sec; training trials were of equivalent duration. To ensure attention to the task of reporting movement direction, rivalry

trials fo
gratings
probe sti
by the su
was pres
response
performa
correct re
and, for
terminate
being a t
Another
had been

Experin
monkeys.
performa
consisted
was run i
min break
one exper

For the
rivalry tes
As similar
cycles per
the results
was consta
120 rivalry

For mac
training tr
subjects, a
consequen
trials. For
experiment
in two and

RESULTS

When or
gratings m
direction o
there was c
(Table 1),

trials for all subjects terminated in 'probes' in which the direction of one of the gratings was reversed so that both eyes viewed the same direction of movement. The probe stimulus always moved in the direction opposite to the direction last reported by the subject. Thus, at some variable time after the beginning of rivalry, the subject was presented with a stimulus to which there was an objectively defined correct response which could be differentially reinforced. Such probes of the subject's performance were intended both to maintain and assess the accuracy of reporting. A correct response within 800 msec of the begining of the probe produced a brief tone and, for the macaques, fruit juice as a reinforcement; otherwise the probe terminated without reinforcement. Non-reinforced probes resulted in the next trial being a training trial identical to those described for the final stages of training. Another rivalry trial could not occur until correct performance on a training trial had been reinforced.

Experimental sessions were approximately one hour in duration. For individual monkeys, training and test procedures were selected that resulted in best performance. For one monkey, DJ, three sessions were run daily; each session consisted of three 15-min passes separated by 5-min breaks. The other monkey, TH, was run in two sessions daily; each consisted of nine 5-min passes separated by 2-min breaks. The latter procedure was used with human subjects who participated in one experimental session per day.

For the first macaque, DJ, grating frequency during both final training and rivalry testing was constant for each pass but varied between passes within a session. As similar results were obtained with several frequencies, only one frequency (two cycles per degree) was used with the second macaque and human subjects, and only the results for this frequency are reported below. For all subjects, grating velocity was constant for each trial but varied randomly between trials within a pass. At least 120 rivalry phase durations at each velocity were obtained for each subject.

For macaque subjects, the procedure called for at least 60% of all trials to be training trials randomly interleaved among rivalry presentations. For human subjects, all trials were rivalry presentations except those training trials initiated as a consequence of failure to respond correctly on the probes which terminated rivalry trials. For all human subjects, sufficient rivalry data were collected in two experimental days, and for the macaques TH and DJ, sufficient data were collected in two and four days, respectively.

RESULTS

When one eye viewed gratings moving in one direction and the other eye viewed gratings moving in the opposite direction, the rate of perceived alternation in direction of movement was an increasing function of grating velocity. Although there was considerable inter-subject variability in the absolute rates of alternation (Table 1), the alternation rate increased with increasing grating velocity for each

154

RATE OF ALTERNATION (ROA) AND GAMMA DISTRIBUTION PARAMETERS (n AND λ) FOR DIFFERENT STIMULUS VELOCITIES

ROA is given in alternations per second.

	Subject	Velocity								
		2°/sec			4°/sec			6°/sec		
		ROA	n	λ	ROA	n	λ	ROA	n	λ
Macaques	DJ	0.239	2	6.23	0.278	2	5.6	0.364	2	5.38
	TH	0.517	3	4.73	0.709	7	9.6	0.767	6	7.28
Humans	EM	0.751	6	6.35	1.09	14	15.9	1.22	19	22.0
	JM	1.06	25	25.1	1.41	30	30.0	1.58	30	30.0
	JA	1.53	30	29.7	1.73	30	29.6	1.84	30	29.8

individual subject, both humans and macaques. As shown in Figure 2, there is an extremely close correspondence between the normalized alternation rate data (rate for a given stimulus velocity as a percentage of the subject's mean rate for all three velocities) obtained from human subjects and those obtained from macaque subjects. Only data from those rivalry presentations which terminated with correct probe performance were included in the present analysis. For human subjects, this represented 96% of all rivalry presentations; for macaque subjects, this represented 94% of all rivalry presentations.

The same data were also analyzed by examining the distributions of rivalry phase
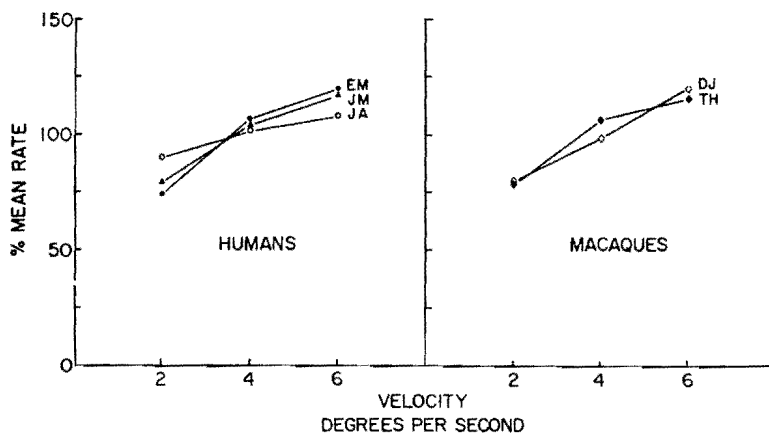

Figure 2. Percentage of mean rate of alternation as a function of stimulus velocity for human and macaque subjects. For each subject the mean value of the three rates of alternation (ROA) was calculated and then divided into each ROA for that subject to obtain the values plotted on the ordinate. The stimulus was a vertically oriented square-wave grating with a spatial frequency of 2 cycles/degree.

S (n AND λ) FOR		
sec		
A	n	λ
64	2	5.38
67	6	7.28
2	19	22.0
8	30	30.0
4	30	29.8

2, there is an
ate data (rate
e for all three
que subjects.
correct probe
ubjects, this
s represented

rivalry phase

r human and
was calculated
ordinate. The
s/degree.

durations. A rivalry phase was defined as the interval from a report appropriate to the view from one eye until the next report appropriate to the view from the other eye. The probability density distributions of rivalry phase durations were calculated for each subject at each grating velocity. As previous investigators of binocular rivalry have done (Levelt, 1965; Fox and Herrmann, 1967), we described these distributions using the gamma probability density function. The gamma function parameters, n and λ for the form given by McGill (1963), characterize the shape of an observed distribution of phase durations. As the value of n increases, the shape of the gamma distribution changes systematically from exponential ($n = 1$) to gaussian (for large values of n) while the mean is always equal to n/λ (McGill, 1963). For approximately gaussian distributions corresponding to large n, changes in n produce negligible changes in the form of the gamma distribution (Central Limits Theorem, see Hogg and Craig, 1970) and therefore in curve-fitting an upper bound of 30 was fixed for values of n.

As is customary (e.g., Levelt, 1965; Fox and Herrmann, 1967), the means of the distributions were set equal to one in the present analysis. The estimates of n and λ obtained by the method of least squares are given in Table 1. The values of both parameters are increasing functions of the rate of perceived alternation in direction; the correlation coefficients are 0.95 for n and 0.94 for λ. The systematic change in distribution form with increasing alternation rate was most dramatic between subjects (Table 1) but may be clearly seen within individual subjects in Figure 3. Note the similar distributions of rivalry phase durations for human and macaque subjects of similar mean rate of alternation (compare the two center panels of Figure 3).

The mean percentage of the variance for the three velocities accounted for by the gamma distribution was 95, 94, and 93% of the variance for human subjects EM, JM, and JA, respectively, and 92 and 61% for macaque subjects TH and DJ, respectively. DJ's distribution were of the same skewed shape as those shown in Figure 3 except that they did not decrease to as low a level at high phase durations. This property is apparently responsible for the poorer fit of the gamma distribution in this case. It should be noted that the ratios of the n and λ parameters in Table 1 do not always equal one, the mean of the normalized distributions. This indicates that the mean of the theoretical and observed distributions are not always equal, and the size of the discrepancy is related to the goodness of fit.

The first monkey, DJ, continued to respond for two subsequent months of binocular rivalry testing which explored other parameters of moving grating stimuli. The second monkey, TH, responded for less than two weeks after the sessions reported here. After a brief retraining period on the discrimination of grating orientation, she was tested with rivalrous stimuli consisting of gratings of orthogonal orientation presented to each eye. As of this writing, the latter rivalry procedure has been successfully employed with TH for more than two months.
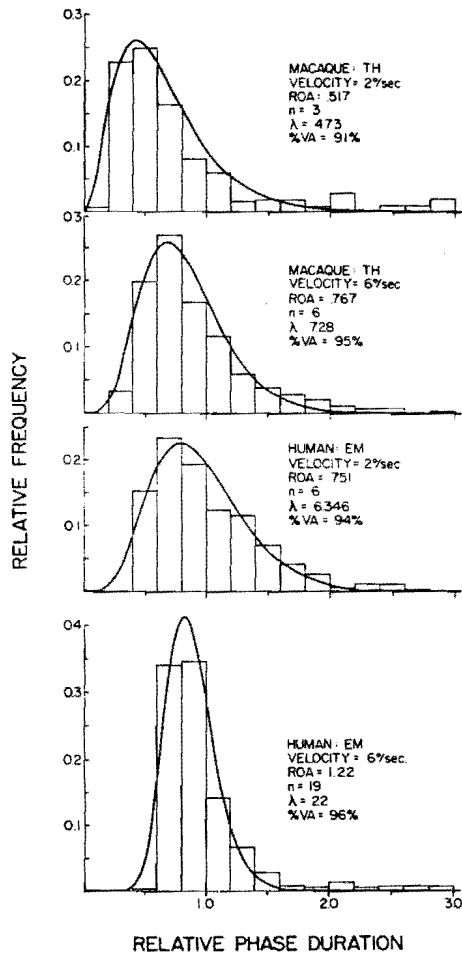
Figure 3. The relative frequency of phase durations and the least mean squares best-fitting gamma distribution plotted for one human subject (EM) and one macaque subject (TH) at two velocities. The phase duration data plotted along the abscissa have been normalized for all the graphs by dividing by the mean phase duration for each graph. Relative frequency of occurrence of each phase duration is plotted along the ordinate. %VA is the percentage of the variance of the relative frequency data accounted for by the plotted gamma function. ROA is the rate of alternation of left and right phases per second reported by the subject. The stimulus used was a 2 cycle/degree vertical square-wave grating.

DISCUSSION

Using operant conditioning techniques, macaques were trained to report the direction of movement of vertical square wave gratings. Humans were given verbal instructions to make similar reports. Both human and macaque subjects then gazed into a haploscope to view gratings with one eye that moved in the opposite direction

from those viewed by the other eye. Quantitative analysis of reports of changes in direction of movement provided a basis for comparison of binocular rivalry in macaque and human subjects.

In order to evaluate the accuracy of the monkeys' reports, probes were inserted into the rivalry situation. The monkeys' probe performance was found to be highly accurate and virtually identical to that of human subjects. The accuracy of the monkeys' reports may also be evaluated indirectly by means of quantitative comparisons of binocular rivalry in humans and macaques. The most parsimonious interpretation of the quantitatively similar properties of responses to rivalrous stimulation in both species is that they are the consequences of similar perceptual phenomena. This is consistent with results of a previous study in the squirrel monkey (Todd, 1972) employing optokinetic nystagmus as an indicator of binocular rivalry (Fox et al., 1975) which suggested that non-human primates experience rivalry.

When rivalry was induced by gratings moving in opposite directions for the two eyes, the perceptions reported by humans and macaques were similarly affected by grating velocity: the rate at which all subjects reported perceived alternations in the direction of grating movement increased with the velocity of the gratings. Normalizing alternation rate by dividing by a subject's mean alternation rate for all three velocities revealed a remarkable similarity not only between subjects of different species but also between subjects of the same species with markedly different mean rates.

The similarity of binocular rivalry in humans and macaques also extended to the form of the distributions of rivalry phase durations as well as to the relationship between form distribution and alternation rate. The gamma-like form of the phase duration distributions is in agreement with the results of previous experiments using human subjects and a variety of other procedures (Blake et al., 1971; Cogan, 1973; Fox and Herrmann, 1967; Fox et al., 1975; Levelt, 1965; Wade, 1975). For similar mean alternation rates, there was an exceedingly close correspondence in distribution form between human and macaque in the present study. As indicated by the parameters of the best fitting gamma distributions, increased alternation rate was associated with a systematic shift from more exponential to more gaussian distribution forms in both human and macaque subjects. The gamma description of normalized phase distributions permits comparison with the results of previous studies which presented results in this form. However, no theoretical model is assumed and other mathematical functions may describe rivalry data with equal accuracy (Cogan, 1973).

Although rates of alternation reported by macaques were slower than those reported by humans for corresponding grating velocities, the small numbers of subjects of both species make it impossible to tell whether this is due to species differences or intersubject variability. Assuming that the differences between the species are real, it is quite likely that they are due to differences in response criteria

rather than differences in perception, or bias rather than sensitivity differences in signal detection terminology. Such differences in criteria will affect the reported rate of alternation in rivalry (Cogan, 1973), and the training procedure for macaques, in which false alarms were costly, might well lead to conservative response criteria and lowered alternation rates.

Psychophysical comparisons of vision in humans and macaques have revealed remarkable similarities in color vision (DeValois, Morgan, Polson, Mead and Hull, 1974), spatial luminance contrast sensitivity (DeValois, Morgan and Snodderly, 1974), stereopsis (Bough, 1970; Cowey, Parkinson and Warnick, 1975; Harwerth and Boltz, 1979a, 1979b; Julesz, Petriz and Buttner, 1976; Sarmiento, 1975) and other visual functions (e.g., Maguire, Meyer and Balzer, 1978; Scott and Milligan, 1970). The present experiment demonstrates that the similarity of the macaque and human visual systems extends to the phenomenon of binocular rivalry. It has been argued (e.g., Walker, 1978) that the competition between the two eyes in binocular rivalry is not fundamentally different from other selective or 'attentional' processes in which stimuli compete for the control of behavior. Thus, binocular rivalry may represent a simple instance of a generally more complex class of perceptual phenomena. In addition to providing valuable comparative data, animal models of binocular rivalry potentially provide a number of important advantages for the experimentalist. These include subjects whose prior experience may be rigorously controlled and in whom linguistically-mediated processes may be ruled out. Finally, the existence of animal models of rivalry, as demonstrated in the present study, may make it possible to investigate the physiological basis of this perceptual phenomenon in behaving monkeys.

ACKNOWLEDGEMENTS

REFERENCES

Blake, R.R., Fox, R. and McIntyre, C. Stochastic properties of stabilized image binocular rivalry alterations. *Journal of Experimental Psychology*, 1971, 88, 327–332.

Blough, D.S. The study of animal sensory processes by operant methods. In W.K. Honig (Ed.), *Operant Behavior: Areas of Research and Application*. New York: Century-Crofts, 1966.

Bough, E.W. Stereoscopic vision in the macaque monkey: a behavioral demonstration. *Nature*, 1970, 225, 42–44.

Cogan, R. Distributions of perception in the binocular rivalry of contours. *The Journal of General Psychology*, 1973, 89, 297–304.

159

Cowey, A., Parkinson, A.M. and Warnick, L. Global stereopsis in rhesus monkeys. *Quarterly Journal of Experimental Psychology*, 1975, 27, 93–109.

Curry, R.E. A random search algorithm for laboratory computers. *Behavior Research Methods and Instrumentation*, 1975, 7, 369–376.

DeValois, R.L., Morgan, H.C., Polson, M.C., Mead, W.R. and Hull, E.M. Psychophysical studies of monkey vision − I. Macaque luminosity and color vision tests. *Vision Research*, 1974, 14, 53–67.

DeValois, R.L., Morgan, H. and Snodderley, D.M. Psychophysical studies of monkey vision − III. Spatial luminance contrast sensitivity tests of macaque and human observers. *Vision Reserach*, 1974; 14, 75–81.

Fleshler, M. and Hoffman, H.S. A progression for generating variable interval schedules. *Journal of the Experimental Analysis of Behavior*, 1962, 5, 529–530.

Fox, R. and Herrmann, J. Stochastic properties of binocular rivalry alternations. *Perception and Psychophysics*, 1967, 2, 432–436.

Fox, R., Todd, S. and Bettinger, L.A. Optokinetic nystagmus as an objective indicator of binocular rivalry. *Vision Research*, 1975, 15, 849–853.

Harwerth, R.S. and Boltz, R.L. Behavioral measures of stereopsis in monkeys. *Physiology and Behavior*, 1979a, 22, 229–234.

Harwerth, R.S. and Boltz, R.L. Stereopsis in monkeys using random dot stereograms: The effect of viewing duration. *Vision Research*, 1979b, 19, 985–991.

Hogg, R.V. and Craig, A.T. *Introduction to Mathematical Statistics*, 3rd edition. London: The Macmillan Co., 1970.

Julesz, B., Pertriz, B. and Buttner, U. Fast determination of stereopsis in rhesus monkey using dynamic random dot stereograms. *Journal of the Optical Society of America*, 1976, 66, 1090.

Lack, L.C. *Selective Attention and the Control of Binocular Rivalry*. The Hague: Mouton Publishers, 1978.

Levelt, W.J.M. *On Binocular Rivalry*. Institute for Perception RVO–TNO, National Defense Research Organization TNO, Soesterberg, The Netherlands, 1965.

Maguire, W.H., Meyer, G.E. and Balzer, J.S. Behavioral demonstration of McCullough effect in the monkey. *Society for Neuroscience Abstracts*, 1978, 4, 635.

Malott, R.W. and Malott, M.K. Perception and stimulus generalization. In W.C. Stebbins (Ed.), *Animal Psychophysics: The Design and Conduct of Sensory Experiments*. New York: Appleton-Century-Crofts, 1970.

McGill, W.J. Stochastic latency mechanisms. In R.D. Luce, R.R. Bush and E. Galanter (Eds.), *Handbook of Mathematical Psychology*, Vol. 1, Chaps. 1–8. New York: John Wiley and Sons, Inc., 1963.

Meadey, D.B. Reaction time as an index of sensory function. In W.C. Stebbins (Ed.), *Animal Psychophysics: The Design and Conduct of Sensory Experiments*. New York: Appleton-Century-Crofts, 1970.

Sarmiento, R.F. The stereoacuity of macaque monkey. *Vision Research*, 1975, 15, 493–498.

Scott, T.R. and Milligan, W.L. The psychophysical study of visual motion aftereffect rate in monkeys. In W.C. Stebbins (Ed.), *Animal Psychophysics: The Design and Conduct of Sensory Experiments*. New York: Appleton-Century-Crofts, 1970.

Todd, S. *Optokinetic nystagmus: An objective indicator of binocular rivalry*. Ph.D. Thesis, Vanderbilt University, 1972.

Wade, N.J. Binocular rivalry between single lines viewed as real images and afterimages. *Perception and Psychophysics*, 1975, 17, 571–577.

Walker, P. Binocular rivalry: Central or peripheral selective processes? *Psychological Bulletin*, 1978, 85, 376–389.