BEHAVIORAL CONTROL OF VISUAL FIXATION OF THE RHESUS MONKEY¹

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A paradigm for the control of visual fixation of the *macaque* monkey in vision experiments was described. Using a Maxwellian view, the procedure permits the placement of discrete test-light stimuli in a specific area of the retina as the monkey fixates a primary target. This procedure holds foveal fixation as other behaviorally significant visual stimuli are presented to the visual field. By a methods-of-limits procedure, the sensitivity of the monkey eye was measured at different retinal locations under both photopic and scotopic visual adaptation.

Key words: visual fixation, perimetry, vision, rhesus monkey

The rhesus monkey (*Macaca mulatta*) has a visual system much like that of man, both in terms of sensitivity (Sidley and Sperling, 1967; Sidley, Sperling, Bedarf, and Hiss, 1965; Sperling, Sidley, Dockins, and Jolliffe, 1968) and anatomical features (Polyak, 1957; Rolls and Cowey, 1970). The better our understanding of the mechanisms of vision of the rhesus, the more useful this monkey becomes for experimentation into some of the visual problems of man. In addition, with such understanding, the value of this research animal for investigations of basic behavioral and sensory processes increases.

Most of the data gathered on the sensitivity of the rhesus visual system have been obtained for stimuli presented without regard to where the image fell upon the retina. The exceptions to this have used a diffusing surface for transmitting or reflecting the visual stimulus, thereby making the quantification of the stimulus energy at the retina very difficult. It has usually been assumed that the monkey would employ the most sensitive areas of the retina (central vision) to solve the visual problem in any particular experiment, especially so in the cases where threshold spectral sensitivity curves have been obtained (Harwerth and

Sperling, 1971). As shown by Crawford (1975), when the increment-threshold is determined against a photopic background, the rhesus monkey uses variable extrafoveal fixation of the target for all stimulus intensities except those just at threshold. The monkey would be of far greater value as a research animal if control could be gained over the placement of the test stimulus upon the receptor surface consistently and repeatedly for above-threshold vision. This would, of course, require that the monkey fixate upon some target as the test stimulus is applied to the retina.

A number of researchers have described efforts to control visual fixation by the *macaque* monkey in behavioral and electrophysiological experiments. Scott and Milligan (1970) reported a visual task for the monkey that presumed foveation of a small light during data collection as judged by an observer using an infrared viewing system. Appropriate responses were reinforced only as the monkey was judged to be fixating by the observer. No data were included to indicate the efficacy of this method in holding foveation while the continuous attention by a human observer was required.

The best known method for controlling fixation by a *macaque* monkey was described by Wurtz (1969) and used by Goldberg and Wurtz (1972a, b) and Wurtz and Goldberg (1972a, b) in a series of reports where receptive fields for neurons of the striate cortex and the superior colliculus were mapped. Briefly, by reinforcement of successive approximations, the fixation by the monkey of a small light

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projected upon a tangent screen was held to within 3° visual angle as measured by the electrooculogram. The presentation of the light to be fixated occurred as the monkey pressed and held down a lever. A brief dimming of the light served as the discriminative stimulus for release of the lever. Lever release responses were reinforced by a small quantity of liquid. During this sequence, other behaviorally irrelevant visual stimuli were flashed or moved about on the tangent screen so as to map the receptive fields for visual neurons. This procedure has not been applied where other behaviorally significant visual stimuli compete with the fixation light for foveation by the monkey. On the face of it, the use of a luminance change in the fixation target as the discriminative stimulus would not assure that the monkey would hold foveal fixation in that extrafoveal retina is quite sensitive to flux density changes, and particularly so under mesopic or scotopic levels of adaptation.

The present paper describes a behavioral paradigm similar to that reported by Wurtz, but with a more stringent requirement: the discriminative stimulus is a change in orientation of the fixation point rather than luminance change. Used with a Maxwellian view optical system this program is demonstrated to hold the foveal fixation by the *macaque* monkey to within $\pm 1^\circ$ visual angle as behaviorally significant visual stimuli compete for visual foveation.

METHOD

Subjects

Three *Macaca mulatta*, 2 to 5 yr of age, were maintained on a chronic liquid deprivation schedule, with most of the liquid requirement obtained during training or experimental sessions. Otherwise, the monkeys were freely fed lab chow supplemented with fruit.

Two male human subjects having normal vision were also used.

Apparatus

Figure 1 includes a drawing of the three-channel optical system. Emanating from a 900-W xenon arc lamp (A) were two light paths. The lower path was designed to provide a narrow bandwidth spectral background through a monochromator (3), while the intensity of this path was adjusted by the neutral

density filters at F2. When a white background was required, super-imposition or substitution by a path from a tungsten halide lamp (B) was made through a beam splitter (B3). It was at B3 that a portion of the background path was diverted through a system of elevated front surface mirrors to an X-Y plotter where a pair of angled mirrors converted the horizontal positioning of a small rectangular image formed by (A3) into positions within the vertical plane of the background as it was added through another beam splitter at B2. A neutral density filter (F3) attenuated the background path so as to make the small rectangular image of A3 appear with low contrast in the final background field, which was determined in size (18 degrees visual angle) by the aperture at A5. As A3 was a disc with two rectangular slits oriented 90° to each other, and mounted on a bidirectional stepping motor, the orientation of the image could be changed by 90° with less than 2 msec rise or fall time. This image served as the fixation point of the system.

The upper path of the system provided a test light through a tandem pair of monochromators. A shutter at S1 allowed control of the duration of the test light with <2 msec rise or fall time, while the intensity was controlled by a combination of neutral density filters and a wedge (F1, W1). The variable aperture A4 permitted the control of the test flash, which was added to the background field at B1. The final lens of the system produced a small focal point, which was made available to either the right eye or left eye pupil by rotation of a mirror in the eyepiece assembly.

Illustrated on this figure, as an example, is the relationship between the visual field for the right eye of the monkey and the test-flash location on the retina if the fixation point, S1, were placed in the center fovea. Here, S2 (the test flash) is shown to be located on the nasal side of the fovea near the edge of the receptor-free optic disc.

The experimental chamber was built by the Industrial Acoustics Company while all scheduling and control functions were done on a Massey Dickinson Company logic system.

Procedure

The behavioral paradigm. Figure 2 presents a complete schematic of the behavioral sequence and may be described as follows:

Fig. 1. The optical system and the manipulanda for the monkey. The relationship between visual field targets and their location on the retina is shown. The components of the optical system are not drawn to scale.

The Cycle Start was signalled by the onset of an auditory stimulus, a clicker (20 pps), which served as the discriminative stimulus for the response of pressing and holding down

a lever with the right hand. The subsequent variable period of from 1 to 10 sec contained either one or two significant events. Stimulus S(1) was a variable train of flashes of a hori-

Fig. 2. A behavioral paradigm for holding visual foveal fixation by the rhesus monkey on target (S1) as a second test target (S2) is moved about in the visual field.

zontal bar presented at some position within the 18 degree visual angle background field. The size and contrast of S(1) was set by preliminary experiments to tax the resolution limit of the primate eye, thereby requiring foveal fixation for optimum detection of a change in orientation. It was the change in the orientation of S(1) from horizontal to vertical [S(1)]^A that started the 500-msec limited hold or catch period in which the monkey had to release the spring-loaded lever to the central position. On approximately half of the trials, and at a variable interval preceding S(1)^A, there occurred a central test flash termed S(2), which was manipulated as to size, wavelength, and intensity. A release of the lever within the limited-hold period of 500 msec (labelled Stimulus Catch) was reinforced by a tone signalling a choice response period—the response being to press one of two buttons. The monkey was to press the left button if S(1)^A was preceded by S(2), and press the right button if S(1)^A occurred alone. Correct choices were followed by a tone (and by juice on a variable-ratio schedule, VR 5), the program was then cycled through a short timeout of 3 sec, and then back to the Start. Incorrect choice responses or other undesirable lever releases occurring outside the Stimulus Catch or Choice Response period were punished by cycling the program through a longer 10-sec timeout period. Additional responses within the Long Timeout maintained that period.

For the electrophysiological experiment, this paradigm allows the positioning of the test flash S(2) upon the area of the retina that supplies input to the electrode positioned in the lateral geniculate nucleus (LGN) or in the visual cortex, thereby making co-extensive the retinal field for the neuron and the retinal field for the monkey's detection response. For the psychophysical experiment, it permits the measurement of the sensitivity of the retina at discrete locations over a large area of central vision.

Tactics on training. Subjects had been trained to criterion on the first half of a program described by Sidley and Sperling (1967) where the monkey, deprived of liquids, was seated in a primate chair before the eyepiece of an optical system. The monkey was then trained by successive approximations to depress and hold down a spring-loaded lever located on the waistplate of the chair. Artifi-

cial orange juice (Tang) was delivered to a mouthpiece strategically located so as to position the eye before the eyepiece. From the outset, the delivery of juice was paired with a brief (1 sec) tone (600 Hz), allowing thinning of the delivery of juice to a variable ratio of eight to one (VR 8) in the well-trained monkey. Initially trained to release the lever when a test light of 50 msec duration appeared on the center of the background field, the monkeys attained a 99% detection rate for test flashes 0.5 log units above threshold. With these well-trained monkeys, control of the lever release response was then transferred from the test flash to a novel visual stimulus, which was to serve as a fixation point. Initially positioned in the center of the background and flashing at a frequency above flicker fusion for a human subject, the fixation point appeared as a horizontal bar, which would change to a vertical orientation after a variable period. Lever releases within the limited-hold period after the change in orientation of the fixation bar were reinforced, as was the case before with the test flash. As the percentage of correct detections of the change in fixation orientation increased above 75%, the fixation stimulus parameters were made more stringent. The size was reduced to a visual subtense of 5 by 15 min of arc visual angle with the contrast of the rectangle being adjusted to the lowest that the monkey could detect. At this point, the position of the fixation bar within the background field was slowly changed. As the task became more difficult, the monkey would occasionally lose the fixation point in the large (18°) field. Therefore, the flash rate of the fixation bar was reduced well below flicker fusion, which served to aid in its location in the field. With the bar flashing, human subjects could locate the fixation bar within the field, but could not identify the orientation without looking directly at the target. Seven to 12 sessions were required to transfer and attain the 99% detection level for the fixation bar, as had been demonstrated for detection of the test flashes.

To develop the second component of the program, the lever was removed from the waistplate and two response buttons were added on the side of the waistplate opposite to that where the lever was normally located. Using a closed-circuit TV camera, it was relatively easy (within two sessions) to shape the

button-pressing response using the combination of the 600-Hz tone and juice on a VR 5 reinforcement schedule, as had initially been the case with the lever release. The next step was to introduce both a new tone of 1000 Hz, which defined the period when a response on either of the buttons was subject to being reinforced, and a timeout period of 10 sec. Button presses that occurred in the absence of the 1000-Hz tone produced the timeout, and additional button presses maintained that period. Within about eight 2-hr sessions, the animals were emitting very few responses in the absence of the 1000-Hz tone. To develop control of responses upon the two buttons, a large bright test light was presented in the center of the background field. In the presence of the light, a response on the left button was reinforced; in its absence, a response on the right button was reinforced.

When the lever was put back in place and the first half of the program was signalled by the onset of the clicker, the lever release following the change in orientation of the fixation bar initiated the 1000-Hz tone, and the second half of the program was in effect. Of course, at this stage the test light was on and steady with the 1000-Hz tone. The test light onset was extended to precede the change in the orientation of the fixation bar. Next, the test-light duration was slowly shortened so as to end before the choice button response occurred. The test light subsequently was shortened to a flash of 50 msec duration, which preceded the change in the fixation bar. Finally, the interval in which the test flash occurred was made variable within the already variable foreperiod for the change in orientation of the fixation bar, and the full program was achieved.

With a $p = 0.5$ of a test flash occurring on any single trial, the monkeys attained a training criterion of 90% correct choices within a block of 600 to 1000 trials. Since the size (5 min by 15 min visual angle) and the low contrast of the fixation target precluded the detection of a change in orientation by human subjects unless they foveated the fixation target, it was likely that the monkey was also foveating the target in order to attain 99% detection of the change in fixation target orientation. And, it was judged that the monkey must be seeing the test flash, attested to by its subsequent high correct response per-

centage (90 to 99% for test flashes 1.0 log unit above behavioral threshold).

Procedure proper. Direct evidence of the monkey's stability of foveal fixation was obtained by presenting the test flash to the light-adapted retina across the boundary of the receptorless optic disc, determining the stability of fixation by the spread of points at which the test flash was not seen, *i.e.*, how repeatedly the test flash fell either on or off the optic disc.

The field stop for the adapting 3000 troland white background was shifted to permit a separation of the test flash and the fixation point by up to 18° (the limit of our present optics). Beginning with a modest separation, and with the monkey working steadily on the task, the fixation bar was moved along a horizontal path away from the fovea, across the temporal retina so that the test flash approached the lateral edge of the optic disc. Upon a failure by the monkey to detect a test flash presented twice in succession, the direction of movement was reversed and another parallel lateral excursion made, reversing again upon the second of two misses of the test flash. By this procedure, the lateral edge of the optic disc contour was mapped in one monkey using two sizes of test flash on different days. By removing the primate chair and providing a chin and forehead rest, comparable measurements were made on two human subjects; the same procedures were employed.

Another indicator of the foveation of the fixation target was obtained by placing a monkey in the experimental chamber for 1-hr dark adaptation. The wavelength of the fixation bar was set at 700 nm and of an intensity sufficient to be detected by a human subject by central foveal cones but not by peripheral rod vision. The wavelength of the 15-min diameter test flash was an optimal 500 nm for rod sensitivity. Threshold rod sensitivity for the test flash was measured by the method of limits using decreasing intensities at points along the central 12 degrees of the horizontal retinal meridian. As before, comparable measurements were made on a human subject. Were the monkey or human subject foveating the fixation bar, rod sensitivity to the test flash was expected to decrease as the test flash fell on retina approaching the center of the fovea, where the density of rods decreases closer to

the fovea and becomes absent in the foveal center.

Finally, to determine the comparability of data obtained by the present paradigm to data obtained by Sidley and Sperling (1967), the photopic spectral sensitivity of the central fovea was measured for a monkey and a human subject using both behavioral procedures. A 2° diameter test flash was presented to the center of an 18° diameter, 3000 troland white background. By the present paradigm, the white fixation target was centered upon the test-flash location, while the fixation bar was omitted when the other paradigm was used. By the method of limits using decreasing intensity steps of 0.08 $\log_{10}$ units, threshold sensitivity for 28 test-flash wavelengths between 400 and 690 nanometers was determined. A radiometer (EG&G Model 580) was used to measure the irradiance of the unattenuated test-light path (watts/cm^2). The product of this reading $\times$ the test-flash area (cm^2) $\times$ the test-flash duration (seconds), when divided by the product of h (Planck's constant) and ν (frequency of the light) results in the average number of quanta/test flash at the behavioral threshold. The $\log_{10}$ of the reciprocal of this value was used to compare sensitivity of the human or monkey eyes to the various colored test flashes.

RESULTS AND DISCUSSION

An indication of the degree of control over foveal fixation may be seen in the precision with which the boundary of the optic disc was mapped. Figure 3A is a composite of determinations of the lateral optic disc contour for one monkey taken on two separate days by either a 1° or 2° diameter test flash. All data points are the retinal locations of the first of two misses of the test flash upon approach to the optic disc. They are shown to scale on a drawing of the rhesus monkey retina. As can readily be seen, the optic disc boundary is clearly indicated and the shape of the contour is consistent for two test flashes presented on different days. Figure 3B presents the same determinations for two human subjects who, using the same procedures, worked the same task as the monkey. The separation of fixation point and optic disc are seen to be about the same as that of the rhesus monkey (13.5°) for human subject DG (filled squares), while it is

somewhat less (11.5°) for MLJC (filled circles). The optic disc for DG appears rotated upward, probably resulting from the reluctance of the human subject to press the eyepiece into the corner of his eye, as was common for the monkey. The ventrolateral optic disc points for MLJC were determined by vertical excursions beginning about 5° below the optic disc.

Fig. 3. Contours of change in sensitivity at the temporal boundary of the receptorless optic disc. A: The threshold contour of the edge of the optic disc of the light-adapted rhesus eye for two test-flash sizes, 1° and 2° [50 msec duration, 540 nm, $\log$ quanta/flash = 9.917 (2°)] shown on a scale drawing of the rhesus eye. B: Comparable contour curves for the optic disc from two human subjects using the 1° test flash. ■ D.G.; ● M.L.J.C.

As the points along the optic disc contours for the monkey eye were stable between days and with different test-flash sizes, and appear to define a contour comparable to those optic disc contours obtained on the human subjects who did fixate and who did find the task a difficult one, it was concluded that this demonstrated a high stability of foveal fixation by the monkey using these procedures.

The precision of the estimation of these points in the monkey is indicated in Figure 4, where the per cent correct detections of test flashes in blocks of 50 trials are presented for several fixed locations approaching the optic disc along the horizontal meridian. For the 2° test flash, 90% or better correct choice percentages are seen as the optic disc was approached at 14° . This percentage correct dropped close to chance at 15° . With the smaller 1° test flash, the initial percentage correct was somewhat less, but the curve is equally steep, indicating high precision in detecting the optic disc boundary between 13° and 14° in the nasal retina away from the point of fixation. The constant difference in position on the X-axis is most probably due to the difference in diameter of the two stimuli.

The control of the behavioral paradigm in

Fig. 4. The percentage of correct detections of the 1° and 2° diameter test flashes by the rhesus monkey at discrete locations approaching the optic disc from the foveal side. Each point is based upon 50 test-flash trials.

holding foveation under dark adaptation conditions is seen in Figure 5, where rod sensitivity of both rhesus monkey and man is seen to decrease in a similar manner as the test flash was moved closer to the center fovea. The two sensitivity curves, normalized for sensitivity at central fovea, illustrate comparable sensitivity symmetry over the central fovea, as well as being quite similar in range of sensitivity loss. These rod sensitivity contours parallel the density of receptors as described by Polyak (1957) for both man and rhesus monkey. Were foveation of the fixation bar variable, the degree of symmetry and smoothness of contour seen here would have been unlikely.

Figure 6 illustrates spectral sensitivity curves for a human subject and a rhesus monkey col-

Fig. 5. Rod sensitivity of the dark-adapted human (unfilled circles) and rhesus monkey (filled circles) eyes along the central 12° of the horizontal retinal meridian. The data were obtained with a 15-min diameter, 500-nm test flash, and a dim 700-nm fixation bar. The two curves were normalized for the central fovea location where the rod sensitivity was $1.7 \log_{10}$ units less than at the 2° eccentric location.

lected by the present paradigm. They are compared with data taken by the earlier paradigm described by Sidley and Sperling (1967). The Y-axis is the logarithm of the reciprocal of the average number of quanta contained in the 2° diameter test flash at threshold. The X-axis is labelled as the wavelength of the test stimulus and plotted on a wavenumber scale. The two curves for the monkey are on a relative sensitivity scale, but are displaced downward from the human data by 1 log unit. First, it can be seen that the form of the curves for both the human subject and the monkey are quite similar for the two methods, the only differences being small changes in overall sensitivity. Vertical lines were drawn through the data points of the monkey curve obtained by the present method to show the range of the four threshold estimates taken on four different days at each of 29 wavelengths between 400 and 690 nm. As seen, the variability was rather small. If the curves for the monkey are shifted upward by 1 log unit, it is clear that man and monkey

Fig. 6. Spectral sensitivity curves for a human observer (large symbols) and a rhesus monkey (small symbols) obtained by two behavioral paradigms. Unfilled data points were obtained by the method described by Sidley and Sperling (1967), filled data points by the paradigm described in this paper. The monkey data curves have been shifted down by 1 log unit. All data were collected by a method-of-limits procedure using only descending intensity sequences. The stimulus conditions were: a 2° diameter test flash, 50 msec duration, presented to the center fovea on a 3000 troland white background.

have about the same overall spectral sensitivity. [For a detailed description and comparison of the shapes of spectral sensitivity curves for rhesus monkey and man, see Sperling and Harwerth (1971)].

In summary, the behavioral paradigm described in the present paper has been shown to control the visual fixation by the rhesus monkey and to produce data on the spectral sensitivity of the primate eye that are quite comparable to data obtained by established techniques. The paradigm and the associated apparatus allow description of the change in sensitivity at discrete locations within central vision of both the light-adapted and dark-adapted primate eye.

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