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MINIATURE EYE MOVEMENTS OF FIXATION IN RHESUS MONKEY[1]

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Abstract—Two-dimensional eye movements were recorded from four rhesus monkeys during training on two tasks aimed at showing they were capable of as accurate fixation control as man. Extensive training on a difficult acuity/vigilance problem caused only three monkeys to occasionally fixate the display for periods over 10 sec with stability of eye position comparable to man. Changing the task to directly reward monkeys for keeping targets within a criterion distance of the fovea increased numbers of long fixations and produced human-like fixation stability in all four monkeys. Monkeys, like man, used slow control to maintain fixation.

Large saccades, smooth pursuits and vergence movements of rhesus monkey and man have been shown to be qualitatively similar (Barmack, 1970; Fuchs, 1967; Keller and Robinson, 1972). We asked whether this similarity extended to both accuracy and eye movement patterns in maintained fixation. The answer was yes. Fixation eye movements of rhesus monkeys are quite similar to man *if* the monkey is instructed to "look at the target" by appropriate behavioral training. We found that naive monkeys are capable of producing small (< 10′ amplitude) saccades and slow control, but they normally do not use these patterns for maintained fixation unless forced to do so. Specifically most monkeys will adopt human-like fixation patterns if forced to perform a very difficult visual acuity discrimination. All monkeys adopt good fixation when required to keep their eye within a criterion distance of a target.

METHODS

Eye movement recording

Four juvenile male rhesus monkeys (*Macaca mulatta*) weighing between 3 and 5 kg served as subjects in these experiments. The procedure used for recording eye movements has been described in detail before (Fuchs and Robinson, 1966; Robinson, 1963) and will only be summarized here. Each monkey was implanted with a coil of fine wire wound around the eye just behind the insertions of the four rectus muscles. When implanted animals were placed in two alternating magnetic fields kept in temporal and spatial quadrature, potentials induced in the coil permitted simultaneous recording of horizontal and vertical eye position. Potentials proportional to eye position were recorded on magnetic tape and later retrieved on photosensitive paper by mirror galvanometer recorder. Overall system bandwidth was 1 kHz and eye position could be resolved to within 1′ in final measurements. The eye on which the coil was implanted retained its full oculomotor range and monkeys had no observable heterotropia.

Each monkey was also implanted with a metal crown (Friendlich, 1973) that was clamped to the primate chair to hold the monkey's head rigidly in place. Recordings of horizontal and vertical head rotations made to test the effectiveness of the crown in immobilizing the head revealed low frequency (0·5–3 Hz) oscillation of the head with a peak to peak amplitude of about 0·7′ combined with occasional abrupt rotations whose peak to peak amplitude did not exceed 1·5′. Thus head movement was not sufficient to seriously contaminate the eye movement recordings and was, in fact, designed into the mechanical properties of the head restraining device to reduce transmission of distracting mechanical vibrations from the building to the animal's skull via the crown.

All monkeys were given 75,000 units of penicillin every 3·5 days for the first 2 post-operative weeks after the first eye-coil implant and also each time the coil was re-implanted. Otherwise, no prophylactic antibiotics were administered. Consequently, leukocyte counts were somewhat elevated because penetration of the skin by the implants served as chronic sources of infection. In addition, each animal was administered about 50 mg ketamine hydrochloride (a short acting anaesthetic) at intervals of about 2 weeks to tighten or reposition crowns.

In general, each animal was given one or two 45-min training sessions per day, 5 days per week. All monkeys were water deprived during this period and were forced to earn all of their water intake during training sessions. They were permitted free access to water on the 6th day and deprived again on the 7th. Then this cycle was repeated. Water deprivation was severe and all animals were hypoglycemic because prevention of food-associated drinking caused them to limit their caloric intake. However, this schedule did permit nearly continuous running of training sessions for periods in excess of 1 yr without substantial (greater than 10%) short-term weight losses and long-term body weights slowly increased.

In all training sessions monkeys were permitted to see targets only with the eye on which the recording coil was implanted. Vision in the other eye was obscured by a light proof baffle.

EXPERIMENTS

(1) *Eye movement patterns during successively finer visual discriminations*

The most direct way to train monkeys to place the image of a fixation target on their retinal locus of preferred fixation and keep it there would be to reward this behavior each time it occurred. However,

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a major technical problem prevents doing this from the outset. Specifically, it is not currently possible to align a sensitive eye movement recording system sufficiently accurately to insure that rewards would be delivered only when a target image fell within a few min arc (~15) of the preferred fixation locus except by behavioral technique. In essence, the recording system could be aligned only when it was certain the organism was fixating a particular target. Consequently, it was necessary to first train monkeys to perform a visual discrimination involving both acuity and vigilance which was designed to elicit good fixation.

Monkeys were required to identify the spatial location of a briefly illuminated disc of light relative to a continuously visible target. Five tungsten lamps were arranged in the form of a cross with diffusers and circular apertures placed in front of the bulbs. The central lamp was continuously illuminated. Peripheral lamps were switched on one at a time for about 100 msec in a random order. Time between flashes was pseudo-random, varying between 1 and 12 sec with a mean of about 6 sec. Initially, discs of light were large, 2·5° dia, and separated by 5·0° between centers. Traditional differential reinforcement techniques were used to shape monkeys to press a lever within 0·8 sec of the onset of the left lamp of the display. Correct responses were rewarded with a small (about 0·5 cm^3) squirt of water or orange juice. Errors (pressing the lever following switching-on of any but the left lamp or during periods none were illuminated) caused the entire display to be extinguished for 10 sec. About 38 (range = 36–40) training sessions were required for each animal to perform this discrimination at a level of 80% correct responses with less than 5% errors. All animals were implanted with the eye movement recording devices at this stage of training. After a 2-week recovery period, discrimination was recaptured. Then, target diameter and separation were gradually reduced keeping proportions of the display constant and target luminance uniform at about 10 mL.[4]

Intuitively, it seemed that this discrimation would yield good fixation because it required the monkey to detect a relatively rare event in a given spatial locus. When both target diameter and separation were reduced, good detail vision would be necessary and the monkey would be forced to fixate the display foveally. Our intuitions were confirmed. When target separation was about 30′, all monkeys confined their lines of regard sufficiently close to the display that their eye coils could be calibrated by moving the entire display through known angles with respect to the subject's head. At this early stage of training, monkey saccade rates were comparable to human rates; i.e. 1–2/sec with occasional intervals of more than 2 sec between saccades. However, monkey eye movement patterns differed from human fixation in two important aspects: (1) their saccades were very large (>30′ amplitude) compared to fixation microsaccades; and (2) their fixation positions were quite variable. These features may be seen in the representative recordings of monkey fixation patterns reproduced in Fig. 1.

Detailed statistical analyses of these patterns for all monkeys were not attempted because they frequently made large saccades outside the recording limits of the apparatus and precluded accurate statistical descriptions of the patterns. For one monkey, horizontal and vertical eye position measures were made at randomly selected times within successive 0·5-sec periods of 10 of the longest fixation intervals. Duration of fixation was about 5 sec. Mean S.D.s of eye position were 28′ on the horizontal and 33′ on the vertical meridian. Mean saccade amplitude was 68·4′ (S.D. = 60·4′) for 100 saccades made during these fixation intervals. These measures confirm that monkey fixation stability at this early stage of training was quite sloppy. However, monkeys improved their fixation control remarkably when the entire visual display was made much smaller.

Reduction of target size was simply continued. Training proceeded more slowly requiring an average of 70 (range = 56–101) more 45-min training sessions to achieve about 80% correct responses with fewer than 5% false alarms when target diameter was 2·5′ and target separation was 5′. Representative recordings of horizontal and vertical eye position made at this stage of training are reproduced in Fig. 2. Note that the monkey's line of regard was confined to the vicinity of the discrimination display for much longer periods of time. Variability in eye position was markedly reduced because most saccades were small (<20′ amplitude).

For each subject the 10 longest fixation records from one training session were selected for exhaustive measurement. For each fixation, horizontal and vertical eye positions were measured at randomly selected times within successive 0·5-sec periods of the fixation interval. Eye position measures for each trial were adjusted by adding a constant so that mean eye position superimposed across trials. Descriptive statistics of fixation stability for each monkey were based on pooled position measures for all 10 trials. Amplitudes and intersaccadic intervals of 100 saccades occurring during fixation were also measured. Transient peaks seen in the records during saccades were excluded from measures of amplitude. Summary statistics of the quality of the monkeys' fixation control are shown in Table 1 along with values taken from an experiment in which one of the authors (AS) served as subject. Actually, data for AS is representative of his performance in a number of different experiments and also of a number of different human subjects (see Ditchburn, 1973, for a compilation of data describing human fixation control).

Standard deviations of horizontal and vertical eye positions were used to calculate bivariate contour ellipse area, a convenient index of variability in 2-dimensional measures having a bivariate normal distribution. The scatter of such data can be expressed by the area of an ellipse which is analogous to the

[4] Actual luminances of the targets used varied between 13·1 and 1·4 mL over the displays used in this size "fading" procedure. This casual approach to the control of target luminance (and also spectral composition) was adopted for convenience in instrumentation because it was felt that the quality of fixation would not depend on these variables. Prior work with humans by Steinman (1965) has shown that neither the spectral composition nor luminance of the target contributed importantly to fixation control if the target was photopically visible. Our experience with the monkey indicates that their fixation performance was also not effected appreciably by these variables.

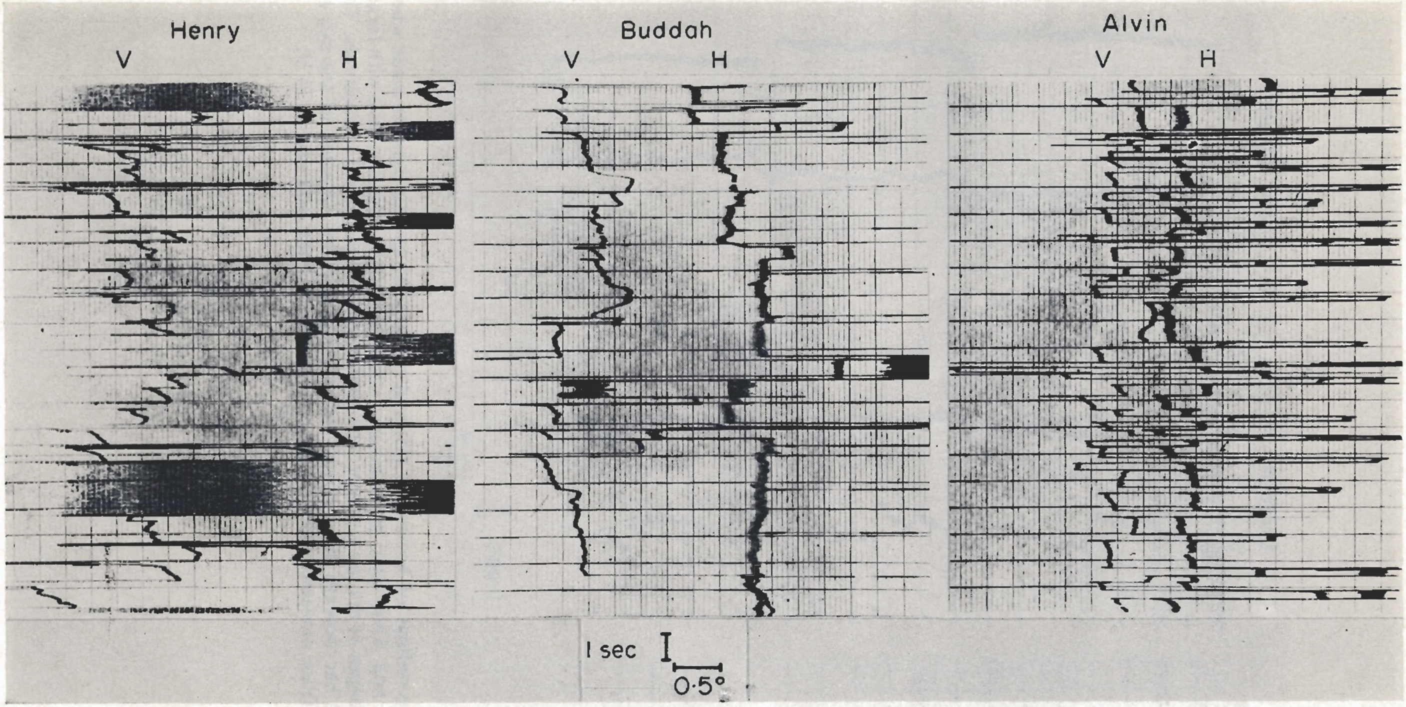

Fig. 1. Representative recordings of horizontal (H) and vertical (V) eye movements of subjects Henry, Buddah and Alvin performing a visual discrimination (see text) with target separations of 0·5° at an early stage of fixation training. Time began at the top and repetitive horizontal stripes indicate 1 sec intervals. The length of the horizontal bar beneath the records corresponds to a 0·5° rotation on both meridians. High frequency oscillations seen when tracings are near the edge of the record reflect saturation of tape recorder amplifiers caused by eye movements made outside the recording limits. Trace movement to the right corresponds to right in H and up in V.

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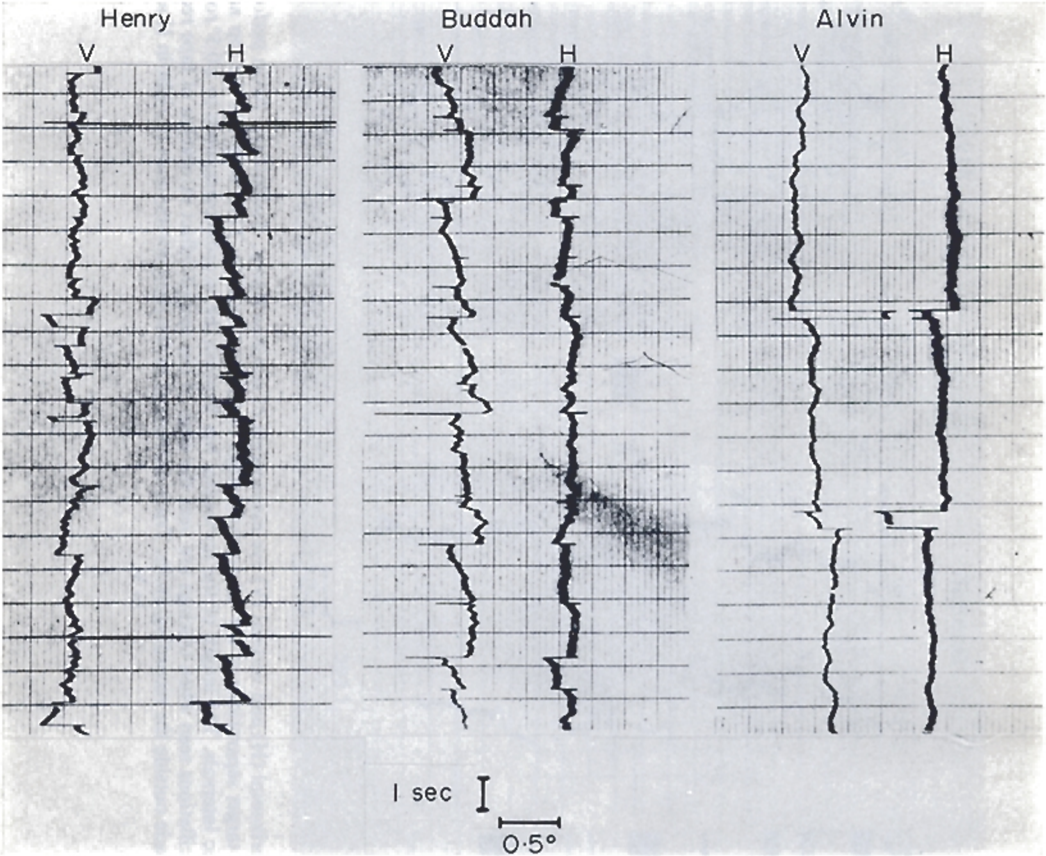

Fig. 2. Representative recordings of horizontal (H) and vertical (V) eye movements made when subjects Henry, Buddah and Alvin were performing a visual discrimination (see text) with target separations of 5′. Time began at the top and repetitive horizontal lines indicate 1 sec intervals. The length of the horizontal bar beneath the records corresponds to a 0·5° rotation of the eye on both meridians. Trace movement to the right corresponds to right in H and up in V.

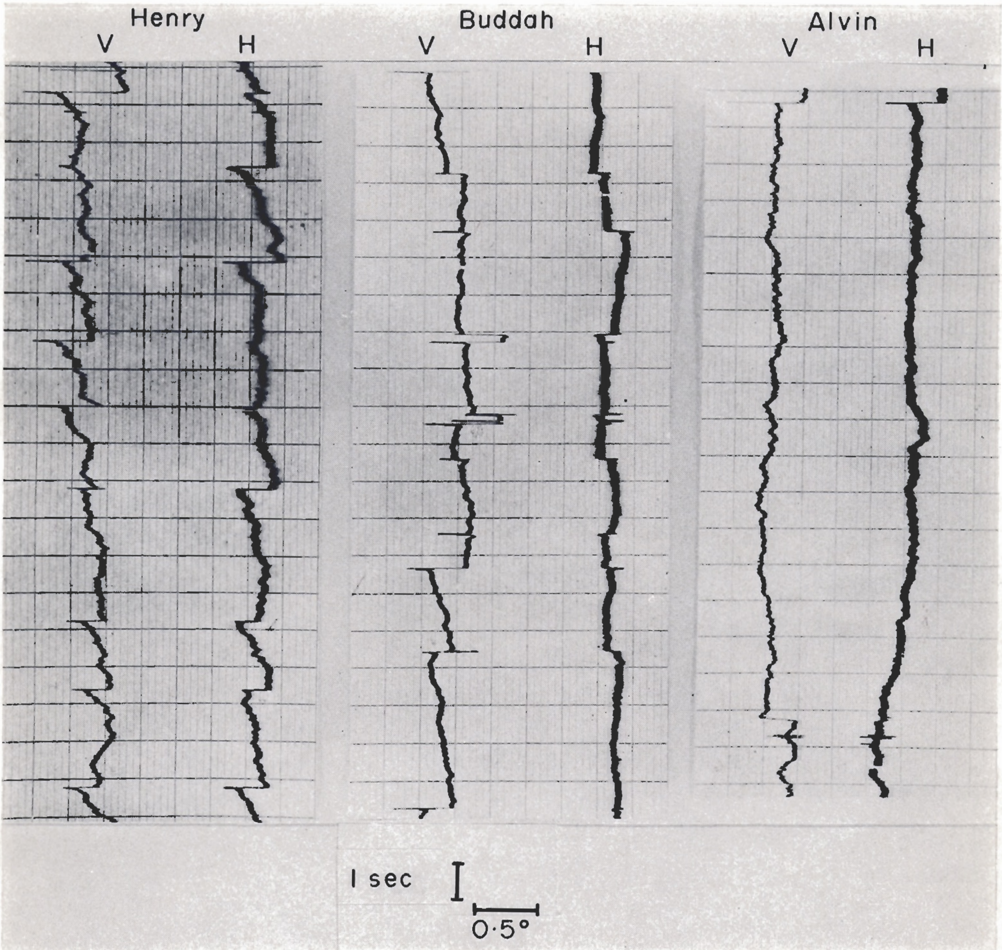

Fig. 4. Representative recordings of horizontal (H) and vertical (V) eye movements made when subjects Henry, Buddah and Alvin were attempting to keep their eye within 12′ of a single 2·5′ dia target seen in total darkness. Time began at the top of the records and repetitive horizontal lines indicate 1 sec intervals. The length of the horizontal bar beneath the records corresponds to a 0·5° rotation of the eye on both meridians. Trace movement to the right corresponds to right in H and up in V.

Table 1. *Fixation interval*, standard deviations on the horizontal (SD_H) and vertical (SD_V) meridians, bivariate contour ellipse areas (*BCEA*), median *saccade amplitude* and *intersaccadic intervals* for 10 long fixations of monkey subjects are shown on the left

Subject:	Henry	Buddah	Alvin	Albert	Man
Fixation Interval (sec)	11.5	17.0	15.0	17.0	10.0
S D H (min arc)	5.4	4.6	4.2	7.5	4.0
S D V (min arc)	4.2	6.4	5.8	22.6	4.9
BCEA (68%)	150	213	171	1214	134
Intersaccadic Interval (sec)	0.8	1.2	7.4	2.0	0.6
Saccade Amplitude (min arc)	9.9	16.4	18.6	40.3	7.7

For *man*, values for these same parameters representative of AS's performance in a comparable task are shown on the right. Measures of fixation stability were based on at least 230 horizontal and vertical eye position measures. Median saccade amplitudes and intersaccadic intervals were based on 100 measures.

S.D. for 1-dimensional data[5] (Nachmias, 1959; Steinman, 1965). For the first three monkeys, this parameter, as well as median saccade amplitude and median intersaccadic interval, lie within the range of those reported for man (Ditchburn, 1973). However, one monkey, Albert, was able to perform the discrimination adequately while maintaining sloppy control of eye position. Bivariate contour ellipse area for this animal was about 6 times larger than that for any other monkey or man. Finding such poor control in one animal forced us to conclude that most, but not all, rhesus monkeys share with man the ability to maintain precise control of eye position for prolonged periods of time. A subsequent experiment will show that all of our monkeys can fixate as accurately as human subjects.

Precision of fixation at this stage of discrimination training owes largely to a reduction in saccade magnitude. As the discrimination became more difficult monkeys switched strategies from making large saccades shown in Fig. 1 to searching the vicinity of the display with saccades that rarely took the display off the fovea. This finding raised an interesting question regarding the development of the fixation pattern. An extensive body of research on human maintained fixation suggests that the microsearch pattern and microsaccades may be learned during development of fine discriminations of minute visual details (Steinman, Haddad, Skavenski and Wyman, 1973). The present experiments offered an opportunity to examine this suggestion. In particular, we asked whether monkeys had to learn to make small (> 10′) saccades in order to perform this discrimination and whether the pattern of microsaccades changed with training. The following analysis shows the naïve monkeys make microsaccades but that their temporal pattern changes with training.

We measured the amplitude of about 100 saccades that occurred in a number of long fixations that were randomly selected from early, intermediate and final stages of fixation training for each monkey. The early stage was taken as the training session in which eye coils were first calibrated as described above. Intermediate and final stages were taken as each monkey's first exposure to target separations of about 10′ and 5′ respectively. Distributions of absolute saccade magnitudes at each stage of fixation training are reproduced in Fig. 3 for Buddah, a subject whose performance is representative of all of the monkeys except Albert, the monkey with poor fixation stability.

The distributions of Fig. 3 make clear that the visual discrimination used in the present experiment did not cause monkeys to learn to make their first microsaccades. Small but consistent percentages of saccades of less than 10′ amplitude occurred during early training on larger displays. Although rare, miniature saccades could also be found in the earliest records made when monkeys had just completed training of displays with 5° target separation. Thus we conclude that the microsaccade is in the rhesus monkey's behavioral repertoire by the time he is about 2 yr old. Whatever its cause, the acquisition of motor skills requisite to the execution of microsaccades will have to be studied in the infant primate. Our training simply encouraged monkeys to make more microsaccades, a shift that was very difficult for the monkeys to master because it required a minimum of 40 training sessions under conditions designed to optimize their motivation. Albert, the monkey with poor fixation stability, produced a saccade amplitude histogram similar to the one at the top of Fig. 3 after 100 training sessions. The present experiment provided few clues about why monkeys had such inordinate difficulty redistributing eye

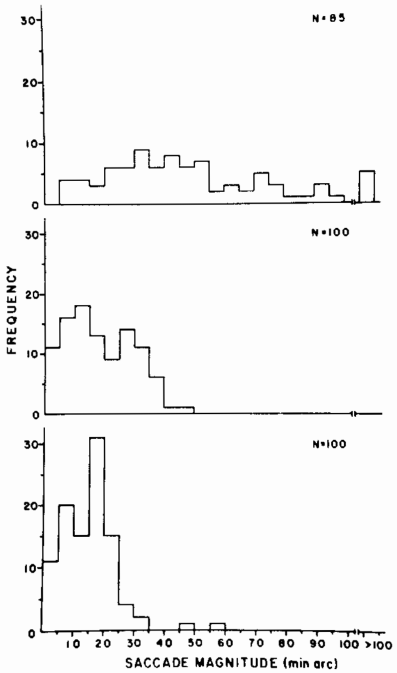

Fig. 3. Frequency histograms of the amplitudes of saccades that occurred in long fixation intervals as the visual discrimination problem was made successively more difficult (top to bottom) for subject Buddah. Target separations were 30′, 10′ and 5′ for the top, middle and bottom histograms respectively.

[5] Bivariate contour ellipse area is actually the solid angle in (min arc)^2 subtended at the eye by an ellipse projected on a plane surface parallel to Listing's plane. Steinman (1965) verified that eye position data meet the assumptions underlying use of this measure.

movements that were already in their behavior repertoires.

(2) *Fixation patterns under direct reward control*

Monkey fixation control produced by the acuity/vigilance problem described above was inadequate for two reasons. First, all monkeys rarely fixated the display for periods longer than 10 sec (about a dozen long fixations occurred in a typical 45-min session). Consequently, those investigators seeking a technique for reliably obtaining long fixations would find that method unsatisfactory. Second, some monkeys can perform such visual discriminations with very sloppy control of eye position. Our argument that monkey fixation is like human fixation depends crucially on showing that all monkeys are like people. Therefore, we sought a better technique for encouraging monkeys to control eye position. It consisted simply of rewarding monkeys each time they produced the desired behavior.

Specifically, an electronic window comparator was connected to the output of the eye movement recording system to permit delivery of water rewards when a monkey kept his eye within a small area around a single fixation target (on both horizontal and vertical meridians) for a predetermined time interval. Training began with the discrimination task described above so the output of the eye movement recorder could be centered in the electronic window when the monkey fixated the display. Then, all but the center target of the display were switched-off. In addition, the training chamber was made totally dark for all monkeys. A warbling 2-kHz tone defined the time interval in which accurate fixation would produce a reward. Initially monkeys were only required to keep their eyes within 0·5° of the target for 5 sec. As training progressed, they were required to stay within ever-decreasing areas about the target for successively longer periods of time. Progress was slow, requiring a mean of 40 training sessions for the monkeys to learn to stay within 15′ of the target for 15 sec. However, it was also effective. All monkeys would immediately fixate the target as soon as the warbling tone was switched-on and would complete about 40 of approx 100 trials started in a session. Thus, this was a good technique for reliably producing long fixations in all monkeys.

Fixation stability was also good as can be seen in representative recordings of horizontal and vertical eye position during maintained fixation that have been reproduced in Fig. 4.

For each monkey, random 0·5-sec eye postion measures were taken from 10 trials of 15 sec duration selected at random from a single training session. Bivariate contour ellipse areas, calculated exactly as outlined in the first experiment, were 297, 165 and 86 (min arc)^2 for Henry, Buddah and Alvin respectively and were comparable to those shown in Table 1. Albert also produced good control here with S.D.s of 4·8′ and 7·8′ on horizontal and vertical meridians respectively. Bivariate contour ellipse area was 256 (min arc)^2. There was a corresponding reduction in his median saccade amplitude to 18·7′. Therefore, we conclude that all of the monkeys could fixate as accurately as man.

Another interesting feature of the fixation patterns can be seen in the right panel of Fig. 4. During fixation intervals, Alvin made no saccades on more than 80% of the completed trials. Alvin spontaneously adopted the use of slow control to keep his eye on target. This mode of control was very stable as the small bivariate contour ellipse area reported above indicated. The value reported corresponds to a S.D. of 3·5′ on an average meridian. Thus, at least one monkey shares with man (Steinman *et al.*, 1973) the ability to maintain eye position using slow control alone and we next asked whether all monkeys shared this ability.

Figures 2 and 4 reveal that Henry and Buddah also occasionally used slow control to effectively maintain eye positon for periods of 2–4 sec. However, these same records contain systematic drifts that clearly moved the eye away from the target and were terminated by small return saccades. All of Albert's drifts on the vertical meridian were of this "noisy" type. His eye drifted up at a rate of about 12′/sec and he never made a corrective drift on the vertical median. However, his slow control on the horizontal meridian was very good. Thus, in general, most monkeys seem unable to use slow control to completely confine the image of a target to a small region of the fovea for long periods of time. However, this does not imply that monkeys do not have effective slow control as can be seen in the next analysis.

Steinman, Cunitz, Timberlake and Herman (1967) and Skavenski and Steinman (1970) have shown that in humans slow control is an active process requiring visible visual details. In total darkness, human subjects drift toward a neutral position that is usually near the primary position. Long-term rates depended on the distance of the eye from the primary position and were on the order of 0·5°/sec, although Becker and Klein (1973) report somewhat higher velocities. A single point of light was sufficient to reduce this long term drift to less than 2′/sec or in most cases, to completely eliminate it. Rhesus monkeys also exhibited drift when placed in total darkness but their patterns differed from human patterns in two important aspects; viz. drift velocities were large and neutral positions were up and far outside the normal oculomotor range. Consequently, in total darkness, all monkeys drifted up at rates and in directions that did not depend on initial eye position. Often there was a horizontal component to this drift but its direction was not systematic across monkeys. Return saccades were frequently executed resulting in nystagmus.

Monkeys, like man, use slow control to markedly attenuate the drift that occurs in the dark. This reduction is shown in Table 2 where mean drift velocities on the horizontal and vertical meridians are listed for all monkeys when they made spontaneous eye movements in total darkness and when they fixated a single 2·5′ target.[6] Each mean was based on the algebraic sum of at least 100 samples of drift between

[6] In the dark, drift samples were measured within 30 sec of the time animals were placed in total darkness. For three of the monkeys, drift velocity stabilized within about 5 sec in the dark. However, Henry's drift velocity continued to increase for about 1 min after the time all light was extinguished. Maximum drift rate was brisk (41°/sec) in this animal. The present series of experiments did not permit us to explain this difference between monkeys.

Table 2. Mean drift velocities on the horizontal (H) and vertical (V) meridians are shown for periods when monkeys made spontaneous eye movements in the dark (Dark) and when they fixated a small target (Target)

Subject	Drift Velocity (min arc/sec) Dark		Target	
	H	V	H	V
Henry	122.3 (29.9)	74.3 (49.6)	5.9 (6.8)	7.9 (9.3)
Buddah	25.3 (42.6)	57.9 (30.5)	-0.1 (7.5)	1.9 (9.9)
Alvin	-8.6 (14.7)	18.5 (18.5)	-0.3 (8.9)	0.3 (9.6)
Albert	33.3 (32.1)	64.9 (55.6)	0.5 (7.7)	11.9 (7.8)

Each mean was based on the algebraic sum of 100 samples of 0·1 sec drift and are shown in parenthesis. Negative signs indicate net drift to the left or down.

0·1-sec eye positon samples taken during intersaccadic intervals. Thus, mean drift represents the net rate of change in eye position caused by drift alone. Net drifts in Table 2 show that the presence of a single point of light was sufficient to activate the slow control system and this system reduced net drift by a factor of about 25 (range = 6–50).

The fact that the monkeys used this means of effectively stabilizing the eye combined with demonstrations of effective slow control in cats (Winterson and Robinson, 1975) and rabbits (Collewijn and Van Der Mark, 1972) indicates that this mode of control is not restricted to humans, but rather is an effective position controlling system in a number of species.

CONCLUSIONS

In addition to quantitative data presented above, we have observed three more monkeys trained to fixate visible targets using these same procedures. Their fixation patterns and accuracy were the same as those reported above. Specifically, two resembled Henry. The third monkey's fixation behavior closely parallels Albert's. These results suggest that the rhesus monkey can control eye position as well as man. In addition, the fact that both species used slow control and microsaccades to fixate is consistent with the notion that similar neural structures are responsible for producing these movements. This finding, combined with recent reports by DeValois, Moran, Polson, Mead and Hull (1974) and DeValois, Morgan and Snodderly (1974) indicating close similarity of *macaque* monkey and human abilities to discriminate luminance, color and fine visual detail, supports use of monkeys as models of the human oculomotor system in neurophysiological and behavioral studies which cannot be conveniently adapted to human subjects. The implication of the qualitative difference in the eye movements of these two species in the dark for such modelling is not yet clear.

Finally, this work provides a technique for establishing fixation in animals and also issues a word of caution to investigators using fixation tasks to "immobilize" eyes of intact and alert animals. Our finding that some monkeys (2 out of 7) can perform fine visual acuity discriminations with sloppy fixation control suggests that such discriminations cannot be assumed to guarantee stable eye position. Consequently, if the investigator is concerned with precisely defining an animal's eye position, a sensitive eye movement recording system must be used in conjunction with direct behavioral control of *eye position*.

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