FIXATION BY THE ALERT BUT SOLITARY CAT

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Abstract—Two-dimensional eye movements of three alert cats, whose heads were restrained, were recorded with a magnetic field search coil technique while they fixated stationary objects of their own choosing in a lighted room and also while in darkness. With visible targets the cats used slow control (drift correction) to maintain fixation. Microsaccades were not observed. The stability of eye position was as good as man's but 0·2-sec drift velocities were almost twice as fast. Slow control was lost in the dark. These results do not agree with prior reports based on horizontal eye movement records.

This paper describes the pattern of eye movements that a cat makes when it maintains fixation on objects of its own choosing. Previous studies on cat fixation (Pritchard and Heron, 1960; Hebbard and Marg, 1960) were inadequate for two reasons. First, only horizontal rotations of the eye were recorded, and, as we will show, the microsaccades reported were probably small horizontal components of large vertical saccades rather than miniature movements. Second, the cats, although given some time to recover, had received depressant drugs to prepare them for recording and may not have been fully alert when the measurements were made. We found that drowsy cats show uncompensated drifts but alert cats use corrective drifts exclusively to maintain the line of sight.

METHODS

Eye movements were recorded by means of a scleral search coil in a magnetic field (Robinson, 1963). Briefly, a coil of stainless steel wire, surgically inserted behind the extraocular muscles, is exposed to two alternating magnetic fields in spatial and temporal quadrature. Voltages induced in this coil, when processed through electronic phase detectors, give rise to two signals proportional to the horizontal and vertical eye positions. Post-surgically the cats had a full oculomotor range ($\pm 20°$) and normal saccadic dynamics which suggests that the implanted coil did not mechanically interfere with normal eye movement. Eye movements were calibrated by rotating the magnetic field coils around the stationary cat by known angles, quickly, during periods when the cat's eye was fixating. Calibration accuracy is, thus, better than 5%. The frequency response of the overall system was 1 kHz. The noise level was low enough so that an eye movement of 1′ could be resolved.

Body movements of the cats were restrained by placing the animal into a loosely-fitting plexiglas box. Head movements were prevented by bolts chronically implanted in the animal's skull. The subjects were three normal cats that were studied many weeks after surgery and had, in that time, been treated, more or less, as pets in the laboratory. They were thoroughly used to the experimental procedure of restraint and were thus free from any sort of mental stress. They were kept awake and alert by conventional physiological procedures, i.e. the experimenters barked, clapped, whistled, and hissed in the adjacent room whenever they suspected that the animal had lost interest in the experiment. The experimenters could not be seen by the cat and their antics could not provide visual input that might influence motions of its eye. The cats were simply allowed to look about the experimental room as they pleased. Their field of view included a peg board upon which a variety of objects were suspended.

RESULTS

(1) *Cats use slow control to maintain fixation*

The three cats studied used slow control (Steinman, Cunitz, Timberlake and Herman, 1967) exclusively to maintain fixation on stationary objects of their own choosing. That is, eye drift was not corrected by microsaccades but by equal and opposite slow drifts which insured that mean eye position did not change. Figure 1 shows the typical eye movement pattern of two of the cats looking about in the experimental room. The pattern consists of one or more large saccades that shift the line of sight a number of degrees. Then, the cat uses slow control to maintain its line of sight until it chooses to make another large saccade that shifts the line of sight once again. Fixation durations are summarized for each of the cats in Table 1.[3]

(2) *Cats do not make microsaccades when they maintain fixation*

Microsaccades (saccades smaller than 10′) were never observed in 6000 sec of recording as can be seen in Fig. 2 which summarizes the saccade vector magnitudes observed in two of the cats. This result is contrary to one of the previous papers (Hebbard and Marg, 1960) where occasional microsaccades were reported in cats but this observation was based on recording of only horizontal eye movements. Occasionally, we also observed small saccadic motions on

[3] Certain periods were chosen during which the cat's eye stayed within any region of size $\pm 6°$ in both meridians by movement of any type. Statistics in Table 1 and Fig. 2 were based on data during those periods. This selection process gives preference to longer fixation intervals and excludes all saccade amplitudes that exceeded about 6°.

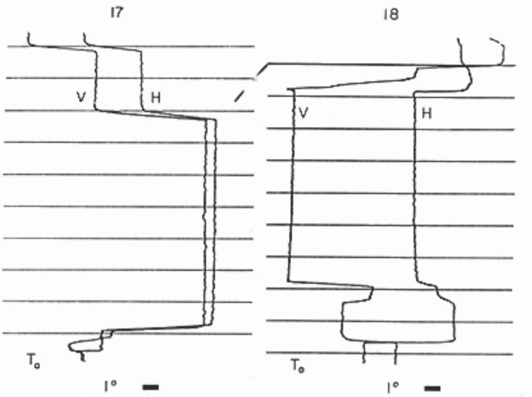

Fig. 1. Typical 2-dimensional search patterns of two cats, 17 and 18. The records begin at T_o. Repetitive horizontal lines show 1-sec periods of time and the black bars show 1° on the horizontal (H) and vertical (V) meridians.

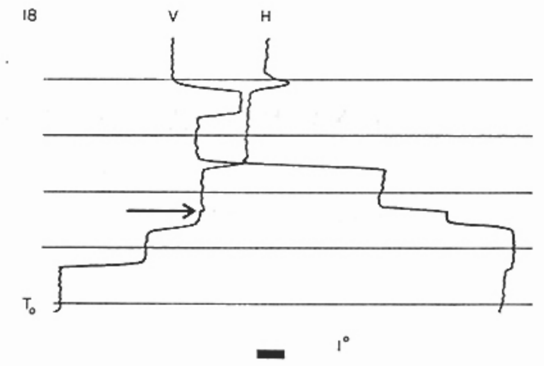

Fig. 3. A small horizontal component (indicated by black arrow) of a large vertical saccade. The record begins at T_o, repetitive horizontal lines show 1-sec periods of time, and the black bar shows 1° on the horizontal (H) and vertical (V) meridians.

one meridian, but such motions always proved to be a small component of a much larger saccade on the other meridian. This is illustrated in Fig. 3.

We cannot rule out the possibility that cats never or cannot make microsaccades. It might be within their power to do so because the cat's visual acuity (Smith, 1936; Blake, Cool and Crawford, 1974) could provide adequate error signals for shifts of eye position smaller than 10′. Also, the cat has a high degree of central anatomical specialization (Stone, 1965). Such specialization is often suggested to provide a need (or an advantage) for making microsaccades, i.e. they place a detail of interest onto the region of the retina where vision is best. But, as Steinman (1975) has suggested, this explanation is inadequate for microsaccades in humans because Millodot's (1966) measurements of visual acuity show that it is relatively uniform over a region 24–50′ dia. Human microsaccades are much smaller (~5′). Such microsaccades could not serve the purpose of improving detail vision. We doubt that the cat does make microsaccades because the rhesus monkey, who has a visual and oculomotor system much like man's, does not naturally, although he can be trained to do so (Skavenski, 1974). It seems likely that microsaccades in the rhesus monkey and the cat are probably as useless to them as they are to humans (Steinman *et al.*, 1973).

(3) *The eye is stable when slow control maintains eye position*

The stability of the cat's eye when it looks at an object of its choice is at least as good as stability of the human eye instructed to maintain eye position in the same way. To measure stability, deviation of eye position during fixation periods from mean position was randomly sampled every 0·5 sec. Standard deviations of horizontal and vertical eye position samples are shown in Table 1. They range from 1·6′ to 4·5′. The cat is as stable as humans using slow control (Steinman *et al.*, 1967; Murphy, Haddad and Steinman, 1974).

Also, like humans, stability can be maintained over long periods of time. An example of this can be seen in Fig. 4.

Table 1. Fixation characteristics of three cats: numbers 17, 18, and 20. Their mean fixation durations (FD) and standard deviation (parentheses) of fixation durations are given in seconds. Inverse fixation stability (IFS), i.e. the standard deviations of eye position measures on the horizontal (H) and vertical (V) meridians, are also given in min arc. Mean drift velocities in the light (DVL) and dark (DVD) are given in min arc/sec. They were determined as absolute mean velocities between successive position samples every 0·2 sec for horizontal (H) and vertical (V) components or along the direction of the movement (vector). These determinations are based on at least 50 samples

CAT	FD	IFS		DVL			DVD
		H	V	H	V	Vector	H
17	7.3 (5.1)	2.6	2.4	10.0	9.6	16.0	23.5
18	4.2 (2.7)	4.5	4.3	9.8	10.2	15.5	54.5
20	*	1.6	3.4	7.0	9.0	12.7	*

* Only high-gain recordings in the lighted room were made for cat 20 which made the records unsuitable for computations of fixation durations.

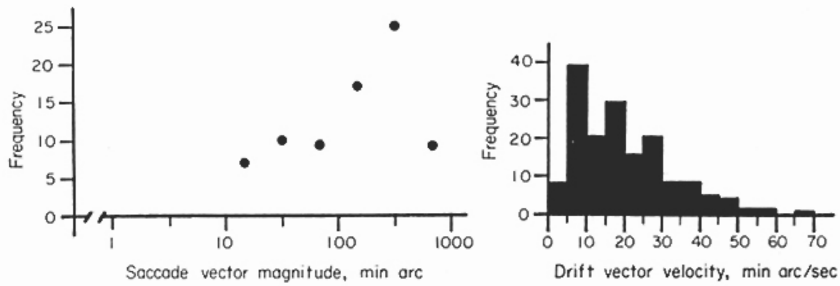

Fig. 2. Left: Frequency of saccade vector magnitudes observed in cats 17 and 18. Right: Frequency of 0·1 sec drift vector velocities observed in cat 20.

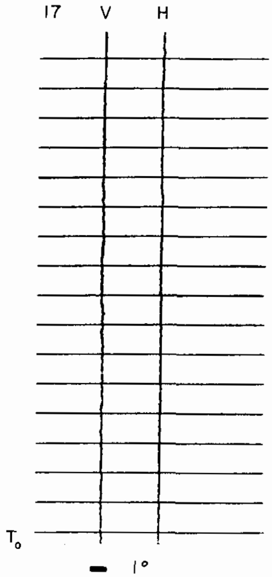

Fig. 4. A 2-dimensional record of cat 17 using slow control for 17 sec. The record begins at T_o, repetitive horizontal lines show 1-sec periods of time, and the black bar shows 1° on the horizontal (H) and vertical (V) meridians.

These results do not agree with a previous report on drifts in the cat. Pritchard and Heron (1960) reported occasional drifts whose "amplitude could exceed 2°". We only observed such drifts in the dark or when an animal dozed off. A loud noise awakened it and reestablished effective slow control. An example of this can be seen in Fig. 5.

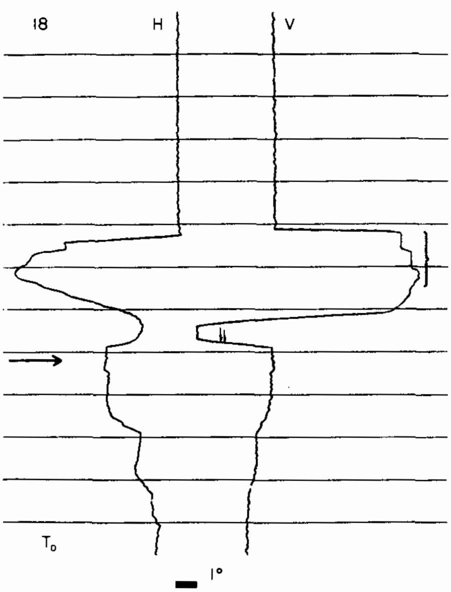

Fig. 5. A 2-dimensional record of a drowsy cat, its awakening, and subsequent performance. The record begins at T_o, repetitive horizontal lines show 1-sec periods of time, and the black bar shows 1° on horizontal (H) and vertical (V) meridians. The arrow indicates when shouting began in the next room in order to arouse the cat. Arousal was accompanied by two large saccades. The bracket indicates when the amplifiers were adjusted to bring the eye position signals within the recording limits and the final 5 sec shows the typical fixation pattern of the alert animal.

(4) *The eye moves irregularly as it maintains its position*

The fine grain nature of slow control is shown in Fig. 6. Notice that drifts in one direction tend to be followed by similar drifts in the opposite direction, resulting in an irregular oscillating pattern which keeps long-term mean eye position from changing by more than negligible amounts (e.g. 3′ in the 9 sec shown in Fig. 6).

The optokinetic reflex in mammals is well known to have a latency of about 150 msec. A feedback system with this delay can exhibit a tendency to oscillate near 3·3 Hz (the reciprocal of twice the delay). This fact could account for the emphasis of this frequency component seen in the drift records of all three subjects. The mean eye velocities occurring in this pattern were estimated from a random sample of drifts between 0·2-sec samples in order to compare drift velocities of the cat to drift velocities of man where 8′/sec have been reported (Steinman, 1965). The result of this analysis is summarized in Table 1 where it can be seen that the cat drifts almost twice as fast as man (mean drift velocity over all three subjects was 14·7′/sec). Drifts between 0·1-sec samples were also measured because the cat's oscillations are of higher frequency than man's and 0·2-sec samples underestimate eye velocity. The frequency distribution of 0·1-sec drift vector velocities for one of the cats is shown in Fig. 2. Its mean 0·1-sec drift vector velocity was 21·7′/sec, S.D. = 13·7.

(5) *Slow control is visually activated*

The stability of the cat's eye is achieved by a visually activated mechanism. Two of the cats were placed in total darkness and stability was lost. This is shown in Fig. 7 for one cat. Uncompensated drifts and higher drift velocities were observed in the dark

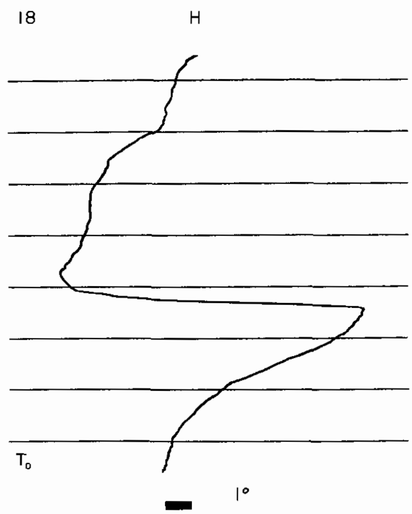

Fig. 7. Horizontal (H) eye movements of cat 18 trying to maintain its line of sight in total darkness. The records begin at T_o, repetitive horizontal lines show 1-sec periods of time, and the black bars show 1°.

than when visual targets were available (see Table 1).

In summary, the cat uses slow control to maintain fixation on objects of its own choosing and does so without microsaccades. Drifts of the eye in one direction are corrected by subsequent drifts in the other direction. The mechanism by which this is accomplished uses visual input because in darkness the eye drifts rapidly and the cat loses its ability to maintain its line of sight.

The fact that the cat uses slow control to maintain eye position is not surprising. Every animal (man, rabbit and monkey) whose fine-grain 2-dimensional fixation pattern has been studied previously either normally uses or can use this pattern of eye movement to maintain eye position (Steinman *et al*., 1973; Collewijn and Van Der Mark, 1972; Skavenski, 1974). The addition of one more species (the cat) that normally uses slow control strengthens the conjecture made by Walls (1962) that slow control (or "the collicular-field holding reflex" as he called such control) is probably a universal characteristic of all vertebrates with mobile eyes. This universal pattern seems likely to be sufficient to maintain vision in the cat as it does in the human being. The characteristics of this pattern might provide a guide as to how to move the stimulus most appropriately in electrophysiological studies of the visual system of this animal.[4]

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[4] A recent report (Movshon, 1974) shows that about 25% of simple cortical cells of the cat prefer velocities which fall within the range of velocities that we found in the normal fixation pattern of the alert cat. Since simple cells also discharge well over a 10 to 1 range below their preferred velocity, 81% of the simple cells would be well activated by velocities of 15′/sec. The thrust of our conclusion is that it is these cells that are likely to be significant for the transmission of the visual message because their activity would be maintained by the natural fixation eye movements of this animal.

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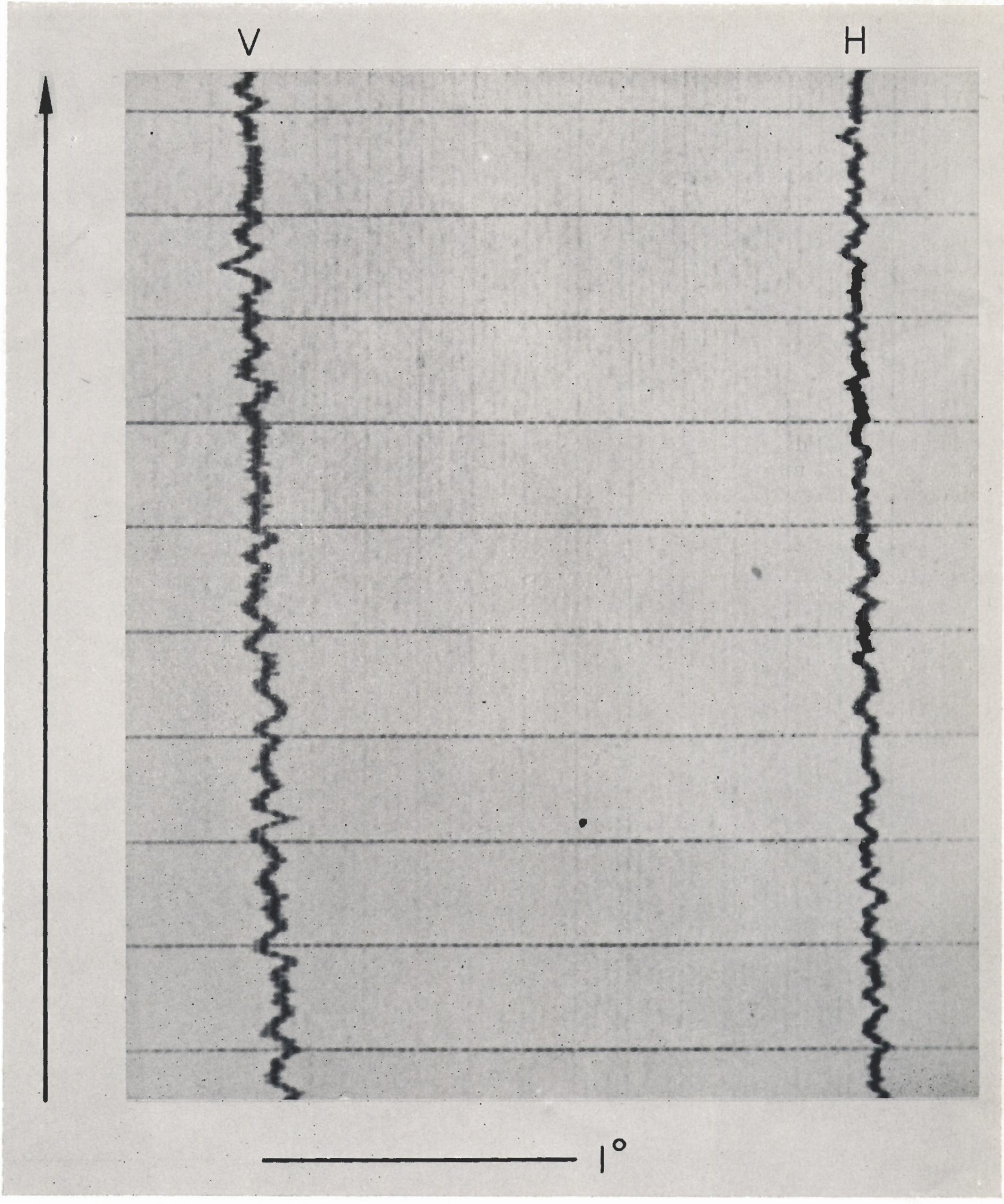

Fig. 6. High-gain 2-dimensional record of a 10-sec period of slow control. The record begins at the bottom, repetitive horizontal lines show 1-sec periods of time, and the black bar shows 1° on the horizontal (H) and vertical (V) meridians.