

SACCADIC AND DISJUNCTIVE EYE MOVEMENTS IN CATS

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INTRODUCTION

AT FIRST sight, cats rarely seem to move their eyes at all. Indeed, when a cat does change its gaze from one thing to another it appears to do so mainly with a movement of its head. Since the cat has only an area centralis (a meager caricature of the primate's fovea) one might question whether it is even capable of fixation in the normal sense of the word. However, PRITCHARD and HERON (1960) have managed to measure ocular tremor, flicks and drift in conscious cats looking fixedly at interesting targets, and the properties of these eye movements are not so startlingly different from those in humans fixating a stationary object.

Although students of the oculomotor system have recently concentrated their efforts mainly on monkeys and men (DICHGANS and BIZZI, 1972), there is far more information about the anatomy and physiology of the cat's visual pathways. We know, for instance, about the orientation-selective and disparity-detecting neurons arranged retinotopically within its visual cortex (HUBEL and WIESEL, 1962; BARLOW, BLAKEMORE and PETTIGREW, 1967; BISHOP, 1970). We know that it has direction-selective, movement-sensitive neurons in the superior colliculus (STERLING and WICKELGREN, 1969) and that stimulation of this structure elicits eye movements (APTER, 1946; STRYKER, 1972; M. STRYKER and P. H. SCHILLER, in preparation). In fact BLAKEMORE (1970) has speculated that different groups of cortical cells, segregated into separate columns, may provide the error signals for the initiation and control of saccadic and disjunctive movements in cats. So it seems sensible to investigate the spontaneous eye movements of cats.

METHODS

Restraint of the body and the head

We selected three cats for their tameness, and handled them for about 1 week prior to surgery. They were prepared using full sterile technique and Nembutal anaesthesia with four bolts attached to the calvarium in the manner of EVARTS (1968). The threaded ends of these bolts, led through puncture wounds in the scalp, allowed us to attach the head firmly to a superstructure, which could either be clamped to restrain the head totally, or loosened to permit free head movements in a horizontal plane. In two of the cats we chronically implanted silver/silver chloride electrodes (modified from BOND and HO, 1970) in the bone at four points around the orbit of one eye for d.c. electro-oculography. Leads from these electrodes ran under the skin to a Sheats pedestal connector mounted on the skull. In addition, these two cats were implanted with a 21-g tube (SCHILLER and KOERNER, 1971) for inserting microelectrodes into the superior colliculus for another experiment. With one exception, the data on spontaneous eye movements reported here were obtained before the introduction of any microelectrode: however, we saw no difference in eye movements in one cat after six penetrations into its superior colliculus.

The cat lay snugly in a cloth bag, drawn together loosely with a string at the neck, inside a 15-cm dia. hard cardboard tube fixed to a wooden platform under the apparatus to which the head was attached. Foam padding between the cat and the tube provided greater comfort.

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After a little training the cats exhibited no distress in this strange situation. Far from showing the usual signs of alarm, such as dilatation of the pupil and loud mewing, all the cats purred in the apparatus and often became drowsy; one cat actually fell asleep frequently and had to be roused for the experiment to continue. The superstructure was loosened to allow free horizontal head rotation when we were not actually measuring eye movements.

Videotape technique

We obtained videotape records from all three cats. Incandescent lights illuminated the room sufficiently to constrict the cat's pupils to a width of 1.8–2.2 mm. A Shibaaden HV-15S low-illumination video-camera was used with a Panasonic NV-505 videotape recording system and a 19-in. television monitor; the entire system scanned at 60 frames per second and was calibrated for linearity. The camera had in view simultaneously both the cat's eyes and a fast stop-watch, which ran continuously throughout the session. More precise timing was achieved by counting frames in slowmotion playback: 3 frames corresponded to 50 msec. Two points 20 deg to the left and right of the cat's sagittal plane were marked on a horizontal eye-level perimeter 85 cm from its eyes. The experimenters positioned their faces, one at each point, and alternately attracted the cat's attention from one to the other, indicating on the video record when the cat appeared to be looking straight at them. A series of four of these movements to each side was sufficiently consistent to serve as a calibration. Then version and vergence eye movements were elicited by moving exciting objects around the room, and toward and away from the cat.

Eye movements were measured by playing back the videotape and noting the position of the center of the fissured entrance pupil of each eye on a 1-mm ruled transparent overlay, which was taped to the monitor screen. The overall magnification of the videotape system was 3.5 times in the plane of the cat's eye. Pupil position was read with an accuracy of ± 0.5 mm on the monitor screen ($\pm 1.4^\circ$ of eye rotation, according to the calibration). The videotape was advanced either 15 frames (250 msec) or 3 frames (50 msec) between readings. The calibration taken above allowed conversion of pupil position on the monitor to equivalent degrees of eye rotation. We recorded only horizontal eye positions, and did not take measurements either when the cat was looking more than a few degrees up or down, or when the size of the entrance pupils changed noticeably, in case the pupil expanded asymmetrically, thus anomalously changing the locus of its center.

Accuracy of the calibration

Our behavioral calibration shows that about 2.2 mm of lateral displacement of the center of the entrance pupil corresponds to 20° of rotation of the eyeball. VAKKUR and BISHOP (1963), in their schematic cat's eye, show a point in the crystalline lens as the center of an approximately circular arc formed by the posterior scleral surface of the globe. (This scleral surface is shown exactly circular for over 90° of arc). If we assume, as is reasonable, that the eyeball rotates against this posterior scleral surface, then the center of rotation is that point in the crystalline lens, shown at a distance of 4.68 mm from the anterior surface of the lens (against which the fissured pupil lies). Thus, 20° of rotation of their schematic eye should cause a lateral displacement of the real, constricted pupil by about 1.63 mm. The entrance pupil is the view of the real pupil seen through the cornea. If we assume that a small rotation of the eye hardly displaces the cornea laterally (since the center of curvature of the cornea is quite close to the center of rotation of the eye), then, during a movement, the entrance pupil is displaced by an amount equal to the translatory motion of the real pupil magnified by the cornea. VAKKUR and BISHOP (1963) estimate that the magnification for a pupil between 0 and 3 mm is about 1.18. So a 20° movement of their schematic eye should displace its entrance pupil by about $(1.63 \times 1.18) = 1.93$ mm. Keeping in mind the fact that our cats all weighed as much as the heaviest of VAKKUR and BISHOP's, we consider the behavioral determination of $2.2 \text{ mm}/20^\circ$ to be in excellent agreement with this theoretical value.

Electro-oculography

The potentials between the pairs of horizontal and vertical silver/silver-chloride electrodes on two cats were amplified by two Hewlett-Packard 8803A chopper-stabilized d.c. differential amplifiers and written out on a Sanborn strip chart recorder or on a Honeywell "Visicorder" direct-writing oscillograph. These records were calibrated in a manner similar to that for the videotape. Although electro-oculography can be unstable under conditions of changing illumination, frequent recalibration, and in one session cross-calibration with the videotape, was possible. Electro-oculography was used only to follow version movements since the electrodes sensed the position of only one eye.

RESULTS

Figures 1 and 2 show selected records of spontaneous eye movement, taken from the videotape. The positions of the cat's two eyes are plotted in the middle, with the mean position (version) above and the difference in position (vergence) below. The angular scale

of rotation is derived from the calibration procedure, in which the cat's gaze was attracted to two points, 20° to each side. On the ordinate for the version record, zero is straight ahead. For the ordinate of the vergence record the scale is the total convergence angle of the two visual axes: zero is the vergence position with the visual axes parallel, fixating a point at infinity, on the assumption that during the calibration procedure the cat converged to fixate the experimenters, 85 cm away. Note that the time scales on the two figures are very different. These records are all for cat 1, but we noted no qualitative differences between the three animals.

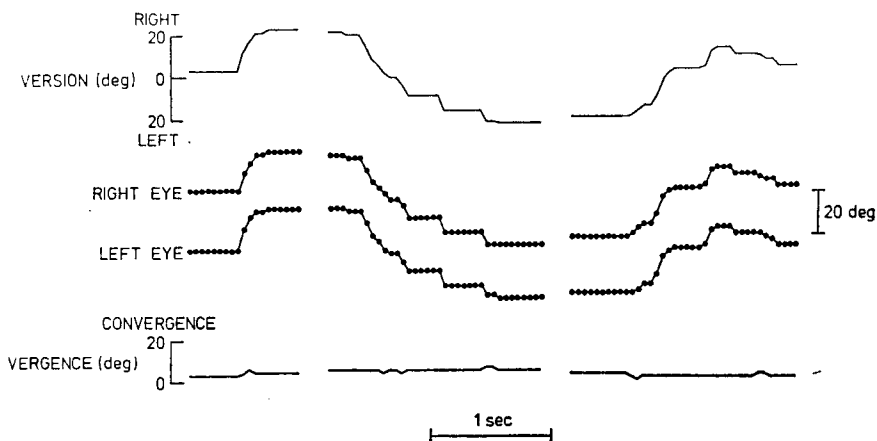


FIG. 1. Examples of saccadic movements, with virtually no change in convergence angle, in cat 1. The solid circles plot the translations of the centers of the pupils, measured from the videotape records at 50 msec intervals. Above is the mean eye position (version); the ordinate indicates the deviation of gaze from straight ahead. Below is the difference between the positions of the two eyes (vergence); the ordinate is the total convergence angle, i.e. the angle between the two visual axes. Zero indicates that the eyes are diverged to infinity and that the visual axes are parallel. The time scale is indicated.

From these sets of records, three facts are clear:

- (1) The cat can hold its fixation quite steady for periods between a few hundred msec and a few sec.
- (2) It can make pure conjugate saccades without any accompanying change in vergence angle.
- (3) It can make pure yoked disjunctive movements without any net version. Thus the observed changes in convergence cannot be the result of sloppy, non-conjugate saccades.

Version movements

Figure 3 plots the peak velocity for 100 saccades against their amplitude. The data are from two animals: the open circles represent 90 successive spontaneous saccades from cat 2, recorded by the d.c. electro-oculographic system when it was cross-calibrated with the videotape display. The 10 filled circles indicate saccades from cat 1 measured with the videotape system. Peak velocities increase from about $50^\circ \text{ sec}^{-1}$ for 5° saccades up to almost $300^\circ \text{ sec}^{-1}$ for some saccades of 20° . However, even many 30° movements had peak velocities of only $100\text{--}150^\circ \text{ sec}^{-1}$. This variability was not due solely to differences in the

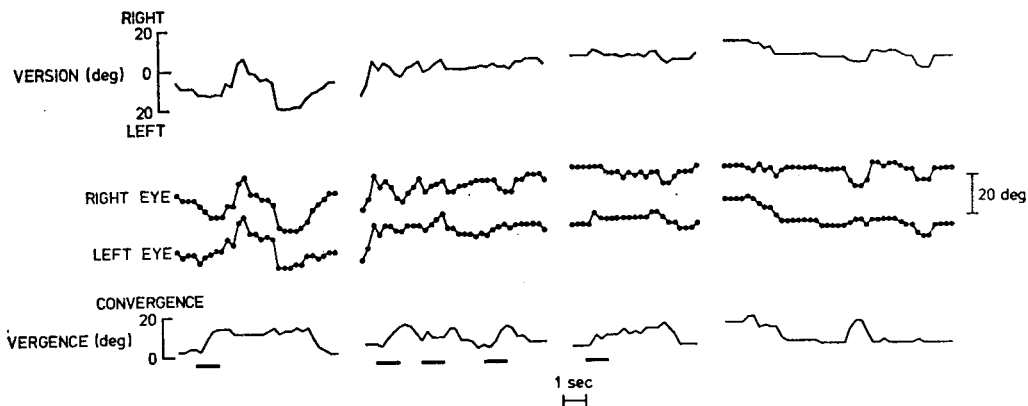


FIG. 2. Similar records to those in Fig. 1, but showing large changes in convergence angle, sometimes almost without any conjugate deviation. The solid bars under the vergence record show occasions when a note was made on the videotape record of the sudden approach of an object from about 80 cm to about 15 cm from the cat's eyes. Notice the difference in the time scale from Fig. 1.

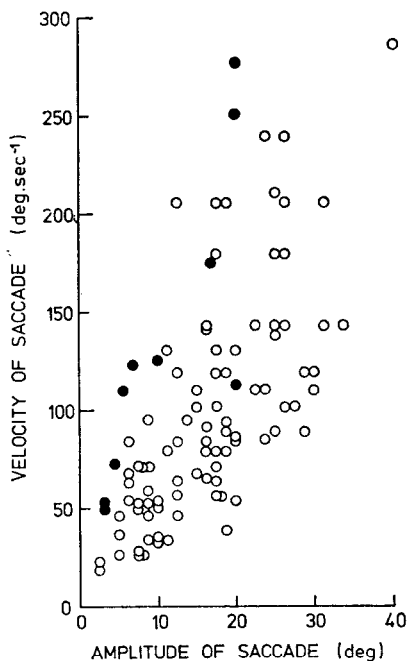


FIG. 3. The maximum velocities of version movements of different amplitude. The open circles represent 90 successive saccades from electro-oculographic records on cat 2, the solid circles are 10 selected saccades from the videotape records for cat 1.

direction of the movement or in the initial position of the eyes. So, although saccades in the cat are slower than in monkey (FUCHS, 1967) or in man (WESTHEIMER, 1954; HYDE, 1959; ROBINSON, 1964), the positive correlation between saccade velocity and amplitude is present in all three species.

Vergence movements

As in man (YARBUS, 1957), spontaneous shifts of fixation in the cat usually involve changes in both direction and convergence. The disjunctive movements, when they happened, were fairly well related to the approach or retreat of an object. Thickened bars under the vergence records in Fig. 2 indicate specific occasions, noted on the videotape records, when a shaking finger or pencil was suddenly thrust up from about 80 cm away to about 15 cm from the cat's eyes. In these cases the cat followed the object quite closely, since the 14° or so of convergence recorded agrees well with the calculated disparity of an object 15 cm from this cat, whose inter-pupillary distance was 42 mm. Certainly in these examples the fixation disparity is less than our measuring error.

At other times, however, the approach of an object would only cause the cat to look away, or would fail to elicit any reaction. On still other occasions the cat would track an object in from 2 m to about 40 cm while the object itself continued to move in to 20 cm, corresponding to an apparent fixation disparity of 6° , certainly much greater than the limit of accuracy of our techniques. Of course, the main problem in all these experiments is that we had no guarantee that the cat was watching the thing we wanted him to watch. We cannot be sure that he was not tracking with perfect accuracy the experimenter's hand holding the object. The most we can state with certainty is that we have elicited as much as 14° of convergence by moving novel objects close to the cat, and that when these objects move away the cat's eyes diverge appropriately.

Since our cats were following objects moving towards them but not exactly in the sagittal plane, it is not surprising that a few of the vergences in Fig. 2 were apparently produced by movement of only one eye. This is not a peculiarity of the cat for we have also seen it in our records of human subjects tracking the same moving targets, and the electromyographic data of BREININ (1955) are similar.

We must emphasize the crucial importance of novelty in the stimulus for disjunctive eye movements. If the same object was repeatedly thrust at the cat, it almost always failed to provoke more than two or three convergence movements. These effects were cumulative, because we almost never saw any large disjunctive movements towards the end of our experiment sessions, after the first 30 min.

The distinction between version and vergence is further emphasized by the difference in their velocities. Figure 4 plots the peak velocity for 50 vergence movements from the same session as the filled circles of Fig. 3. Again, as in man (RASHBASS and WESTHEIMER, 1961), the maximum velocity of a disjunctive movement increases with its amplitude. This cat's peak velocities for each eye during vergence movements were about one-tenth of the peak velocities for equal size saccades. In man, too, version and vergence can be distinguished on the basis of their velocities (ALPERN, 1969).

DISCUSSION

The cat's eyes suddenly seem to come to life when its head is immobilized: restraint reveals a wealth of oculomotor activity that usually passes unnoticed. To be sure, even this richness may still be slight by comparison with men and monkeys, but we hope that this

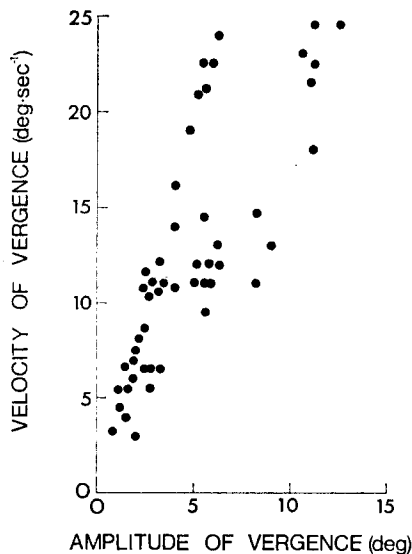


FIG. 4. The maximum velocities of vergence movements of different amplitude. Data are from videotape records for cat 1 from the same session as the filled circles of Fig. 3. The abscissa is the total change in convergence angle (whether due to a convergent or a divergent movement), so the actual angle moved by each eye is half this value and the true peak velocity for each eye alone is half the value on the ordinate.

demonstration of spontaneous version and vergence may validate the use of cats in studies of the anatomy and physiology of the oculomotor system and may add weight to extrapolations between the properties of visual neurons in the cat and human visual perception.

We should take care, however, to point out the peculiarities of the cat's eye movements. First of all, it is clear from all our records that cats simply do not move their eyes over more than $\pm 20^\circ$: this should be contrasted with $\pm 45^\circ$ in man and monkey. Most of the spontaneous saccades in Fig. 3 are smaller than 20° , and almost never is a movement greater than 30° , even when the starting position of the eye is far to one side. Those who study the effects of stimulating the cat's oculomotor centers should bear in mind this limited total range of eye movement.

Second, although all three cats we studied showed large convergence movements, it was often difficult to gain the cat's attention, and the movements were not elicited repeatedly by our stimuli. This may explain why we were not able to produce fusional vergence by placing prisms (from 2 to 12 dioptres, base-in and base-out) in front of one eye. We only attempted this experiment towards the end of a session, when single, moving, novel stimuli would rarely elicit a disjunctive movement anyway. This difficulty in obtaining repeated, reliable convergence may partly explain why HUGHES (1972 and personal communication) did not record large disjunctive movements in some of his cats. However, this cannot be the whole reason and it may be, as Hughes points out, that learning and practice are very important in the development of convergence. In other ways the results of his careful experiments are in excellent agreement with ours. The problem of obtaining secure, repeatable eye movements has not been adequately stressed in the past. We have seen a similar phenomenon with optokinetic nystagmus in the cat. The first presentation of moving stripes in a

daily session evokes a strikingly strong nystagmus: after a few minutes (or sooner, if the stripes are stopped and restarted) the cat responds weakly or not at all. Even 2 hr later, at best a very weak and occasional optokinetic response can be elicited.

Third, from Fig. 3, the cat's saccades seem much more variable in velocity than those often reported in primates: we feel that this apparent difference between carnivore and primate is the result of different experimental conditions. FUCHS' (1967) data were gathered in an operant situation where the monkeys were required to fixate and pay attention to the targets presented in order to obtain their reward: results on man were usually obtained in similar situations with subjects instructed to follow the targets (WESTHEIMER, 1954; HYDE, 1959; ROBINSON, 1964). Under such conditions the primate's eye movements show small variability in velocity and duration. However, DICHGANS, NAUCK and WOLPERT (1972) found that the velocity of human nystagmus and saccadic movement is strongly influenced by the subject's attention and vigilance. Monkeys also produce saccades of widely varying velocity after facing a blank screen for 1 hr, with the head restrained (M. STRYKER, unpublished observations). So our results probably do represent the true variability of eye movements in the normal, unrestrained cat: perhaps we should look to the influence of attentional factors on the discharge patterns of oculomotor neurons to explain this variability. (Of course, we must also keep in mind that our data were collected by waving objects in front of the cat, so some of the slowest movements in Fig. 3 may have been smooth pursuit movements rather than true saccades.)

The cat's ability to converge to near objects appears to be slightly greater than his accommodative capacity, which is 4–5 dioptres according to ELUL and MARCHIAFAVA (1964): 4.5 dioptres accommodation is equivalent to about 11° of convergence in our cat 1, in which we have seen as much as 14° of convergence (Fig. 2). ALPERN, KINCAID and LUBECK (1959) showed that, in man too, convergence to near objects exceeds accommodative power (which has a maximum of about 5 dioptres).

REINHART and ZUBER (1971) recorded from cat abducens neurons that have similar properties to those reported in the monkey (SCHILLER, 1970). The current results demonstrate similarities between the actual eye movements of cats and primates.

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Abstract—We monitored eye movements in cats with their heads immobilized, using videotaped television recordings of pupillary translations and d.c. electro-oculography. Cats only deviate their eyes by up to 20° from the midline: they hold fixation quite constant for up to several seconds: they can make pure conjugate saccades without changing convergence angle; they can converge and diverge their eyes by many degrees to follow interesting objects. The disjunctive movements are difficult to elicit repeatedly and are generally much slower than the conjugate movements, whose velocity increases with amplitude up to about 300° sec⁻¹.

Résumé—On enregistre les mouvements des yeux chez les chats avec la tête immobilisée, par l'analyse en télévision des translations pupillaires et l'électro-oculographie en courant continu. Les yeux des chats ne dévient que jusqu'à 20° de la position centrale; ils maintiennent pendant plusieurs secondes une fixation presque constante; ils peuvent faire de pures saccades conjuguées sans changer de convergence; ils peuvent converger et diverger de plusieurs degrés pour suivre un objet intéressant. Les mouvements disjoints sont plus difficiles à produire d'une façon répétée et sont généralement beaucoup plus lents que les mouvements conjugués, dont la vitesse augmente avec l'amplitude jusqu'à environ 300° sec⁻¹.

Zusammenfassung—Wir zeichneten die Augenbewegungen bei Katzen mit fixierten Köpfen auf, wobei wir Videoband-Fernsehaufnahmen der Pupillentranslationen und Gleichspannungs-Okulographie zu Hilfe nahmen. Katzen weichen mit ihren Augen nur bis zu 20° von der Mittellinie ab; sie halten eine Fixation bis zu mehreren Sekunden ziemlich konstant; sie können reine konjugierte Sakkaden ohne Änderung des Konvergenzwinkels durchführen;

sie können ihre Augen um mehrere Grad konvergieren und divergieren, um interessanten Objekten zu folgen. Die disjunktiven Bewegungen können nur schwer wiederholt hervorgerufen werden und sind i. a. viel langsamer als die konjugierten Bewegungen, deren Geschwindigkeit mit der Amplitude bis zu etwa 300 Grad/s zunimmt.

Резюме—Регистрировались движения глаз у кошек при неподвижной голове; использованы видеомагнитофонная запись перемещений центра зрачка и окулография на постоянном токе. Амплитуда движений глаз у кошки не превышает 20 градусов от средней линии; они способны удерживать совершенно точную фиксацию на протяжении нескольких секунд; саккадические движения выполняются чисто, без изменения угла конвергенции; конвергенция и дивергенция имеют значительную амплитуду при прослеживании интересных объектов. Трудно вызывать вергенционные движения несколько раз подряд; скорость вергенции много ниже скорости саккад; последняя нарастает с увеличением амплитуды, достигая примерно 300 град/сек.