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Physiological Nystagmus in the Cat*†

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Cats were prepared by the *encéphale isolé* technique. A small plane-mirror mount was sutured to each cornea without obstructing vision, and eye movements were recorded using the optical-lever method. The records showed physiological nystagmus similar to that in man, although the cats had fewer and smaller saccades. Some saccades were binocular, but usually they were uniocular. The fine tremor varied in frequency from 35–65 cps, averaging 50 cps, and in amplitude from 4–52 sec of arc, averaging 22 sec. Curare decreased and ultimately abolished eye movements and physiological nystagmus, whereas neostigmine increased them. Physiological nystagmus is therefore mediated by efferent neural stimulation of the eye muscles. Tremor was also recorded from the detached inferior oblique muscle, as well as from the eyeball with most of the extraocular muscles detached. Fine tremor was also found in finger pointing in man. The significance of physiological nystagmus to vision is briefly discussed.

INTRODUCTION

THE small involuntary eye movements which occur even during attempted steady fixation comprise the so-called physiological nystagmus. Its existence in man has been well established,[1–5] and it is usually described as consisting of at least three components: (1) tremor, or micronystagmus; (2) saccades, jerks, or flicks; and (3) drifts and "waves." In a dozen healthy males between the ages of 20 and 30 studied in this laboratory using the optical-lever method, reflecting light from a mirror mounted on a small stalk attached to a contact lens, the tremor had a mean amplitude of 10–14 sec of arc and a mean frequency of 85 cps, which varied little among subjects, although in any subject the frequency for different half-second intervals varied between 65 and 100 cps. The saccades occurred in most subjects at a rate of 1–2 cps with an amplitude of 5–6 min.[6] A typical record is shown in Fig. 1.

A search of the literature has failed to uncover any report of physiological nystagmus in animals. Yet, if it is not present, there will clearly be need for re-evaluation of proposals that physiological nystagmus in man is valuable or even essential for vision. Therefore a study was made to determine (1) whether it exists in the cat and, if so, (2) the effect of certain drugs which increase or decrease the end-plate potentials at the myoneural junction, and (3) the contribution of individual muscles. To determine whether tremor might normally be found in muscles other than those of the eye, records were also obtained of the movement of (1) the pinna of the cat's ear, (2) the human index finger while pointing, and (3) the elbow while held in a fixed position.

EXPERIMENTAL METHOD

In order to record eye movements without having the cats under general anesthesia, they were prepared by the *encéphale isolé* technique of Bremer[7]: i.e., with the cat under ether anesthesia, the spinal cord was cut at the level of the first or second cervical vertebra after injecting 0.05 cc of 1% procaine at the site of the section. Artificial respiration through a tracheal cannula was started when natural respiration failed. Use of ether was then discontinued. After 1–2 hr its effects disappeared, and the cat showed signs of consciousness. In a good preparation it would appear alert, and its eyes would sometimes follow a moving light. Head movements could occur but were greatly restricted with a harness. The rest of the body was, of course, paralyzed.

The animal was prepared for eye-movement recording while it was still under ether anesthesia. The nictitating membranes were removed and the eyelids were sutured open. Mirror holders were sutured to the

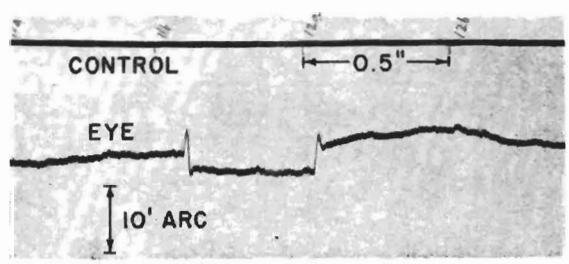

FIG. 1. Physiological nystagmus in man. The horizontal arrow indicates one-half sec of time; the vertical arrow shows 10 min of eye rotation. Two saccades, tremor, and drift are evident.

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[1] G. Dohlman, Acta Oto-laryngol., Suppl. No. 5 (1925).

[2] F. H. Adler and M. Fliegelman, Arch. Ophthalmol. (Chicago) **12**, 475–483 (1934).

[3] F. Ratliff and L. A. Riggs, J. Exptl. Psychol. **40**, 687–701 (1950).

[4] Riggs, Armington, and Ratliff, J. Opt. Soc. Am. **44**, 315–321 (1954).

[5] R. W. Ditchburn and B. L. Ginsborg, J. Physiol. (London) **119**, 1–17 (1953).

[6] F. W. Hebbard, Eye Movements During Fixation and Fusion, Ph.D. Dissertation (University of California, 1957).

[7] F. Bremer, Compt. rend. soc. biol. **122**, 460–467 (1936).

corneas, and a small screw holding a mirror was mounted in the skull, for recording horizontal eye and head movements, respectively, by means of the optical-lever principle.

Topical anesthesia, renewed periodically, was applied wherever it would be valuable: tetracaine on the corneas, procaine on the wounds. The corneas were kept moist by 1% methyl cellulose in Ringer's solution.

The corneal mirror mount, which weighed only 0.56 g, was sutured around the limbus and consisted of a metal ring having a 1-cm arm to which a plane front-silvered mirror 0.25-in. in diameter was attached. Direct vision was completely unobstructed. Horizontal movements from one or both eyes were recorded on photographic paper moving 7.9 cm per sec. The optical lever was 3.5 m long, so that a 1-mm displacement of the trace was equal to 29.5 sec rotation of the eye. Horizontal head movements could be recorded simultaneously.

The effect of individual muscles was investigated by two methods. (1) Eye movements were recorded after detaching the muscles one at a time. (2) The movement of an individual detached muscle was recorded. For this we selected the inferior oblique muscle, which was the most accessible oculorotary muscle in the cat, and appeared to us to be second in mass only to the medial rectus. A nylon suture was attached to the tendon, and the suture was drawn over a light-weight, low-friction pulley having a diameter of 20 mm, which is almost equal to that of a cat's eye. The suture was kept taut by hanging various small weights to its free end. A tiny mirror for use with the optical lever was attached to the pulley shaft. Since the shaft was horizontal, a contraction of the muscle produced a vertical displacement of the optical lever. For photographic recording, this was optically rotated to a horizontal displacement by means of a Dove prism. Precautions were taken to keep the detached muscle free from drugs.

Movement of the pinna of the cat's ear was recorded by the same method as for the detached muscle, except that the suture was attached to the pinna. Movement of the right index finger was recorded by having the subject rest his hand on a table, and point the finger so that the optical lever, reflected from a small mirror glued to the finger tip, was directed to the camera aperture. Movement of the right elbow was recorded by gluing a mirror on it and having the subject place his right hand on his right shoulder and "point" so that the optical lever was directed to the camera.

RESULTS AND DISCUSSION

Eye Movements and Physiological Nystagmus

Eye movements occurred over a range of about 40° horizontally and 20° vertically. In general the movements of the two eyes were coordinate, although at times they failed to coordinate. These larger movements made it difficult to direct the optical levers to the camera, which had a horizontal aperture wide enough to record a total amplitude of only 45 min of eye rotation.

The "physiological nystagmus" in these cats, of which a typical record is shown in Fig. 2, was at times indistinguishable from that of man (see Fig. 1). The fine tremor varied in frequency from 35–65 cps, averaging 50 cps, and in amplitude from 4–52 sec of arc, averaging 22 sec. The tremors in the two eyes were not synchronous, which agrees with the findings of Riggs and Ratliff[8] for man. The cats had far fewer and somewhat smaller saccades than are usually found in man. Some saccades were binocular, but most were uniocular. This contrasts with man, in whom all but a few of the saccades are binocular.[6] However, it may be questioned whether the physiological nystagmus obtained with the cats so prepared is truly physiological.

Effect of Detaching Muscles

Records of the movement of the detached inferior oblique muscle indicated that there usually was no measurable tremor present. However occasionally a tremor, sometimes associated with changes in the length of the muscle, was recorded having a frequency of 6–20 cps, averaging about 10 cps, and an amplitude which varied from 7–18 sec of arc-equivalent eye rotation, averaging 10 sec (Fig. 3). When larger contractions of the muscle were not too rapid, they could be resolved into small steps of about 10 cps frequency. This steplike character could also sometimes be detected in the tremor.

Records of eye movement made after detaching the inferior oblique muscle from the globe were almost identical in amplitude, frequency, and general appearance to those made prior to detachment, indicating that this muscle makes little contribution to the horizontal component of physiological nystagmus in the cat.

Eye movements recorded after detaching all the extraocular muscles except the retractor bulbi and medial rectus still showed considerable physiological nystagmus, including some small saccades. When the medial rectus was detached, some tremor remained,

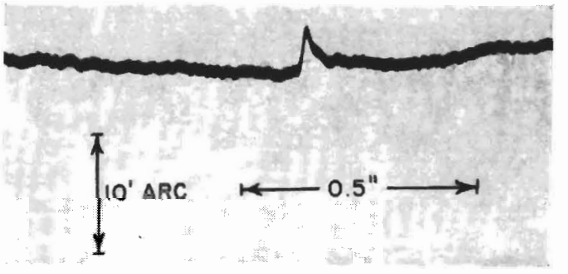

FIG. 2. Physiological nystagmus in cat. A typical cat saccade is shown, as well as tremor. The mean frequency of the tremor here was 56 cps; mean amplitude was 21 sec.

[8] L. A. Riggs and F. Ratliff, Science **114**, 17–18 (1951).

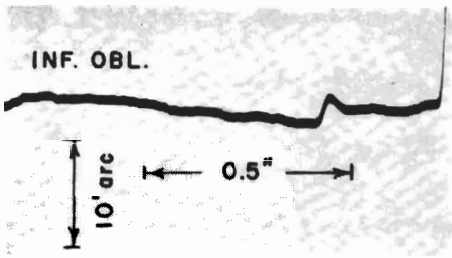

FIG. 3. Movement of the detached inferior oblique muscle in cat. The vertical arrow represents the eye rotation which would occur if the effective contact of the tendon were tangent to the globe.

although saccades were not found. This was not an artifact, since retrobulbar injection of procaine abolished all tremor.

The principal source of the horizontal component of physiological nystagmus in the cat is thus in the medial and lateral rectus muscles. A lesser contribution is made by the four small muscles which comprise the retractor bulbi, whereas the inferior and superior obliques make a negligible contribution.

Effect of Drugs

Nembutal

Preliminary studies of cats under Nembutal anesthesia, intraperitoneally injected and without *encéphale isolé*, had shown that physiological nystagmus was absent, but it gradually appeared as anesthesia became less deep. However, even when cats were kept warm they usually showed slight shiver during lightened anesthesia, causing the head to exhibit tremor. Such shiver is difficult to avoid with barbituates, of which Nembutal is a form, because they affect the temperature control centers in the brain. Although the head tremor and eye tremor were not synchronous, we did not consider the results of such experiments to be adequate, on the grounds that the head tremor might induce an eye tremor even though an eye tremor might not normally exist. Yet, on several occasions head shiver was absent, and a few records showing only physiological nystagmus were obtained.

Curare

The reputed selective responsivity of the extraocular muscles to the paralyzing action of curare[9–12] led us to record physiological nystagmus under its influence. Intravenous injection of 100 units (u) of Squibb *d*-tubocurarine chloride in *encéphale isolé* cats at first increased the amplitude and, to a slight extent, the frequency of the tremor, but then both gradually decreased and disappeared in about 25 min, when all gross eye movement had ceased. As curare took effect, it is likely, after the brief initial stimulative phase lasting no more than 5 min, that individual motor units were progressively affected until, when paralysis was almost complete, only a few active motor units remained. As paralysis occurred, the eyes started to exhibit rhythmic movements which were synchronous with the pulse and as large as 2.5 min of arc in some preparations, although the average amplitude was nearer 1 min, as in Fig. 4.

The 100-u dosage of curare compares, according to standards recommended by the manufacturer, with 40–60 u used with general anesthetics in man to provide greater musclar relaxation during surgery, followed by an additional 20–30 u in 3–5 min and repeated later if necessary. The 100-u dose in the cat was sufficient to eliminate all large eye movements and ear twitches.

Other records were made after administering the same dosage per pound as recommended for humans. With 4 u of *d*-tubocurarine, a slight increase in tremor amplitude was observed after 5 min, but the amplitude and frequency were both considerably lower in another 3 min. The injection of another 4 u 15 min after the initial injection was insufficient to cause the tremor to disappear. Larger eye movements were also present, as were twitches of the pinna, resulting from gentle touching of hairs near the ear.

In humans intravenously injected curare is effective within 3 min, and its effect is of short duration—about 10 min. According to Roche,[9] even after a "completely paralyzing dose," a patient can walk unassisted 30 min afterwards. The usual dose to minimize voluntary ocular movement is 50 u, but doses as high as 140 u may be required. However, reflex eye movements still remain.

These findings with the cat cannot be directly compared with those in man, since physiological nystagmus is not a voluntary activity. Whether voluntary movement in the cat was minimized by a dose proportionate to that given man could not be determined. Reflex eye movements, as well as physiological nystagmus, were

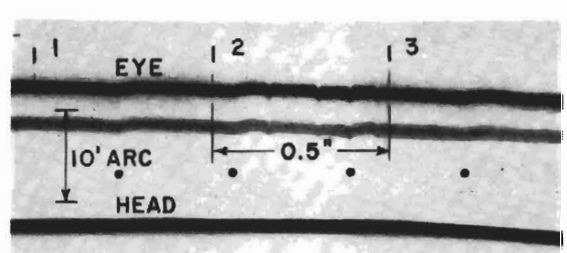

FIG. 4. Movement of a cat's eye 20 min after injection of 100 u of curare. The large eye movements had almost disappeared. Ignore the lower and fainter eye trace. Four real tremors can be seen in half-sec interval No. 2, but such tremors were then infrequent. The almost continuously present very fine vibration of the eye trace here is an artifact, since it persisted after death. The "pulse movements" of the eye are indicated by the dots and occurred 180 times per min. In this cat the pulse movements were smaller than usual.

[9] J. R. Roche, Am. J. Ophthalmol. **33**, 91–94 (1950).
[10] F. C. Cordes and R. S. Mullen, Am. J. Ophthalmol. **34**, 557–564 (1951).
[11] Drucker, Sadove, and Unna, Am. J. Ophthalmol. **34**, 543–553 (1951).
[12] H. Farquharson, Am. J. Ophthalmol. **34**, 554–555 (1951).

still present in the cat, even though their activity was reduced. Total loss of physiological nystagmus required much larger doses. However, these findings are not inconsistent with those reported by Cogan[13] and Gifford.[14] Gifford, working on rabbits, found when adminstering curare by retrobulbar injection and using the retraction syndrome as a measure of reflex activity, that it required very close to a lethal dose for loss of reflex activity. Cogan also found, with orbital injection, that the dose required for paralysis was almost lethal. However, orbital adminstration is criticized by Roche[9] on the grounds that it is no more effective than intravenous injection, since curare must reach its site of action by diffusion from the blood stream. Intravenous injection is said to be safer because diffusion is quicker and dosage can more easily be controlled.

Since the classical experiments of Claude Bernard over 100 years ago, it has been known that curare produces a highly selective paralysis of the motor endplates in skeletal muscle.[15] Confirmation has come from recent microelectrode recording of potentials in cats, demonstrating that curare depolarizes the endplate, which becomes unresponsive to incoming stimuli while the electrical excitability of the muscle fiber remains unchanged.[16] Hence, on the basis of our experiments, tremor of the extraocular muscles appears to be mediated by efferent neural stimulation and is not a property of unstimulated muscle fibers.

Neostigmine

Subcutaneous injection of 2.5 mg of neostigmine in previously nondrugged *encéphale isolé* cats increased the mean amplitude of the physiological nystagmus to 1.8 of that usually found, and decreased the mean frequency to 0.6 normal (Fig. 5). There was an increase in the frequency of what appeared to be saccades. Neostigmine increases the end-plate potentials and therefore reduces the threshold for muscle-fiber activity.[16] This experiment also demonstrates that physiological nystagmus is mediated by efferent neural stimulation.

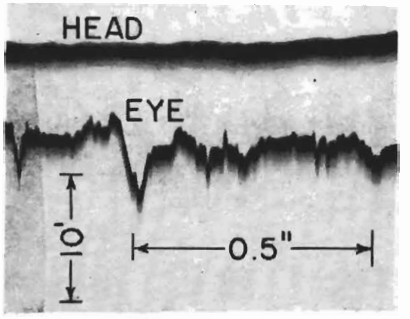

FIG. 5. Movement of a cat's eye 33 min after injection of neostigmine. A similar record was obtained 45 min later.

[13] D. G. Cogan, Am. J. Ophthalmol. **33**, 95 (1950).
[14] H. Gifford, Am. J. Ophthalmol. **33**, 95 (1950).
[15] L. S. Goodman and A. Gilman, *Pharmacological Basis of Therapeutics* (The Macmillan Company, New York, 1955).
[16] I. A. Boyd and A. R. Martin, J. Physiol. (London) **132**, 61–91 (1956).

Hypotheses

The preceding findings are consistent with the following hypotheses: (1) that the fine ocular tremor represents a continuous variation of the total activity of the acting individual motor units of the extraocular muscles, mediated by efferent neural stimulation; (2) that the normal tonus of these muscles effectively damps potential pulse movement; and (3) that the saccades originate, at least in part, in the binocular motor areas, whereas the fine tremor is entirely peripheral to binocular control.

Tremor in Other Muscle Systems

Records of the movements of the pinna of the cat's ear showed occasional tremor, with a frequency of about 20 cps (Fig. 6).

Records of the movements of the right index finger of apparently healthy men of ages 21–24 showed tremor of about 30 cps during pointing (Fig. 7), with an amplitude of 5 sec to 1.5 min, averaging 33 sec. Tremors larger than 15 sec occurred at a rate of about 18 cps. Halliday and Redfearn[17] also found finger tremor. Using a frequency analyzer, they concluded that muscle energy was fed to the finger at 5–15 cps, with a peak amplitude of about 10 cps. The higher frequency which we find, probably results from the greater sensitivity of our experimental method. Since a frequency analysis has not been made with our records, we do not know at what frequency the energy peak occurs.

There was no similar fine tremor of the elbow (Fig. 8), although small undulations of up to 10 cps could be seen in the trace. Even if tremor were present in those muscles maintaining the position of the elbow, the heavier mass of the arm as compared with the finger would help to dampen its effect.

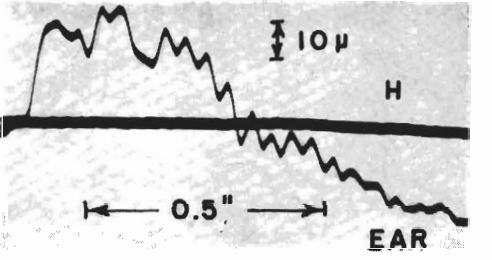

FIG. 6. Movement of the pinna of a cat's ear. Trace *H* indicates head movement. The vertical arrow indicates the movement of the trace produce by a 10 μ movement of the tip of the pinna.

[17] A. M. Halliday and J. W. T. Redfearn, J. Physiol. (London) **134**, 600–611 (1956).

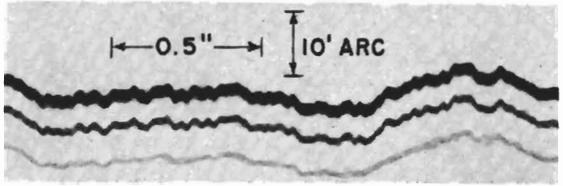

FIG. 7. Movement of the pointing right index finger in man. The record shows three traces because of unscreened multiple reflections from the light source used for the optical lever. The tremor frequency here was about 25 cps.

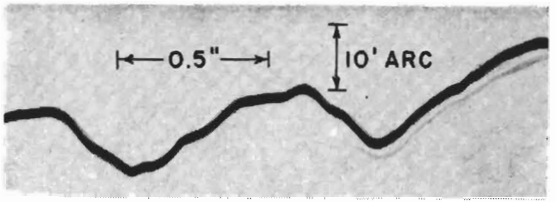

FIG. 8. Movement of the positioned elbow in man. The same subject was used as for Fig. 7.

Significance to Vision

Does physiological nystagmus have a value, or is it simply a useless and perhaps undesirable byproduct of the ocular motility apparatus? Both viewpoints have been held, but majority opinion is that it is helpful. Research has indicated that it helps to prevent the fading away of detailed vision which occurs when the retinal image is optically immobilized,[18–20] although it can reduce resolution.[21] Some proposals[22,23] have suggested that physiological nystagmus is utilized by the visual apparatus so as to improve certain forms of acuity beyond that explainable by the anatomy of the retina alone; e.g., vernier thresholds of 2 sec of arc can be reached even though the smallest foveal cones are many times that large.

The existence of physiological nystagmus in the cat suggests that it may be inevitable in animals with good ocular motility. This, however, does not say whether or not it is valuable in vision. Since cats are believed to have relatively poor resolution acuity ($\frac{1}{5}$ that of man[24]), there is no support for the extreme idea that it is a mechanism devised especially to obtain even better performance from an otherwise maximally developed visual discrimination apparatus.

ACKNOWLEDGMENTS

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[19] R. W. Ditchburn and B. L. Ginsborg, Nature **170**, 36–37 (1952).

[20] Riggs, Ratliff, Cornsweet, and Cornsweet, J. Opt. Soc. Am. **43**, 495–501 (1953).

[21] F. Ratliff, J. Exptl. Psychol. **43**, 163–172 (1952).

[22] E. Hering, Ber. math.-phys. Classe Königl. Sächs. Gesellschaft der Wissenschaften zu Leipzig, naturw. Teil, 16–24 (1899). Reprinted in *Wissenschaftliche Abhandlung von Ewald Hering* (Georg Thieme, Leipzig, 1931), Band 2.

[23] E. E. Andersen and F. W. Weymouth, Am. J. Physiol. **64**, 561–591 (1923).

[24] G. L. Walls, *The Vertebrate Eye* (Cranbrook Institute of Science, Bloomfield Hills, Michigan, 1942).