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SACCADES AND THE QUICK PHASE OF NYSTAGMUS

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ALTHOUGH seldom explicitly stated, it seems to be often assumed that the two forms of rapid eye movements, the saccade and the quick phase of vestibular nystagmus are identical (COHEN and SUZUKI, 1963; MACKENSEN and SCHUMACHER, 1960; REINHART and ZUBER, 1969; ROBINSON, 1968 and WESTHEIMER, 1954). This notion probably originates in the desire for the simplicity which results when it is assumed that both these movements are generated by the same rather than separate neural mechanisms. A search of the literature seems to indicate that this idea has not yet been substantiated by quantitative experimental results. Such results were not provided in the studies by COHEN and SUZUKI (1963), GOTO, TOKUMASI and COHEN (1965), PULEC (1968) and UEDA and SUZUKI (1965), to mention only a few. If saccades and the quick phase of nystagmus were distinctly different, that finding would considerably complicate our ideas of the organization of the oculomotor system.

For quick phases to be the same as saccades, the shape of their time courses and the relationship between their amplitude and duration should be the same. Such a quantitative comparison cannot be found in the literature. In fact, many of the quick phases in published records of nystagmus, elicited by various methods such as caloric or electrical stimulation, show little resemblance to saccades in their amplitude–duration relationship or the shape of their trajectories (COHEN and SUZUKI, 1963; PULEC, 1968 and YAMANAKA and BACH-Y-RITA, 1970). Consequently, the present study was undertaken to compare the shape and amplitude–duration relationship of saccades and quick phases of vestibular nystagmus in the alert monkey.

It has also been generally assumed that the time course of a quick phase of nystagmus was independent of the method by which it was induced and also independent of the nature of the visual surroundings. It turns out that these things make marked changes in the quick phase and saccadic time courses and this investigation also describes the nature and extent of these changes.

METHODS

Experiments were carried out on five monkeys. Under pentobarbital sodium anesthesia, each had chronically implanted in it a coil for recording eye movements, a crown to immobilize the head and a chamber through which stimulating electrodes could be lowered to the cerebellum and brain stem.

The coil of fine wire was implanted on the monkey's globe beneath Tenon's capsule and the four recti insertions. When used in conjunction with alternating magnetic fields, the coil provides an accurate method for recording vertical and horizontal eye movements with a sensitivity of 15′ arc and a bandwidth of 2 kHz. These techniques have been described in detail elsewhere (FUCHS and ROBINSON, 1966; ROBINSON, 1963). The

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crown was a light aluminum ring that encircled the calvarium and was fastened to it by eight stainless steel screws whose sharpened tips penetrated the upper table of the skull. The chamber was implanted over a trephine hole in the skull. The dura was left intact and electrodes or cannuli were passed into the brain within a sterile guard tube. The identification of stimulated sites was later verified by histological reconstruction (RON, 1971). The animals were supported post-operatively by chloramphenicol and penicillin.

All the experiments were done, in subsequent daily recording sessions, on the unanesthetized, alert animal. Normal saccades were studied by utilizing the spontaneous movements the alert animal made in looking about the laboratory (referred to as a structured visual field). Spontaneous saccades were also studied in total darkness and with an illuminated ganzfeld by placing a blank opaque surface just in front of the monkey's eyes. Saccades under these conditions were studied when the animal was kept alert by food and novel auditory stimuli (periods of ganzfeld and darkness were kept short to prevent loss of alertness) and also when alertness was allowed to decrease by periods of quiet when the animal appeared to be bored or drowsy.

Vestibular nystagmus induced by rotation was also studied under these three visual conditions. To obtain rotational nystagmus, the primate chair and eye movement measuring system were mounted so that the animal could be rotated in a horizontal plane. A potentiometer measured the angle of the head in space and the magnetic field eye monitor measured the angle of the eye in the head.

Vestibular nystagmus was artificially induced by electrical stimulation of the vestibular nuclei, injecting KCl into the flocculus, and caloric irrigation. Monopolar electrical stimulation was done with a cathodal train of constant current, 0·5 msec pulses at a frequency of 500/sec and a typical stimulus train length of 2 sec. About 40 sites were stimulated in the vestibular nuclei and vestibular nerve.

The method of cortical spreading depression (by injecting potassium chloride) has been used extensively to achieve temporary, functional elimination of certain parts of the central nervous system (MEGIRIAN and BUREš, 1970). Floccular spreading depression was caused by injecting 1–6 μl. of 25% KCl into the flocculus through a 25 gauge hypodermic tube. Nystagmus results presumably by depolarization of Purkinje fibers, projecting from the flocculus, causing disinhibition of the vestibular nucleus on that side. Subsequent histological reconstruction verified the location. These experiments were repeated three times (separated by intervals of at least one hour) at five different flocullar sites in one monkey.

To evoke caloric nystagmus, water at various temperatures (0°, 10° and 20°C) was injected in the right ear. Ten trials were made when both ears were irrigated: the right ear with cold water and the left ear with hot water (max. 58°C). A total of 26 caloric stimulation experiments were done on four monkeys.

All the data were recorded on a tape recorder, retrieved from the tape and printed by an ultraviolet mirror galvanometer direct writing recorder with a frequency response (−3 dB) of 1·9 kHz.

RESULTS

Alertness and visual field structure

Figure 1(a) shows some typical spontaneous saccades made by an alert monkey. The relationship between the amplitude and duration (A and D, Fig. 1(a)) of a saccade is well known for man (BECKER and FUCHS, 1969) and monkey (FUCHS, 1967). Our own data, which agrees with those of others, are shown in Fig. 2, curve S.F., for the typical juvenile rhesus monkey. We have adopted the attitude that any rapid eye movement which is not reasonably described by this curve is not "normal".

The velocity of saccades is evidently a sensitive index of alertness. As an animal becomes used to the experimental situation it soon becomes listless and if no attempt is made to interest it, it often falls asleep. Figure 1(b) shows examples of "saccades" made by a drowsy monkey whose eyes, however, are still open. They have been chosen as extreme examples to illustrate how slow the movements can become. A few more examples are shown by the data points in Fig. 2 marked *x*. They resemble many of the abnormal eye movements seen during REM sleep episodes in this animal by FUCHS and RON (1968). In intermediate states between alertness and drowsiness, less dramatic but statistically significant slowing of saccades occurs. We have not attempted to quantify this because we have no independent measure for alertness. In fact, saccadic eye velocity is probably a more sensitive measure of alertness than most other parameters commonly used. Whenever eye movements are analyzed from recording periods when little control over alertness was exercised, saccadic