FUNCTION OF THE PHASIC AND TONIC SYSTEMS OF THE OCULOMOTOR APPARATUS IN POST-ROTATORY AND OPTOKINETIC NYSTAGMUS

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The oculomotor apparatus (OMA), which assists the optic analyzer [3] in the course of its many different activities, constantly performs two essentially different functions: it facilitates fixation of the eye and its change from one object to another by means of various forms of muscular activity: first, by means of postural tone and relatively slow movements (movements of fusion or scanning movements), and second, by very rapid and brief movements (saccades). A high speed (short duration) of the saccades is an essential quality of these movements, because during their performance vision is interrupted [8]. The author's earlier investigations [4-6] revealed this dual function of the OMA in mammals, and the existence of highly specialized phasic and tonic systems resembling the homologous systems in the locomotor apparatus of amphibians [4-6].

These results, in agreement with morphological findings [10], have subsequently been fully confirmed [9].

It may be concluded from facts now established [6, 9] that all the slow movements of the eyes in mammals and, evidently, in man also are performed by a special tonic system, and the rapid movements by the phasic system of the OMA. However, more concrete information can be obtained only by experimental investigation of the working of the eye muscles responsible for the slow and rapid movements of the eyes. The activity of the phasic system of the OMA may be judged from the rapid biphasic action potentials of the mass of phasic fibers on the electromyogram (EMG), while the activity of the tonic system may be judged from the slow, monophasic potentials on the EMG – the potentials of the motor end-plates of the nonconducting tonic fibers [4, 5].

As the simplest forms of natural activity of the OMA, including both slow and rapid movements, post-rotatory and optokinetic nystagmus were selected.

These phenomena have already been investigated electromyographically, but with no attempt to analyze the forms of the potentials [7].

EXPERIMENTAL METHOD

Experiments [8] were carried out on unanesthetized rabbits with an intact brain. Under local anesthesia the lateral rectus muscle of one eye was dissected, needle electrodes were inserted into it (one into the belly, the other into the tendon) and the EMG was recorded. The investigated muscle worked in isometric conditions; it was periodically bathed with a warm mixture of mineral oil and paraffin.* At the same time, the electro-oculogram (EOG) was recorded by means of needle electrodes inserted into the skin near the "angle" of the opposite eye. The EMG and EOG were recorded on continuously moving film (at winding speeds of 3.3 and 8.35 cm/sec), which was then examined under an enlarger. The frequency characteristic curve of the cathode-ray oscillograph used in the experiments was linear within the range 1-3000 cps.

Post-rotatory (labyrinthine) nystagmus (LPN) was evoked by rotating the rabbits 10 times on a manual centrifuge in either direction (10 turns in 10-15 sec). Optokinetic nystagmus (OKN) was evoked by rotating

*In some experiments its contractions were recorded by an oscillograph using a piezocrystal.

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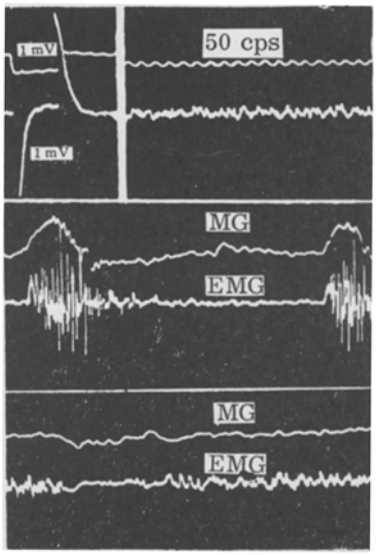

Fig. 1. Recordings of post-rotatory nystagmus of the lateral rectus muscle of a rabbit. MG(Mechanograms (recorded by means of a piezo-crystal); EMG) electromyograms. Top series) Calibration of amplitude of MG and EMG, time scale and background EMG; middle series) active work of the muscle in the rapid phase of nystagmus; bottom series) active work of the muscle in the slow phases of nystagmus.

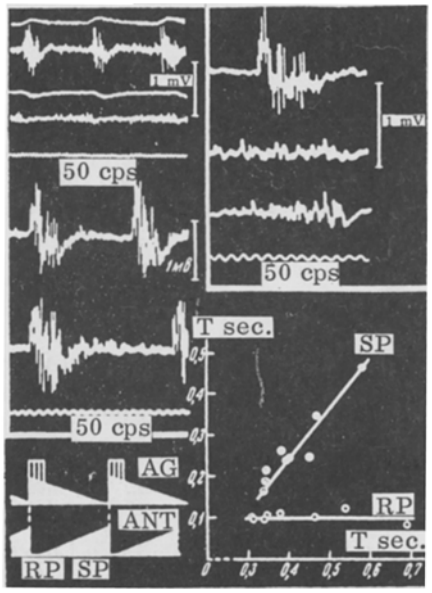

Fig. 2. Characteristics of labyrinthine post-rotatory nystagmus (LPN). On the left, from top to bottom) EOG and EMG of the lateral rectus muscle in the rapid phases of nystagmus; EOG and EMG of the same muscle in the slow phases of nystagmus in the opposite direction. Two examples of activity of the muscle in the rapid phases of nystagmus of different frequency (constant duration of the volleys of biphasic AP). Scheme of working of the phasic (shaded) and tonic (white portion) of the systems of the agonist (AG) and antagonist muscle (ANT) in the rapid phase (RP) and slow phase (SP) of LPN. On the right, from top to bottom) forms of the EMG of the rapid (top) and slow (2 bottom tracings) phases of nystagmus. Graphs showing the relationship between the duration of the SP and RP and the duration of the periods of nystagmus (T).

a "white" cylindrical screen with vertical black bands around the experimental animal. The visual angle of the bands was 4° and the distance between neighboring bands 20°; the velocity of rotation of the cylinder was 15 deg/sec; the duration of rotation was varied.

When defining the direction of nystagmus in the rapid phase, the investigated muscle will be called the agonist if it takes an active part in the rapid phase and an antagonist if it plays an active part in the slow phase of the nystagmus (in the opposite direction).

EXPERIMENTAL RESULTS

The rapid phase of nystagmus in the investigated muscle (as agonist) took the form of a relatively short "parcel" of rapid biphasic action potentials (AP), combined with a slight increase in the amplitude of the slow waves (mainly monophasic in form). During the subsequent slow phase, slow waves of diminishing amplitude and frequency were recorded (Figs. 1-3).

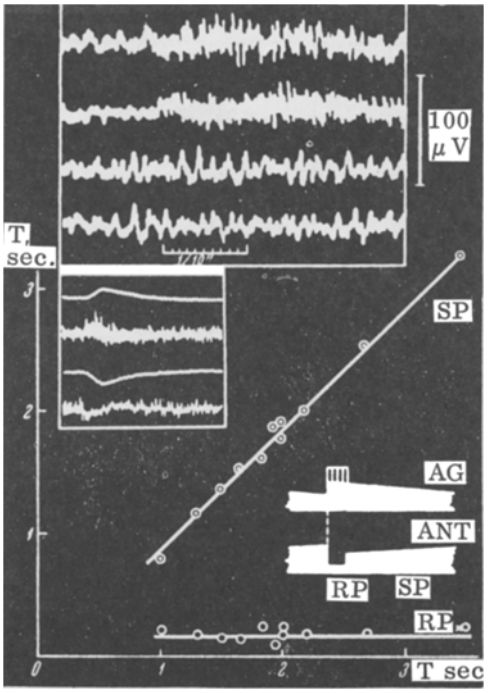

Fig. 3. Characteristics of optokinetic nystagmus (OKN). From top to bottom) EMG of the lateral rectus muscle during activity in the rapid phases of nystagmus (2 tracings) and the slow phases of nystagmus (the 2 bottom tracings); EOG and EMG of the same muscle in nystagmus in a different direction (fragments of a tracing during slow winding of the film). Scheme of working of the phasic (shaded) and tonic (white portion) systems in OKN. Graph showing the relationship between the durations of the RP and SP and the duration of the period of nystagmus (T).

When the investigated muscle worked as an antagonist, the rapid phase of nystagmus appeared as the more or less complete inhibition of electrical activity and the slow phase as a gradual increase in the amplitude and frequency of the slow monophasic potentials (Figs. 1-3). Judging by the shapes and the time parameters, the rapid biphasic waves must be taken as the AP of the muscle fibers of the phasic system and the slow, monophasic waves as the potentials of the fibers of the tonic system (see Figs. 1-3 and the table).

The rapid phase of nystagmus is thus brought about by the combined work of the phasic and tonic systems (agonist muscles). This dual mechanism is fully justified: the phasic system gives the movement its speed, while the tonic system provides for maintenance of the position achieved as the starting point for the subsequent slow movement in the opposite direction.

The slow phase of nystagmus is performed mainly by the tonic system of ocular muscles, the activity of which in the agonist and antagonist changes in opposite directions (Figs. 2 and 3). Similar conclusions may evidently be made from examination of certain EMG tracings of human ocular muscles presented in the literature without analysis [7].

The schemes of the relationships between the activity of the phasic and tonic systems in the forms of nystagmus studied in these experiments are shown in Figs. 2 and 3.

The results showed that the durations of the rapid phases of nystagmus – the saccades (in contrast to the durations of the slow phases) were not clearly correlated with the durations of the nystagmic periods, but were approximately constant during phasic volleys of different strengths (saccades; see Figs. 2 and 3). This fact evidently indicates the existence of special mechanisms for limiting the duration of the saccade (as a factor obliterating the image on the retina and disturbing vision).

The limitation of the duration of the saccade explains the direct relationship between the velocity of the saccade and its amplitude, which has been known for some time [8].

The investigated LPN and OKN were identical in all these respects.

So far as differences in the investigated types of nystagmus in the conditions described above are concerned, the duration of the periods in LPN was much shorter (the frequency was higher) than in OKN. The period in LPN increased as the nystagmus diminished (the frequency fell). The period (and frequency) of OKN, with a constant velocity of rotation of the "striped screen" varied about a constant level. The activity of the tonic system in the slow phases of LPN and OKN increased differently: in the slow phase of LPN almost uniformly, but in the slow phase of OKN (in a scanning movement), at first rapidly, and then very slowly (see Figs. 1 and 2, schemes). A slight difference was found in the mean durations of the rapid phases of LPN and OKN and in the mean durations of the slow waves in the EMG during LPN and OKN (see the table), but these differences were not statistically significant within the range of the material obtained. The observed differences between LPN and OKN are reminiscent of the similar slight variants of "anesthetic" nystagmus, reported in the literature [2].

Characteristics of Investigated Forms of Nystagmus of the Lateral Rectus Muscle of the Eye

Parameter	Labyrinthine post-rotatory nystagmus	Optokinetic nystagmus
Duration of period (T; in sec)	0.3-0.7	1-4.9
Duration of rapid phase (t_r; in sec)	0.09 ± 0.01 (0.064-0.121)	0.14 ± 0.03 (0.067-0.293)
Coefficient of correlation between t_r and T	−0.19	+0.25
Duration of slow phase (t_s; in sec)	0.2-0.6	0.8-4.7
Coefficient of correlation between t_s and T	+0.93	+0.99
Duration of biphasic AP in the rapid phase (in msec)	No more than 3 (in both phases)	Not more than 3 (in both phases)
Duration of monophasic potentials in the slow phase (in msec)	10 ± 1 (7-14)	13 ± 1 (9-17)

Note: With intracellular recording the duration of the AP of the phasic fibers of the ocular muscles was 2-3 msec, the duration of the potentials of the excited tonic fibers (potential of the motor end-plate) 10-20 msec [4, 5].

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