TONIC REFLEX IN OCULAR MUSCLES ON RHYTHMIC ELECTRICAL STIMULATION OF VESTIBULAR RECEPTORS

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It was found in an earlier investigation that horizontal nystagmus could be produced by rhythmic electrical stimulation of the ampulla of a horizontal semicircular canal. The rapid and slow components of the nystagmus were differently affected by the rate of stimulation, or in other words, the afferent flow [3]. A natural inference was that a "pure" labyrinthine, tonic reflex would be dependent on afferent flow in much the same way as the slow (tonic) component of nystagmus.

The aim of this investigation was to produce a tonic labyrinthine reflex in the eye muscles by rhythmic electrical stimulation of receptor formations in one vestibule and to determine the nature of the relationship between the reflex and the frequency of stimulation.

EXPERIMENTAL

Receptors in the vestibule of one labyrinth were stimulated with rectangular pulses in a series of acute experiments on six rabbits. A bipolar electrode was inserted into the vestibule through the horizontal semicircular canal and its ampulla (the method has been described earlier [3]). Stimulation was only effected when there was no nystagmus. Pulse length was 0·2 msec, the rate was 10-90 cps and the series lasted from 1 to 20 sec. The rate of stimulation was kept constant throughout a series. The animal was in a prone position, its head was fixed relative to its body and the mouth was horizontal. Eye movements on the side opposite to that of the stimulate labyrinth were recorded by a photonystagmograph [1, 2]. A horizontal strip of white paper was applied to the anesthetized cornea to give better contrast. The animals were killed with an electric current at the end of an experiment, and the positions of the electrodes were determined by examination under an operating microscope (this in three animals; in the others the electrode was withdrawn from the vestibule for stimulation of the ampulla).

RESULTS

Rhythmic electrical stimulation of one vestibule regularly produced conjugate movements of both eyes in the frontal plane. The eye on the side of stimulation was turned upwards and that on the opposite side, downwards. The movement developed after a latent period of 30-400 msec. The longest latent period was associated with the lowest rate of stimulation producing distinct vertical movements of the eyes—a rate of 20 cps. The amplitude of the movement increased as the rate of stimulation increased (Figs. 1 and 2).

With low rates of stimulation, the amplitude of movement remained constant during the period of stimulation (Fig. 1I). With rates of 80 and 90 cps, the eye oscillated gently in its new position (Fig. 1IV). The rapidity of the eye movement depended on the rate of stimulation, increasing as the rate increased (Fig. 3). The rate at which the eye returned to its original position, which it did as soon as stimulation ended, was always greater than the speed of deviation, increasing with increase of amplitude. When the eye returned to its original position some degree of overcorrection (the eye passing beyond its zero level) was observed in most cases (Fig. 1III and IV). The eye then

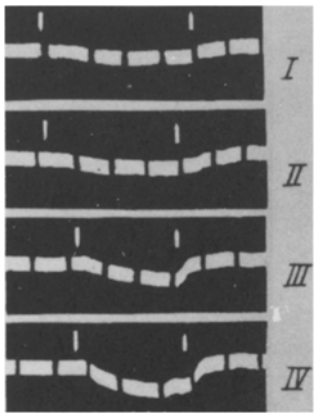

Fig. 1. Vertical deviation of eye on intact side on rhythmic electrical stimulation of vestibular receptors. Arrows indicate beginning and end of stimulation. Time (vertical bands) 500 msec. Stimulation rates: I) 30 cps, II) 50 cps, III) 70 cps, IV) 90 cps.

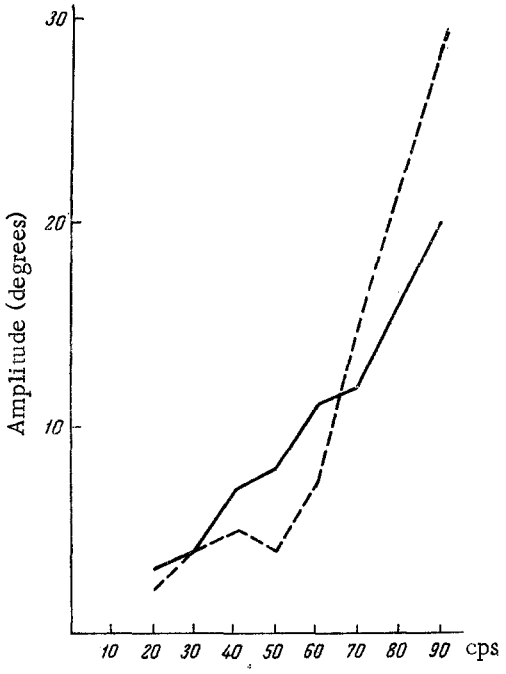

Fig. 2. Amplitude of vertical deviation of eye in relation to rate of stimulation. Abscissa) rate (cps); ordinate) amplitude (degrees). Voltage on electrode: interrupted line) 40 V; continuous line) 30 V. Interelectrode resistance) 3 MΩ.

returned to its original position, possibly with some slight oscillations, in the course of 1-1 1/2 sec. Contractions of cervical muscles, in addition to the eye reflex, were seen with stimulation rates of 90 cps. Stimulation at 10 cps failed to produce a distinct reflex. Reversal of the poles of the electrode had no effect on the results. The tip of the electrode was afterwards found to be in the vestibule, at the level of the utricle.

On this evidence it was reasonable to regard the tonic movement of the eyes, in response to local rhythmic stimulation of receptors in the vestibule, as the result of a difference in the afferent impulse activity reaching the two vestibules: on the side there was a synchronous afferent flow, produced by pulses between the poles of the electrode in the labyrinthine fluid, and on the other, spontaneous afferent impulse activity from receptors in the intact vestibule. The afferent flow on the side of stimulation was composed of spontaneous activity with its natural frequency and stimulation of known frequency. This view is supported by the fact that the eyes resumed their normal positions in the intervals between stimulations, which meant that the actual introduction of the electrode did not produce any significant disturbance of the balance between tonic influences in the two vestibules. The tonic reflex would then naturally be more intense, the higher the rate of stimulation, as this meant a greater afferent flow. Conditions in these experiments could be compared with those prevailing when there is loss of one labyrinth. When impulse activity in one labyrinth is eliminated (or at least greatly reduced) by poisoning or removal, the tonic influence of the other labyrinth was then predominant. Consequently, the eye on the side of the lesion deviated downwards, and the other upwards. When the head is inclined to the side of the intact labyrinth, the degree of deviation of the eyes increases with increase of the angle of inclination [5]. In the present experiments one of the labyrinths had a constant level of spontaneous impulse activity (which could be compared to the zero level on the side of loss). The level of afferent activity in the other (stimulated) labyrinth was higher, and it could be compared to the afferent activity in the intact labyrinth of the unilaterally labyrinthectomized animal. An increase in the rate of stimulation produced an effect similar to that observed in a unilaterally labyrinthectomized animal when the head was inclined to the intact side.

The essential difference between this type of experiment and experiments in which one labyrinth was inactive or removed was that, in our case, the levels of afferent impulse activity were different only for receptors in the vestibule and only during periods of stimulation. Consequently, a tonic reflex could be produced in "pure" form, while the eye remained in the normal position in the intervals between stimulations. The local nature of the stimulation is proved by the fact that the tonic reflex was replaced by horizontal nystagmus when the electrode was withdrawn from the vestibule into the ampulla of the horizontal semicircular canal. The latent period in our experiments was about the same as that observed on direct mechanical stimulation

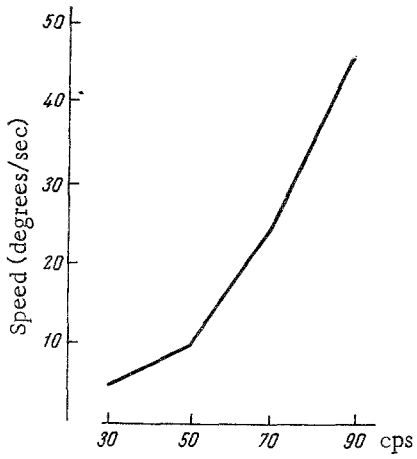

Fig. 3. Speed of deviation of eye in relation to rate of stimulation. Abscissa) rate (cps); ordinate) speed (degrees/sec).

of vestibular receptors in the cat [6]. The absence of a reflex when the stimulation rate was 10 cps can be explained by the fact that, if effect summation is to occur, the intervals between successive pulses should not exceed a few tens of milliseconds [4].

Opinions differ as to the nature of the vestibular receptor responsible for tonic vertical deviation of the eyes. Some authors are of the opinion that it is a reflex from the sacculus [5], while others [4] doubt if there is any strict specificity of individual vestibular receptors. If the position of the electrode in these experiments is any guide, the vertical tonic deviation of the eye was the result of stimulation of the utricle. The tonic vestibular eye reflex is effected over a three-neuron arc, like the slow component of horizontal nystagmus. The relationship the reflex bears to the frequency of stimulation, like the similar relationship demonstrated previously between the slow (tonic) component of horizontal nystagmus and the rate of stimulation [3], is ultimately referable to the level of afferent impulse activity.

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