THE RATE OF THE RAPID NYSTAGMUS MOVEMENT DURING RHYTHMICAL ELECTRICAL STIMULATION OF THE AMPULLARY RECEPTOR (RELATION BETWEEN THE RAPID COMPONENT AND THE VESTIBULAR APPARATUS)

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M. M. Levashov

Laboratory of the Physiology of the Auditory Analyzer (Head, Professor G. V. Gershuni),
I. P. Pavlov Institute of Physiology (Director, Academician V. N. Chernigovskii)
AN SSSR, Leningrad
Presented by Academician V. N. Chernigovskii
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At present there is no agreed opinion as to whether the rapid component in vestibular nystagmus is anything more than a compensatory eye movement which depends entirely upon the slow component, or whether there is a direct relationship between the rapid component and the vestibular apparatus. We have found that during nystagmus the rate of the rapid component reaches its maximum value earlier than does the rate of the slow component, after which a period follows in which the rate of the rapid component is reduced. The minimum rates of the rapid component occur at the same time as the maximum velocities of the slow component (Fig. 1A). Later, when the rate of the slow component has fallen the rate of the rapid component has again increased. These effects were found to occur regularly and at corresponding times in various animals.

The idea has been put forward that these changes might be related to a system having characteristic temporal characteristics, i.e., related to the ampullary apparatus whose action resembles that of a damped torsion pendulum [11, 12, 14]. If we suppose that the rate of the rapid component is to some extent determined by the position of the cupula, then this rate should depend on the flow of afferent impulses from this receptor. There is electrophysiological evidence that the deflection of the cupula is associated with a change in the frequency of afferent impulses [7]. The frequency of the impulses is proportional to the angle of deviation of the cupula [13]. Thus, in the flow of afferent impulses induced by a postrotational ampullipetal displacement of the cupula there will be a single maximum. We may suppose that this highest frequency itself corresponds to the greatest rate of the slow component. The rate of the rapid component during the same period is twice as great. On this account the idea was put forward that there is an optimal frequency for the rapid component, i.e., a frequency which evokes a rapid component of maximum rate. If this optimal frequency is less than the greatest frequency of the range generated by the receptor, then in the post rotational flow of afferent impulses it should be observed twice: once in the period before the maximum deviation of the cupula, and once in the period of return of the cupula to the original position. The rate of the rapid component at a frequency greater than the optimal frequency should be reduced.

The object of the present investigation was to confirm this theory experimentally. We have attempted to determine whether the rapid component depends upon the frequency of afferent impulsation, and if there is such a dependence to find whether there is an optimal frequency for the rapid component.

EXPERIMENTAL METHOD

We carried out 12 acute experiments on adult rabbits. The animal was fixed to a stand with a special head-holder, and a fenestration of the horizontal semicircular canal was performed under amytal and local novocaine anaesthesia. A bipolar electrode having an interelectrode separation of 0.1 mm was introduced into the canal in the

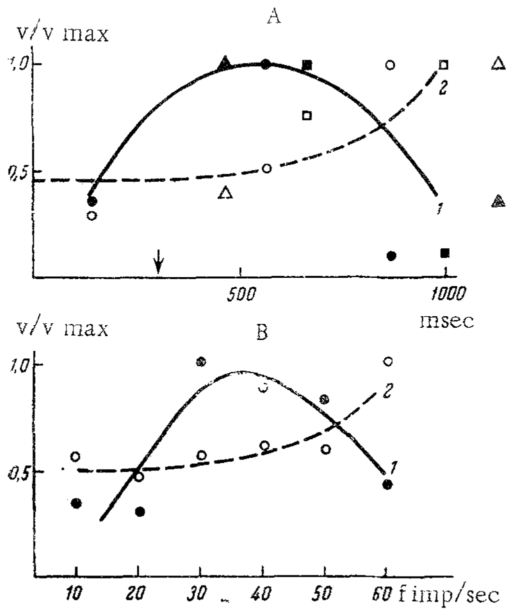

Fig. 1. Mean results of the rate of the rapid (1, black symbols) and of the slow components (2, light symbols) components of vestibular nystagmus after stimulation (A) and nystagmus during electrical stimulation (B), Square, triangle, circle—successive experiments on 1 animal. In both drawings the ordinate represents the ratio of the velocity of each of the components to the maximum velocity. Abscissa: A) time from start of nystagmus until the transiition of the slow component into the rapid component; B) frequency of stimulation.

direction of the ampulla. The experiment was started 5-7 h after the anaesthesia had been given, and after recovery from it. A volley of 0.2 msecond square-wave stimuli lasting 5 sec was applied via the electrode. We determined the minimum voltage necessary to elicit a nystagmus directed towards the side of the stimulated labyrinth. The frequency of impulses was 10, 20, 30, 40, 50, and 60 per sec. These frequencies were within the range corresponding to afferent impulsation in the ampullary nerve [8, 9]. The stimulation was repeated several times, and the sequence of frequency changes was random.

To record the nystagmus we used a photographic method [1]. Stimulation of the receptor is a "release mechanism" of vestibular reflexes [5], and therefore, on the assumption that the nature of the stimulus will affect principally the initial part of the nystagmus reaction, in every case we made measurements on the first 2 nystagmic movements which immediately followed the onset of stimulation. After measurement of the actual velocities of both components we calculated their mean value for each frequency of stimulation in each experiment, and then expressed them in relative units. The results of the different experiments were then combined for a statistical evaluation [6].

EXPERIMENTAL RESULTS

After the action of the anaesthetic had worn off we observed a nystagmus which was due to trauma and was directed towards the side of the operated labyrinth. In clinical terms this would be called a "nystagmus of stimulation" (here and below the direction is described in terms of the rapid component). Later we observed a "deficit nystagmus" directed towards the intact side. In most of the experiments stimulation was applied after the nystagmus had ceased and when the eyes were motionless.

The results of the experiments are given in the table. Stimulation evoked a horizontal nystagmus directed towards the stimulated labyrinth (animals Nos. 1-8). The latent period varied between 0.3 and 3 sec. Sometimes the stimulation caused only 2-3 nystagmic movements, but in most cases the nystagmus lasted throughout the whole period of stimulation and continued for from 1-2 sec to 1 min. If stimulation was applied during a nystagmus already present the nature of the nystagmus was altered, both components being affected (animal No. 10). The "deficit nystagmus" was inhibited by stimulation, and in some cases its direction was changed (animals Nos. 11 and 12). After the end of stimulation the "deficit nystagmus" was renewed in the original direction. In one experiment (animal No. 9) stimulation evoked an irregular deviation upwards of the eye on the stimulated side, while the opposite eye deviated downwards. This effect appeared to be the result of stimulation of vestibular receptors resulting from excessively deep implantation of the electrode.

The results given in the Table indicate that in experiments in which the nystagmic reactions were present over the whole frequency range of stimulation (or over most of it) there was an optimal frequency for the rapid component (animals No 1-7, and 10). Figure 1 shows the result of an experiment which may be considered typical. It gives the results of the measurement of the nystagmus after-effect from its onset until the slow component attained its maximum value (A); it also shows the rates of both components for various frequencies of stimulation (B). In this experiment the optimum frequency is that which elicits the maximum velocity of the rapid component (30 impulses/sec). The difference is significant at frequencies of 20 and 30 impulses/sec, and even for frequencies of 30 and 60 impulses/sec ($P < 0.02$). The velocity of the slow component was increased with increase of frequency of stimulation.

The difference in the optimal frequencies in the different experiments may be attributed to the level of the innate or "residual" [4] impulsation in the ampullary nerve at the moment of stimulation. The minimum optimal frequency occurred in the experiment with animal No. 10, when there was enhanced activity, as shown by the direction

Results of Experiments with Rhythmical Electrical Stimulation of the Ampullary Receptor of the Horizontal Canal

Animal	Initial nystagmus	Effect of rhythmical electrical stimulation	Frequency (impulses/sec) which produce the effect	Optimal frequency (impulses/sec)*
1	none	Horizontal nystagmus directed towards the stimulated labyrinth at all frequencies of stimulation (or at some frequencies)	10-60	30
2	"		10-60	30
3	"		10-50	30
4	"		20-50	30
5	"		10-50	30
6	"		20-50	40
7	"		10-60	50
8	"		30 and 40	—
9	"	Vertical ocular deviation	10-60	—
10	Directed towards the operated side	Change in rate of both components	10-50	20
11	Directed towards the intact labyrinth	Inhibition of nystagmus (sometimes to complete cessation). In certain cases nystagmus towards stimulated labyrinth.	Most marked at 30 and at 40	—
12				—

* The optimal frequency is designated as that at which the rate of the rapid component evoked by stimulation was greater than at adjacent frequencies in the range (lower and higher frequencies). The — sign indicates experiments in which no optimal frequency was found.

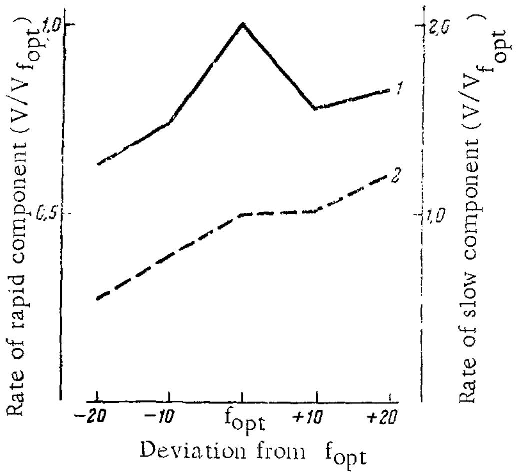

Fig. 2. Mean results giving the relationship of (1) the rapid and (2) the slow components of nystagmus to the frequency of electrical stimulation of the ampullary apparatus (rabbits Nos. 1-7, 10). Abscissa - frequency of stimulation in relative units; frequency measured as deviation from optimal frequency f_{opt}. Ordinate - ratio of rapid to slow components.

of the initial nystagmus. In 2 experiments in addition to an increase in the speed of the rapid component which occurred in the middle of the stimulus-frequency range we also found an increase in velocity in the case of the highest stimulus-frequency value used in the experiment.

Figure 2 shows the lumped results of 8 experiments in which there was an optimal frequency for the rapid component. The rates are given in relative units. In contrast to Fig. 1 the velocities at the optimal frequency in each experiment are taken as the unit for the rapid and for the slow component. The difference between the optimal frequencies in the different experiments is eliminated by the use of a common abscissa in which the middle of the frequency range is the optimal frequency. The mean difference in the velocities in the rapid component and the optimal frequency and at the 2 adjacent frequencies differing by 10 impulses per sec is statistically significant ($P < 0.05$ and is less than 0.01). In the curve of the velocity of the slow component the mean difference in the levels for the least and optimal frequencies is significant ($P < 0.02$).

In our use of electrical stimulation we were guided by the idea that although the labyrinth and cupula did not remain intact during introduction of the electrode the nervous terminations of the ampullary nerve remained sensitive to the stimulus from the electrode immersed in the fluid of the labyrinth; subsequent microscopic observation showed that the cupula was in no way damaged. As a result of stimulation of the ampullary nerve a discharge of impulses synchronous with the stimulus frequency should be generated. In other words the experiment may be regarded as a close model of afferent stimulation from the ampullary nerve induced by varying degrees of displacement of the cupula.

Of course this is only a rough approximation. We may note that the chief difference between our model and the normal functioning of the receptor is that in a normal ampulla the mechanism operates by virtue of impulses at different requencies. In our experiment we used only a single frequency. However, the model has supplied the answer to the problem to be investigated. The rate of the rapid component depends upon the frequency of the afferent impulses, and the relationship is more complex than in the case of the slow component.

Results obtained in the present investigation agree with those obtained by I. V. Orlov [2, 3] which indicated that the contralateral and ipsilateral neck muscles of the pigeon were related in different ways to the frequency of labyrinthine electrical stimulation.

It is widely known that there is a difference in the optimum frequencies. It seems to us that the fact of principal importance is not so much the existence of a frequency optimum so much as that the relationship is different for the slow and the rapid components: whereas the speed of the slow component increases with increase of frequency,for the rapid component there is a frequency optimum which elicits maximum velocity of movement. This last fact indicates that both components are directly linked with the vestibular apparatus but that the linkages are anatomically and functionally distinct.

SUMMARY

In acute experiments on rabbits nystagmus was induced by rhythmical electrical stimulation of the ampullary receptors. Square-wave stimuli at 10-60 impulses per sec were applied by means of a bipolar electrode inserted in the ampulla of the horizontal semicircular canal. The nystagmus was recorded by my own photographic method, and the results were analyzed statistically. The ratio of the speed of the fast and slow components of the nystagmus to the stimulus frequency was determined. It was found that for the fast component there was an optimum stimulus frequency. The speed of the slow component continued to increase with increase of frequency. The results are in line with data on the analysis of nystagmus following stimulation and show that there is a direct relationship between the rapid component of the nystagmus and the vestibular apparatus.

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