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Research Report

EFFECTS OF PROLONGED CALORIC STIMULATION UPON OCULOMOTOR, VESTIBULOSPINAL, AND SEGMENTAL SPINAL ACTIVITY*

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SUMMARY PAGE

THE PROBLEM

A disturbance of dynamic state of balance between the vestibular discharges from the two ears occurs during caloric stimulation of one ear as reflected objectively by the appearance of nystagmus. Clinical use of this phenomenon is limited to brief caloric stimulation, the effect of which is explained by convection currents in the endolymph, the nystagmic response being in agreement with predicted movements of that field. Prolonged caloric stimulation produces serial changes in direction of nystagmus. The object of this study is the analysis of the primary and secondary nystagmus produced by prolonged stimulation.

FINDINGS

The effects of prolonged caloric stimulation with hot (45° C) or ice water have been studied upon eye movements, vestibulospinal, and segmental spinal activity. The results obtained under this variety of test conditions demonstrate that continuous irrigation with water of extreme temperatures evokes, in addition to the effects upon the position of the cupula by endolymphatic convection currents according to the theory of Bárány, an initial excitatory thermal effect giving rise to an increased afferent firing which is followed by a paralyzing effect upon the vestibular sensori-neural structures. In order to localize more specifically the site of action of thermal stimulation, experiments were carried out upon labyrinthectomized squirrel monkeys and monkeys with the three semicircular canals plugged. These results, and those obtained by recording the cochlear microphonic and neural components to click stimulation during maximal cold and warm irrigation of the ear, indicate that the effect is upon the peripheral nerve fibers somewhere along their course from the ampulla to the internal auditory meatus. Earlier theories which have predicted this direct effect on the nerves are mentioned, but, for the present, without comment as to their respective importance in explaining paradoxical caloric reactions.

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INTRODUCTION

The vestibular organs initiate a considerable spontaneous neural discharge which is easily recorded from single primary neurons of amphibians and fish (22, 28), from cell bodies scattered along the vestibular portion of the eighth nerve or from primary neurons of the cat (13, 29), and from the vestibular nuclei of cats and rabbits (1, 9). This activity must be in appropriate functional balance between the two sides while the head is at rest. A disturbance of the dynamic state of balance occurs during caloric stimulation of one ear as reflected objectively by the appearance of nystagmus. The effect of brief caloric stimulation is explained by convection currents in the endolymph, the nystagmic response being in agreement with predicted movements of that fluid (3). It is interesting to note that prolonged irrigation produces a nystagmus which is directionally independent of head position and may be explained as an effect of thermal stimulation upon peripheral receptors and/or peripheral nerve fibers.

The present study is directed toward analysis of the primary and secondary nystagmus produced by prolonged caloric stimulation. Experimental findings currently available appear to be insufficient to permit a clear choice among several possible explanations for directional reversal of nystagmus. It is possible that several causes may be operative, depending upon the particular stimulus situation, and that only the end result, i.e. inversion of the nystagmus, is common to all conditions (7).

The effect of maximal cold and warm stimulation of the ear has been studied, not only by the primary test of recording eye movements, but also by recording cochlear activity in response to click stimulation (6, 11, 20), and vestibulospinal (14), and segmental spinal activity (15, 16, 21, 31, 32). The collective data obtained under this variety of test conditions have demonstrated that prolonged, extreme caloric stimulation, either hot or cold, initially evokes a powerful excitatory effect upon the peripheral labyrinthine structures and/or their nerve fibers and that this effect is superseded eventually by a strong depression.

APPARATUS AND PROCEDURE

Squirrel monkeys, securely fixed in a rigid holder, were used for recording the nystagmus evoked by prolonged caloric stimulation. Leads from electrodes placed on the skin at the outer canthus of each eye and on the crown at the midline of the skull were plugged into a two-channel Sanborn polygraph recorder. Ice water or water of about 45° C was used for caloric stimulation in total darkness. The temperature reading was obtained by measuring at the nozzle of the probe.

Cats under Nembutal anesthesia were used for recording the round-window response to single click stimulation before and after warm or cold water irrigation of the external auditory canal of the same ear. The recording electrode was a 38-gauge enamel-insulated silver wire with a saline-soaked wick at the tip. Acoustic clicks were produced by an Altec 802C high frequency driver-horn assembly to which pulses of 0.1 msec duration were fed from a Tektronix pulse generator and power amplifier. The horn was placed about 1 cm outside the external auditory canal after the external ear had been removed. The click stimuli were presented at the rate of one every two seconds. Cochlear potentials were amplified and displayed on a Tektronix type 555 dual-beam oscilloscope.

In another series of experiments on decerebrated cats, the peripheral branches of the left vestibular nerve were exposed and fitted with stimulating electrodes by a technique previously described (2). After immobilization with Flaxedil, single shock electrical stimuli, usually of 0.3 msec duration, were delivered at intervals of two seconds. The evoked vestibulospinal responses were recorded from ipsilateral lumbosacral ventral roots before, during, and after prolonged caloric stimulation.

The effect of hot and cold water irrigation of the external auditory canal on spinal segmental activity was studied on decerebrate cats placed in a symmetrical, sphinx-like position. A lumbar or sacral ventral root and its corresponding dorsal root, ipsilateral to the ear to be irrigated, were divided intradurally and placed on bipolar silver electrodes for recording and stimulating purposes, respectively.

RESULTS

THERMAL EFFECTS UPON VESTIBULAR ORGAN AND PERIPHERAL NERVOUS STRUCTURE

The effect upon eye movements of prolonged caloric stimulation with ice water is demonstrated in Figure 1 A-F. An unanesthetized squirrel monkey was tilted backwards to place the horizontal semicircular canals in optimal position. Ice water irrigation of the right (intact) ear was then begun. At the onset of irrigation, a nystagmus with quick phase to the left appeared (Figure 1 A). This is due to the well-known effect of endolymphatic convection currents acting upon the cupula. This follows Ewald's law; that is, because of the ampullofugal deviation of the cupula, the resting discharge from the right horizontal canal has diminished or stopped, while the resting discharge from the left persisted, the resultant being a leftward directed nystagmus. If the irrigation continues, this nystagmus may stop, but if so, it can be restarted immediately by a pinprick to the skin (Figure 1 B). As irrigation was continued, a stage was reached at which the same stimulus still reactivated the nystagmus, but only after a certain delay (Figure 1 C), and, still later, a stage when repeated pinpricks no longer produced the restarting effect at all (Figure 1 D). At this point, after 55 minutes of continuous irrigation, there is reason to believe that excitatory thermal effects were now acting directly upon the sensori-neural structures, thus setting off afferent firing which is independent of cupular position. An alternative hypothesis is that the entire labyrinth had been homogeneously cooled to the point that no convection currents could occur. This, in turn, allowed the cupula to return to its neutral position and the resting discharge to be resumed. Both hypotheses, because of the transient disappearance of nystagmus, must rest on an assumption of a resting discharge in

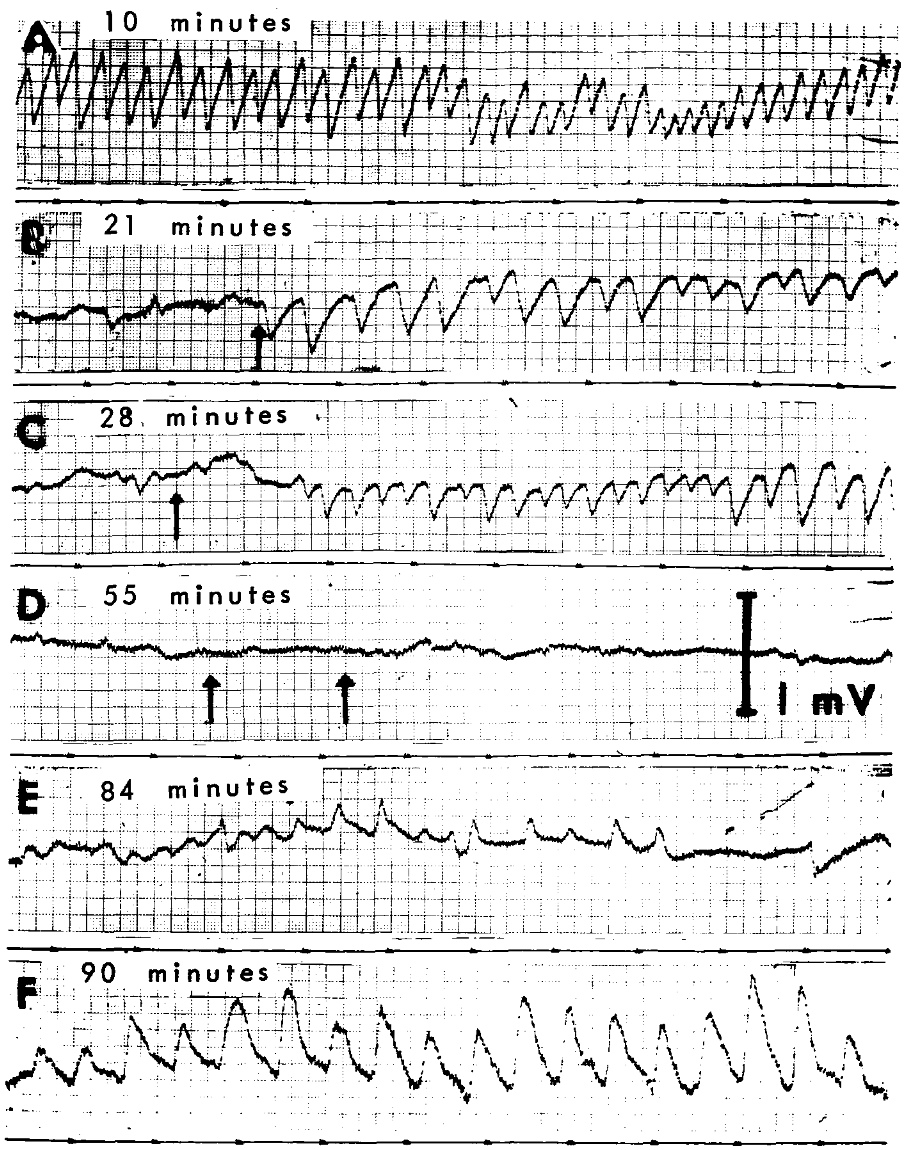

Figure 1

Squirrel monkey, labyrinths intact. Caloric stimulation, ice water, right ear. Downward deflection, nystagmus to the left; upward deflection, nystagmus to the right. Time scale in 1 second intervals. Arrows mark application of pin-prick to animal.

Note delay on onset of nystagmus in response to cutaneous stimulation (C). Note nystagmus to right (E) and strong nystagmus to right (F).

functional balance with that from the opposite ear. The effect of continuous ice water irrigation lends stronger support to the first hypothesis.

As the irrigation continued still further, a new phenomenon was added, namely, the appearance of a rightward directed nystagmus (Figure 1 E), and this reversal became clearly established in Figure 1 F. The presumptive explanation is that now the peripheral sensori-neural structures of the right ear were more powerfully excited by thermal stimulation, resulting in firing at a level distinctly higher than that of the resting discharge of the left ear. If the irrigation continued, the direction of the fast component would reverse once again (not illustrated), implying that cooling had progressed to the point of producing a paralyzing effect, allowing the resting activity of the left ear to regain the ascendancy to the extent of evoking a resumption of the leftward directed nystagmus.

It can be postulated from the foregoing results that three different effects of prolonged irrigation with ice water, as judged by the eye movements, are evoked in sequential fashion. These are: 1) the well-known effect of endolymphatic convection currents on the cupula, 2) an excitatory thermal effect on receptor cells and/or vestibular afferent fibers, and 3) an ultimate paralyzing effect upon the same structures. A further analysis of these events was attempted in the following series of experiments.

The effects of prolonged irrigation of the ear with hot water have also been studied on labyrinthectomized squirrel monkeys, and on monkeys in which the three semicircular canals had been plugged some months or weeks before testing. This is illustrated in the sequential nystagmograms in Figure 2 obtained from a monkey (whose three left canals had been plugged two weeks before) during a prolonged period of irrigation of the left ear. No nystagmus is seen during the first 12 minutes of irrigation, despite pinprick stimulation (Figure 2 A). The first sign of nystagmus appeared after 30 minutes of irrigation (Figure 2 B). Inasmuch as the plugging of the canals permits us to rule out influences of endolymphatic convection currents on the cupula, a likely explanation is that the horizontal nystagmus toward the left is due to an excitatory thermal effect on receptor cells and/or vestibular nerve fibers, especially those of the horizontal canal. As with ice water irrigation, the excitatory phase during prolonged warm water stimulation became gradually weaker (Figure 2 C, D, E, taken after 53, 57, and 102 minutes, respectively). In Figure 2 E, the firing rate of the left ear was presumably equal to that of the right side; consequently, the nystagmus ceased and did not reoccur in spite of multiple efforts to arouse the animal by pinpricks. In Figure 2 F, taken 103 minutes after the onset of irrigation, the nystagmus is reversed, i.e. to the right. Thus, as judged by the occurrence and direction of the nystagmus, the previous excitatory thermal effect was now superseded by a paralyzing or depressive effect upon the peripheral nervous structures; consequently, spontaneous firing from the opposite ear must gain unopposed command of the oculomotor activity.

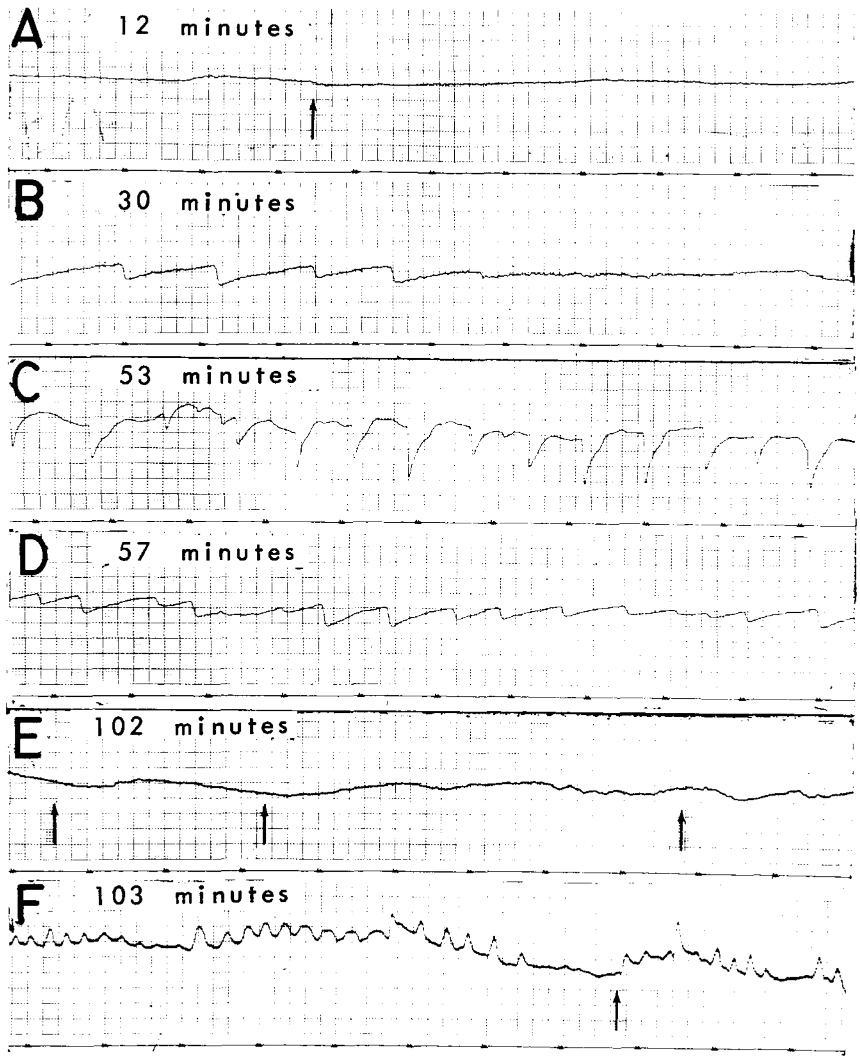

Figure 2

Squirrel monkey, left semicircular canals plugged. Caloric stimulation, hot water (45° C), left ear. Time scale in 1 second intervals. A - F = nystagmograms at the indicated intervals after the beginning of continuous irrigation. Arrows mark application of pinprick to the animal. Note reversal of nystagmus in F.

THERMAL EFFECTS UPON COCHLEAR RECEPTOR AND PERIPHERAL NERVE ACTIVITY

The cochlea and its nerve should be affected by thermal stimulation in a fashion similar to that of the vestibular organs and nerve fibers; therefore, it seemed reasonable to expect that a comparison of thermal effects on the two systems might add to the information on site of action of excitatory and paralyzing effects of hot or cold irrigation of the auditory canal. Moreover, the auditory system offers the additional advantage of a differential test of end organ as contrasted with cochlear nerve function, based on recording from a single electrode placement. Accordingly, responses to click stimulation were recorded from the round window before and after irrigation of the external auditory canal with ice water and with hot water. The response consists of three components, the aural microphonic, which is generated in the cochlea; and the two neural components, N_1 and N_2, which reflect action potentials of the cochlear nerve. The control response to single free-field click stimulation is shown in Figure 3 a. The stimulation was then stopped and the ear irrigated with ice water for 120 minutes. Following this period, resumption of stimulation and recording revealed that clicks now evoked responses showing a marked decline in amplitude and increase in latency of the N_1 and N_2 components while the microphonic component showed only slight change (Figure 3 b). The responses returned gradually to control values over a period of two to three hours (Figure 3 b - f). Figure 3 g shows a control response recorded just prior to a 120-minute irrigation of the ear with hot water. The end result was the same as that with ice water, as can be seen in Figure 3 h - l. In most cases of prolonged periods of warming, however, it was not feasible to achieve complete recovery of the response even though testing was continued over extended periods of time.

Although the foregoing experiments yield some information as to the general localization of thermal influences, the obvious drawback of not being able to follow continuously the effect of cooling and warming on the round-window response makes necessary a further experimental approach in the analysis of thermal stimulation.

THERMAL EFFECTS UPON EVOKED VESTIBULAR ACTIVITY

Single shocks applied to the vestibular nerve evoke responses which can be recorded from peripheral motor nerves or from spinal ventral roots. If the peripheral vestibular nerve fibers are exposed in the vestibule by a ventrolateral approach through the bulla, the external auditory canal remains intact, making it possible to record descending vestibulofugal reflex activity while the ear is continuously irrigated. Figure 4 a depicts a control response recorded from the ipsilateral L_7 ventral root, and Figure 4 b shows the increase in amplitude of the response after 80 minutes of ice water irrigation. In addition to the increase in size, there was a tendency to repetitive firing which followed the response proper. The paralyzing effect of prolonged cooling is shown in Figure 4 c, taken after 120 minutes of irrigation. Figure 4 d shows the response when threshold stimulation was applied to the vestibular nerve.

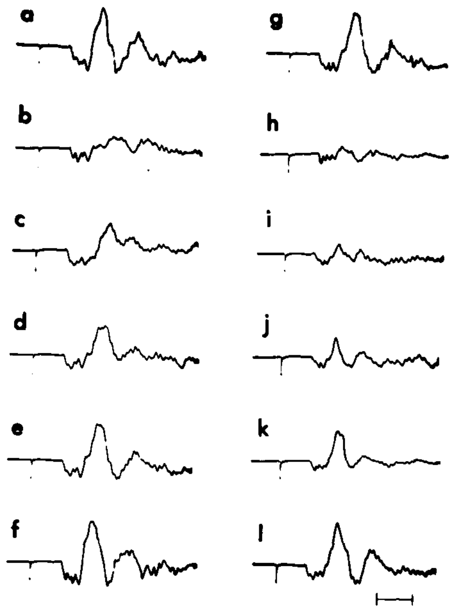

Figure 3

Cat, Nembutal. Responses to single click stimulation recorded from round window. Time scale = 1 msec.

a = Control response.
b = After 120 minutes of continuous ice water irrigation.
c = 35 minutes after irrigation discontinued.
d = 65 minutes after irrigation discontinued.
e = 95 minutes after irrigation discontinued.
f = 190 minutes after irrigation discontinued.

g = Control response.
h = After 120 minutes of continuous hot water (45° C) irrigation.
i = 40 minutes after irrigation discontinued.
j = 70 minutes after irrigation discontinued.
k = 115 minutes after irrigation discontinued.
l = 220 minutes after irrigation discontinued.

After 90 minutes of hot water irrigation, the response became clearly augmented (Figure 4 e) before continuous warming reduced its amplitude or abolished it (Figure 4 f).

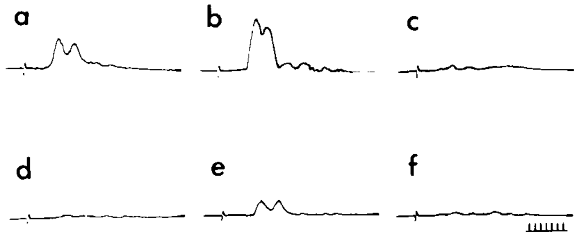

Figure 4

Cat, decerebrate. Ipsilateral L_7 ventral root response to single shock vestibular nerve stimulation. Time scale in msec intervals.

a = Control response.
b = After 80 minutes of continuous ice water irrigation.
c = After 120 minutes of continuous ice water irrigation.
d = Control response to threshold stimulation.
e = After 90 minutes of continuous hot water (45° C) irrigation.
f = After 115 minutes of continuous hot water (45° C) irrigation.

EFFECT OF THERMAL STIMULATION UPON SPINAL SEGMENTAL REFLEX ACTIVITY

The spontaneous stream of afferent impulses traversing the vestibular nerve contributes strongly to an increased excitability of the spinal cord. This series of experiments concerned reversible changes in spinal motor pool excitability as reflected by amplitude variations of segmental reflex discharges during prolonged caloric stimulation. Figure 5, insert a, depicts the control response to single shock stimulation of dorsal root L_7 recorded from the corresponding ventral root (upper tracing). The lower tracing demonstrates the spontaneous discharge in the ventral root. The remarkable increase in amplitude of the monosynaptic component of the segmental reflex response and in spontaneous firing after 80 minutes of ice water irrigation is shown in Figure 5, insert b. Continuous irrigation for 160 minutes, measured from the start, revealed the paralyzing effect upon the peripheral vestibular nervous structure. In the absence of the facilitatory support of descending vestibular impulses (Figure 5 c, lower tracing) the amplitude of the test response was reduced (Figure 5 c, upper beam).

· The temporal sequence of the effects of ice water irrigation upon the amplitude of the monosynaptic component of the segmental reflex discharge is also illustrated in Figure 5. A similar sequence of effects was produced by irrigating the ear with hot water.

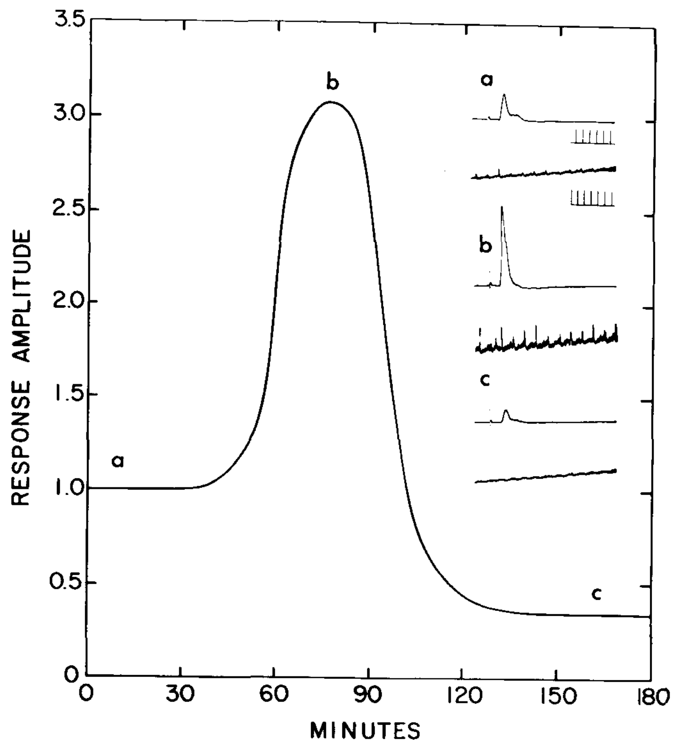

Figure 5

Amplitude variations of monosynaptic component of segmental lumbar reflex response relative to control = 1.0 plotted against irrigation time in minutes.

Insert a = Control response to supramaximal dorsal root L_7 single shock recorded from corresponding ventral root (upper beam). Spontaneous activity of that ventral root (lower beam).

Insert b = The evoked reflex response and spontaneous activity after 80 min. of ice water irrigation.

Insert c = After 160 min.

Upper time scale in msec intervals, lower in 10 msec intervals. The letters on the curve mark when records of inserts were taken.

DISCUSSION

The value of caloric stimulation for studying vestibular function lies chiefly in the assumption that one can determine whether the end organ functions normally or not at all; however, the test falls far short of precision, for the literature abounds in cases in which caloric nystagmus appears even after a loss of labyrinthine function. There are several methods of performing a caloric test. Because of the considerable distress evoked by prolonged irrigation with water of extreme temperatures, it cannot be performed upon human subjects. Thus, the findings presented in this report may be of theoretical interest only, except perhaps as they apply to brief but repeated caloric tests over a limited period of time. Under these conditions, a nystagmus may appear eventually, which is not the result of endolymphatic convection currents changing the position of a normal cupula, but rather of cumulative thermal effects acting upon the peripheral nervous structure. Such an effect has been postulated by Bartels (4) and demonstrated by several authors who found that the nystagmus elicited by caloric stimulation was sometimes independent of the position of the head (13, 17, 19).

Both the prompt, indirect convection current effect and the delayed, direct thermal effect upon the nervous structure by prolonged irrigation is readily demonstrated upon squirrel monkeys with intact ears. The direct effect of thermal stimulation may be upon the receptors and/or the peripheral nerve fibers. In an effort to distinguish between these two possibilities the experiments were performed upon monkeys with the three semicircular canals plugged or with the end organs completely removed. These operations were performed at intervals varying from several months to several weeks prior to caloric testing. Only four monkeys out of eight failed to show prompt nystagmus when tested, demonstrating the fact that paradoxical caloric reactions (caloric test positive, rotatory test negative) may still be elicited after the semicircular canals have been plugged or destroyed or the entire labyrinth removed (24, 27).

Those four monkeys and two labyrinthectomized animals were selected for the present experiments. In these animals, endolymphatic convection currents or thermal effects on receptors alike could be ruled out; nevertheless, it was still possible to evoke clear-cut nystagmus, the first sign appearing after 30 - 40 minutes of irrigation with either hot water or ice water. These experiments indicate that the thermal effects are exerted upon the peripheral nerve fibers somewhere along their course from the ampulla to the internal auditory meatus. As seen in Figure 6, the horizontal ampullar nerve is located more antero-medially than the lateralmost point of the bony horizontal canal and most of the ampullar nerve is covered by the VIIth nerve and its bony canal. This anatomical configuration may explain the long delays between the onset of irrigation, the appearance of nystagmus, and its directional reversal. It has been demonstrated that the cooling progresses as a wave through the petrous bone in such a way that immediately after the test, the most lateral part of the horizontal canal remains the coolest point (3, 8, 26, 30). Thereafter, the cold wave proceeds, cooling the more medial parts of the labyrinth, until finally the temperature of the most

Figure 6

Photomicrograph, squirrel monkey, horizontal section through labyrinth. Arrows show direction of postulated termperature progress when heating and cooling the external auditory canal (X), lateral part of horizontal semicircular canal (H), horizontal ampullar nerve (N), and facial nerve and bony canal (F). 20 microns. Hematoxylin-eosin. 10 X.

medial point of the canal is lower than that of the lateral. This may cause a flow of endolymph in the direction opposite to the initial one, thus explaining the reversal of caloric nystagmus. In the present experiments, however, the reversal of nystagmus and the increase and decrease of vestibular afferent firing, as compared to the resting activity, occurred during prolonged caloric stimulation despite the fact that the lateral point of the canal must remain cooler (or, at least, never warmer) than the medial during ice water irrigation. Under these conditions, it is not reasonable to expect reversal of endolymphatic convection currents. It must be kept in mind that prolonged irrigation with water of extreme temperatures influences not only the horizontal canal and its afferent branches, but also the vertical canals and their neural connections and the fibers from the otolith organs. This explains why an initially horizontal nystagmus later begins to show rotatory components as the peripheral nervous structures less accessible than the vertical canals begin to be affected by gradually penetrating heat or cold. Since the cochlea is accessible to thermal stimulation, the otoliths must also be affected; and, while nystagmus of otolith origin is still an open question, increased or diminished firing in the otolith afferent fibers must be reflected strongly in vestibulospinal and segmental spinal activity during prolonged irrigation.

The differential effect of temperature upon latency and amplitude of the components of the round-window response supports the assumption that the thermal effect is mainly upon the nerve fibers and to a lesser extent upon the receptors. The amplitudes of microphonic and neural components decrease during prolonged heating or cooling, but the neural component declines more rapidly than the microphonic and it disappears at a temperature where the microphonic is still clearly defined (6, 11, 20). It may also be significant to note that Hensel and Zotterman (18) were able to show that mechanically sensitive units of the tongue are not easily excited by thermal stimulation.

It is well known that impulses can be elicited in nerve fibers by applying any of the following forms of energy: mechanical, chemical, electrical, or thermal. The study of many physiological mechanisms has been advanced through the use of temperature as a variable, and it has been shown that temperature changes influence all excitable tissues to a greater or lesser extent (5). Different types of peripheral nerve fibers show different thermosensitivity (10, 23, 25). An analysis of the fiber spectrum of the stato-acoustic nerve of monkey and cat has been presented by Gacek and Rasmussen (12).

The present experiments demonstrate that continuous irrigation of the external auditory canal with water of extreme temperatures will cause the fibers of the vestibular nerve to become depolarized and to generate a significantly increased number of impulses after approximately 40 minutes of irrigation (Figure 5). The evidence of this augmented afferent firing is obtained by recording eye movements, evoked vestibulospinal activity, and the effect of descending vestibulofugal activity on the excitability level of spinal motor cells before, during, and after prolonged irrigation. This thermal excitatory effect upon the nerve fibers is superseded eventually by a strong depression probably due to metabolic changes or to alterations of the physicochemical properties of the nerve fibers. In the absence of substantially more information, it is meaningless to press the speculation beyond this point because too many dubious assumptions would be required. It can be stated, however, that the depression is a reversible phenomenon. If the irrigation is stopped at this point and enough time is allowed for the ear to return to a more normal temperature, a stage similar to the prewarming or precooling one can be achieved, although it is more difficult to do so after warming than after cooling the ear.

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13. ABSTRACT The effects of prolonged caloric stimulation with hot (45°C) or ice water have been studied upon eye movements, vestibulospinal, and segmental spinal activity. The results obtained under this variety of test conditions demonstrate that continuous irrigation with water of extreme temperatures evokes, in addition to the effects upon the position of the cupula by endolymphatic convection currents according to the theory of Bárány, an initial excitatory thermal effect giving rise to an increased afferent firing which is followed by a paralyzing effect upon the vestibular sensori-neural structures. In order to localize more specifically the site of action of thermal stimulation, experiments were carried out upon labyrinthectomized squirrel monkeys and monkeys with the three semicircular canals plugged. These results, and those obtained by recording the cochlear microphonic and neural components to click stimulation during maximal cold and warm irrigation of the ear, indicate that the effect is upon the peripheral nerve fibers somewhere along their course from the ampulla to the internal auditory meatus. Earlier theories which have predicted this direct effect on the nerves are mentioned, but, for the present, without comment as to their respective importance in explaining paradoxical caloric reactions.

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