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Vestibular nerve and nuclei unit responses and eye movement responses to repetitive galvanic stimulation of the labyrinth in the rat

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Summary. Two-second cathodal current pulses were applied at one-minute intervals at a point external to the round window in the ear of each albino rat subject. Responses were recorded in the vestibular nerve ganglion, the vestibular nuclei (single units), or in the eye movements (search coil recording method) of anaesthetized, decerebrated, or alert rats. The unit responses to the galvanic stimuli were characterized and compared with responses to galvanic and rotational stimuli reported in the literature. The main focus of the study, however, was effects of stimulus repetition. In both the vestibular nerve and vestibular nuclei recordings, the responses of many units were substantially larger or smaller at the end of a 13-pulse stimulus train than at the beginning. In the vestibular nuclei, but not in the nerve, there was a slight bias towards a decrease in response magnitude, with 10/88 units showing decreases great enough to be considered as reflecting an habituation process. In contrast, the eye movement responses showed more consistent response decrements, especially in the alert condition, but also in the other conditions (none of the unit recordings were done in alert rats). It is concluded that some of the modifications underlying habituation of the vestibuloocular reflex probably occur in portions of the neuronal reflex pathways that are downstream from the vestibular nuclei.

Key words: Vestibular habituation – Vestibular nuclei – Scarpa's ganglion – Vestibuloocular reflex – Galvanic stimulation

Introduction

Vestibular habituation has been studied mainly by measuring the vestibuloocular reflex (VOR) responses to repeated stimuli such as caloric irrigations and angular velocity steps or ramps (Collins 1974). The progressive diminution of nystagmic responses (which can be quantified by measuring cumulative slow phase deviation) to repeated velocity steps has been extensively studied in the cat (Collins 1964; Jeannerod et al. 1976; Schmid and Jeannerod 1985; Courjon et al. 1985). There is good evidence that as habituation progresses, a strict correlation between the VOR gain and time constant is maintained. In acquisition (responses measured during a habituating session) there is a decrease of both parameters, and in retention (responses measured several hours or days after the last session) a diminution in both parameters is maintained (Dodge 1923). In contrast to the many behavioral studies, there have been only a few investigations of vestibular habituation at the neuronal level (Kileny et al. 1980; Jäger and Henn 1981). In order to learn more about the neuronal basis of this phenomenon we compared, in the rat, the responses to repetitive galvanic vestibular stimulation at different levels of the system: vestibular nerve units, vestibular nuclei units and eye movements.

Galvanic vestibular stimulation, which is the application of a direct current at a point external to the labyrinth, is believed to have its primary action mainly on 8th nerve fibers (see Discussion). Cathodal currents cause an increase in vestibular afferent spike activity and anodal currents cause a suppression. As Kornhuber and Da Fonsca (1964) have pointed out, galvanic stimulation is therefore analogous to caloric stimulation or to rotation (cathodal current, warm water irrigation, and ipsiversive acceleration all cause increases in vestibular afferent activity and ultimately in contraversive slow phase eye movements). Galvanic stimulation, which has not been used previously in studies of habituation, was chosen for this study because it is easy to control and may facilitate

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eventual synaptological investigation of the phenomenon, which would be difficult if rotational or caloric stimuli were to be used.

Material and methods

Surgical procedures

SIVZ (Sprague-Dawley stock) albino rats were anaesthetized with chloral hydrate and injected with atropine (0.5 mg atropine sulfate i.p.) before undergoing surgery. All the animals were reinjected with chloral hydrate every 1–2 h except for the decerebrated rats, which were anaesthetized only until completion of the decerebration procedure (precollicular transection). Each rat in which eye movements were recorded in the alert condition was anaesthetized for the surgical procedures (implanting the stimulus electrode and attaching a skull socket for head fixation). A volatile anaesthetic (air-halothane mixture) was used for re-anaesthetization when the search coil was attached to the eye.

For unit recording in Scarpa's ganglion the cerebellar hemisphere including the flocculus and paraflocculus was removed by aspiration and the recording electrode was introduced in the ganglion under visually guided control. Vestibular nuclei units were recorded through the cerebellum. The animal's body temperature was monitored and maintained at about 36° C with a heating pad.

Electrical stimulation

Each rat was implanted with a silver-silver chloride (non-polarizable) wire electrode, insulated with teflon except for 0.5 mm of the tip, placed adjacent to the round window. An indifferent electrode was inserted in the neck musculature. Stimulating currents were applied in the ear ipsilateral to the recording site (1) to evoke field potentials with 0.1 ms single shocks, and (2) to test units or eye movements for habituation to a negative (cathodal) d.c. stimulus of 2 s duration given at 60 s intervals at least 13 times. A constant stimulus current was produced by a Hi-Med, Isolator Hg 203/100, stimulus isolation unit. The voltage changes across a resistor in series with the animal were monitored with an oscilloscope to confirm that the current was really constant for the 2 s stimulation pulses. For nerve and vestibular nuclei unit recordings, stimulus amplitude (pulse current) was chosen as 1/2 the threshold current for field potential appearance (threshold was about 80 μA). Units that did not show a clear response to this galvanic stimulus were discarded.

Recording procedure

Single unit activity was recorded extra-cellularly in Scarpa's ganglion or in the vestibular nuclei with glass micropipettes filled with 2 M NaCl (impedance 10 to 20 MΩ). The amplified signal from the electrode was fed to a window discriminator, and the discriminator output fed to a Mormira event frequency meter. The electrode was advanced by an electronically controlled microdrive (Nano-Stepper, WSE Electronic).

Eye movement recording

In separate experiments eye movements were elicited by the same galvanic stimulus used in the unit experiment (i.e. 2 s duration) and stimulus amplitude was chosen to be comparable with the amplitude used in the unit recording experiments (about 40 μA).

Eye movements were recorded using a magnetic field search coil technique. The small wire search coil (1.8 mm diameter) was glued to the cornea of the animal (Hess et al. 1985).

Results

Vestibular nerve unit responses to a single galvanic stimulus

43 Scarpa's ganglion units recorded in 14 anaesthetized rats responded to cathodal current, duration 2 s, amplitude 39 ± 19 μA. The initial response amplitude (firing rate during the first 400 ms of the stimulus minus the resting firing rate) was 71.0 ± 72.3 spikes/s. All but three of these units showed a tonic response; an increase in firing lasting the duration of the stimulus. Most of the tonic units (34) had regular resting discharges of 31.1 ± 20.0 spikes/s (Fig. 1A), but 6 did not (Fig. 1C). The remaining 3 units had phasic responses to the stimulus (Fig. 1D) and one of these had a resting discharge. In response to an anodal current pulse, the tonic units with resting activity showed a tonic decrease in firing (Fig. 1B).

Vestibular nuclei localization and unit characterization

When a single shock (cathodal pulse, approx. 100 μA, 0.1 ms) was applied via the stimulating electrode, a characteristic field potential was recorded from a micropipette inserted in the vestibular nuclei area. The potential consisted of an initial positive deflection (P) related to the current evoked in primary vestibular fibers, followed by a large negative wave, N1, related to the currents generated monosynaptically by the excitatory action of vestibular fibers in secondary vestibular neurons and a smaller negative potential, N2, composed of currents generated by polysynaptic activation of vestibular neurons (Precht and Shimazu 1965; Sirkin et al. 1984).

The field potential characteristics were used to locate the vestibular nuclei area. When a unit was found, it was discarded if it was not reliably activated, giving a spike superimposed on the field potential, by a single shock stimulus of about 160 μA, or twice the amplitude required to elicit a minimally observable field potential. In addition, some of the recording electrodes were filled with pontamine blue in order to mark the recording sites. The marked locations, according to the demarcations in the Paxinos and Watson atlas (1982), were between 10.8 and 11.3 mm posterior to Bregma in

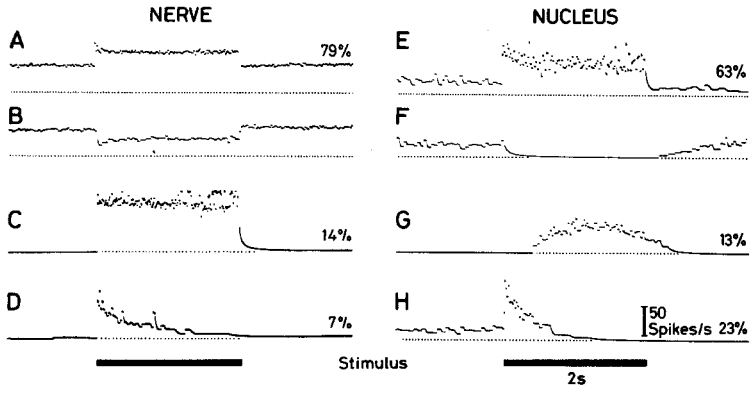

Fig. 1A–H. Types of spike frequency profiles (Mormira meter output) of single unit responses to cathodal current pulses recorded in anaesthetized rats. **B**, **F** are the responses to anodal current of the same units shown in **A**, **E** respectively. Percentages on the right in each case indicate the percentage of units in the population having the type of response profile illustrated

the medial and lateral vestibular nuclei and in the medial part of the superior vestibular nucleus. None of them was located outside the vestibular nuclei complex.

Whenever possible, units were tested for rotational sensitivity by rotating the preparation around a vertical axis. This stimulation was not canal-specific because the head was fixed such that the plane of the horizontal canal (Fischer et al. 1979) was about 50° from the vertical.

Vestibular nuclei unit responses to a single galvanic stimulus

The responses of 57 vestibular nuclei units to cathodal current (duration 2 s, amplitude 30 ± 16 μA) were recorded in 31 anaesthetized rats. The initial response amplitude was 54.4 ± 30.4 spikes/s. Tonic responses were shown by 63% of the units (Fig. 1E), phasic responses were shown by 23% (Fig. 1H), and responses characterized by a delayed onset and termination, and a slow build-up and decay were shown by the remaining 13% (Fig. 1G). These three kinds of responses were found in the subpopulation of units responding to rotation and also in the subpopulation of units not responding to rotation. Forty-six of the vestibular nuclei units exhibited a clear resting activity of 12.6 ± 7.3 spikes/s. In most cases this spontaneous activity was irregular.

In an additional set of experiments using the decerebrate, non-anaesthetized preparation, the same response patterns elicited by cathodal current, duration 2 s, amplitude 47 ± 17 μA, were found in 31 vestibular nuclei units (resting discharge 11.3 ± 4.7 spikes/s, initial response amplitude 46.4 ± 27.9 spikes/s) recorded in 10 rats. However, the proportion of units having tonic responses was much larger (94%), and that having phasic responses reduced to 3%.

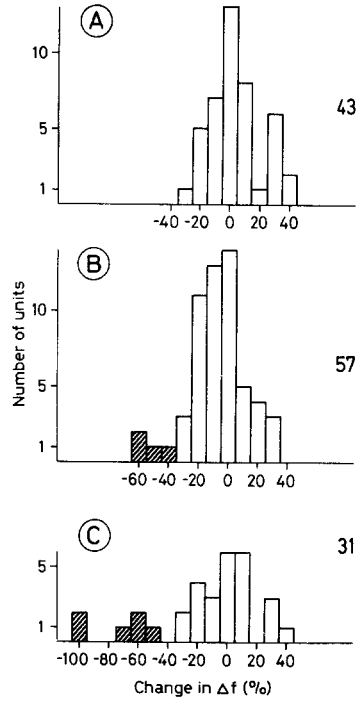

Fig. 2A–C. Distribution of percent changes in response magnitudes (Δf) of nerve units (**A**), nuclei units in the anaesthetized preparation (**B**), and nuclei units in the decerebrate preparation (**C**) following repeated galvanic stimulation. See text for explanation of method of calculation. Shading indicates units showing large decreases in response magnitude (more than 40%)

Unit responses to repeated galvanic stimulation

The units described in the previous section were examined for response modifications by applying to each of them the same galvanic stimulation repeated at least 13 times (see Methods). In order to evaluate a possible modification of response resulting from stimulus repetition, the change in firing rate (Δf) was calculated for the first and second responses and for the 12th and 13th responses (Δf = average firing rate

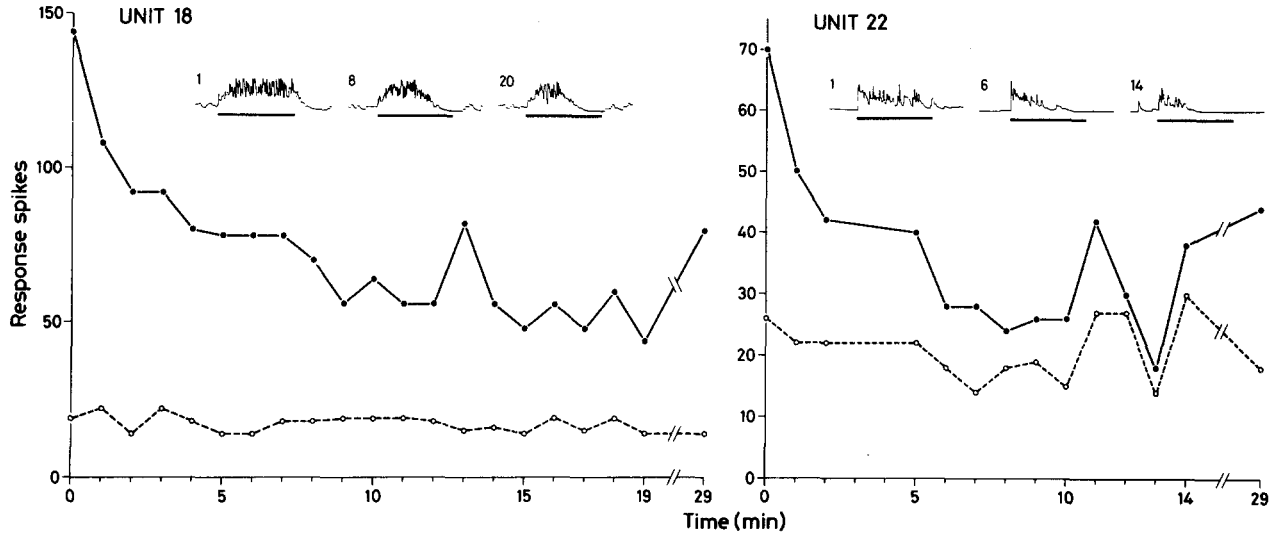

Fig. 3. Examples of vestibular nuclei units exhibiting strong reductions of their responses to repeated galvanic stimulation. The magnitude of the response to each stimulus is expressed in terms of response spikes (spikes not accounted for by resting discharge) counted over the entire 2 s period during which current was passed (filled circles, solid lines). The number of response spikes counted over the first 400 ms of the stimulus period is also shown (open circles, dashed lines). Across the top, the instantaneous frequency profiles of the first response and two subsequent responses (stimulus numbers indicated) are shown for each unit

during the 2 s stimulus minus the resting rate). The mean Δf of the first and second responses (Δf_i) was compared with that of the 12th and 13th responses (Δf_f) by calculating the percentage increase or decrease in Δf: $(\Delta f_f - \Delta f_i) \times 100/\Delta f_i$. The distributions of changes in Δf were similar for units showing tonic, phasic, and slow responses, so we grouped units with these different response types together to simplify the analysis.

For nerve unit recording, only 4 cells showed no changes in Δf, but the changes in the other units were distributed symmetrically about zero (Fig. 2A). There was also no significant change in the resting rate (31.1 ± 20.0 spike/s initial resting rate vs. 31.5 ± 20.2 spike/s final resting rate).

The distribution of the percentage changes in Δf for vestibular nuclei units in anaesthetized rats is shown in Fig. 2B and for vestibular nuclei in decerebrate rats in Fig. 2C. The mean resting activity was identical before and after the stimulus series, except in a very few cases. However, the distributions of changes in Δf were not symmetric about zero. Four of the units recorded in the anaesthetized rats and six of those recorded in the decerebrate rats had decreases in Δf of more than 40% (shaded areas of Fig. 2B, C); whereas no unit had an increase in Δf of more than 40%. Moreover it is interesting to note that in the decerebrate preparation, first, a larger percentage of units showed large decreases in Δf (19% versus 7%), and second, two of these units showed a complete disappearance of their response.

Some characteristics of the 10 vestibular nuclei units that had large decreases in Δf after repeated stimulus presentation were studied. The progressive decreases in response to a repeated galvanic stimulus for two units are shown in Fig. 3. The upper curves (solid lines, filled circles) are the total numbers of response spikes due to the stimulus during the 2 s during which the current was passed (i.e. $2 \times \Delta f$). The lower curves (dashed lines, open circles) are the number of response spikes during the first 400 ms of passing current. It can be seen from these lower curves that the first 400 ms of each response did not show a progressive decrease in either unit. The same was also true for the other 8 units showing large decreases in Δf. Thus, the progressive decrease in total response spikes (upper curves) reflects response decrements exclusively in the portions of the response occurring after the first 400 ms. Note also in the upper curves that 10–15 min after the last stimulus in a train, when another test stimulus was given, the response had only partially recovered, i.e. there was a partial retention of the response decrement. We were able to test for this phenomenon in only the two cells shown and one other cell (which had a similar partial retention).

Two of the 10 cells with large response decrements had progressive decreases of their resting discharges in addition. In the other 8 cells, the resting discharges did not change. The responses to the first stimulus were tonic in 7, and phasic in the remaining 3 cells. Most noteworthy is that among these 10 cells,

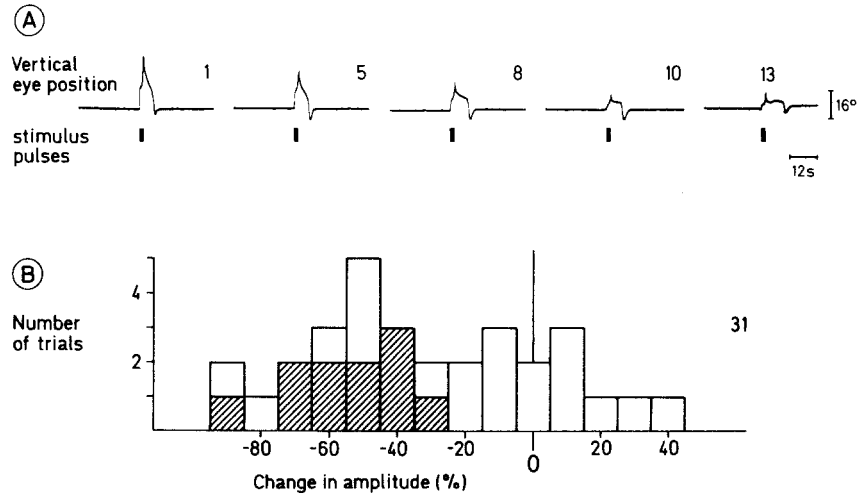

Fig. 4. A Vertical eye movements evoked by repeated galvanic stimulation. The stimulus number is indicated for each response. **B** Distribution of percent changes in vertical eye movement amplitude following repeated galvanic stimulation. Shaded portion of histogram represents experimental trials in decerebrate and alert rats; unshaded portion in anaesthetized rats

only 1 (10%) had no response to rotation, as compared to 65% of the total sample in the anaesthetized rats and 52% in the decerebrate rats.

Eye movements

Typically, a 2 s galvanic stimulus elicited a complex eye movement trajectory. The vertical component was usually larger than the horizontal component. Because of this, and because of the fact that the vertical component is directly related to the search coil current induced by the vertical field (whereas the horizontal component is related in a complicated way to the currents induced by both the vertical and horizontal fields), we chose to examine vertical eye movements for the presence of habituating responses. Similar movements were recorded in 5 anaesthetized rats, 3 alert rats, and 1 decerebrate rat. In almost all cases, the movements were tonic deviations, as seen in Fig. 4A, rather than nystagmus). In several trials of repeated stimulation the amplitude of eye movement (maximum excursion of the vertical component was measured) was clearly reduced, as in the case shown in Fig. 4A. The percentage changes in amplitude were quantified in the same way as were the percentage changes in the unit responses: $(a_f - a_i) \times 100/a_i$, where a_i is the average amplitude of the first and second responses, and a_f is the average amplitude of the 12th and 13th responses. The results of all the trials are shown in Fig. 4B. In the anaesthetized preparation (unshaded blocks), in 60% of the trials a decrease in amplitude was observed. In alert rats, the same repeated stimulation resulted in a progressive and clear decrease in amplitude in all trials. Similar results were obtained with one decerebrate preparation. The trials performed in alert or decerebrate preparations are indicated in the figure by shaded blocks. Five of fifteen minutes after stopping the stimulus repetition, if the same stimulus was given again, the response amplitude was intermediate between a_i and a_f (partial retention of the response modification) in almost all cases.

Discussion

Resting discharges

The average resting rate of units recorded in Scarpa's ganglion was similar to what we previously reported for a larger sample of such units (Sirkin et al. 1984) and slightly lower than what Curthoys (1982) has reported. The resting activity we found in the vestibular nuclei was significantly lower than that in the ganglion, in agreement with prevous findings (Markham et al. 1978).

Properties of unit responses to galvanic stimulation

A difference between our data and those of Markham et al. (1978), who studied neuronal responses to angular acceleration steps, is that we found units having "phasic" response profiles. These were especially frequent among the central vestibular units (see Results). It should be noted that these "phasic" responses are quite different from the "adapting" responses mentioned by Markham et al., which are similar to those described previously in the cat (Blanks et al. 1975). The "phasic" responses reported here were so called because the firing rate increases due to the galvanic stimulus decayed rapidly, the

firing rate returning to baseline within the 2 s stimulus period (see Fig. 1D, H). The "adapting" units described by Markham et al. showed a gradual response decay after many seconds of a constant acceleration stimulus. It should be noted that responses of the type shown in Fig. 1G were also not reported by Markham et al.

Galvanic stimuli are thought to bypass the sensory transduction apparatus of the labyrinth, and to have their effect directly on 8th nerve fibers, since galvanic stimuli are still effective when the labyrinth is removed (e.g. Huizinga 1930; Pfaltz 1969). However, the occurrence of phasic responses in our study appears not to reflect a peculiarity of the galvanic stimulus, but rather of the anesthetized, intact preparation (Markham et al. used encephale isolé). If the phasic responses recorded in vestibular nuclei units reflected a peculiar action of the galvanic stimulation, one would expect a comparable proportion of phasic responses to have been found in the nerve units. In fact, there were only 7% phasic units among the nerve units as opposed to 23% among the nuclei units in anaesthetized rats (significant at the 5% level in a Chi-squared analysis). Also, Goldberg et al. (1984) reported no phasic responses to galvanic stimuli in the vestibular nerve afferent fibers of the anaesthetized squirrel monkey.

Anaesthesia is known to affect the responses of central vestibular units (Buettner et al. 1978). The proportion of phasic responses recorded was smaller when we used decerebrate, unanaesthetized preparations (1/30 as opposed to 13/57 in the anaesthetized perparations). This difference in the proportion of phasic responses was not accompanied by any difference in the average resting rate of the units. In addition to using encephale isolé preparations, Markham et al. made large ablations of the cerebellum for visually guided electrode placement in the vestibular nuclei. This may also be important. In preliminary experiments in which we recorded central vestibular units in anaesthetized rats following complete cerebellar ablation, 21/21 units had the tonic response type to the galvanic stimulus.

Effects of stimulus repetition on eye movement and unit responses

In most trials in anaesthetized rats, and in all trials in decerebrate or alert rats, stimulus repetition resulted in a decreased amplitude of eye movement response (Fig. 4). We suggest that this response decrement is an example of habituation. In experiments performed in the cat on VOR habituation (Jeannerod et al. 1976) it was found that during the first session (10 postrotatory stimuli) of the first day, there was a progressive and substantial response decline. The tenth response (cumulative slow phase deviation) was sometimes less than half as large as the first. The results we obtained in the rat with galvanic stimulation were quite similar and might therefore indicate a similar mechanism of acquisition (see Introduction). Where along the vestibuloocular reflex pathway do changes occur that result in this behavioral response amplitude decrement? First of all, since we used galvanic stimuli, which are thought to bypass the receptors (see previous section), the receptors can be ruled out. The next two possible sites are the vestibular afferents and the vestibular nuclei neurons. As elaborated below, our unit data indicate that changes in the responses of afferents are not responsible, and changes in the responses of vestibular nuclei neurons are partially, but probably not completely, responsible for the behavioral response amplitude decrement. Thus the important changes seem to occur in the vestibular nuclei and in more central elements of the vestibuloocular reflex circuit.

The fluctuation of unit responses was quite significant, with decrements or increments in Δf of 20% or more not uncommon (Fig. 2). Similar fluctuations were previously reported in the responses of vestibular nuclei units in the cat to rotational stimuli (Kileny et al. 1980). In our recordings from the vestibular nerve, the distribution of fluctuations was rather symmetric about zero (Fig. 2A), but in our vestibular nuclei recordings there was a clear bias towards response decrements (Fig. 2B, C). Furthermore, in the responses of nuclei neurons that were considered to have been habituating, there was some degree of retention, as also in the eye movement responses that habituated, which is a well known characteristic of vestibular habituation (Collins 1974; Jeannerod et al. 1976). Kileny et al. (1980) found no such evidence for habituation in the cat vestibular nuclei, probably because the stimuli they used were not appropriate for causing vestibular habituation.

The response decrements in vestibular units and eye movements that we have considered to be examples of habituation cannot easily be dismissed as fatigue effects. The interstimulus interval we used (1 min) is too long to cause neurotransmitter depletion. The fact that resting discharge did not change in habituated units also speaks against a fatigue effect. Finally, perhaps the strongest argument is that in all the groups of units, and in the group of eye movement trials performed in anaesthetized rats, there were examples of responses that actually increased with repeated stimulation.

Compared to habituation of vestibular nuclei unit responses, habituation of eye movement responses

was more frequent (100% in decerebrate and alert rats) and more complete. Thus our data are in agreement with the view of Horn (1970) that habituation is found more rarely in cells, the closer they are to the sensory apparatus. In his view, not until cells that are separated by three or four synapses from the sensory receptors is there a high probability of encountering habituation. Most studies in mammals have not reported habituation in sensory fibers, even when low frequency stimulation that results in habituation more centrally is used (Segundo and Bell 1970).

It is not surprising that we found only a relatively small indication of habituation in the vestibular nuclei neurons as a group considering Horn's theory, because most of these neurons can be presumed to have been separated by only two synapses from the receptor cells. In addition, previous studies that analyzed response time constants in vestibular nuclei neurons of the cat, found that there seems to be very little information processing between the afferent fibers and the vestibular nuclei neurons (Melvill Jones and Milsum 1971; Shinoda and Yoshida 1974). Finally, previous studies in cat (Keller and Precht 1979) and monkey (Lisberger and Miles 1980) reported that large adaptive modifications of the vestibuloocular reflex were accompanied by only minor changes in sensitivity and no changes in the resting rates of vestibular nuclei neurons.

Nevertheless our data did yield some examples of habituation in vestibular nuclei neurons, although the habituating units comprised a small subpopulation. How are we to interpret this finding? The first speculation is that this subpopulation had a privileged input to the motor system and thus might at least partially explain the habituation observed at the behavioral level. In any case, our result suggest that the property of plasticity might be unevenly distributed among neurons in the central nervous system. It is interesting that the units designated as habituating showed response decrements only in the portions of the responses beginning 400 ms after stimulus onset. This observation could be interpreted to indicate that vestibular habituation is characterized by a shortening of the time constants of the responses. In fact such an observation was made by Jaeger and Henn (1981) in studying habituation to natural stimuli of vestibular nuclei and eye movement responses.

A final interesting observation is that almost all of the central vestibular neurons that we considered to have habituated to the galvanic stimulus were units that responded to rotation (i.e. presumed semicircular canal units). The phenomenon of vestibular habituation as it is known today is limited to the canal system. It may be that a comparable mechanism does not exist in the otolith system.

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