Exp. Brain Res. 27, 523–538 (1977)

Experimental Brain Research

Neuronal Activity in the Vestibular Nuclei of the Alert Monkey during Vestibular and Optokinetic Stimulation*

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Summary. Recordings from neurons of the vestibular nuclei were performed in alert monkeys. Type I and type II units were identified by rotating the monkey about a vertical axis. All neurons responded also when only the visual surround was rotated around the stationary monkey. The combination of visual and vestibular stimulation points towards non-algebraic summation characteristics for the two inputs, with each input dominating the response over a certain range.

Key words: Vestibular neurons – Optokinetic nystagmus – Visual-vestibular interaction – Alert monkey

Introduction

More than 100 years ago Ernst Mach performed a series of experiments on the vestibular system and came to the conclusion: "Wie es scheint, können also optische Empfindungen durch Bewegungsempfindungen modifiziert werden. Umgekehrt werden aber auch Bewegungsempfindungen auf optischem Wege angeregt. Dies soll durch einige Experimente demonstriert werden." (Mach, 1875; translated in Henn and Young, 1975: "Apparently, optical sensations can be modified by motion sensation. Conversely, motion sensation can also be stimulated by optical means; this can be demonstrated by some experiments.") The question, at which neuronal level this interaction first occurs, could be answered only recently, because it was first necessary to use microelectrode techniques in alert animals.

Klinke and Schmidt (1970) reported on recordings from afferent fibers from the semicircular canals in the goldfish, whose activity was modulated if an optokinetic pattern, displayed in front of the immobile fish, was moved in different directions.

* Supported by Swiss National Foundation for Scientific Research 3.044.76 and Emil-Barell-Foundation of Hoffmann-La Roche, Basel, Switzerland

In the following years these studies were extended to recordings from the vestibular nucleus complex in goldfish and rabbits (Dichgans et al., 1972, 1973). It could be shown that large moving visual fields induced activation or inhibition in units which were otherwise thought to be specific vestibular afferents. All these animals were paralyzed, preventing them from making any movements. Results from unit recordings from the vestibular nuclei in monkeys gave similar results (Henn et al., 1974). In these experiments the monkeys were alert and made spontaneous eye movements. All units which were activated by vestibular stimulation could also be activated by moving optokinetic patterns.

In this report we will present and discuss quantitative data from units in the vestibular nuclei. The specific questions raised are: 1. what is the time course of frequency change to optokinetic stimuli; 2. what is the relation between different velocities of the optokinetic stimulus and the unit activity; 3. how are the visual and peripheral vestibular inputs summated in the vestibular nuclei.

Methods

Six rhesus monkeys (Macaca mulatta) were chronically prepared. Under halothane-nitrous oxide anaesthesia a plug was implanted stereotaxically over a trephine hole in the skull. DC-electrodes (Bond and Ho, 1970) were implanted around the boney orbits to measure horizontal and vertical eye position, and head bolts were attached to the skull in order to fixate the head during the following experiments. The monkeys sat in a primate chair, the limbs were loosely restrained and the head fixed at an angle of 25° downwards to bring the horizontal semicircular canals into the plane of rotation. Strain gauges were mounted to the head holder for measuring head torque. The monkey could be rotated about a vertical axis by a servo-controlled motor. This rotating platform was enclosed by a cylinder covered with black and white stripes on the inside, which also could be moved about a vertical axis around the monkey by another servo-controlled motor. The cylinder's diameter was 124 cm, its height 86 cm, stripe width 7.5°.

Stimulation consisted of rotating the monkey in the dark (pure vestibular stimulation) using a trapezoid velocity profile. The animal was accelerated, turned at constant velocity, and then decelerated. The cylinder could be rotated around the monkey in just the same way (visual stimulation) while the cylinder was illuminated from the inside (photopic range). Finally the monkey could be turned in the light in front of the stationary cylinder (combined visual-vestibular stimulation).

Units were recorded extracellularly with varnish-insulated tungsten wires, having an impedance of 4–8 MΩ (measured at 1000 Hz). At the end of the experiments, a selected recording site was marked by anatomical tracers. Animals were perfused under deep anaesthesia. Frozen sections of the brainstem, taken every 320 μ, were stained with cresyl violet. The recording sites were then reconstructed.

Experiments with the fully alert monkeys were performed every second day. In order to guarantee a constant level of alertness small doses of amphetamine were given (0.5 mg/kg i.m.). Unit data, horizontal and vertical eye position, head torque, turntable and cylinder velocity, a signal for lights on and off, and a digital time code were stored on FM tape. All analyses were performed off-line. Instantaneous and average frequency of units were determined. The time interval for determining the running average could be varied between 0.25 and 2 sec, and was adjusted according to the regularity of the unit firing. Slow phase nystagmus velocity was obtained by differentiating the horizontal eye position. Eye movements were calibrated by determining slow phase nystagmus velocity during rotation of the animal in the light (rotation velocity 30°/sec and 60°/sec).

Results

Characteristics of Neuronal Activity during Vestibular Stimulation

Neurons were selected according to their response to stimulation of the horizontal semicircular canals. All the units considered in this report consistently exhibited frequency changes during rotation of the animal about a vertical axis. Of the 59 units 37 (63%) were type I units according to the classification of Duensing and Schaefer (1958), i.e. excited during acceleration to the ipsilateral side and inhibited during acceleration to the contralateral side. 22 units (37%) were of type II characterized by a mirror-like response.

The average spontaneous activity of all units was 38 impulses per sec, extremes ranged from 2 to 100 Hz. Nine neurons had a rather regular discharge pattern with spontaneous changes less than ± 10% of the average resting discharge. When animals were stationary, 21 neurons (36%) exhibited some modulation of resting discharge which could be related to changes of eye position and/or to rapid eye movements (Miles, 1974; Keller and Daniels, 1975; Fuchs and Kimm, 1975). When animals were subjected to vestibular stimulation, average frequency characteristics in these units did not differ from other units, in which no relation to eye movements was evident. The frequency increase or decrease for the eye movement related neurons during nystagmus was larger than could be attributed to increased number of rapid eye movements or the change of average eye position.

The vestibular stimulation consisted of a trapezoid velocity profile with an acceleration of 8°/sec^2 and end velocities up to 120°/sec. The peak frequency above or below resting discharge at the end of the acceleration period was set to 100%. Using the same velocity profiles the activation or inhibition which occurred while animals were exposed to pure visual or visual-vestibular stimulation could then be expressed for each unit as a percentage of the response to pure vestibular stimulation (Fig. 1). The change of unit frequency after the end of the acceleration period in darkness can be approximated by an exponential function. Time constants for these functions were mostly in the range between 15 and 40 sec (Miles and Henn, 1976). The time constant was taken as the time elapsed between maximal frequency deviation and the point at which the frequency returned to 37% of that value.

Histological examination showed that most neurons were recorded from those parts of the vestibular nucleus complex which comprise the lateral and superior nucleus and the rostral pole of the medial nucleus. No neurons were included in this study which, although responding to vestibular stimulation, lay outside the boundaries of the vestibular nucleus complex.

Characteristics of Neurons during Visual Stimulation

Consistent with our earlier report (Henn et al., 1974), all units which were influenced by the horizontal semicircular canals, could also be influenced by large moving visual stimuli, i.e. in our case the striped drum rotating around

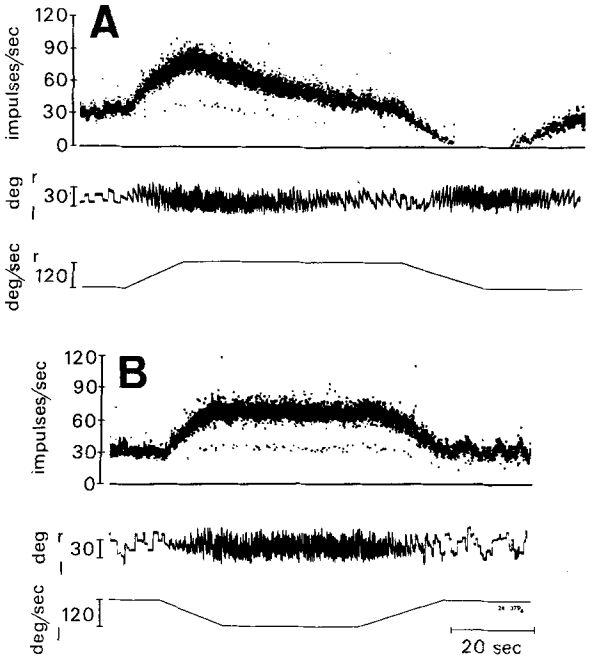

Fig. 1. Type I unit during table rotation in the dark (**A**, vestibular stimulation) and drum rotation around the stationary animal in the light (**B**, visual stimulation). The top trace is the instantaneous frequency rate; middle trace, horizontal eye position; below, the chair or cylinder velocity. Note that chair movement to the right (**A**) gives a similar increase in discharge rate and nystagmus response as drum rotation to the left (**B**). During constant velocity rotation in the dark, the unit activity returns to the level of spontaneous activity, and is inhibited during deceleration (**A**). During constant velocity rotation of the cylinder the unit maintains its activity, and during deceleration activity parallels stimulus velocity (**B**). The average peak of frequency at the end of acceleration in A is 75 imp/sec, or 45 imp/sec above resting discharge, and this value is set to 100%. The average frequency reached during visual stimulation is 67 imp/sec or 37 imp/sec above resting discharge, i.e. 82% of the frequency obtained during vestibular stimulation

the stationary animal. Type I units which were excited by acceleration to the ipsilateral side, were also excited by the visual stimulation moving in the opposite direction (Fig. 1). It should be noted that these two different stimuli elicit nystagmus into the same direction. Type I units were inhibited when the direction of the acceleration or drum rotation was reversed. Type II units showed for both the direct vestibular and visual stimulation a mirror-like behavior. In only two units was an exception to this general rule found. In these units acceleration and drum rotation in the same direction yielded an increase in frequency. It should be noted that these two different stimulus situations produce nystagmus in opposite directions. As these units represent a minority, comprising less than 4%, they are not discussed further in this context. With the exception of two units, which exhibited a higher resting discharge in the light, unit activity was the same in darkness as in light.

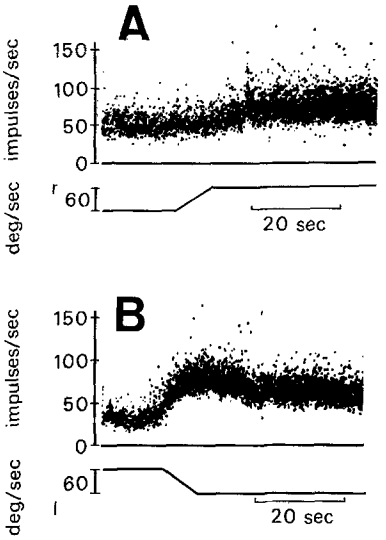

Fig. 2. Different types of frequency increases for vestibular neurons using the same visual stimulus. Instantaneous frequencies are displayed. The cylinder was accelerated at 8°/sec^2 from zero to an end velocity of 60°/sec (bottom trace is velocity profile of cylinder). In **A** a type II unit reaches maximum frequency deviation only very slowly, about 25 sec after the end of acceleration. In **B** a type I unit reaches maximum immediatly at the end of acceleration of the visual stimulus, and then slowly returns to some level above resting discharge

The velocity profile of the visual stimulus was the same as that of the vestibular stimulus. The drum was accelerated to a terminal velocity which was held constant over at least 30 sec, then the drum was decelerated and came to rest. Using an acceleration of 8°/sec^2 and a terminal velocity of 60°/sec, the acceleration period lasted 7.5 sec. Typically units exhibited an increasing deviation from resting discharge, which reached a plateau and then stayed more or less constant until deceleration begun (Fig. 1). The time at which the frequency reached its maximum deviation varied: it could be immediately at the end of the acceleration period, or be delayed by up to 25 sec (Fig. 2A). Five units, all of which had a peak of activity immediately after the end of the acceleration, exhibited a decline of frequency towards baseline activity, but still remained above it (Fig. 2B). Such phasic behavior was the same for the excitatory as well as for the inhibitory direction. There was a general trend that type I neurons reached the maximum of frequency changes earlier, usually 2.5 to 7.5 sec after end of acceleration, whereas type II neurons reached that maximum later, usually 7.5 to 25 sec after end of acceleration. Average results from repeated acceleration periods for ten units are shown in Figure 3. The average latency between start of drum rotation and first signs of frequency change was 2.4 sec (S.D. ± 1.6 sec). There was no difference whether the induced frequency change was an activation or inhibition. The rate of change of frequency could be approximated by an exponential function. The average time constant for these ten units was 9.4 sec (S.D. ± 2.4 sec) using an acceleration of 8°/sec^2 to a terminal velocity of 60°/sec. No significant difference in the

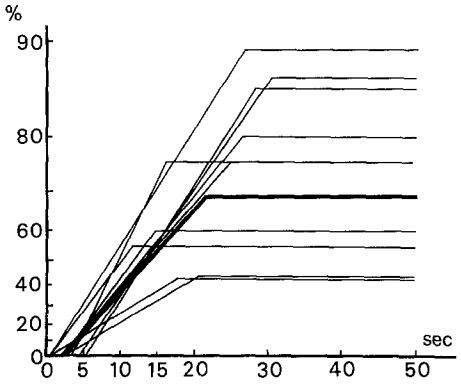

Fig. 3. Unit activity during cylinder rotation for 10 neurons (averages of 4 to 10 trials for each neuron), the heavy line indicating the combined average. The lines represent linear regression lines through the values of frequency deviation. Abscissa is the time in seconds after start of cylinder rotation, which consists of acceleration for 7.5 sec to a constant end velocity of 60°/sec. Ordinate is unit activity. 100% is the maximum frequency deviation obtained for each neuron during vestibular stimulation, using the same velocity profile. Note the slow increase of unit activity, which can be approximated by an exponential function, and which is followed by a plateau

values was found for acceleration into the inhibitory or excitatory directions. If the maximum frequency change obtained by the vestibular stimulation is set at 100% for each neuron, then the values for changes in frequency during visual stimulation ranged between 30 and 90%, the mean for the ten units in Figure 3 being 69%. Only in one case out of 59 units was the change of frequency during visual stimulation 100% i.e. as strong as the vestibular stimulation. Absolute values of frequency deviations from level of spontaneous activity were mostly around 10–50 Hz, an extreme value being 160 Hz. Many units responded asymmetrically to vestibular stimulation. Usually the frequency increase was larger than the decrease in frequency with the opposing stimulus. In such cases the response to visual stimulation showed a similar asymmetry.

21 units were also investigated using different end velocities of the rotating drum. Acceleration was held constant at 8°/sec^2, but end velocities were systematically varied between 7.5°/sec and 120°/sec, so that acceleration periods lasted up to 15 sec. Neurons with a regular resting discharge and a strong response to visual stimulation exhibited reliable frequency changes already at drum velocities of 7.5°/sec (Fig. 4). With increasing velocities frequency changes concomitantly increased but only to a certain level, when they saturated. The level of saturation was most often around 60°/sec and varied between 45°/sec and 120°/sec (Fig. 5). In this context it should be remembered that the velocity of optokinetic nystagmus (slow phase velocity) which is elicited using such a stimulus, saturates only at velocities well above 120°/sec (Komatsuzaki et al., 1969): indicating a dissociation between neuronal activity and nystagmic response. The level of saturation contributed to certain nonlinearities of unit activity. For the unit in Figure 4 activity follows cylinder ve-

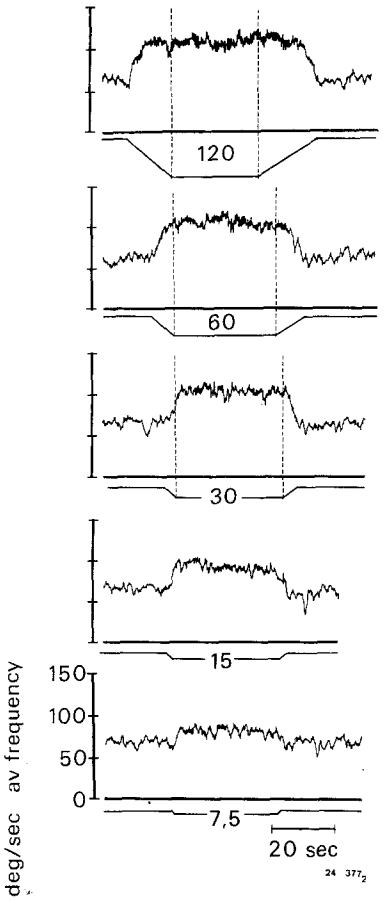

Fig. 4. Frequency display (running average over 1 sec) for a type I unit during cylinder rotation with different velocities. The ramp below each frequency trace is the velocity profile of the cylinder, end velocities ranging from 7.5 to 120°/sec. The unit saturates between 30 and 60°/sec to the visual stimulus. With an end velocity of 120°/sec the neuron reaches its maximum frequency already during acceleration, and the frequency begins to decline 13 sec after the start of deceleration, i.e. at a velocity of about 40°/sec

locities up to about 60°/sec. Above 60°/sec unit activity reaches a plateau already during the acceleration phase and remains there until in the deceleration phase velocity drops below a value of about 40°/sec.

During deceleration the first frequency change occurred when the velocity was reached at which the neuron had previously saturated to the visual stimulus. This introduced varying values of latencies between start of deceleration and frequency changes, which depended on the previous end velocity, the level at which the neuron saturated, and the rate of deceleration. Below the saturation velocity frequency roughly followed the shape of the velocity profile (Figs. 1, 4). Resting discharge was reached immediately after the end of deceleration. For the majority of units no rebound activity was seen, although in a

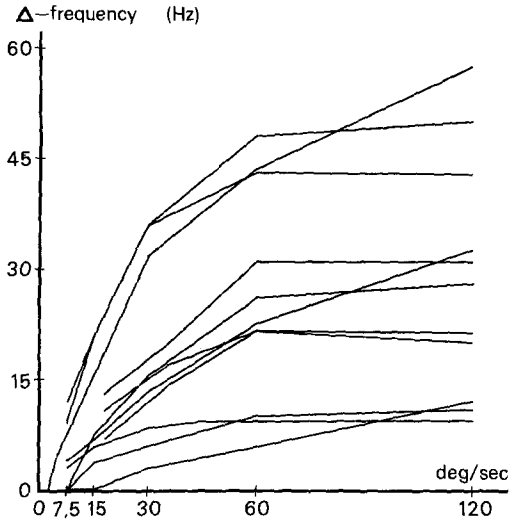

Fig. 5. Responses of eleven neurons to different velocities of the visual stimulus. Abscissa is the velocity of the visual stimulus. Ordinate is the average frequency increase above resting discharge for individual neurons. At the lower velocity range the frequency increases with higher stimulus speeds, but above a certain velocity there is no further frequency increase. Most neurons become saturated at about 60°/sec

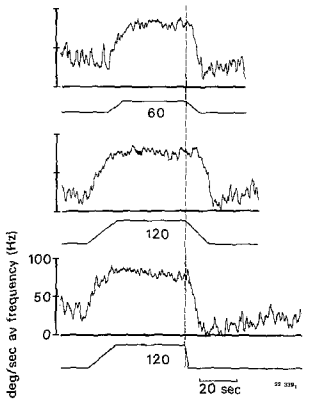

Fig. 6. Frequency display (running average over 1 sec) of a type II neuron during cylinder rotation at different velocities and with different rates of deceleration. Below each frequency display the velocity profiles of the stimulus are plotted in degrees per sec. Note the long-lasting depression of activity after the end of deceleration

few a rebound in the direction opposite to that of the resting discharge was seen, and this rebound was stronger when the cylinder came to a sudden stop (Fig. 6). In such cases it usually took 20–40 sec for the activity to reach the level of spontaneous discharge again. Five units were encountered which displayed some phasic activity during acceleration and deceleration of the visual stimulus (Fig. 2B).

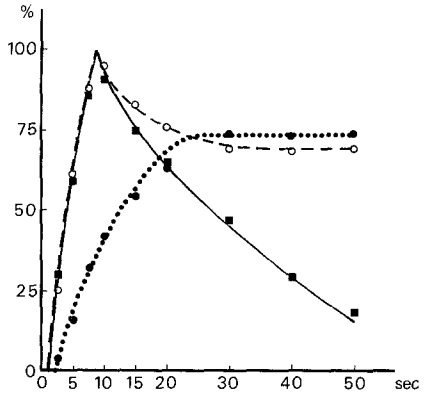

Fig. 7. Average frequency responses from 6 neurons (3 type I and 3 type II units) during chair rotation in the dark (solid line), chair rotation in the light (broken line), and cylinder rotation around the stationary animal (dotted line). Abscissa is time in seconds after start of a 7.5 sec acceleration, after which stimulus maintains a constant velocity of 60°/sec. Ordinate is the normalized response. 100% is the maximum activation of units while animals are turned in the dark. Note that initially the response to animal rotation in the dark and the light are similar. During the plateau phase frequencies are not significantly different for turning the animal in the light or turning the cylinder around the stationary monkey

Combined Visual-Vestibular Stimulation

Again the same trapezoid velocity profile was chosen to test the different effects of vestibular, visual and combined visual-vestibular stimulation. The combined visual-vestibular stimulation consisted of rotating the animal in the light.

Acceleration Phase: The response to vestibular or visual-vestibular stimulation during and immediately following the acceleration period was virtually the same (Figs. 7, 8, 9). The latencies of the frequency changes at the start of acceleration were less then 1 sec, the time of occurrence and the maxima were also similar. If the maximum frequency deviation for vestibular stimulation is defined as 100%, the same value is reached for visual-vestibular stimulation. However, after that peak of frequency change, there were pronounced differences between the pure vestibular and the combined stimulation, which will be discussed in more detail below. During pure visual stimulation latencies were longer and increase in activity was slower (Fig. 7). Frequency deviations during the visual acceleration were less than deviations obtained by vestibular stimulation.

Constant Velocity Period: During pure vestibular stimulation, frequency returned to the resting discharge, whereas during rotation of the animal in the light, frequencies never returned to baseline levels. Mostly there was a slight initial reduction, followed by a plateau, which remained more or less constant at values between 30 and 90% (in one unit 100%) of the initial maximum frequency deviation (Figs. 7, 8, 9). For each individual unit the value of the sus-

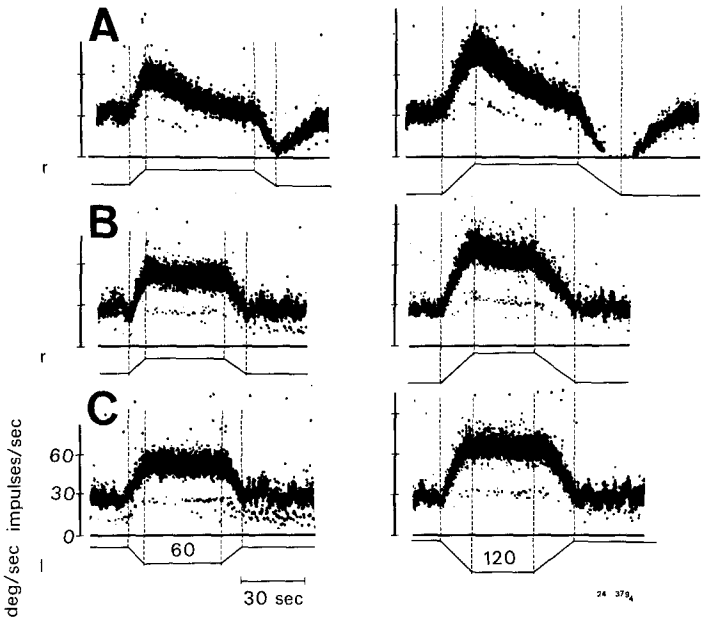

Fig. 8. Instantaneous frequency of a type I unit during rotation in the dark (**A**), rotation in the light (**B**), and cylinder rotation around the stationary animal (**C**). On the left side, end velocities were all 60°/sec, on the right side 120°/sec. Velocity profiles in degrees per sec are shown below each frequency display. Peaks of unit activity in A and B are similar; afterwards in **A** there is an approximately exponential decline towards resting discharge; in **B** there is only a small decline with velocity of 60°/sec, but more with velocity of 120°/sec, because the unit saturates to visual stimuli at a velocity of about 90°/sec. In **C** with the pure visual stimulation at a deceleration from 60°/sec the unit responds immediately; with 120°/sec there is some latency (5 sec) in the response, i.e. activity declines only after the stimulus reaches again about 90°/sec (deceleration 6°/sec^2)

tained response was the same as that reached during the plateau phase of pure visual stimulation. Since the pure visual response saturates at a certain stimulus velocity, the initial decline in response is more marked for higher stimulus velocities (Fig. 8). The response then declines to the maximum level the unit can hold during pure visual stimulation.

Deceleration Period: During deceleration with the visual-vestibular stimulus, frequencies returned from the previous plateau to the level of resting discharge (Figs. 8, 9). In detail, the behavior differed. It depended on the previous velocity, the degree the neuron could be influenced visually, and the value at which the neuron became saturated to the visual stimulus. Neurons which could be weakly influenced by the visual stimulus, that is by less than 70% compared to the vestibular stimulus, did exhibit some rebound activity during visual-vestibular deceleration (Fig. 9A). Units which could be influenced to more than 70% by the visual stimulus, mostly type II units, did not show such a rebound (Figs. 8, 9B). If the previous velocity of the visual stimulus was below saturation for any respective neuron, then the frequency just returned to baseline levels. Above saturation level, frequency during deceleration first returned to

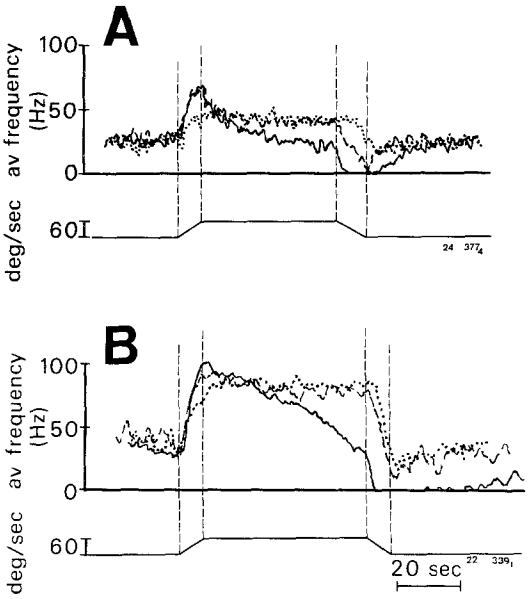

Fig. 9. Running average of two different neurons (type I in **A**, and type II in **B**) during animal rotation in the dark (solid line), animal rotation in the light (broken line), and cylinder rotation around the stationary animal (dotted line). During acceleration there is no difference in activity when rotating the animal in the dark or in the light. Afterwards while the animal is rotated in the light activity decreases and stays at the level of unit activity which is otherwise reached when the cylinder is rotated around the stationary animal. In **A** the unit was saturated at about 45°/sec to the visual stimulus. Therefore decline of frequency during deceleration starts only after velocity decreased to about 40°/sec. During deceleration with the combined stimulus there is an initial decline in unit activity with a rapid return of frequency to resting discharge after the end of deceleration. In **B** the unit is not saturated to the visual stimulus and the percentage influence during visual stimulation is more than 70% of the vestibular response. Therefore during deceleration activity elicited by the visual stimulus alone or the combined stimulus is not significantly different

the direction of baseline activity with a profile similar to that seen with the vestibular stimulus alone. Near the point at which the velocity of saturation to the visual stimulus is crossed the steep change in frequency is markedly slowed down (Fig. 9A), and levels of baseline activity are quickly reached. This dissociation in activity between visual and vestibular-visual stimulation during deceleration was more pronounced the higher the previous velocity was above saturation level.

Discussion

All vestibular units recorded from the vestibular nuclei which can be influenced by stimulation of the horizontal semicircular canals, also show consistent frequency changes when animals are exposed to moving visual fields. Rotation of animals in the dark in one direction, or movement of the visual stimulus in

the opposite direction around the stationary animal excited more than 95% of the units. Inhibition occurred when the direction of the stimuli were reversed. Less than 5% of the units were exceptions from this general rule. In terms of behavior therefore, most units are activated during nystagmus in a certain direction, independent of whether it was induced by animal rotation (vestibular) or surround rotation (optokinetic), and similarly the units are inhibited with nystagmus in the opposite direction. The same behavior has been found in the goldfish and rabbit (Dichgans and Brandt, 1972; Dichgans et al., 1973; Klinke and Schmidt, 1970). Therefore this powerful influence of moving visual stimuli seems to represent a more general characteristic of the organization of the vestibular system. As all the described phenomena are also elicitable in the paralyzed goldfish, any major contribution from extra-vestibular receptors (cutaneous or joint receptors, muscle spindles) as a result of possible postural reactions is excluded.

In retrospect it seems astonishing that this visual influence on vestibular nucleus neurons escaped notice until recently. Apparently the experimental procedures are responsible for that. The visual channel conveys the rather abstract information about velocity of the visual surround. For such a multisynaptic pathway to function physiologically, alert preparations are necessary. Also it seems important that the visual stimulus covers large parts of the peripheral visual field – large enough to elicit nystagmus.

The visual response has a latency which lies in the range of seconds, and beyond that it usually takes several seconds after the acceleration period is over until most units are maximally activated or inhibited by the visual stimulus. Therefore any high frequency visual stimulation would not have much effect on vestibular nucleus units (Keller and Daniels, 1975). On the other hand, our study emphasizes that in all experiments involving the vestibular system one would have to be very careful to exclude any visual input, if one is interested only in that part of the response which comes from the peripheral vestibular apparatus.

Pathways from the Visual System

The pathways by which the visual influence is transmitted, are unclear at the moment. Recently it had been shown that the flocculus receives an input from the visual system (Maekawa and Simpson, 1972), and from primary vestibular neurons (Ito et al., 1973). The Purkinje cells in the flocculus mainly project to superior vestibular nucleus (Angaut and Brodal, 1967). Single unit recordings from the flocculus in alert monkeys showed a strong modulation to vestibular stimuli of these units when the vestibulo-ocular reflex was suppressed by visual fixation (Lisberger and Fuchs, 1974; Miles and Fuller, 1975). Lesions of the flocculus in monkeys led to an impairment of the visually mediated suppression of the vestibulo-ocular reflex in the light (Takemori and Cohen, 1974). Taken together it seems possible that the flocculus mediates the visual influence which we observed in vestibular nucleus units, however, a direct proof is lacking.

Type II units, for the most part, probably get their input from contralateral type I units, i.e., they can be considered as tertiary neurons relative to the end organ (Shimazu and Precht, 1966). As type II units can be more strongly influenced by visual input than type I units, it is concluded that the pathways from the visual system end on type I as well on type II units with the result that type II units thus get a twofold input from the visual system, a direct one, and an indirect one via the contralateral type I units, resulting in a greater modulation to the moving visual surround. At higher levels of the nervous system, such as in the thalamic projection area of the vestibular nuclei, it was shown that visual-vestibular interaction is more complex and that many units are found there which could be influenced visually just as strongly as by adequate vestibular stimulation (Büttner and Henn, 1976). This suggests an increasing convergence of vestibular and visual inputs centrally.

Summation of Peripheral Vestibular Input and Visual Input on Central Vestibular Neurons

The present data allow some comments on how the visual and the vestibular input converge onto central vestibular cells. Theoretical possibilities include an algebraic summation of inputs, a weighted summation, or a switching mechanism. By switching mechanism we mean that either the visual *or* the peripheral vestibular input is allowed to pass activity onto the units while the other input is turned off. A combination of these different mechanisms is also possible, each working over a certain range.

For the acceleration and constant velocity period experimental evidence seems to favour the switching hypothesis. To proove this one has to compare the results of vestibular-visual stimulation with either stimulation alone (Figs. 7, 8, 9). The period of acceleration and the time immediately after seems to be dominated entirely by the vestibular stimulus.

During the period of constant velocity the response was entirely dominated by the visual input, i.e., there was no difference in unit activity whether the animal was rotated in the light or whether only the surround was rotated around the stationary animal. The period of switch-over from the vestibular to the visual dominance is particularly interesting. At the point where the vestibular activity falls to the level of visual activity, the visual input seems to take over and determine the further response (Figs. 7, 9). During deceleration the visual input dominates the response in type II units, if the visual channel is not previously saturated (Fig. 9B). For type II units with the visual input saturated, and most type I units, the vestibular response is added to the visual one. It seems that in such situations the visual input is not strong enough to shunt off the vestibular input. The moment the velocity of saturation was approached and crossed, the visual input again contributed and balanced off the vestibular input. The conclusions reached should be regarded as hypotheses which still have to be tested over the whole range of stimulus accelerations and velocities. Also, it would be desirable to test the units while animals are exposed to conflicting stimuli, i.e. the turntable and the visual surround moving in the same direction, or the two moving with different accelerations and velocities.

Comparison with Data from the Goldfish

So far, in only one other animal, the goldfish, has a similar investigation been done (Allum et al., 1976). Results are similar in that all central vestibular units in the goldfish can be influenced by whole-field optokinetic stimulation. There are however differences when comparing the two sets of data quantitatively. In particular it is important to consider: 1. the monkey has a vestibular projection to the thalamus and cortex, where a further interaction between vestibular and visual input occurs, 2. the goldfish were paralyzed and could not move their eyes. In the monkey comparable open-loop experiments have been done (Koerner and Schiller, 1972): while stimulating one eye that was immobilized, nystagmus was recorded from the other eye, which could move normally. Under such conditions even very small optokinetic stimulus velocities (less than 5°/sec) evoked nystagmus velocities more than 30 times faster than stimulus velocity. For the monkey, and possibly for the goldfish also, it would mean that most vestibular units were already saturated to the input of the visual channel. In the goldfish, experimental results pointed towards a weighted summation of visual and vestibular input, a result which is comparable to the monkey experiments if the visual stimulus is always in the range above saturation.

Possible Functional Significance of Visual Channel Acting on Vestibular Neurons

The functional significance of the visual signal modifying vestibular unit activity seems to be to provide the animal with an accurate velocity signal rather than only with information about acceleration (Dichgans et al., 1973). The vestibular system if relying solely on peripheral vestibular input primarily gets information about accelerations. Fernandez and Goldberg (1971) determined transfer functions for peripheral vestibular neurons while animals (squirrel monkey) were rotated sinusoidally. Only in the upper frequency range, i.e. above 0.1 Hz, did unit activity reflect stimulus velocity. In the lower frequency range an increasing phase angle was seen, so that at low frequencies unit activity could be closer related to acceleration.

Preliminary experiments in our laboratory show that the phase angles of vestibular nucleus units at low frequencies are similar to those of peripheral units. This is in agreement with experiments done in the cat (Melvill Jones and Milsum, 1971) and the gerbil (Schneider and Anderson, 1976). From the present experiments we would predict that the visual stimulus in combination with the vestibular one would abolish the large phase angle at low frequencies in central vestibular units resulting in a transfer function that, over the whole frequency range up to about 1 Hz, would accurately represent velocity. Assuming that a velocity signal might be the important parameter for the animal, then this combination of the two inputs reduces the shortcomings of either transfer characteristics alone, i.e. the poor vestibular response at low frequencies, and the poor visual one at high frequencies. If the combination of visual and vestibular input occurs already at the level of the vestibular nucleus, then the in-

formation as to which peripheral channel transmits the information about velocity or acceleration gets lost. However, reflex actions like nystagmus or postural changes should be the same. A combination of vestibular and visual input at the level of the vestibular nucleus would ensure this.

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Received October 10, 1976