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The Velocity Response of Vestibular Nucleus Neurons During Vestibular, Visual, and Combined Angular Acceleration*

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Summary. In alert Rhesus monkeys neuronal activity in the vestibular nuclei was measured during horizontal angular acceleration in darkness, acceleration of an optokinetic stimulus, and combined visual-vestibular stimulation. The working ranges for visual input velocity and acceleration extend up to 60°/s and 5°/s^2. The corresponding working range for vestibular input acceleration is wider and time-dependent. During combined stimulation, that is acceleration of the monkey in the light, a linear relation between neuronal activity and velocity could be established for all neurons. Type I vestibular plus eye movement neurons displayed the greatest sensitivity and had a small linear range of operation. Other vestibular neurons were less sensitive but had a larger range of linear response to different values of acceleration. Accelerating the animal and visual surround, simultaneously but in opposite directions, results in neuronal activity proportional to relative velocity over a limited range.

Key words: Vestibular nucleus neurons – Visual-vestibular stimulation – Nystagmus – Alert monkeys

For several species it is documented that vestibular nucleus neurons, receiving their input from the horizontal canals, can reliably be modulated by optokinetic stimulation (Allum et al., 1976; Azzena et al., 1974; Dichgans and Brandt, 1972; Dichgans et al., 1973; Henn et al., 1974; Keller and Precht, 1978; Waespe and Henn, 1977a). The functional interpretation put forward is that thereby a true velocity signal becomes available even during periods of constant velocity rotation and during deceleration in the light. For the alert monkey, we have shown that neurons saturate to higher values of constant velocity visual stimulation, the saturation velocity on the average being 60°/s (Waespe and Henn, 1977a). In all studies including our own, only short durations and very limited values for the acceleration of the optokinetic and vestibular stimulus

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were used. To investigate the working ranges of neurons during different values of vestibular, visual, or combined acceleration, the present study was undertaken. Fully alert animals were exposed to different combinations of visual and vestibular stimulations to which they responded with adequate nystagmus, while single neurons were recorded in the vestibular nuclei.

Methods

Three Rhesus monkeys (Macaca mulatta) were chronically prepared by implanting a ring for fixing the micromanipulator above a trephine hole in the skull, Ag–AgCl-electrodes to monitor eye position, and skull bolts to clamp the animal's head during experiments (further details, Waespe and Henn, 1977a, b). Neuronal activity was recorded extracellularly with varnish-insulated tungsten electrodes. Animals were placed on a servo-controlled turntable with their heads bent forward and fixed to bring the lateral semicircular canals into the horizontal plane. The turntable was totally enclosed by an optokinetic cylinder, which could be accelerated independently. During vestibular stimulation in the dark, this cylinder served as a lightproof enclosure. During optokinetic stimulation, the cylinder was illuminated from within and rotated around the stationary monkey. During combined stimulation, the monkey was rotated inside the stationary illuminated cylinder. Finally, both the turntable and cylinder were rotated simultaneously but in opposite directions, therefore doubling the relative accelerations and velocities of either stimulus alone.

Animals were kept light-adapted except for the short periods of vestibular stimulation. Eye movements were calibrated by rotating the optokinetic cylinder at constant velocity. Nystagmus velocity then equals stimulus velocity up to about 100°/s (Cohen et al., 1977).

At the conclusion of all experiments lesions were placed to histologically verify the recording sites. All relevant data: neuronal activity, horizontal and vertical eye position, turntable and optokinetic stimulus velocity, head torque, a photocell-signal, and a digital time code were stored on an FM tape recorder for later analysis. Neuronal activity was averaged over 250–1000 ms (running average) and together with the other stored information written out on a rectilinear oscillograph, from which further measurements were taken.

Results

Neurons within the vestibular nuclei will be considered, which receive their peripheral input from the horizontal semicircular canals. Histology showed that they were mostly located in the rostral pole of the vestibular nuclei complex. They are conveniently classified as type I (activation during angular acceleration to the ipsilateral side) and type II with a mirror-like behavior (Duensing and Schaefer, 1958). 71 neurons were recorded, 62% were type I, 38% type II. The averaged spontaneous activity was 43.1 Hz with a range between 1 and 112 Hz. Acitivity in 48% of all neurons (66% of all type I neurons and only 19% of type II neurons) was also related to parameters of individual eye movements and/or eye position. To differentiate, neurons are classified as "vestibular plus eye movement", or "vestibular only" neurons (Fuchs and Kimm, 1975; Keller and Daniels, 1975; Miles 1974; Waespe et al., 1977; Waespe and Henn, 1979).

Vestibular Stimulation

For vestibular stimulation, monkeys were rotated about a vertical axis in complete darkness. With an acceleration value of 1.25°/s^2, 79% of the type I

neurons showed a modulation exceeding 10% of the resting discharge (Fig. 1). Type II neurons rarely responded to such low accelerations (Shimazu and Precht, 1965). With acceleration values of 2.5°/s^2, 89% of the neurons responded, with 5°/s^2 all neurons responded. During prolonged constant acceleration in the excitatory direction, the firing frequency increased with rising velocity. After 3–15 s, the frequency increase became progressively smaller and finally maintained a plateau until the end of acceleration. Neurons with low threshold and high sensitivity reached the plateau earlier than others (Figs. 1A, 3A). Type I vestibular plus eye movement neurons were the most sensitive neurons with the greatest increase in firing rate in response to increasing velocities (Fig. 3A; Waespe and Henn, 1979). Type I vestibular only or type II neurons had a lower sensitivity and reached the plateau only in the late phase of acceleration (Figs. 1A, 2A, 4A). During constant velocity rotation, frequency decayed with a time constant between 10 and 25 s (Buettner et al., 1978). The same observations can be made for accelerations in the inhibitory direction. This decremental time constant depended on the state of habituation of the monkey, and was similar to the time constant of nystagmus. At any given time, it was similar for all neurons tested.

The incremental time constant during acceleration (Shimazu and Precht, 1965), however, differed for different types of neurons in the same animal. The smallest values were found for type I plus eye movement neurons (Fig. 3A), and larger values for type II neurons (Fig. 4A). These different values reflect the different linear working ranges of the vestibular response. Also, incremental time constants progressively decreased with increasing acceleration values: from 6.7 s (range 3.8–13 s) at 2.5 deg/s^2 to 4.6 s (range 3.0–7.8 s) at 10 deg/s^2 (n = 9). Similar small values have been reported in anesthetized animals (Shinoda and Yoshida, 1974).

In conclusion, the vestibular response is time-dependent: above a lower limit of acceleration and up to about 5 s, neuronal activity is proportional to actual velocity; for accelerations exceeding 10 s, neuronal activity becomes proportional to acceleration.

Optokinetic Stimulation

For optokinetic stimulation, the visual surround was rotated around the stationary monkey. All neurons responded to the optokinetic stimulus above a certain absolute velocity. The response was direction specific, i.e., neurons were activated (or inhibited) when the cylinder and chair rotation were in opposite directions, each eliciting nystagmus into the same direction. Neurons were tested with the same stimulus parameters as for vestibular stimulation. If acceleration was below 5°/s^2, the response was strictly proportional to the instantaneous velocity over a wide range. With an acceleration of 1.25°/s^2 neurons showed the first sign of frequency increase when a velocity of 3.3°/s was reached (averaged values from 15 neurons, range 0.3 to 11.5°/s). The average upper velocity limit, beyond which no further activity increase occurred was 60°/s with a range between 40 to 100°/s (n = 18 neurons). Type I vestibular plus

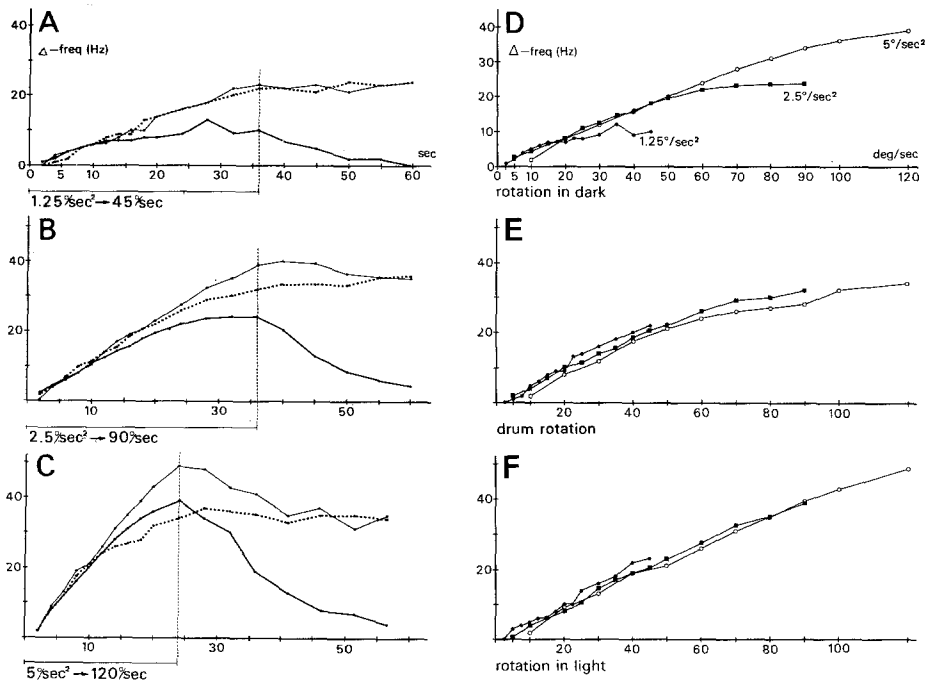

Fig. 1A–F. Activity of a type I vestibular only neuron. Abscissa is time (**A–C**) or velocity (**D–F**) after start of acceleration, ordinate is frequency increase above resting discharge taken from single measurements. In **A–C**, different values of acceleration and angular velocity were used as shown below each figure; length of bar indicates duration of acceleration. Heavy line is response to vestibular stimulation, dotted line to visual, and thin line to combined visual-vestibular stimulation. In **D–F**, the same accelerations are replotted on a velocity scale as abscissa for the three different stimulus conditions. During visual stimulation in **E**, neuronal activity saturates, when a velocity of 80°/s is reached. In **F**, during acceleration in the light, a linear relationship between neuronal activity and velocity can be established over the whole range tested, independent of the value of acceleration

eye movement neurons had the lowest saturation values (Fig. 3B), whereas type I vestibular only and type II neurons could reach much higher values (Fig. 1E). Deviations from the velocity function occurred with visual accelerations exceeding 5–10°/s² for most neurons: activity increase then lags the velocity signal. During constant velocity rotation, neuronal frequency remained constant. With low values of visual acceleration neuronal activation is always stronger than with the equivalent vestibular stimulation. For type I neurons the visual input is stronger for accelerations up to 2.5°/s² (Fig. 3) and for type II neurons up to 5°/s² (Fig. 2, 4), when related to stimulus velocity.

In conclusion, the visually mediated input to the vestibular neurons discriminates velocities between 3 and 60°/s, and accelerations between 0 and 5°/s². Within these limits, neuronal activity is proportional to actual velocity independent of the duration of the stimulus.

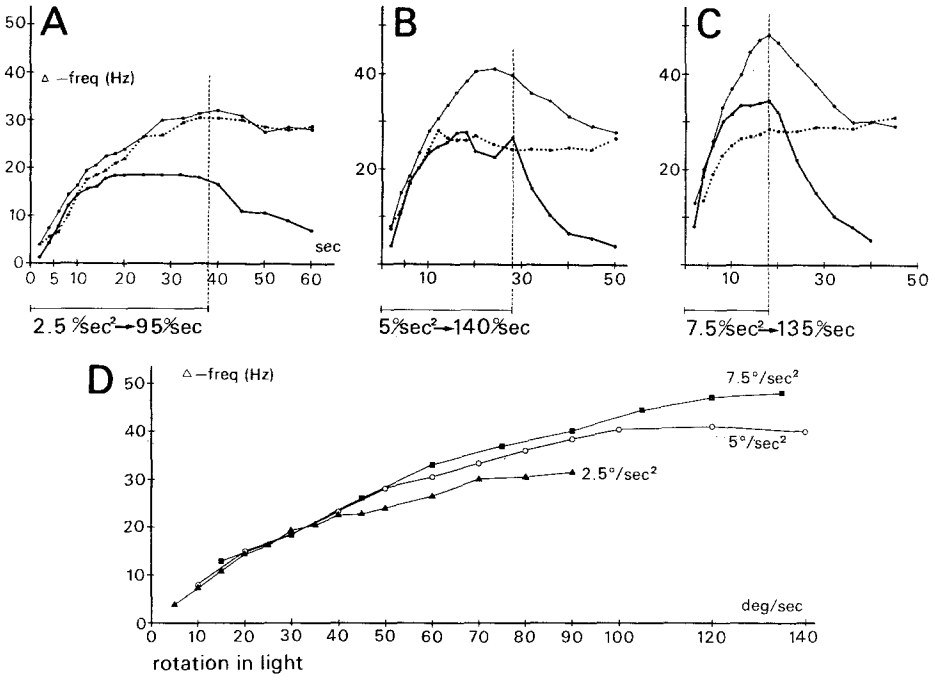

Fig. 2A–D. Activity of a type II vestibular only neuron over a range of vestibular, visual, or combined accelerations. Values averaged from 2–5 single measurements. In **A–C,** abscissa is time in s after start of acceleration, ordinate is frequency increase above resting discharge. In **A**, acceleration was 2.5°/s² to a constant velocity of 95°/s, in **B** and **C** as indicated; length of bar shows duration of acceleration. Heavy line represents neuronal activation during vestibular stimulation, dotted line during visual stimulation, and the thin line during combined stimulation. In **D** the same values obtained during combined stimulation are replotted for the acceleration phase: ordinate again is frequency increase, abscissa is instantaneous velocity. Over a wide range, a linear relation between velocity and neuronal activity, independent of the value of acceleration can be established

Combined Visual-vestibular Stimulation

For combined stimulation, the monkey was rotated inside the stationary optokinetic drum in the light. Again, neurons were tested with the same ranges of accelerations and velocities, and results were compared to those with vestibular and optokinetic stimulation alone (Figs. 1–4). As a general result, during combined stimulation, neuronal activity is proportional to actual velocity over a wider range compared with the ranges found with vestibular or visual stimulation alone. Figure 1 illustrates an example: During rotation in the light (F) neuronal frequency is a function of velocity over the whole range tested up to 120°/s. At that velocity a frequency increase of 46 Hz was measured, a frequency neither reached during vestibular nor visual stimulation alone (D and E). Certain characteristic differences could be noted between the different types of neurons. Type I vestibular plus eye movement neurons usually had a high sensitivity (ratio of frequency increase to velocity increase), but a limited range

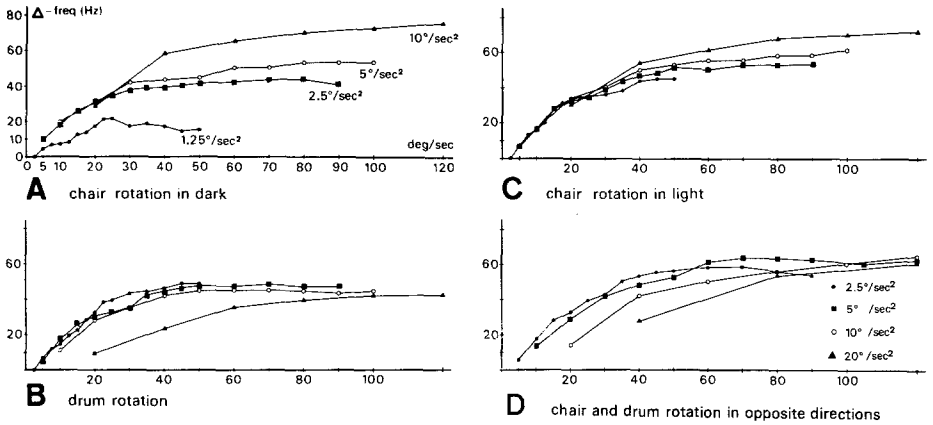

Fig. 3A–D. Type I vestibular plus eye movement neuron under different stimulus conditions with varying values of acceleration. Abscissa is instantaneous velocity of the respective stimulus, ordinate frequency increase above resting discharge averaged from 2–4 single measurements. In **A**, during vestibular stimulation, acceleration with 1.25°/s^2 gives only little response. In **B**, during visual stimulation, activity lags stimulus velocity with acceleration of 10°/s^2. Only in **C**, during combined visual-vestibular stimulation, is there a linear relationship independent of the value of acceleration up to about 20°/s. In **D**, turntable and optokinetic drum were rotated in opposite directions, so that the relative velocity between surround and monkey doubles (all numbers refer to relative velocity or acceleration). Therefore, at high acceleration values neuronal activity lags stimulus velocity

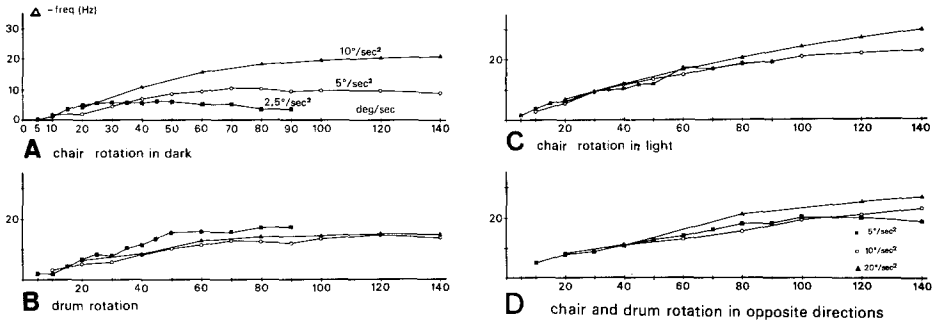

Fig. 4A–D. Type II vestibular only neuron. Format of display the same as in Fig. 3, values averaged from 3–5 single measurements. Again only during rotation in the light (**C**), neuronal activity can be linearly related to actual velocity, independent of the value of acceleration

over which activity was proportional to velocity (Fig. 3C). The high sensitivity can be seen as a strong increase in neuronal activity to velocities between 5 and 20°/s. Beyond 20°/s neuronal activity rises only slowly and reaches a plateau at about 60°/s. For the neuron in Fig. 3 the frequency increase between 5 and 20°/s is linear, and independent of the acceleration applied (sensitivity 1.78 Hz/deg.s^{-1}, regression coefficient r = 0.98).

Other type I vestibular plus eye movement neurons exhibited similar features. The relationship between stimulus velocity and frequency increase

Table 1. Range of linear velocity function for different types of neurons during combined visual-vestibular stimulation

	Number	Linear velocity function (r>0.9)		Sensitivity	
	n	Up to an average of deg.s^{-1}	Upper limit of range deg.s^{-1}	Average Hz/deg.s^{-1}	Range Hz/deg.s^{-1}
Type I vest. plus eye mov.	14	40	15–90	1.63	0.48–4.33
Type I vest. only	7	75	35–>140	0.76	0.40–1.16
Type II (all subgroups)	10	105	60–>140	0.38	0.16–0.54

could be linearly approximated (r>0.9) for velocities up to values between 15 and 90°/s independent of the acceleration applied (Table 1). For higher velocities frequency approached a plateau similar to that shown in Fig. 3C. Type I vestibular only neurons characteristically exhibited a lower sensitivity and a wider linear range (Fig. 1). Type II neurons also had, on average, a low gain and a wide linear range over which neuronal activity was proportional to velocity (Figs. 2D, 4C). All neurons tested over the appropriate range of stimuli fitted the above generalizations.

Differences between type I vestibular plus eye movement, vestibular only and type II neurons point towards a separation of widely overlapping working ranges. The one common feature is that visual and vestibular inputs combine in such a way as to produce a signal which is proportional to actual velocity independent of the values of acceleration. This linear relationship covers a wider range of velocities or accelerations than the vestibular or visual stimulation alone.

Different Combinations of Visual-vestibular Stimulation

Knowing the velocity and acceleration ranges over which neurons respond linearly to vestibular and visual stimulation, these two modes of stimuli can now be combined in arbitrary ways. One such combination is to accelerate the monkey in one direction and the optokinetic drum into the other direction with the same stimulus parameters. This leads to a relative visual acceleration which is double the angular acceleration of the turntable (Figs. 3D and 4D). Turntable acceleration of 1.25 and 2.5°/s^2, doubled by visual acceleration to values of 2.5 and 5°/s^2, lead to a neuronal activation related to velocity in the same way as is turntable rotation alone. For the type II neuron with low sensitivity and a wide linear range in Fig. 4D, the increase in activity can be related to relative velocity up to accelerations of 10°/s^2, being doubled by the visual stimulus to 20°/s^2. However, the activity of the type I neuron in Fig. 3 lags velocity at these higher acceleration. In all cases, the behavior of neurons during combined stimulation with a rotating optokinetic drum and a counter-rotating-turntable could be predicted from the response to the two stimuli given separately.

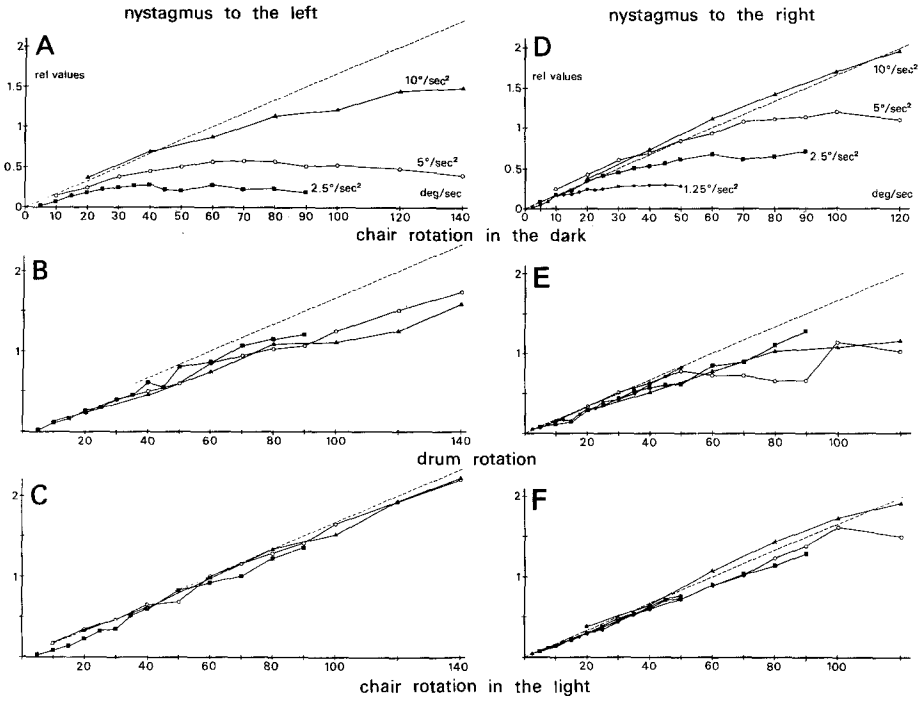

Fig. 5A–F. Slow-phase of nystagmus, velocity measurements on monkey 32. The nystagmus to the left shown in **A–C** occurred during the recording of the neuron shown in Fig. 4 (type II). Nystagmus to the right shown in **D–F** occurred during the recording of the neuron in Fig. 3 (type I). Nystagmus slow-phase velocity is plotted in the same format as the figures displaying the concomitant neuronal data. Nystagmus slow-phase velocity closely followed the single neuron activity, but always had a wider range of linearity. During prolonged acceleration in the dark, nystagmus slow-phase velocity lags actual velocity. During optokinetic stimulation, nystagmus has a gain near unity up to about 50–70°/s, and gain decreases for higher velocities. During combined stimulation nystagmus has a gain near unity independent of nystagmus asymmetry (compare the two upper graphs **A** and **D**). Values for a gain of unity are shown by a dotted line

Another combination of visual-vestibular stimulation has already been described (Waespe and Henn, 1978). In these experiments the monkey was rotated together with the drum so that during acceleration in the light no visual displacement took place as long as no nystagmus was elicited. As expected, the vestibular input dominated the response during high acceleration, and the visual input dominated at the low acceleration values.

Nystagmus Slow-phase Velocity

In all experiments, nystagmus was measured continuously. The values of nystagmus slow-phase velocity closely followed the changes in single neuron activity, but nystagmus had a wider range of linearity. Figure 5 shows a

typical example, measured during the recording of neurons in Figs. 3 and 4, and plotted in the same format. During prolonged acceleration in the dark, nystagmus slow-phase velocity already lags actual velocity after a few seconds. During acceleration of the optokinetic stimulus, nystagmus has a gain of near unity up to about 50°/s, which decreases at higher velocities. During constant velocity optokinetic stimulation gain remains at unity for values exceeding 100°/s, however such velocities are reached only several seconds after termination of acceleration. During combined stimulation, slow-phase velocity has a gain near unity independent of the duration of acceleration. Any asymmetries in vestibular nystagmus, or some spontaneous nystagmus in the dark, is fully compensated for during acceleration in the light (Fig. 5). Acceleration of monkey and visual surround into opposite directions resulted also in a nystagmus response with a gain near unity (tested for relative accelerations up to 20°/s^2).

In conclusion, vestibular nystagmus and optokinetic nystagmus combine in such a way that during combined stimulation nystagmus gain is near unity and is proportional to velocity over a much wider range than during vestibular or optokinetic stimulation alone.

Discussion

In the series of experiments presented above the acceleration of a visual, vestibular, or combined stimulus was systematically varied. For optokinetic stimulation, results showed that all neurons changed their frequency according to the relative velocity between visual surround and animal as long as acceleration values did not exceed 5°/s^2. In a previous paper we defined the upper working range of vestibular neurons in response to constant velocities of visual stimulation (Waespe and Henn, 1977a). On the average neuronal activity saturated at constant velocities above 60°/s (range 40–120°/s). The present experiments confirm and extend these observations by defining the lower limit of the velocity signal to activate the neurons as 3.3°/s on the average (range 0.3 to 11.5°/s).

Type I vestibular plus eye movement neurons showed a high sensitivity and had lowest saturation velocities. Type I vestibular only and type II neurons were less sensitive and responded to higher velocities of visual stimulation. With these measurements the working range of the visual input can be defined: for type I vestibular plus eye movement neurons it is a relative visual velocity of up to 40°/s and accelerations between 0 and 5°/s^2. For the other neurons the upper velocity limit is up to 120°/s, and effective accelerations can reach values of up to 10°/s^2.

Combined visual-vestibular stimulation, i.e., rotating the animal within the stationary cylinder, has the effect that the working range becomes extended and independent of the acceleration applied. During combined stimulation the working range is now defined by the lower limits of the visual input and the higher limits of the vestibular input. Within this range instantaneous velocity during acceleration and neuronal activity are linearly related. For type I

vestibular plus eye movement neurons this linear range extends over velocities between 0 and 90°/s. For other types of neurons the range extends up to more than 140°/s. The advantage of presenting the data in this format is that the neuronal response can be described by one linear equation, independent of the value or duration of acceleration. It also permits the prediction of the neuronal response to combined stimulation, knowing the response to either stimulus alone.

It emerges that vestibular neurons can be separated in groups with high sensitivity and limited linear range of the response, and neurons with a lower sensitivity which respond over much wider ranges of velocities. During low constant accelerations, first the highly sensitive neurons would become active, and only later would the other neurons be recruited. An interesting problem then is whether the summed output of all these neurons is equivalent to a linearly rising activity in response to a constantly increasing velocity.

Making the assumption that during most movements under natural conditions, a combined visual-vestibular stimulation occurs, neurons in the vestibular nuclei then transmit a signal which is proportional to actual velocity. Constant angular velocity rotation probably occurs rarely under natural conditions, so that the visual saturation to constant velocities above 60°/s would pose no severe limitation. Also, in our investigation, only the visual input was considered although information from other sensory systems converge onto the vestibular nuclei, especially from proprioceptive systems (Rubin et al., 1977). Therefore we tend to consider the vestibular nuclei as a system which gathers and conveys information about velocity. Only if the vestibular nuclei are deprived of some of their physiological inputs, a signal is measured which is proportional to acceleration rather than velocity.

When different combinations of stimuli were applied by rotating the turntable and drum simultaneously into opposite directions, the visual input could strongly modify the vestibular signal in the low acceleration range, so that again neuronal activity was in fact proportional to the relative velocity between the visual surround and the animal. This mechanism is obviously of advantage to compensate for asymmetry in vestibular activation or for spontaneous nystagmus. Therefore, vestibular activity again becomes symmetrical, and neuronal activity proportional to actual velocity during rotation in the light, even in animals with some spontaneous nystagmus in the dark and after small brainstem lesions.

Several attempts have been made to describe visual-vestibular interaction quantitatively and to model it. Allum et al. (1976) used goldfish data, Robinson (1977) monkey data. Also, other models, originally developed for nystagmus generation (Raphan et al., 1977), or subjective sensation (Young, 1970; Zacharias and Young, 1979) have proved to be valuable. In a previous paper (Waespe and Henn, 1977a), we proposed a "switching" between visual and vestibular input to describe the behavior of neurons during combined stimulation. The data presented above show that such a description is insufficient.

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