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The Effect of Tilt on the Response of Vestibular Nucleus Neurones to Horizontal Angular Acceleration in the Rat

LAURENCE R. HARRIS*

From the Department of Psychology, University of Durham, Durham, England

The vestibular nucleus (VN) is a site of considerable convergence of information. The signal leaving the VN of an alert animal contains information about eye position (Fuchs & Kimm, 1975) and visual slip (Cazin et al., 1980), as well as head movement. In the cat, angular and linear acceleration signals converge on cells in the VN (Duensing & Schaefer, 1959; Curthoys & Markham, 1971).

When an animal is rotated about an axis that is tilted with respect to gravity (an off-earth-vertical axis: OEVA) the vestibulo-ocular reflex is affected (Goldberg & Fernandez, 1982). Such a rotation represents changes in linear acceleration due to changes in orientation with respect to gravity with concomitant angular accelerations. The pattern of eye movement evoked suggests a convergence between information about angular and linear acceleration. In this paper I describe the effect of simultaneous changes in linear and angular accelerations which occur during rotation about an OEVA on responses of VN neurones.

METHODS

VN neurones responding to horizontal angular acceleration were recorded in eighteen normally-pigmented rats, lightly anaesthetized with urethane (25 mg/kg/h; IV). The animal was mounted in a stereotaxic apparatus on a table that could be rotated by a DC servo motor (motor 1). The animal's eyes were occluded with masking tape. The head was tilted so that the horizontal canals were approximately orthogonal to the axis of rotation. The entire table (including motor 1) could also be rotated about an earth horizontal axis by a second servo motor (motor 2). The two motors were controlled by a PDP 11/34 computer which produced the following patterns of stimulation illustrated in Fig. 1: (*a*) Sinusoidal rotation about an EVA (Fig. 1*a*). (*b*) Sinusoidal roll (Fig. 1*b*) or pitch (Fig. 1*c*). (*c*) Rotation in the plane of the horizontal canals (yaw: motor 1) with the animal in a tilted position, either nose up (Fig. 1*d*) or nose down (Fig. 1*e*) with respect to gravity. In these conditions, sinusoidal yaw produces not only horizontal canal stimulation identical to that produced with the animal horizontal, but also changes in roll and pitch with respect to gravity (Fig. 1*d* and *e*).

Histograms of single cell firing rate were accumulated by the computer which also monitored the position of the tables by means of potentiometers. Sinewaves were fitted by a least-squares linear regression (using 64 bins/cycle) to

$$y=A \sin (x+\varphi)+B$$

where y=firing rate; φ=phase; A=depth of modulation; x=bin; B=dc offset. This process was applied both to the cells' responses and to the signal obtained from the potentiometers attached to the table. The method allows the fitting of a sinewave to even a partial curve so

* Present address: Department of Physiology, University College, Cardiff, Wales.

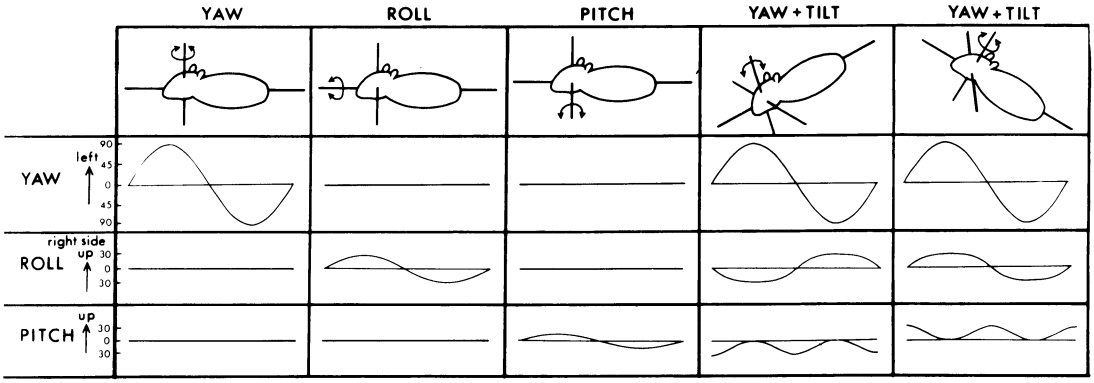

Fig. 1. The position changes through which an animal moves in each plane (yaw, pitch, roll) for five stimulus conditions. While the yaw rotation is shown with respect to the animal (an axis orthogonal to the horizontal semicircular canals) the roll and pitch stimuli are with respect to gravity. Columns *d* and *e* show +/−90 deg sinusoidal yaw rotation about an OEVA with the animal in a tilted position with the nose either 30 degs up (*d*) or down (*e*). The roll and pitch caused by tilting the yaw axis is given by: pitch=arc sin (sin tilt×cos ∅), roll=arc sin (sin tilt×sin ∅), where ∅ is the angle of yaw from the straight ahead. For a +/−90 deg sinusoidal yaw (shown here), the roll component approximates a sinewave of +/− angle of tilt.

that bins with no response (representing inhibition) could be ignored and hypothetical best-fit sinewaves with negative values of firing rate produced.

At the end of an experiment an electrolytic lesion was made and the animal killed by an overdose of Nembutal. The sites of recorded cells were histologically reconstructed. All the cells from which data are presented were located in the medial or superior vestibular nuclei.

RESULTS

Thirty-one VN cells (47%) responded to ipsilateral rotation (type I); thirty-five (53%) to contralateral rotation (type II). All sixty-six cells showed qualitatively the same effect of tilting the axis with respect to gravity. All cells responded both to yaw and roll. The response to yaw depended on the tilt of the axis of rotation with respect to gravity.

Sinusoidal yaw (of constant amplitude) was given at different frequencies around EVA and OEVAs. Fig. 2 shows gain and phase plots (Bode plots) with respect to velocity about the yaw axis in both EVA and OEVA conditions. The shaded areas represent +/−1 SD of the responses of all 66 cells. Gain and phase plots of examples of type I and type II cells are superimposed on the shaded areas.

At low frequencies of rotation about an EVA the phase of response lags behind the velocity of the stimulus and the gain increases with frequency. Above about 0.1 Hz the phase approaches 0 degs with respect to velocity and gain stays roughly constant with further increase of frequency. Tilt of the axis of rotation dramatically increases the gain, especially at frequencies of oscillation below about 0.1 Hz. Phase is also altered by tilt. At low frequencies there is a large increase in phase lag for 30/31 type I cells during nose-down tilt and for 1/31 type I and all type II cells during nose-up tilt. A lead is produced in 30/31 type I cells during nose-up tilt and in 1/31 type I and all type II cells during nose-down tilt.

The difference between the response to rotation around an EVA and around an OEVA

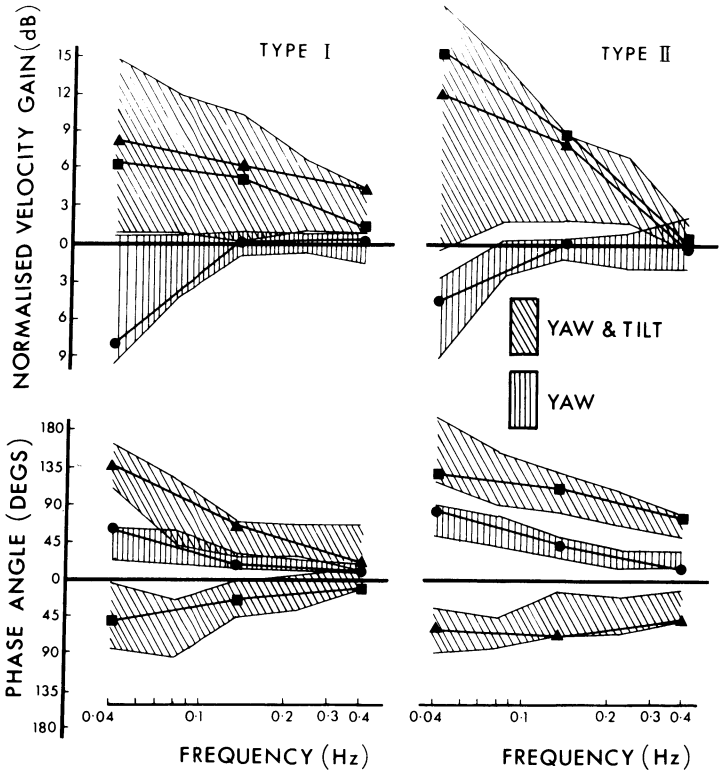

Fig. 2. Bode plots of the response of typical type I (left) and type II (right) cells to rotation around an EVA (●) or an OEVA tilted up (■) or down (▲) by 30 degs. The shaded areas show +/−1 SD of the mean responses. Gain (top graphs) is defined as depth of modulation/peak angular velocity of yaw and has been normalized to the 0.1 Hz stimulus (EVA) and expressed in dB. Phase (bottom graphs) is relative to the peak velocity of yaw.

can most easily be measured and visualized on a polar plot in which the gain is represented as the length of the vector and the phase by its angle.

The effect of a 30 deg tilt on the response at each frequency of yaw oscillation is shown by the vector joining the points representing the responses to stimulation around an EVA and an OEVA. This difference vector can be adequately accounted for by the response of the cell to the rolling motion that is introduced by tilting the yaw axis (see Fig. 1 *d*). The response to rolling (+/−30 degs: i.e. the roll introduced by tilting the yaw axis) is also plotted in Fig. 3 *a* (0.04 Hz) to compare the response to the composite stimulus with the response to each component alone. The sum of the responses to roll and to yaw around an EVA is very close to the response to yaw around the OEVA. This implies a linear addition of information from different parts of the vestibular end organ in the VN. The gain and phase at 0.4 Hz stimulation are shown for +/−15 deg tilts as well as for +/−30 deg. The difference vectors between the response to rotation about an EVA and OEVA tilted by 15 degs is close to half that between an EVA and 30 degs of tilt and with a similar phase angle: the points fall on a straight line.

The source of the roll response could be either the movement-detecting vertical canals or the tilt-detecting otoliths. To distinguish these possibilities some cells were tested with roll around the animal-horizontal position and then with the animal upside down. Stimulation in the roll or pitch planes with the animal upside down should produce a 180 deg phase shift (with respect to the movement of the table) if the response is otolithic in origin (since the orientation of the otoliths has been inverted) but no phase change if the responses are to angular acceleration alone. The response of 10 units successfully held during inversion, showed a 180 deg phase shift implying that the change in response was of otolithic origin.

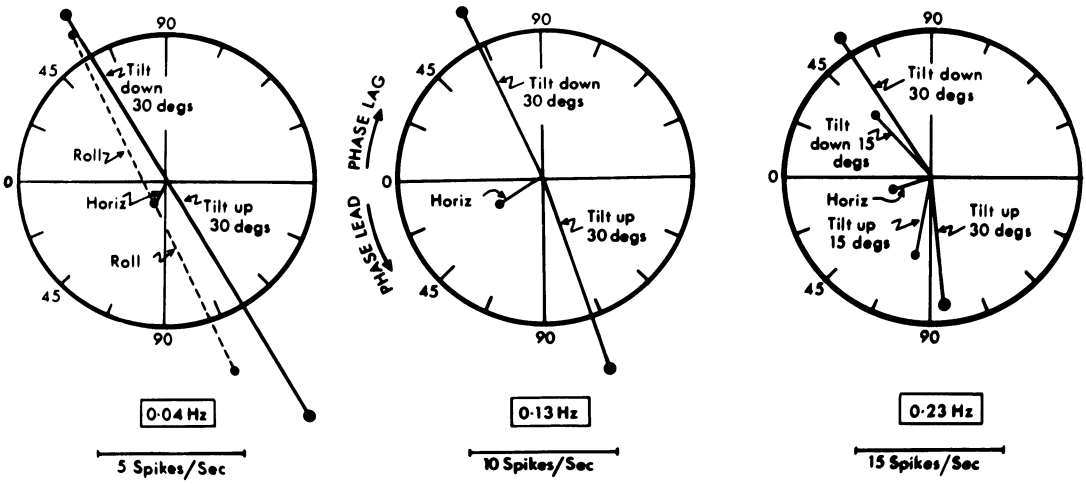

Fig. 3. Polar plots of the response at three frequencies of yaw stimulation around an EVA and an OEVA. The length of the vectors represent the depth of modulation of response (note the different scales for different frequencies shown below each plot). The angle represents the phase relative to the peak velocity of yaw rotation. Also shown for 0.04 Hz (left) is the response to appropriate roll alone (dashed line).

DISCUSSION

Convergence between vestibular signals produced by angular acceleration and those produced by linear acceleration has been demonstrated at many levels. Convergence of the two systems is necessary at some stage to explain the pattern of eye movements produced when an animal is rotated about an OEVA (Goldberg & Fernandez, 1982). Recordings from the primary vestibular fibres innervating the horizontal canal show changes with static tilt (Estes et al., 1975). Primary afferents are, however, not sufficiently sensitive to changes in orientation with respect to gravity to account for the influence of gravity on secondary neurones.

Fibres innervating the otoliths and horizontal canals converge on secondary VN cells (Duensing & Schaefer, 1959). Curthoys & Markham (1971) showed that 53.2% of cat VN neurones responding to angular accelerations change their firing rate in response to static tilt. In fact only 52% (34/66) of the cells in the present study showed an influence of static tilt, but all showed some change in the response to horizontal canal stimulation in the presence of tilt.

It may be significant that these data were obtained from rats—animals that have their eyes laterally positioned. Furthermore, convergence seems to be found on all horizontal acceleration units. It may be that an animal with laterally positioned eyes extracts more advantage from the integration of gravity detectors with angular accelerator detectors.

Since the gain of the response to rotation about an EVA falls off at low frequencies, it is at these low frequencies that the response can most usefully be supplemented by other systems. For example the visual system, which operates best at low velocities, normally improves the efficiency of head movement compensation (Robinson, 1977). Indeed the visual system can improve the low frequency response of VN neurones in the rat (Cazin et al., 1980). It now appears that the low frequency response of VN neurones can also be supplemented by the otolithic system whenever head rotation is not around the true earth-vertical axis.

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L. R. Harris, Department of Psychology, University of Durham, Durham, England.