Response of Mammalian Gravity Receptors to Sustained Tilt

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It has been demonstrated that subjective responses to prolonged angular accelerations may diminish in amplitude, even though the stimulus persists and the output of the sense organ theoretically increases in magnitude.[3] These observations indicate that vestibular responses are made primarily to transient accelerations and that considerable adaptation occurs if the stimuli are extended over time.

Some of this decay can be attributed to changes in the sensory side of the stimulus-response system. It is known that the projections of the horizontal ampulla in the medial vestibular nucleus do not maintain their responses to extended angular accelerations and that the decay of response is at least partially attributable to central neural activity.[2] Lowenstein and Roberts[4] have reported some decay in the response of isolated elasmobranch gravity receptors. Adrian[1] found some decline of the response to prolonged tilt, presumably in the medial vestibular nucleus in cat. In these cases, however, this decline was mentioned only incidentally.

This study was selected as a starting point for studies of vestibular adaptation for two reasons: (1) technical simplicity in operative procedures and in the maintenance of a vestibular stimulus, and (2) a desire to determine if nuclear vestibular responses unadulterated by cutaneous and proprioceptive and other infringements are subject to modification over time, provided the stimulus is held constant. In this study, the stimulus was prolonged tilt at a constant angle. In a practical situation, the stimulus could be steady-state weightlessness.

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METHOD

Cats were anesthetized with pentothal sodium administered intravenously; the common carotid arteries were ligated; and a tracheotomy was performed. The head was rigidly fixed, and the neck, high thorax, and pelvis were encasted in a plaster-of-Paris bandage secured to the cat board. A radical craniectomy was performed. The forebrain and cerebellum were removed by aspiration, sparing only the pons and medulla. Hemostatis was accomplished by intramuscular injections of Koagamin and by local application of Gelfoam. The anterior cranial cavity was packed with cotton, as were the lateral cavities produced by removal of the cerebellum. This provided some support for the brain stem against gross shifting during tilt. Heat and other physiological supporting measures were used as required.

The electrodes used in this study were made from stainless steel wire approximately 75 mm. long and 20 to 50 micra in diameter. They were electropointed to provide tips of 3 to 5 micra and were insulated with air-drying Glyptal. Impedance was approximately 30,000 ohms. These electrodes were sufficiently flexible to maintain their placement in the recording field in spite of minor shifts of the brain stem during tilting. The electrode was coupled to a Grass P-5 preamplifier; the amplified signal was led to a Tektronix 502 dual beam oscilloscope and recorded on a Grass kymograph camera. Visual and auditory monitoring were used throughout the experiment.

The micromanipulator was mounted on a board to which the cat was secured, and the electrode was driven vertically into the brain stem 1 to 3 mm. behind the stumps of the cerebellar brachia. The spinal vestibular nucleus was the target, although electrode placements have not been verified histologically. No real attempt was made to restrict action potentials to those originating in a single cell. When action potentials of two to four different magnitudes were detected, advancement of the electrode was stopped. The action potentials were monitored for any change in frequency concurrent with forward, backward, or lateral tilt of the preparation. If such a change could not be attributed to changes in the pressure exerted by the electrode or to proprioceptive, cutaneous, or ampullar activity, the preparation was adapted to the horizontal position. The camera was then started. The catboard was tipped nose down and propped in this position for approximately one and one-half minutes, returned to the horizontal for the same length of time, tipped and propped in the nose up position, and again returned to the horizontal for one and one-half minutes. The camera was then turned off and a new electrode placement sought. A similar sequence of stimuli was applied for lateral tilt receptors.

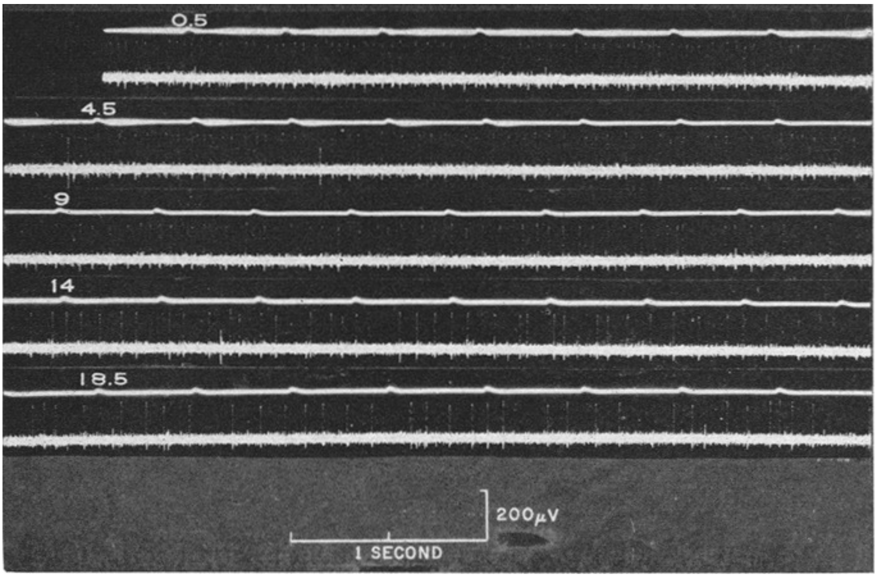

Fig. 1. Response of a single cell in one projection of the otolith organs in cat brain stem to prolonged tilt.

RESULTS

Eleven partial records of activity in the projections of the otolith organs were obtained. Undue jarring of the preparation during manipulation of the board caused dislodgment of the electrode at some point during the interval of recording in most cases. Figure 1 shows samples of the records obtained during one experiment. In this case, the recordings were made continuously from a single cell.

These potentials are approximately 175 microvolts; the time marker is one-half second. The film clip on the top line begins at zero time with side up tilt of approximately 10 degrees. It can be seen that there was a gradual decline in activity as the tilt was maintained. This decline was complete after approximately 20 seconds, and there was no steady-state indication of position. An equal tilt in the opposite direction abolished activity for at least 22 seconds, at which time jarring of the table dislodged the electrode.

Figure 2 shows the results of analysis of the responses to forward and backward tilt in another preparation. In this analysis, the impulses arising from three cell bodies were counted together. The smoothly descending curve through

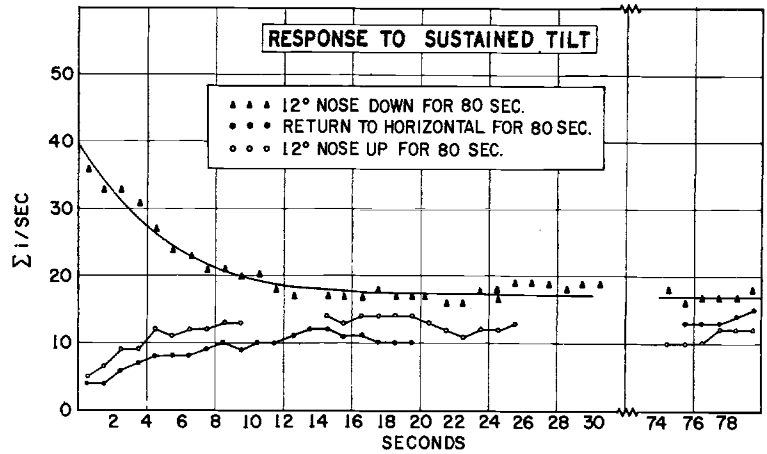

Fig. 2. Responses of three cells to three sustained positions in the gravitational field. In this case, ordinate values represent the number of impulses generated by three cells in successive one second intervals. Abscissa is the time in seconds elapsing after the preparation was established in a given position.

the response to 12 degree nose down tilt was drawn according to the function $e^{-.204t}$. In each of these tracings, the response can be divided into two components: (1) a transient lasting for 15 to 20 seconds, and (2) a steady-state signal, which only feebly represented the tilted position of the head.

This dual nature of the response was characteristic of the other recordings, with the transients disappearing in 15 to 30 seconds. These transients could be approximated by simple negative exponential functions although the exponent varied according to the extent and direction of repositioning. The steady-state signal was relatively weak in comparison to the initial magnitude of the transient.

DISCUSSION

The data obtained in this experiment indicate that in at least some projections of the otolith organs the static function of the gravity receptors is subordinate to dynamic functions in that they do not maintain any sizable response to change in position when the new position is held for any length of time.

This experiment was designed only to describe the response to prolonged tilt and not to investigate the causes for decay of the response. However, the variability in the negative exponential decay function hints that the adaptive processes may be complex even this close to the input.

It is believed the data presented here will be useful in two ways to those concerned with weightlessness during space flights: (1) In the first place, the duration of the transient indicates that steady-state responses to weightlessness should be studied in parabolic flights of more than 30 seconds duration, and (2) The relative dominance of dynamic over static responses offers some hope that the sensori-motor problems of prolonged weightlessness may be minor.

SUMMARY

Studies were made of the behavior of single cells of the projections in the otolith organs in

decerebrate and decellebrate cat as the preparation was maintained for extended times in different positions relative to the earth's gravitational field. In every case studied, it was found that there was a rather vigorous initial response to the tilt and that this response diminished considerably over 15 to 30 seconds; the steady-state signal to tilt was relatively weak.

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