periments were anesthetized with Nembutal, maintained firmly in place by means of a mouthpiece, and stimulated with a Maxwellian field subtending 90 degrees of visual angle through a pupil dilated by either phenylephrine hydrochloride or cyclopentolate hydrochloride or both. A direct-current (d-c) amplification system with silver chloride electrodes recorded both the electroretinogram and the transocular d-c potential simultaneously. One electrode was placed within Tenon's capsule, behind the globe, and the other in a corneal contact lens. The light source was a well regulated 1000-watt high-pressure Xenon arc lamp, the output of which was continuously monitored during the experiments. The monkeys were routinely dark-adapted for 20 minutes before flickering stimuli were presented to the eye. Stimulation was continued until the retinal responses reached a steady-state, the criterion being the production of a constant electroretinogram after each stimulus of the flicker.

With flickering lights which did not raise the retinal illumination greatly from the dark-adapted state, the electroretinogram came to an equilibrium with the stimulus within seconds and there was little or no detectable shift in the transocular potential. If the intensity of stimulation was greater, transient changes in the electroretinogram became prolonged and the transocular potential exhibited a slow transient increase. With moderately bright illumination, the amplitude and waveform of the electroretinogram changed considerably during the first few minutes of stimulation; thereafter the amplitude slowly increased to a maximum at 5 to 10 minutes and then decreased again to a minimum at 20 to 25 minutes. This slow oscillation of the amplitude of the electroretinogram gradually decreased in a lightly damped manner after an hour or more of maintained stimulation. The transocular potential showed a similar oscillation which appeared to be in phase with that of the electroretinogram (Fig. 1). The phenomenon occurred with either sinusoidal or square-wave light functions and with energy from both ends of the visible spectrum. The energies necessary to elicit these changes were not excessively large, being in the order of 10^{13} quanta sec^{-1} deg^{-2} at 502 $m\mu$.

Similar light-induced oscillations in the transocular d-c potential of the human eye have been described (*1*) and this study demonstrates their counterpart in the monkey. Parallel oscillations in the electroretinogram have not been reported hitherto. Biersdorf and Armington (*2*) observed that the human electroretinogram can slowly increase during light adaptation and speculated upon the possible relationship between this and a similar change in the d-c potential of the human eye. This evidence from the monkey eye strongly supports their conjecture and makes it appear likely that the oscillatory changes in the electroretinogram also occur in man.

Methods other than light stimulation which can alter the transocular d-c potential such as either electric current (*3*) or the administration of sodium azide (*4*) also influence the amplitude of the electroretinogram. These effects are relatively rapid. The slow, oscillatory behavior observed in these retinal responses appears to be a unique consequence of light stimulation.

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Vestibular Nuclei: Activity of Single Neurons during Natural Sleep and Wakefulness

Abstract. *The rate of spontaneous discharge of second-order vestibular neurons is higher during wakefulness than during drowsiness and synchronized sleep. The activity of units recorded from the lateral (and superior) vestibular nucleus remains unmodified or is slightly increased during desynchronized sleep, in spite of the complete disappearance of the postural tonus. Units in medial and descending vestibular nuclei show bursts of rapid discharge associated with the eye movements characteristic of desynchronized sleep.*

Sleep characterized by the well-known electroencephalographic patterns of slow waves and spindles (synchronized sleep) is interrupted by short episodes of low-voltage, fast waves (desynchronized sleep) (*1*, *2*). The desynchronized sleep, at least in the cat, appears to be deeper than the synchronized phase (*3*).

During episodes of desynchronized sleep, the electromyogram of the cervical antigravity muscles is silent (*2*), while rapid eye movements suddenly appear (*1*). Neurons localized

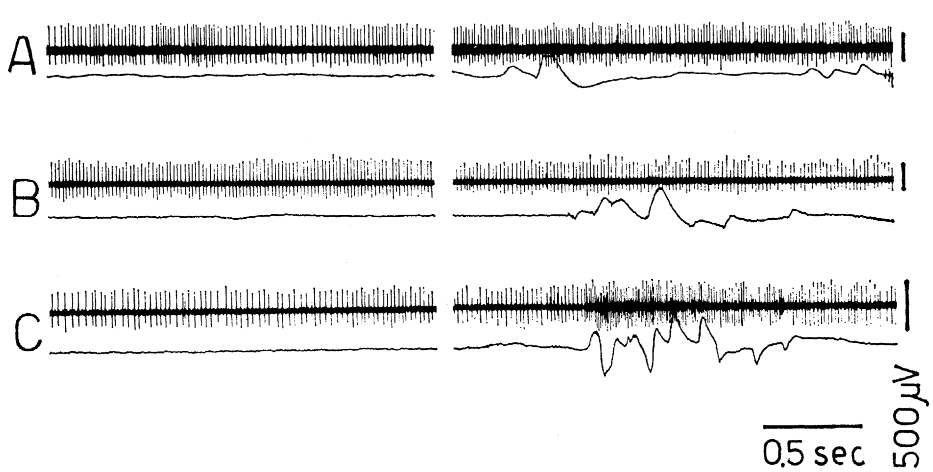

Fig. 1. Spontaneous discharge of single units recorded in different experiments from lateral (*A*), superior (*B*), and medial (*C*) vestibular nucleus during synchronized sleep (left column) and during the episodes of rapid eye movements occurring in desynchronized sleep (right column). Upper records show the unit activity; lower records show the eye movements recorded from electrodes placed above the orbit. Voltage calibrations correspond to 500 μv and apply to the units. Time calibration: 0.5 sec.

in the lateral vestibular (Deiters') nucleus exert a strong facilitatory influence on the antigravity tonus, while other neurons, localized in the remaining vestibular nuclei, control the oculomotor activity (*4*). The experiments described herein were conducted to find out (i) whether the vestibular centers, which control the cervical extensor muscles, namely the Deiters' nucleus, decrease their tonic activity during desynchronized sleep, and (ii) whether the lateral vestibular centers which control the eye muscles increase their activity during the rapid ocular movements occurring in desynchronized sleep.

The activity of single vestibular neurons was recorded in unrestrained, unanesthetized animals by means of a movable electrode system equipped with a microelectrode, described previously by other authors (*5*). Electrodes for recording electroencephalographic activity, the cervical electromyogram, and the eye movements (electronystagmography) were also permanently implanted. A total of 64 units from the brain stem in a series of 22 cats was analyzed and in each unit the spontaneous rate of discharge was recorded during different stages of natural sleep and wakefulness. Electrolytic lesions were made at the bottom of each electrode track, and the positions of the units appeared localized on the histological sections.

Thirteen out of 64 units were localized in the lateral vestibular (Deiters') nucleus. These units discharged irregularly and their mean rate of activity was higher during quiet waking than during synchronized sleep. Recording from units in a strongly aroused animal (acoustic stimulation) was technically difficult because units were frequently lost during sudden and large head movements. During transition from synchronized to desynchronized sleep, no change in spontaneous firing was observed in six units, while only a slight increase in the rate of discharge occurred in seven units. In no instance, however, was a decrease observed in the spontaneous discharge of units of the Deiters' nucleus during desynchronized sleep. Moreover, most of the Deiters' units (11 out of 13) did not show any change of spontaneous rate of firing when the episodes of rapid eye movements occurred during desynchronized sleep (Figs. 1*A* and 2*A*).

Thirteen units recorded from the superior vestibular nucleus showed more regular firing during quiet waking than the units of the Deiters' nucleus. During synchronized sleep the rate of discharge did not change in nine units and slightly decreased in four. In all cases during transition from the synchronized to the desynchronized sleep, the mean rates of spontaneous discharge did not change significantly. No alteration in the pattern of discharge could be associated with the eye movements (Figs. 1*B* and 2*B*), except in two units. These two units showed bursts of high-frequency discharge correlated with eye movements.

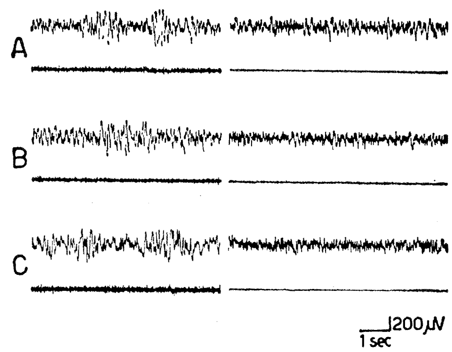

Fig. 2. Electroencephalographic records showing episodes of synchronized sleep (left column) and desynchronized sleep (right column) during which single unit activity from lateral (*A*), superior (*B*), and medial (*C*) vestibular nucleus has been recorded. Upper records show electroencephalographic activity from the temporal region; lower records, the electromyogram of the posterior cervical muscles.

Among the units recorded from the other vestibular nuclei, 18 were localized either in the medial or in the descending vestibular nuclei, while seven units were located in the most rostral part of these nuclei, very close to the caudal portion of Deiters' nucleus. All these units behaved in a similar way. Their spontaneous discharge was quite regular and their rate appeared to be higher in the aroused animal than during either quiet waking or synchronized sleep.

The rate of firing strikingly increased during desynchronized sleep in almost all the units examined. Mean rates were generally two to four times higher during desynchronized sleep than during quiet waking. The pattern of discharge consisted of bursts of rapid firing (80 to 160 spikes per second), each burst lasting for a fraction of a second (but occasionally for several seconds), followed by a period of relative or complete lack of discharge. Bursts were invariably associated with eye movements as recorded by the electrode implanted in the orbit (Figs. 1*C* and 2*C*). A similar pattern of discharge was also observed in 13 units localized in the brain stem reticular formation, in a region ventral to the medial vestibular nucleus.

The units recorded from all the vestibular nuclei never showed any change in their spontaneous firing (i) during electroencephalographic spindles and interspindle lulls, and (ii) during the voluntary eye movements occurring in the awake animal.

These experiments suggest that the abolition of the tonus in the antigravity muscles occurring during desynchronized sleep is not due to withdrawal of tonic descending facilitating influences arising in the neurons of the Deiters' nucleus. Investigations conducted along an entirely different line indicate that these effects are actually due to a supraspinal inhibitory influence exerted on spinal reflexes (*6*). On the other hand, the increased activity of most of the units localized in the medial and descending vestibular nuclei, as well as in the neighboring reticular formation, indicates that these structures are related to the rapid eye movements occurring during desynchronized sleep. The appearance of bursts of rapid discharge occurring synchronously with the eye movements might also be related to the pontine waves (themselves correlated with eye movements) which have been recorded with macroelectrodes during desynchronized sleep (*2, 7*).

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