Using the methods developed by Hubel and others, we attempted to record unitary activity from the lateral geniculate body (LGB) of freely behaving cats. This paper will report how the spontaneous unitary activity of the LGB changes during the sleep-wakefulness cycle, paying special attention to deep sleep (activated sleep).

Methods. Six cats were used. Under Nembutal anesthesia, bipolar electrodes of steel wire, insulated except the tips and stuck together side-by-side, were implanted into the optic chiasm. They were used for electrical stimulation of the optic tract with brief pulses. The skull was trephined on one side in diameter of about 8 mm over the LGB. Then, a cylinder (8 mm in inside diameter and 30 mm in height), made of alloyed aluminium, was vertically fixed to the bone concentrically with the trephined hole. The cylinder held a hydraulic micromanipulator which was made modifying the original type of Evarts. To the LGB on the remaining side, a pair of bipolar electrodes were implanted which served to record spontaneous mass activity. A pair of steel wire electrodes were also implanted to the sensorimotor cortex to obtain the electrocorticogram. Two needle electrodes were inserted acutely into the posterior neck muscles to monitor their spontaneous activity.

The LGB unitary discharges were picked up through a tungsten microelectrode which was varnished with Insl-X. The discharges were led to a conventional cathode follower preamplifier and then to a C-R-coupled amplifier and were displayed on the screen of a twin beam oscilloscope. The electrocorticogram, the electromyogram and the LGB mass activity were recorded continuously on paper. In some experiments the LGB mass activity was recorded simultaneously with the LGB unitary activity on the same film.

Experiments were performed under faint illumination or in complete darkness. A sound-proof room was not used.

Results. Identification of the LGB units was done by applying a single shock to the optic chiasm. Unit discharges which were evoked with short and invariable latencies to a chiasmatic shock...
were taken as being derived from the LGB neurons. The distribution of latency obtained from 42 units is shown in Fig. 1.1)

1. Rate and pattern of the LGB unitary discharges during sleep and arousal. The behavioral states of the freely behaving cats were devided into three, i.e., arousal (resting wakefulness), light sleep and deep one. Two types of sleep were distinguished from each other by the widely accepted, electrographic criteria.13)

Among 119 LGB units recorded, 14 units could be well held to follow their activities through arousal and the two types of sleep. It was found that the discharge rate, measured from continuous records of 10-30 seconds, was decreased from deep sleep to arousal and to light sleep. The average discharge rates obtained from these units were 16.4/sec, 15.7/sec, and 10.9/sec during deep sleep, arousal and light sleep, respectively.

During arousal there were well spaced, continuous spike discharges in the LGB (Fig. 2, A and 3, A). However, the chances to observe

Fig. 2. Sample records of the LGB unitary (upper traces) and mass (lower traces) activities during sleep-wakefulness cycle. A: arousal. B: light sleep. C: deep sleep. D: LGB unitary responses to chiasmatic shocks. Ten sweeps were superposed, among which the spike discharge appeared in three sweeps. Arrows indicate inflections on the downward (positively going) deflection of the spike. Note subliminal EPSPs in the tracings of spontaneous activity. They decreased in frequency from arousal (A) to light sleep (B) and to deep sleep (C). In C, DSWs were seen toward the end of the 4th and 6th sweeps of the mass recording as slow downward deflections.
this pattern of discharge were rather limited. When the animals became attentive toward their surroundings or external stimuli, there was seen a transient increase of the discharge rate. On the other hand, when the animals became quiet, the discharges soon tended to show the pattern which will be described below as the characteristic of light sleep.

When the animals entered light sleep, the pattern of unitary firing changed in the following way. The discharges, when occurring in a sporadic manner, were more spaced than during arousal resulting in a decrease in the mean discharge rate. But it was most notable that there was a tendency for the discharges to occur in a group which was followed for a while by a train of accelerated sporadic discharges. This is seen in the 6th to 7th sweeps and in the 9th sweep of Fig. 2,B. In some cases the grouped discharges appeared in a form of tight combination of many spikes. This is exemplified in Fig. 3,B in which a train of discharges consisting of a burst of 9 spikes and a following regular succession of isolated spikes appeared at a considerably long, silent interval.

The discharge pattern during deep sleep was generally a mixture of those seen during arousal and light sleep, though it was more alike to that during arousal, In a certain phase of deep sleep, the unit discharged regularly at a similar rate to that seen during arousal, but occasionally it tended to show grouped discharges which are characteristic of light sleep. This is exemplified by the record of Fig. 3,C. In the upper half of this figure, there were seen bursts of grouped discharges on a relatively silent background. This is similar to the pattern seen during light sleep (cf. Fig. 3,B). On the other hand, the lower

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**Fig. 3.** The LGB unitary activity during sleep and arousal. The spikes were of negative-positive sequence. A: arousal. Spikes were well spaced. B: light sleep. Grouped discharges consisting of 9 spikes and a following well-spaced regular discharges appeared at a long interval of silence. C: deep sleep. The upper half contained grouped discharges interspaced at a long silent period and the lower one rather regularly spaced discharges.
half of Fig. 3,c contained rather well-spaced, regular discharges which were characteristic of arousal (cf. Fig. 3,A).

There are many descriptions about the spontaneous slow waves which appear during deep sleep simultaneously in the pontine reticular formation, the oculomotor nucleus, the visual cortex, the LGB and other thalamic nuclei. This slow wave activity, called deep sleep wave (DSW) activity by Brooks and Bizzi, has been shown to modify impulse transmission of the LGB.

Fig. 2,c is to show a relationship of the unitary discharges and the DSW activity. In this figure the DSWs were seen toward the end of the 4th and 6th sweeps as a downward slow deflection ending into a long-sustained, low-amplitude upward deflection. As will be seen from this figure, the on-going unitary discharges were temporarily suppressed when the DSW occurred and there appeared discharges of a burst form after the DSW subsided. Also it was noted that when the grouped discharges were present, they were more or less wiped out by the DSW.

2. EPSP of the LGB unitary discharges. Fig. 2,D is a superposed record of 10 sweeps to show the detailed configuration of the spike discharge in response to chiasmatic electrostimulation. There are seen two inflections on the positively going stroke (downward deflection) of the spike (arrows). It is most probable that these two inflections are attributable to the EPSP and IS spike, respectively. The EPSPs were sometimes produced without yielding any further spike potential (subliminal EPSP). The EPSPs subliminal for spike discharge could also be seen as the spontaneous event (Fig. 2A, B, and C). In general, it was found that the frequency of occurrence of the subliminal EPSP decreased from arousal to light sleep and to deep one. As noted above, the frequency of occurrence of the full-size spike is highest during deep sleep and decreases from arousal to light sleep. This means that there are more chances for the EPSP to develop the full-size spike during deep sleep than during arousal and light sleep. However, if the frequency of occurrence of the EPSP is measured including the subliminal EPSPs and those leading to the spike discharge, it was lowest during deep sleep.

In the preceding section it was noted that the DSW acted to suppress the spontaneous spike discharge. This suppressing effect of the DSW seems to be extended to the level of the EPSP, because there was hardly seen the spontaneous EPSP under presence of the DSW.

Discussion. It was found that deep sleep is associated with
an increase in the average discharge rate of the LGB units relative to that during light sleep. This is in good accordance with the results of the previous workers obtained from the visual cortex,\textsuperscript{5,6} the brain stem\textsuperscript{11} and the sensorimotor cortex.\textsuperscript{7}

It was shown in our experiments that the LGB unitary activity tends to appear in a form of grouped discharges when animals are in the state of light sleep. This is consistent with Hubel’s finding.\textsuperscript{10} That the grouped discharges are characteristic of light sleep has also been established with the cortical level, both visual and sensorimotor.\textsuperscript{7,9}

The recordings from the LGB revealed that the discharge pattern of the LGB units during deep sleep is a mixture of those during light sleep and arousal. This may suggest that the state of deep sleep is not steady but fluctuates between the two excitatory states, the one which is similar to light sleep and the other which is close to arousal. However, to generalize this statement must be reserved, because Evarts has reported that the discharge pattern seen with the sensorimotor cortical units during deep sleep is of a particular type which is distinguishable from those during light sleep and arousal.

In some good recordings we were successful to identify the EPSP of the LGB units, and found that the number of the subliminal EPSPs plus the number of the spike-producing EPSPs, averaged per unit time, is lowest during deep sleep. This may suggest that the excitatory synaptic bombardment upon the LGB units is reduced to the lowest level during deep sleep. However, the actual firing of the LGB units was found to occur at the highest rate during deep sleep. This may indicate that there is exerted upon the LGB units some tonic depolarizing effect, so that the excitatory synaptic bombardment, though reduced in frequency of occurrence, becomes relatively effective to keep the spontaneous firing at the highest rate.

Summary. Single unit activities were recorded from the lateral geniculate body (LGB) of freely behaving cats to see how the spontaneous firing was altered during the sleep-wakefulness cycle. Identification of the LGB unit was accomplished by stimulating the optic tract with electrical shocks.

1) With 14 LGB units the average discharge rates were measured during sleep and arousal. They were highest during deep sleep (16.4/sec) and decreased from arousal (15.7/sec) to light sleep (10.9/sec).

2) Arousal was associated with well-spaced, continuous discharges of the LGB units and light sleep was characterized with the grouped
discharges. The discharge pattern during deep sleep was a mixture of those during arousal and light sleep.

3) The LGB units stopped their spike discharges in phase with the deep sleep wave (DSW) activity and following its subsidence, they fired in burst temporarily.

4) In good recordings it was successful to identify the EPSPs which occurred spontaneously with or without association of the spike discharge. They were decreased in number as the animal fell asleep and were hardly observed when the DSW occurred.

References