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26 July 1967

## Neurons in Paradoxical Sleep and Motivated Behavior

**Abstract.** *Single-cell recordings were taken with electrodes permanently implanted in unrestrained rats during normal sleep, paradoxical sleep, quiet awake, and highly motivated awake periods. In most areas, neuronal activity increased when normal sleep changed to paradoxical sleep. The hypothalamus showed a significantly greater increase than most other areas. The hippocampus differed strikingly from all other areas by showing a decrement in all cases. The average firing rates in paradoxical sleep exceeded those of the quiet awake state as well as those of normal sleep. Comparison of paradoxical sleep with motivated behavior illustrated that changes in brain activity during paradoxical sleep were related to anatomically specifiable groupings, but no such differentiation appeared in motivated behavior.*

The state of paradoxical sleep in animals has been a matter of keen interest because of its relation to the state of dreaming in man. The work of Dement and Kleitman (1) established that a paradoxical arousal of electroencephalographic activity occurred periodically during sleep in man and that it was correlated with the state of dreaming. Later Dement (2) showed the similarity of paradoxical sleep in animals and man. The question of the function of the two states of sleep does not have a clear answer. Freud (3) thought dreams constituted a kind of fantasied wish fulfillment, satisfying strong motivational urges and permitting sleep to continue. Motivational interpretations have received some support from work on deprivation of paradoxical sleep in animals (4); these studies might be considered to suggest that dreams constitute the discharge of the brain's unspent motivational energies as a sort of built-in psychothera-

peutic mechanism. The notion of information processing also figures prominently in a nonmotivational interpretation, namely that dreams function in the laying down of memory stores, being involved in the dissipation of weak bits of associational information prior to the placing of stronger bonds in a long-term store (5). From a less theoretical point of view, there are significant questions related to the similarities and differences between dream-sleep and waking; if the brain is active during dream sleep as it is in waking, why is there no behavioral output, and why does experience in this period lack the coherent organization of that of the waking brain?

Contributions toward the understanding of the questions involved have derived from physiological research on paradoxical sleep in man and animals. During paradoxical sleep, as in waking, low-voltage, fast activity appears in the electroencephalograms (EEG) taken from most forebrain and midbrain points, and a higher more rhythmic and slower "theta" pattern with higher voltage is recorded from the hippocampus and related areas. There is also a powerful downstream inhibitory process acting toward the spinal cord; this process expressed in a depressed muscle tone which is even lower in this state than it is in normal sleep and is quite unlike anything observed in the awake animal. These patterns taken together are the defining characteristics of paradoxical sleep (4).

There is a very large increase in neuronal activity in the midbrain and forebrain (6). There is often a greater discharge frequency during paradoxical sleep than during either quiet sleep or quiet awake periods. It is most marked in the reticular formation and thalamus but is also apparent to a lesser degree in caudate, putamen, hippocampus, amygdala, cochlear nucleus, and colliculi.

While the large downstream inhibitory process may account for the lack of output from a generally activated brain there are still unanswered questions about the relation of the dream state and awake states. We have compared neuronal activity during paradoxical sleep not only with that of sleep and quiet awake states but also with that of a highly motivated period in order to answer the following questions. First, can any detailed differences be specified between the dream state and the quiet and motivated awake

states? Second, does the whole brain participate in the activity increments during paradoxical sleep, or do the slow, theta rhythms which characterize hippocampal recordings and those from some other areas during this period indicate an actual depression of activity in some areas? Third, is there a clear and significant predominance of some areas over others during this period of general activation which might help to clarify the relation between informational and motivational interpretations of the process?

In these studies, we implanted six to eight fixed wire microelectrodes in male albino rats. The electrodes were stereotaxically aimed and guided by single-unit recording. Animals were trained to remain motionless for a period of 2 seconds while depressing a pedal to obtain food or water. Recording sessions occurred during a period of 3 to 4 weeks. Units were identified on the basis of amplitude and wave form. Movement was detected by a hearing-aid wire which was wrapped loosely around the cable that carried the microelectrode signals; movement of the cable generated voltages in it. A more complete description of the unit-discrimination procedure has been reported (7).

During sleep and quiet wakefulness, samples were taken at a rate of about one sample every 3 seconds, but they were accepted for computations only if no movement occurred during the 2-second sample period. Records were also obtained during successful 2-second movement-free pedal presses for food. The digital output of five unit-discriminators was recorded on EEG paper during sample periods together with three channels of EEG, a record of movement, and indications of the completion of a successful 2-second sample and pedal pressing (Fig. 1). The same information was punched on paper tape.

Records were taken during extended periods of sleep, usually 2 to 3 hours long. During this time, the animal was monitored visually. Records were also obtained during periods of quiet behavior when the animal was awake and during pedal pressing for food. The EEG records were used to categorize sleep samples as slow-wave sleep or paradoxical sleep. Most of the EEG recordings were monopolar from subcortical locations, and theta activity (6 to 8 cycle/sec) occurred characteristically during paradoxical sleep. The cyclical relation of sleep with slow

Table 1. Median values and ranges for ratios of mean unit activity during three behavioral conditions to mean unit activity during sleep with slow waves for 52 electrodes. *N*, number; Md, median.

Location	Paradoxical sleep			Quiet awake		Bar-Press, food	
	<i>N</i>	Md	Range	Md	Range	Md	Range
Lateral hypothalamus	11	3.52	0.95- 5.17	2.06	0.83- 4.81	2.84	0.89- 9.28
Reticular formation	9	2.80	.97-20.50	1.51	.79- 4.25	1.53	.95-16.25
Ventral tegmentum	6	1.94	.63- 2.75	1.37	.55- 3.41	1.13	.32- 6.20
Lateral preoptic	9	1.79	.49- 3.15	1.31	.92- 1.76	1.57	1.11- 2.44
Anterior thalamus	7	1.49	.73- 3.46	1.48	.94- 3.40	2.45	0.75- 3.30
Parietal cortex	4	1.42	.88- 2.09	1.23	1.01- 1.26	1.21	.98- 1.53
Dorsal hippocampus	6	0.62	.34- 0.87	1.03	0.87- 1.26	0.99	.34- 1.26
Total	52	1.93	.34-20.50	1.37	.55- 4.81	1.58	.32-16.25

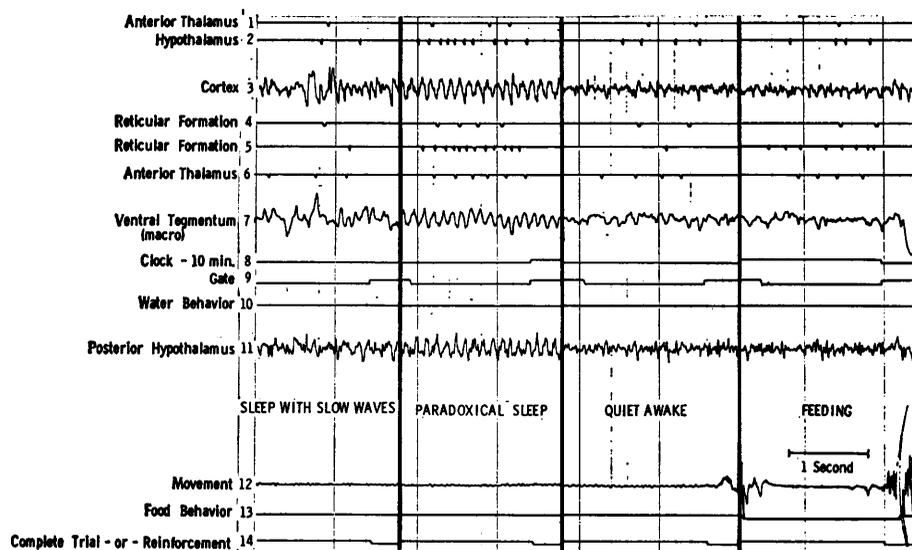


Fig. 1. Sample records of one complete sample interval for the four conditions which were observed. Analog channels are EEG tracings (3, 7, 11) and movement (12); digital channels indicate the readout of unit counters (1, 2, 4, 5, 6) and the state of the behavior sampling system (8, 9, 10, 13, 14).

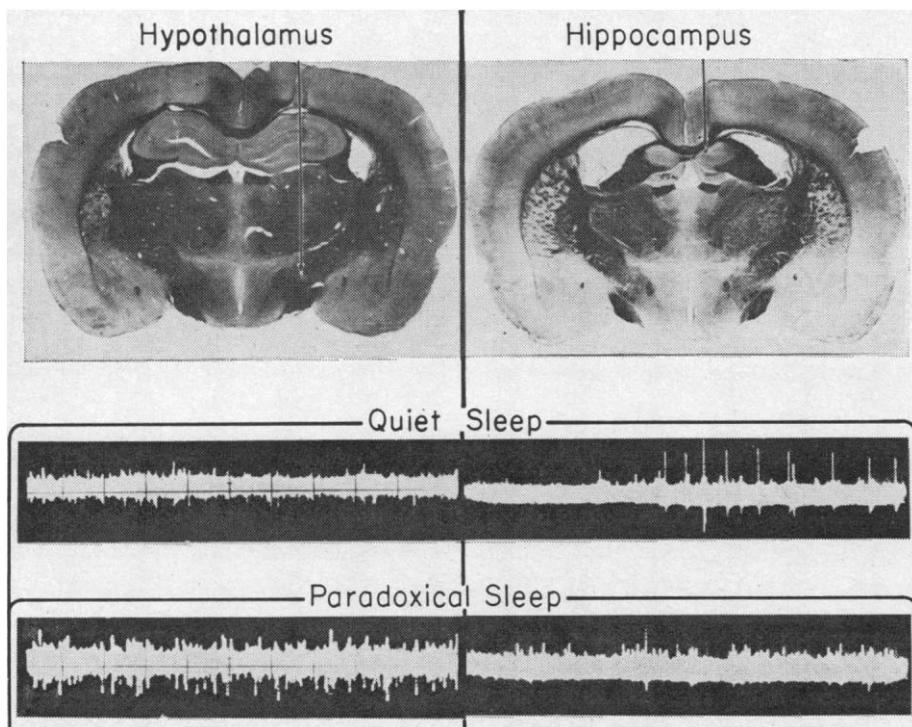


Fig. 2. Samples of neuronal activity in lateral hypothalamus and dorsal hippocampus during normal sleep and paradoxical sleep. Histological sections show the location of the two recording points.

waves to paradoxical sleep in our animals was similar to that reported in rats (8).

A group of 12 animals was observed, providing a total of 52 unit recordings. Electrodes were aimed at the following areas: lateral preoptic area, lateral hypothalamus, reticular formation, ventral tegmentum, anterior thalamus, dorsal hippocampus, and parietal cortex.

The number of 2-second samples varied from 350 to 2000. Because rates of response per 2-second period were greatly different from unit to unit, absolute response rates were not used in comparisons but were converted to ratios of a baseline average response rate obtained during sleep with slow waves. The analyses of results were based on these ratios. The medians and ranges of the ratios were tabulated for each of the stereotaxically defined brain areas (Table 1).

In total neuronal activity, paradoxical sleep surpassed the quiet awake state ( $P < .05$ ), and the latter surpassed quiet sleep ( $P < .05$ ). The motivated awake condition was highly variable, falling above the quiet awake state and below paradoxical sleep in mean value but statistically not differing from either.

The pattern of changes in rate of firing from normal to paradoxical sleep was highly differentiated by brain locus. The hypothalamus and reticular areas showed the highest increments; both changes were statistically significant. The median response rate in hypothalamus was more than 350 percent of the normal sleep rate, and that in reticular formation was more than 250 percent. The thalamic, preoptic, tegmental, and cortical groups had median increments ranging from 42 to 94 percent; each of the latter three groups was significantly below the hypothalamus in the size of the increments. Histological material showed that the highly augmented cases of hypothalamus occurred in the lateral part, in or near the medial forebrain bundle. The involvement of the medial forebrain bundle was also indicated by the characteristic recordings which usually had a small ratio of signal to the background, making units difficult to distinguish from one another (Fig. 2, left-hand column). The units of hippocampus showed a consistent decrease in rate of firing during paradoxical sleep. In fact, a decrease was observed in the rate of every hippocampal unit. The hippocampus as an area was significantly different from all the others, being the only case to show a consistent decrement (Fig. 3). The hippocampal

2									
1									
1, 2									
1, 2	1								
1, 2,	1	1	1	1	1	1			
3	1	1	1	1	1	1			

Fig. 3. Difference between groups of neurons in different brain areas significant at  $P$  equal to or less than .05 by the Mann-Whitney test. Entries are as follows: (1) changes from quiet to paradoxical sleep were different between the two areas, (2) changes from quiet sleep to quiet awake were different between the two areas, (3) changes from quiet sleep to the motivated awake state were different between the two areas.

recordings were regularly taken from the layer of hippocampal pyramidal cells in the dorsal anterior part. Neurons here were identified by their large ratio of signal to background (Fig. 2, right-hand column).

The increments over quiet sleep rates observed in the quiet awake state were not only smaller than those observed in paradoxical sleep, but were also less differentiated by anatomical structure. Units in the lateral hypothalamus again had the largest increments in rates, with an average increase of more than 200 percent, itself significant by statistical tests. Also, the hypothalamic group of neurons differed with respect to the size of the increase from those in reticular formation, parietal cortex, preoptic area, and hippocampus. The other brain areas had average rate increments of 50 percent or less. There were no average decrements and no other significant differences between areas.

There was an almost total absence of differentiation according to anatomical structure when differences between quiet sleep and motivated awake behavior were considered. From the 21 paired comparisons of the seven groups, taken two at a time, only one yielded a statistical significance; this was between the lateral hypothalamus which had the largest increments and the dorsal hippocampus which was unchanged.

Clearly, paradoxical sleep emphasized regional groupings of neuronal

activity based on anatomical structure, whereas motivated behavior emphasized individual differences between units. If one might assume that a differentiated pattern of excitation and inhibition would occur within a structure under the influence of an information process, this would suggest a reduced information content in paradoxical sleep. It might nevertheless be involved in the clearing of temporary information registers on the one hand or in discharging unspent motive force on the other. The clear lead of hypothalamic process might favor a motivational interpretation because of the known "drive and reward" centers housed there. On the other hand, the reduction in hippocampal discharges might contribute to the clearing of any reverberatory processes involved in temporary information stores often suspected to occupy that region. One appealing supposition combines the two views. It is that the organism generates drive processes on the basis of physiological needs, but that there is an excess of drive which provides a cushion or safety factor. Paradoxical sleep would occur after it was established that the needs were filled, and it would function to dissipate the excess drive.

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11 October 1967

## Successiveness Discrimination as a Two-State, Quantal Process

Abstract. The duration of the "psychophysical time quantum" measured through the application of a two-state model of successiveness discrimination is equal in magnitude to the modal zero-crossing interval of the alpha rhythm. The two quantities have similar distributions and they are correlated over individuals.

The most recent review of the concept of a psychological unit of duration is the monograph by White (1). He considers many lines of evidence which indicate the existence of such a unit somewhere within the range from 50 to 100 msec and he raises again the speculation that the unit may be related to some rhythmic brain process. The alpha rhythm of the electroencephalogram has a period of approximately 100 msec and it is often suggested as a correlate. Later experiments by others (2) support this connection by showing associations between certain temporal characteristics of alpha rhythm and of behavior.

I have also presented some reasons for thinking of psychophysical time in quantal terms (3). In that paper, the time quantum is identified with three different behavioral parameters, and measurements show that the magnitude of the quantum is very close to 50 msec in all three cases. This is approximately the same as the interval between zero-crossings of the alpha rhythm, and additional measurements are given which indicate a positive correlation over individuals between this alpha interval and the behavioral quantum. However, the number of experimental subjects was small, and the average values of the behavioral parameters exceeded the average alpha interval by 6 or 7 msec in all three cases.

The present report is concerned with a further analysis of one of the three behavioral parameters and with its relationship to the alpha interval. Additional empirical relationships which support the time quantum hypothesis are also set forth. The parameter under consideration is called  $M$  and it is defined in terms of the successiveness discrimination function: the relationship between (i) the probability of discriminating a successive pair of sensory events from a simultaneous pair of sensory events and (ii) the time interval between the members of the successive pair (4).