to the banana jack and the food shield, and a lining of electrical tape is applied to the inside of the cup for insulation (Fig. 1). Either the vacuum-tube circuit developed by Stellar and Hill (*4*) or a solid-state amplifying circuit (*6*) may be used in order to activate a relay for recording. The active lead of the contact circuit is secured to the banana jack on the eatometer, and the ground lead is secured to the rat's cage.

While the drinkometer measures discrete licking responses, the eatometer measures only contacts with the food shield, and consequently, the record from the eatometer is less refined than a drinkometer record. However, the identification of meals on an eatometer record is relatively simple. Since contacts with the eatometer occur in clusters which are rarely less than 1 minute in duration, it is convenient to define one meal as a cluster of contacts having a duration of more than 1 minute, and two separate meals are recorded when there is an interval of more than 3 minutes between contacts, This definition effectively eliminates the possibility of recording as a meal such an artifact as a rat's poking its paw into the cup, and very few data are lost.

Several eatometers have been used for a few weeks (*7*), and have provided continuous and reliable records of frequency and duration of meals (*8*). Data collected from six rats under free-feeding conditions during one continuous 22-hour period of 11 hours of darkness and 11 hours of light are shown in Table 1. While there was some variation in the pattern of eating (for example, rat 2 ate seven long meals while the others ate numerous shorter meals) the total time spent eating was remarkably consistent from one animal to another (mean, 2.0 hours; range, 1.5 to 2.5 hours). On the average, 75 percent of the total eating time was concentrated in the 11 dark hours of the 22-hour period. The mean frequency of isolated eatometer contacts of less than 1 minute in duration was 2.3, and in each case these brief contacts were clearly distinguishable from the average meal.

Table 1. Frequency and mean duration of meals for six rats during one continuous 22-hour period. A meal was defined as at least 1 minute of sustained contacts with the eatometer. Separate meals were recorded when there was an interval of more than 3 minutes between eatometer contacts.

| Rat | Frequency of meals | Mean duration of meals (min) |
|---|---|---|
| 1 | 16 | 9.10 |
| 2 | 7 | 18.54 |
| 3 | 11 | 11.25 |
| 4 | 18 | 7.37 |
| 5 | 16 | 6.19 |
| 6 | 16 | 5.42 |

In conjunction with a drinkometer, the eatometer may also be used to obtain contingencies between eating and drinking (*7*). Of course, the device may be easily modified for use with species other than rats.

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**References and Notes**

1. W. S. Verplanck and J. R. Hayes, *J. Comp. Physiol. Psychol.* **46**, 327 (1953).
2. D. Bindra and J. Blond, *Can. J. Psychol.* **12**, 74 (1958).
3. R. C. Bolles, *J. Comp. Physiol. Psychol.* **54**, 580 (1961).
4. E. Stellar and J. H. Hill, *ibid.* **45**, 96 (1952).
5. The food cup, including the cover and food shield shown in Fig. 1, is food device LC-306 from the Geo. H. Wahmann Mfg. Co., Baltimore, Md.
6. M. E. Jarvik and J. L. Carley, *J. Exptl. Anal. Behav.* **7**, 82 (1964).
7. F. W. Finger, in preparation.
8. The food which we have used with the eatometer is Purina Lab Chow, ground into a dry powder.
9. Supported by NIMH grant MH 04920 to F. W. Finger and L. S. Reid.

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## Paradoxical Sleep: Deprivation in the Cat

Abstract. *In cats, the paradoxical phase of sleep occupies about 33 percent of the total sleeping time. Cats which were deprived of paradoxical sleep, by being awakened at its onset, required an increased number of awakenings on successive days of deprivation in order to prevent paradoxical sleep. On the first day of recovery after deprivation, when sleep was not experimentally interrupted, the paradoxical phase occupied 53 percent of the total sleeping time.*

Dement and Kleitman (*1*) demonstrated that in humans the phase of sleep characterized by low-voltage, high-frequency waves in the electroencephalogram (EEG) and rapid eye movements (REM) is reliably related to dreaming. In humans this phase of sleep has been called stage 1-REM. A similar phase occurs in chimpanzees, monkeys, dogs, cats, rabbits, rats, and mice (*2, 3*); but it is not known whether the functional significance is the same for animals as for humans. In animals this phase of sleep has been called paradoxical, activated, deep, and rhombencephalic.

The functional significance of stage 1-REM sleep was explored by Dement (*4*) who deprived humans of this phase for 3 to 7 nights and found that an increased number of awakenings was necessary on successive nights of deprivation in order to prevent occurrences of REM sleep. He also found an increase in the percentage of the time spent in stage 1-REM on recovery nights. This finding was recently replicated by Agnew *et al.* (*5*). It is as if a "need" exists for a certain amount of paradoxical sleep, which, if not permitted, will be made up during a recovery period. Also, Dement's subjects demonstrated various degrees of behavioral deterioration as a result of deprivation of paradoxical sleep.

We have attempted to determine whether cats also have a need for paradoxical sleep and whether this species shows signs of behavioral deterioration if deprived of this phase. Electrodes were implanted permanently on the cortex and in deep brain structures of four adult cats, and were also implanted in the dorsal neck muscles for electromyograms (EMG) and in subcutaneous tissue of the forelegs for electrocardiograms (EKG).

Each cat was adapted to a sleep–waking cycle and to the experimental chamber for 2 weeks. According to this cycle the animal was permitted to sleep 10 to 12 hours per day in the experimental box. Between these sessions of sleep the cat was returned to the colony room and placed on a brick in the middle of a pan of water which was the floor of a cage. The animal could not lie down and did not sleep under these conditions. In the morning the cat was fed, permitted to exercise, placed in the experimental box, and connected to the stimulating and recording equipment. Approximately midway through a day's session, the animal was removed from the box and given food and exercise for about 30 minutes.

After the adaptation period, control data were obtained for 5 days by continuously recording the EKG, EMG, and EEG from the cortex and the hippocampus. These electrographic data were used to put the animal's behavioral state into three categories: awake, high-voltage sleep, or paradoxical sleep. A summary of the control data comprises one-half of Table 1 and shows the normal amount of paradoxical

sleeping time relative to total sleeping time under the conditions of this experiment.

During the control period and for the remainder of the experiment, two of the animals were rated according to a scale for emotional behavior designed for cats (*6*) in order to obtain a measure of any behavioral change occurring with deprivation of paradoxical sleep. This procedure was performed at the beginning and end of each day's session.

One animal was then deprived of paradoxical sleep for 3 days, one for 5 days, and another for 10 days. This was accomplished by awakening the cat within 15 to 30 seconds after the onset of paradoxical sleep by high-frequency stimulation of the reticular formation. The criteria for the occurrence of paradoxical sleep were clear-cut changes in the tonus of neck muscle and in the EEG from the cortex and hippocampus.

One cat was used as a control for the effects of being awakened per se. This control animal and the experimental animals were treated in the same manner throughout the experiment except that the control cat was awakened from high-voltage sleep instead of paradoxical sleep. The mean numbers of awakenings from paradoxical sleep on days 1 through 5 were determined for cats CD 1 and CD 13. The control cat was then awakened from high-voltage sleep a corresponding number of times for 5 days.

In recovery sessions each animal was permitted to sleep uninterruptedly as it had during the 2-week period of adaptation and during the 5-day period of collecting control data. The three experimental animals were given 5 days or recovery and the control animal 3.

Tables 1 and 2 summarize the major findings of this experiment. The three experimental cats required an increase in the number of awakenings necessary to prevent paradoxical sleep on successive days of deprivation. A mean of 94 percent more awakenings was necessary on the last day of deprivation as compared to the first day. Also, all experimental animals showed a dramatic increase in the percentage of total sleeping time spent in paradoxical sleep during the first recovery session as compared to the control sessions. (The mean percentage of time spent in paradoxical sleep for the three experimental animals was 52.9 percent on the first day of recovery and 33.2 percent during control days. This difference of 19.7 percent represents a 59-percent increase in the time spent in paradoxical sleep on the first recovery session as compared to the control days.)

Table 1. Paradoxical sleep during both control and recovery days expressed in minutes and as percentage of the total sleeping time. CD 2, CD 1, and CD 13 are experimental animals; CD 8 is the control.

| | Control days | | | | | Recovery days | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 |
| | | | | | *CD 2* | | | | | |
| Minutes | 104 | 157 | 175 | 138 | | 246 | 174 | 184 | 177 | |
| Percentage | 27.6 | 31.7 | 33.4 | 28.1 | | 44.0 | 33.4 | 32.5 | 30.4 | |
| | | | Mean 143.5 min, 30.2% | | | | | | | |
| | | | | | *CD 1* | | | | | |
| Minutes | 85 | 149 | 119 | 121 | 135 | 225 | 120 | 132 | 117 | 122 |
| Percentage | 32.2 | 33.6 | 26.7 | 30.3 | 30.5 | 52.3 | 38.2 | 36.6 | 34.2 | 31.8 |
| | | | Mean 121.8 min, 30.6% | | | | | | | |
| | | | | | *CD 13* | | | | | |
| Minutes | 159 | 165 | 147 | 166 | 152 | 286 | 191 | 160 | 195 | 133 |
| Percentage | 41.7 | 40.1 | 35.4 | 40.1 | 36.9 | 62.5 | 50.9 | 44.5 | 46.0 | 38.4 |
| | | | Mean 157.8 min, 38.8% | | | | | | | |
| | | | | | *CD 8* | | | | | |
| Minutes | 157 | 156 | 171 | 164 | 159 | 159 | 165 | 156 | | |
| Percentage | 40.3 | 39.3 | 39.2 | 36.5 | 38.1 | 36.4 | 41.0 | 38.2 | | |
| | | | Mean 161.4 min, 38.7% | | | | | | | |

Table 2. Awakenings of experimental animals from paradoxical sleep on days of deprivation. The control animal was awakened from high-voltage sleep.

| Subject | No. of awakenings on day: | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| CD 2 | 64 | 117 | 137 | | | | | | | |
| CD 1 | 58 | 58 | 70 | 96 | 93 | | | | | |
| CD 13 | 45 | 73 | 81 | 67 | 93 | 89 | 101 | 92 | 108 | 93 |
| CD 8 (control) | 52 | 66 | 76 | 82 | 93 | | | | | |

Data from the scale for rating emotional behavior failed to show any differences before, during, and after deprivation of paradoxical sleep. The conclusion, however, that deprivation of paradoxical sleep has no behavioral effect may not be warranted since the reliability and sensitivity of this technique are not known.

For all cats, the end of a normal uninterrupted period of paradoxical sleep was marked by a gross body movement and brief arousal. The pattern of events was characterized by a change in the EMG and EEG indicative of the end of a paradoxical sleep episode. This was followed within a minute (usually seconds) by a raising of the head, opening of the eyes, shifting of body position and sometimes stretching, lying down again, and returning to the high-voltage stage of sleep.

This finding establishes another common characteristic of paradoxical sleep in widely divergent mammalian species, namely, mouse, cat, and man. Weiss and Fifkova (*3*) report that in mice paradoxical sleep is usually terminated with a short arousal reaction followed by a return to high-voltage sleep. Dement and Kleitman (*7*) report that in humans cessation of REM periods is often accompanied by a large body movement. Apparently, similar events in the nervous systems of these species occur at the end of a period of paradoxical sleep to produce similar effects.

Previous studies have shown the paradoxical phase of sleep to be a characteristic of a number of mammalian species. This experiment has demonstrated that cats have, in a sense, a need or drive for paradoxical sleep. These results, similar to those reported by Dement (*4*) with humans, and the observation of body movements at the end of a paradoxical sleep period, suggest that paradoxical sleep in animals and stage 1-REM sleep in humans are similar phenomena and have, perhaps, a similar significance across species.

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### References and Notes

1. W. Dement and N. Kleitman, *J. Exp. Psychol.* **53**, 339 (1957).
2. W. R. Adey, R. T. Kado, J. M. Rhodes, *Science* **141**, 932 (1963); E. D. Weitzmann, *Electroencephalog. Clin. Neurophysiol.* **13**, 790 (1961); H. L. Bastel, *ibid.* **12**, 421 (1960); W. Dement, *ibid.* **10**, 291 (1958); J. Faure, *Rev. Neurol.* **100**, 255 (1959); J. Swisher, *Science* **138**, 1110 (1962).
3. T. Weiss and E. Fifkova, *Physiol. Bohemoslov.* **13**, 242 (1964).
4. W. Dement, *Science* **131**, 1705 (1960).
5. H. W. Agnew, Jr., W. B. Webb, R. L. Wil-

liams, *Electroencephalog. Clin. Neurophysiol.* **17**, 68 (1964).
6. S. Norton and E. J. deBeer, *Ann. N.Y. Acad. Sci.* **65**, 249 (1956).
7. W. Dement and N. Kleitman, *Electroencephalog. Clin. Neurophysiol.* **9**, 673 (1957).
8. We thank Dr. A. J. Hance at Stanford University and Drs. Bernice Wenzel and W. D. Winters at UCLA for their assistance in acquiring some of the techniques basic to this research. This work was supported by a grant from the University of Delaware Research Foundation and grant No. GB 1965 from the National Science Foundation to J.S.

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## Evoked Potentials and Correlated Judgments of Brightness as Functions of Interflash Intervals

Abstract. *Computer-averaged evoked potentials were recorded from subjects presented with pairs of flashes having equal light energy but differing in duration of the brief interval separating the flashes. For the experimental conditions studied, the pair was always subjectively fused. Although the brightness did not change noticeably as the interval was varied, the use of the forced-choice psychophysical technique showed that apparent brightness declined with increase in the interval. Analysis of the evoked potentials revealed a correlated change in amplitude and wave form previously demonstrated for changes in flash flux alone.*

Bloch's law (the reciprocal relation of luminous flux and duration) applies for visual thresholds for detecting a flash, so long as the duration remains below a critical value. At least for durations less than 1.5 msec Brindley (*1*) has demonstrated its applicability also to the judgment of brightness of suprathreshold flashes. However, in a study in which flashes of various durations were matched for brightness with a standard 200-msec flash, Katz (*2*) noted an apparent departure from reciprocity as the duration of the test flash was increased from 8 to 25 msec. Wicke, Donchin, and Lindsley (*3*) published records of evoked potentials for foveal stimulation as luminance and duration of the stimulus flash were varied; in commenting on their records they emphasize that, although the latency appeared to be determined largely by the luminance, the wave form and amplitude of the average evoked potentials appeared to depend instead on the product of luminance and duration. Thus, by inference from Bloch's law, wave form and amplitude are closely related to perceived brightness when duration is varied below the critical value. In our study the effects on specific components of evoked cortical potentials were determined for stimuli comprised of pairs of brief flashes (10 $\mu$sec) of the same light energy but with different intervals between the flashes in each pair. We further determined whether such changes in the evoked response resemble those found with change in flash flux alone. Over the range of intervals studied there was no obvious difference in the apparent brightness of the fused flash pairs, but forced-choice judgments revealed the brightness order in which they fell.

The recording apparatus is described in detail elsewhere (*4*). Briefly, a Mnemotron computer of average transients was fed directly by an Offner type R dynograph equipped with a type 9806A input complex. Occipital cortical potentials were recorded with monopolar electrodes. The active electrode was 2.5 cm above the inion and 2.5 cm to the left of the midline. The reference electrode was attached to the left ear lobe. The computed average potentials from a set of stimulus presentations was recorded on graph paper with a Moseley X-Y plotter, model 2D2. The gain settings on all components of the recording system remained fixed during the study.

Flashes were presented to the right eye by a Grass photostimulator, model PS-2, mounted flush against a window (7.5 cm square) of an electrically shielded room. The subject sat inside the room with his eye approximately 90 cm from the window. One-half of a table-tennis ball was secured over his eye, its edges taped to the skin, thus rendering the flash stimulus a ganzfeld—that is, filling the entire field of vision. A low-level prevailing ganzfeld was provided by light from a projector, with filters, coming through a second window immediately below the first. The constant background was such as to raise the flash threshold about one-tenth logarithmic unit above the level found with full dark-adaptation. The photostimulator was operated at scale 1 (the lowest level) with no filters in some trials and with a 90-percent neutral-density filter for others. With no filters, stimuli were approximately four logarithmic units above threshold. All tests were run with a background of white noise well above the level required to mask clicks from the photostimulator.

Each subject was dark-adapted before being tested. Three subjects served in both phases of the experiment, and another was used only in the psychophysical judgments.

Tests were conducted in two phases. In the first, a train of three pairs of flashes, each pair having a different interflash interval, was presented after a "ready" signal. The subject indicated which pair was brightest, even though he may have felt that he was merely guessing. Intervals between pairs of flashes were approximately 2 seconds. Interflash intervals within pairs were 9, 16, and 25 msec; the order of the pairs in a trio was varied from trial to trial, according to a balanced design for a block of 27 trios. Two blocks, or 54 judgments, were recorded for each of the two flash luminances in a day.

In the second phase, evoked potentials were recorded for pairs of flashes having interflash intervals of 9 or 16 msec; no filter was used over the photostimulator. All four channels of the computer were used, two for the 9-msec condition and two for the 16-msec condition; thus we could check the reliability of the findings. Responses were recorded for 25 flash pairs, all of a set having one interflash interval (separation); 25 were then recorded for the other interval, in *A-B-B-A* order, until 100 responses

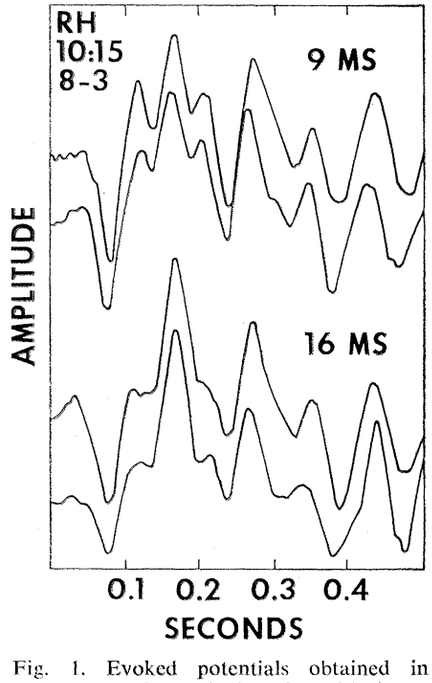


Fig. 1. Evoked potentials obtained in response to fused flash pairs with interflash intervals of 9 and 16 msec. Onset at start of trace, each trace representing the summation of 100 flash pairs in one channel of the computer. All four records obtained during a single session, in counterbalanced order, as described in text. Negativity downward. Equal gain-setting in all four channels.