

implications for the therapy of epilepsy, particularly for the delayed onset forms such as posttraumatic epilepsy, which are most likely to be related to kindling.

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9. This time interval was chosen because of the slow onset of neuronal response to micro-iontophoretically applied ACh. In agreement with others [T. J. Biscoe and D. W. Straughan, *J. Physiol. (London)* **183**, 341 (1966); K. Krnjevic, *Methods Neurochem.* **1**, 129 (1971)], we found that ACh began to excite neurons only after a latent period of several seconds and then induced a gradual increase in firing frequency over a period of several more seconds. A steady level of induced firing was reached by about 15 seconds.
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Sleep and Estivation (Shallow Torpor): Continuous Processes of Energy Conservation

Abstract. *Estivation (shallow torpor) in the round-tailed ground squirrel (Citellus tereticaudus) is entered through electrophysiologically defined states of sleep. Rapid-eye-movement sleep diminishes as body temperature falls in such a way that, at a body temperature of 26° to 28°C, torpor is characterized by almost continuous slow-wave sleep isomorphic with that observed at euthermic body temperatures.*

Hibernation and estivation are similar physiological processes that conserve energy in homeotherms by the lowering of body temperature (T_b) to near ambient temperature (T_a) (1-3). Conventionally, estivation denotes periods of dormancy or torpor occurring at high T_a 's with T_b 's above 15°C, whereas hibernation designates dormancy at lower T_a 's with T_b 's below 15°C (2). Hudson recently sug-

gested that "estivation" is a misnomer since there is little evidence that it is directly triggered by either heat or drought (3), and he regards estivation as synonymous with hibernation. Perhaps the term "shallow torpor," used here, is more appropriate, since it denotes changes in T_b without bearing causal connotations as does estivation.

Recent evidence points to a physiolog-

ical continuity between states of sleep and torpor. Alpine ground squirrels enter hibernation through sleep (4). Subsequent periods of wakefulness are associated with a halting or reversal of the hibernation entrance. The progressive lowering of hypothalamic thermosensitivity during the entrance into hibernation appears to be an extension of that which occurs during the transition from wakefulness to slow-wave sleep (SWS) in euthermic mammals (5, 6). Thus, sleep and hibernation appear to be homologous physiological processes. In this study we found that shallow torpor, induced by depriving desert round-tailed squirrels of food, is also characterized by almost continuous sleep.

We studied one juvenile (weight, 57 g) and three adult (194, 152, and 143 g) male round-tailed squirrels (*Citellus tereticaudus*), trapped on the Mohave Desert. A reentry tube was implanted 3 mm below the dura in the cortex to measure brain temperature (T_{br}), and permanent electrodes were implanted for recording the cortical electroencephalogram (EEG), the hippocampal EEG, the electrooculogram (EOG), and the electromyogram (EMG) (4). The electrocardiogram (EKG) could be recorded from EMG leads during periods of reduced activity. Each animal was housed individually in a 25 by 25 by 43 cm wire cage containing a wooden box with cotton nesting material. Throughout the study, animals were maintained in an electrically shielded incubator ($T_a = 25^\circ \pm 0.5^\circ\text{C}$) under a photoperiod of 12 hours of light and 12 of darkness (lights on at 8 a.m.).

Shallow torpor was induced by food deprivation during the months of July and August (water was continuously available). Although normal (euthermic) T_{br} 's during the day ranged from 34° to 37°C, at night they dropped as low as 32°C (Fig. 1). Therefore, the beginning of an entrance into torpor was defined as the point at which T_b progressively declined below 32°C. Continuous electrophysiological and T_{br} recordings were obtained (Grass model 7 polygraph; paper speeds of 5 or 6 mm/min) over a period of 10 to 26 days, during which time 20 periods of torpor occurred (at least four for each animal). Polygraphic records were scored by 25- or 30-second epochs for wakefulness, SWS, and rapid-eye-movement (REM) sleep (4).

The four animals first entered torpor after 2, 3, 5, and 19 days of food deprivation, respectively. Subsequent periods followed at approximately 24- or 48-hour intervals (Fig. 1). A distinct nocturnal pattern of torpor occurring at the usual

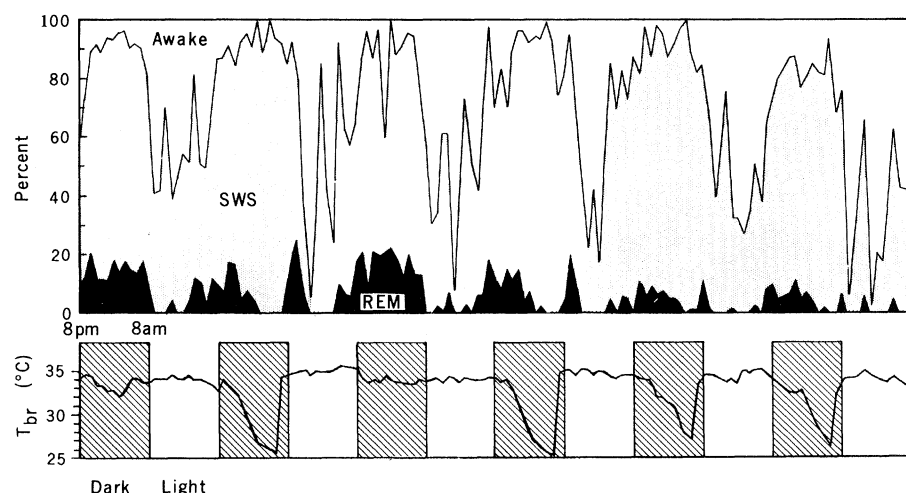


Fig. 1. Hourly sleep and wakefulness percentages and measures of T_{br} for a round-tailed ground squirrel over a 6-day period. Decreases in T_{br} below 32°C indicate bouts of shallow torpor (estivation). Diurnal T_{br} 's in other animals ranged as high as 37°C.

sleep time was present in three animals. During the first half of the night, T_{br} decreased by 1°C every 40 to 50 minutes; it stabilized at 26° to 28°C for 1 to 4 hours, and then increased to euthermic levels over a period of approximately 1 hour. Torpor periods lasted an average of 10 hours, from the initial decrease in T_{br} to the return to euthermia. The return to euthermia was spontaneous and occurred during the last 2 hours of the dark period (6 to 8 a.m.). One adult animal that went 19 days without food before entering torpor exhibited some periods of torpor during the night, but the timing and duration of other periods were variable (7). Thus, the shortest bout began in the afternoon (3:44 p.m.) and lasted 8 hours, whereas the longest bout began in the early morning (4 a.m.) and lasted 18 hours.

Although EEG amplitude, heart rate, and tonic EMG decreased in parallel with T_{br} during the entrance into shallow torpor, sleep and wakefulness could nevertheless be identified according to conventional electrographic criteria at all T_{br} 's. At the lowest T_{br} 's of 26°C, REM sleep was absent, but states of wakefulness and SWS isomorphic with those of euthermia were present (Fig. 2). Wakefulness was characterized by a desynchronized low-voltage EEG (8 to 12 Hz, < 50 μ V) and a high EMG, whereas SWS consisted of a slow, moderate-am-

Table 1. Sleep percentages for four ground squirrels during a single nocturnal period of torpor (the torpor period was defined from the initial decrease in T_{br} below 32°C to the return to a euthermic T_{br}) [and during time-equivalent euthermic periods before and after the torpor (8)] and for comparable complete 24-hour periods (9). Statistical comparisons (analysis of variance followed by Duncan's multiple range test) were made between torpor periods and adjacent nontorpor periods.

Sleep stage	Nocturnal period			24-hour period (8 p.m. to 8 p.m.)		
	Pre-torpor	Torpor	Post-torpor	Pre-torpor	Period including torpor	Post-torpor
Total sleep (%)	82.4*	92.4	87.6	60.1	69.6	66.7
SWS (%)	68.7†	88.1	76.7*	51.7*	64.5	57.7
REM						
(REM/recording time)	13.7†	4.8	14.9†	8.4*	5.1	9.0†
(REM/sleep time)	16.7†	5.1	16.9†	14.1*	7.4	13.6*

* $P < .05$. † $P < .01$.

plitude EEG (0 to 2 Hz, 75 to 125 μ V) with occasional spindles (3 to 6 Hz, 50 to 100 μ V) and a reduced EMG. Heart rate, an index of both arousal and metabolic rate, was 84 percent lower than during euthermia (Fig. 2). Alterations in the distribution of sleep and waking states during entrance into shallow torpor were similar to those reported for alpine squirrels entering hibernation (4). In each instance of torpor, sleep time increased, and the percent spent in REM progressively decreased as T_{br} declined (Fig. 1).

To assess whether the sleep of torpor differed from euthermic sleep, the first

period of torpor was compared with temporally equivalent portions of euthermic nights prior to and subsequent to it (8). Sleep time was significantly greater during torpor than during preceding euthermia (Table 1). This was the case even though torpor was compared to the animal's major sleep period. In addition, SWS increased during torpor, but more dramatic was the reduction of REM sleep. On those occasions when torpor did occur during the day, sleep-wakefulness patterns were essentially the same as during nocturnal torpor and comprised more total sleep and less REM

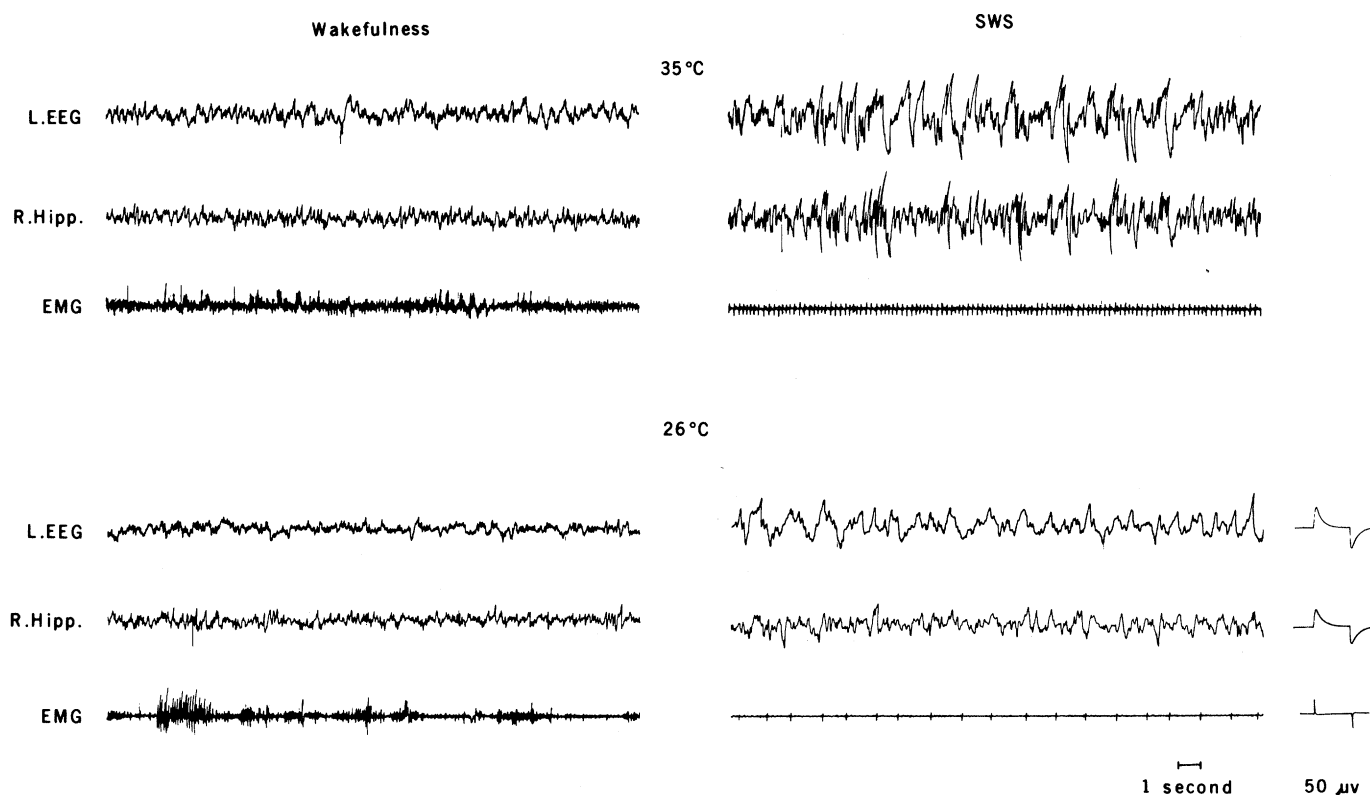


Fig. 2. Examples of wakefulness and SWS in the round-tailed ground squirrel at euthermic levels ($T_{br} = 35^\circ\text{C}$) and during shallow torpor ($T_{br} = 26^\circ\text{C}$).

sleep than during time-equivalent euthermic periods.

Torpor was usually terminated by increased wakefulness soon followed by an increase in T_{br} , but REM sleep was not present. Despite the suppression of REM sleep during torpor, compensatory REM rebounds did not occur in the 24-hour period after the return to euthermia (9) (Fig. 1) (Table 1). The occurrence of shallow torpor did not significantly affect the amounts of total sleep or SWS during subsequent euthermia when compared with pretorpor euthermia.

Daily shallow torpor occurring in some small mammals such as pocket mice is sometimes interpreted as an extension or magnification of the euthermic circadian rhythm of T_b . However, in this study some bouts of torpor occurred independently at times remote from the minor circadian decreases of T_b . Therefore, the decreased T_b of torpor appears to be associated more closely with the sleep state than with a preestablished circadian variation of T_b independent of sleep.

These results also point to the physiological identity of estivation and hibernation. Sleep patterns during shallow torpor in desert ground squirrels were qualitatively and quantitatively identical to those of shallow hibernation in alpine ground squirrels (10). Moreover, changes in EKG, EMG, and EEG activity during bouts of shallow torpor were similar to those of shallow hibernation.

The function of sleep is typically regarded as the restoration of one or more physiological processes degraded during prior wakefulness, in spite of a lack of concrete empirical support for such an interpretation (11). An alternative, but not necessarily exclusive hypothesis is that SWS evolved as an adaptation for energy conservation that partially offset the high costs of endothermy (12-14). Evidence for this hypothesis was until recently confined to correlative studies and included (i) strong positive correlations between metabolic rate and amount of SWS in mammals (15), (ii) the parallel ontogeny of SWS and thermoregulation (14), and (iii) the absence of SWS in ectotherms (13). The finding of a regulated decrease in T_b during SWS indicative of reduced metabolism provided direct support for this hypothesis (5). Since the electrophysiological patterns of SWS and shallow torpor are temporally continuous and essentially isomorphic, it is probable that thermoregulatory adjustments while entering torpor are an extension of those initiated during SWS. There can be little doubt about the bioen-

ergetic adaptive value of torpor, and the physiological homologies between torpor and sleep described point to a unitary primordial function for both states.

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7. The initial weight of this animal was 143 g. After 12 days of food deprivation it weighed 108 g, and after 26 days, 85 g.
8. The first instance of torpor for three animals (torpor entrances at 10:00, 10:10, and 10:28 p.m.) and the second for the fourth animal (9:50 p.m.) served as the data base. Sleep-wakefulness patterns were determined for time-equivalent euthermic periods before the first period of torpor and after torpor. Comparisons between pretorpor, torpor, and post-torpor in this and subsequent comparisons were made by one-way analysis of variance for repeated measurements. Duncan's multiple-range test was used to compare specific means.
9. Euthermic sleep-wakefulness measures were determined in the 24-hour period (8 p.m. to 8 p.m.) prior to the first period of torpor. Although individual animals had experienced differing food deprivation with the varying times of occurrence of the first torpor, sleep-wakefulness measures were as homogeneous as and within the range of normative data reported for another species of squirrel (4). Sleep-wakefulness patterns were measured in the 24-hour period that torpor occurred [same periods of torpor as in (8)] and in the subsequent 24-hour euthermic period.
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Membrane Potential Changes During Chemokinesis in *Paramecium*

Abstract. Intracellular recordings show that (i) *paramecia* hyperpolarize slightly in attractants and depolarize in repellents that depend on the avoiding reaction (an abrupt change of swimming direction), and (ii) *paramecia* more strongly hyperpolarize in repellents and more strongly depolarize in attractants that depend on changes of swimming velocity. These membrane potential changes are in agreement with a hypothesis of membrane potential control of chemokinesis in *Paramecium*.

Paramecia accumulate in or disperse from the vicinity of certain chemical stimuli (1). The animals do this by either of two mechanisms: modulation of frequency of changing swimming direction (the avoiding reaction) or modulation of forward swimming speed (2-4). Neither mechanism seems to involve orientation toward or away from the stimulus, and therefore the behavior is termed chemokinesis rather than chemotaxis (5, 6). Components of both of the mechanisms are under electrical control at the cell membrane: (i) each avoiding reaction corresponds to the generation of a calcium action potential, and (ii) the frequency and angle of ciliary beating, which determine swimming speed, are

controlled by changes from the resting membrane potential (7, 8). Therefore, it is of interest to determine the electrophysiological correlates of the complex behavior of chemokinesis. I have made intracellular recordings from cells in attractants and repellents. The membrane potential (E_m) values from these recordings are presented here and are in agreement with a hypothesis of membrane potential control of chemokinesis (2, 3).

Accumulation of organisms is associated with decreased frequency of avoiding reaction (F_{AR}) or with decreased speed (V) in the area of attractant (5, 9). Conversely, dispersal is associated with increased F_{AR} or with increased V in the