The activity patterns of 6 of the 7 hamsters used in this experiment were only weakly synchronous with the LD cycle at the beginning of the hibernation season (October) when the ambient temperature was 19 °C. Some individuals showed irregular intervals of torpor of up to 36 h. In the two hamsters for which data are presented (fig., A and B), circadian rhythms of locomotor activity were observed during the first 2 weeks of the experiment. The chi-square periodogram analyses for the section from 17 October to 1 November revealed significant periods (τ) around 24.0 h in both hamsters as well as τs longer than 24 h (24.9 h in hamster A and 24.4 h in hamster B). Subsequently, activity became arrhythmic (see periodograms for 18 November to 4 December). After the temperature change from 19 to 10 °C a circadian rhythmicity reappeared in the onsets and ends of locomotor activity during arousal intervals. The initial τs were between 25.5 and 26.0 h in hamster A and about 26.0 h in hamster B. They gradually shortened towards the end of the hibernation season. The other hamsters used in this study showed different responses: In 4 hamsters (2 ♂; 2 ♀) no circadian rhythmicity was evident between arousal intervals. In one female the activity rhythm was entrained to the LD cycle between bouts of hibernation. Re-entrainment of the activity rhythm to the LD cycle was observed in all 7 hamsters at the end of the hibernation season (examples shown in fig., A and B).

To interpret these results, two hypotheses are proposed:

1) With the beginning of the hibernation season the mechanism which is responsible for entrainment of the circadian pacemaker(s) with the LD cycle (Zeitgeber) is 'switched off', or, the system which perceives and/or transmits information about external light conditions is inhibited. At the end of the hibernation season these functions become re-established and the circadian rhythms again entrain to the LD cycle.

2) It is presumed that subsidiary circadian oscillators which control locomotor activity as well as other functions[7,8] become uncoupled from the pacemaker located in the suprachiasmatic nuclei (SCN) of the hypothalamus at warm ambient temperatures during the hibernation season. With the change in temperature and the entry into deep hypothermia, internal coupling becomes re-established and a circadian rhythmicity may reappear at a new phase (as, for example, in the two hamsters of the figure). Whether or not these changes occur may depend on the predisposition of the individual, i.e., the degree of interaction (mutual coupling) between various components of the circadian system before the temperature change, or on other factors (e.g., τ, etc.).

It is important to consider that different individual responses cannot be detected even under LD cycles, if groups of animals are sacrificed and the data are pooled at various stages of an experiment (e.g., Vaněček et al.[6]). In a previously reported experiment with Turkish hamsters hibernating under similar conditions to those in the present experiment, the times of spontaneous arousal as well as the onsets of locomotor activity following arousal were not periodically distributed when the data of all hamsters were pooled[9].

From the previously mentioned finding that the rhythm of melatonin formation in the pineal of the Syrian hamster is abolished during hibernation[6], it may be derived that the sympathetic nervous transmission from the circadian pacemaker in the SCN to the pineal is inhibited during hibernation. Since the rhythms of melatonin synthesis and/or release in the pineal are involved in the photoperiodic control of annual rhythms in hamsters[10], this mechanism may be blocked during hibernation.

In conclusion, the data show that, although the circadian pacemaker controlling locomotor activity continues to run during natural hypothermia, profound changes in the functional state of the circadian system occur during the hibernation season. These may involve changes in the properties of the system by which entrainment to LD cycles is achieved and (or) in the interaction between oscillators controlling different functions and the pacemaker(s). To test these hypotheses, further investigations are required.

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Seasonal changes of circadian pattern in human rectal temperature rhythm under semi-natural conditions[1]

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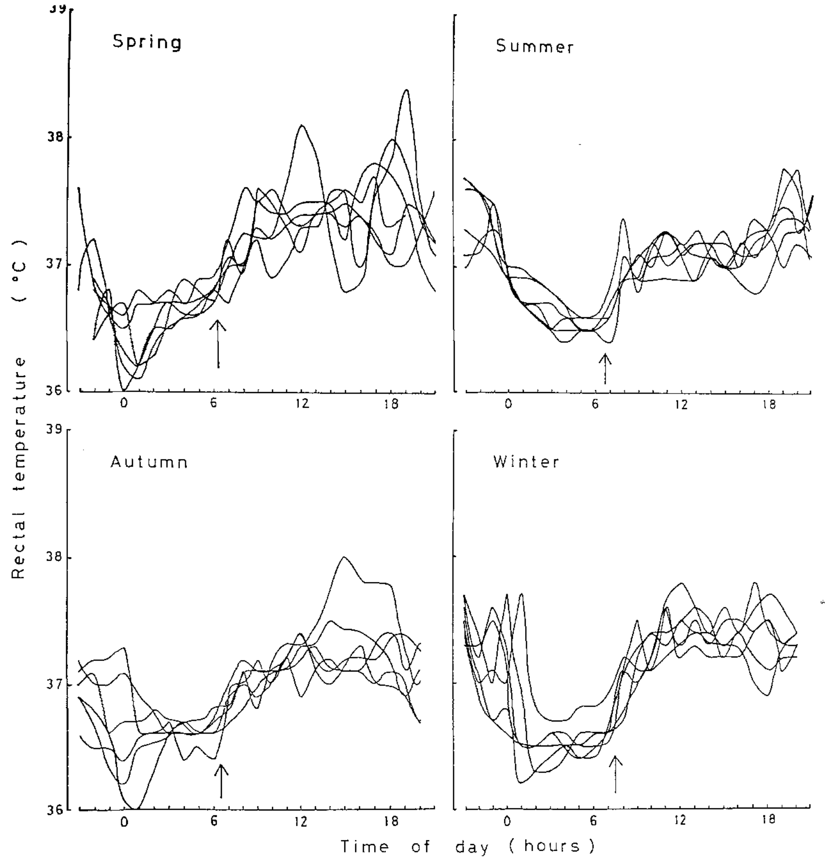
Summary. A phase delay of the circadian rectal temperature rhythm existed in three human subjects leading normal lives under semi-natural conditions: the rectal temperature began to increase later in summer than in the other three seasons.

Key words. Season; rectal temperature; circadian phase; rhythm.

Light affects human circadian rhythms[2]. Temperature cycles can entrain freerunning rhythms not only in poikilothermic animals[3], but also in non-human primates[4,5]. Recently, seasonal change in the freerunning circadian period of the core temperature rhythm in normal subjects isolated from time cues has been shown[6]. With these in mind, it is of interest to know whether the circadian pattern of human physiological rhythms might change annually under the influences of seasonally changing photoperiod and temperature cycles. Therefore, in the present experiment we studied the effects of season on the circadian pattern of rectal temperature rhythm in human subjects leading normal regular lives under semi-natural conditions.

Two males (H. T., 45 years old, N. I., 38 years old) and a female (K. N., 22 years old) served as subjects. The subjects were exposed to artificial light during the evening, and often to both natural and artificial during the daytime. They went to bed when they felt sleepy at night. One (H. T.) of the three subjects did not use an alarm clock when he got up throughout the year. To



Seasonal change of circadian pattern of rectal temperature rhythm in a male subject (H.T.). Arrow indicates average awakening times of each season.

exclude the possibility of the effects of the menstrual cycle on the rectal temperature rhythm, the data were collected only during the follicular phase in the female subject (K.N.). The data for rectal temperature were stored every 5 min in a 'Body Temperature Recorder' (MED-TECH YM-1, 15 × 19 × 3 cm, weight: 275 g) continuously throughout day and night for 7–10 days during spring (April 28–June 8), summer (July 18–September 1), autumn (October 14–November 2) and winter (December 12–January 15), respectively, and printed out on a printer by the aid of a computer after the completion of the experiment. The subjects engaged themselves in work as usual during wakefulness, always carrying the 'Body Temperature Recorder' at their waist. It was laid at the subjects' bedside during night sleep.

The figure shows representative seasonal changes of circadian pattern in the rectal temperature rhythm of a male subject (H.T.). It can be easily seen that the rectal temperature begins to increase latest in summer. Furthermore, decreasing slopes of rectal temperature rhythm from 21.00 to minimum times seem to be steeper in spring and winter compared with those in summer. After the rectal temperature reached the maximum value, it began to fall to the minimum value, which was kept for a few hours, and again began to increase. Although it is known that there are difficulties in defining the 'real' minimum, and there are masking effects of sleep on rectal temperature rhythm[7,8], we took as a reference point the earliest times when the rectal temperature reached the minimum value. As there were no systematic differences between weekdays and weekends with respect to 'rectal temperature minimum', the average times of the minimum rectal temperature, visually determined from the original curves which included data for weekdays and weekends, were seasonally summarized in the table. It is clearly seen that the minimum times are significantly latest in summer, compared with those in the other three seasons. We could not detect any consistent differences among spring, autumn and winter. However, these pilot data suggest probably the existence of summer phase delay of the circadian rectal temperature rhythm in humans spending normal lives under semi-natural conditions.

Seasonal change in the time of rectal temperature minimum in three subjects. Mean ± SD

	Spring	Summer	Autumn	Winter
K.N.	2.8 ± 1.5 h	4.8 ± 1.0 h	2.6 ± 1.1 h	2.8 ± 1.8 h
H.T.	0.1 ± 0.6	5.2 ± 1.3	1.1 ± 1.8	3.2 ± 1.8
N.I.	2.9 ± 1.6	3.9 ± 1.0	1.6 ± 1.8	2.6 ± 1.7

What mechanisms could account for our findings that the circadian phase of rectal temperature rhythm was delayed in summer? The length of the freerunning circadian period under constant conditions is responsible at least partly for the determination of the phase angle difference between circadian rhythm and light-dark cycle[9]. Birds with longer 'natural periods' in constant conditions showed more negative phase angle difference between activity rhythm and the light-dark cycle, compared with that in birds with shorter 'natural periods' under constant conditions[10]. The freerunning period for circadian temperature rhythm was longer in July-August, compared with that in other seasons[6]. Furthermore, the ambient temperature (T_a) of 33 °C lengthened the freerunning circadian period of circadian locomotor activity in the pig-tailed macaque compared with that at a T_a of 17 °C. If this were the case in humans, the higher ambient temperature in summer might have an effect on rectal temperature rhythm by lengthening the period. The average ambient temperatures which surrounded the three subjects were 28.3 ± 2.1 °C (mean ± SD) in summer. These summer values were about 7–14 °C higher than in the other three seasons. Thus, the phase delay of rectal temperature rhythm in summer might be ascribed to interaction of endogenous lengthening of τ and higher ambient temperature. Experimental evidence, however, must still be obtained. Furthermore, it remains to be investigated how different life-styles among individuals could influence the circadian rectal temperature rhythm.

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Sleep in the tortoise *Kinosternon* sp.

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Summary. Individuals of *Kinosternon* sp., previously confined to laboratory conditions, were chronically implanted with electrodes for electroencephalogram, electro-oculogram and electrocardiogram recording. Behavioral states of waking and sleep were clearly observed. Two sleep stages were present: quiet sleep and REM or active sleep. Electrical cerebral activity was polymorphic and irregular. EEG frequencies declined and amplitudes diminished with sleep. Arrhythmic spikes occurred during behavioral sleep and declined with waking. Heart rate decreased when passing from wakefulness to quiet sleep. It was slightly but consistently higher during active sleep compared with quiet sleep.

Key words. Behavioral sleep; quiet sleep; active sleep; REM sleep.

In sleep studies carried out in mammals and birds, scanty attention has been given to the separation of behavioral sleep from electrophysiological sleep. These two parameters generally correlate well enough, so the electrophysiological signs are used as indicators of behavioral sleep.

Sleep in mammals is accompanied by two alternating electro-

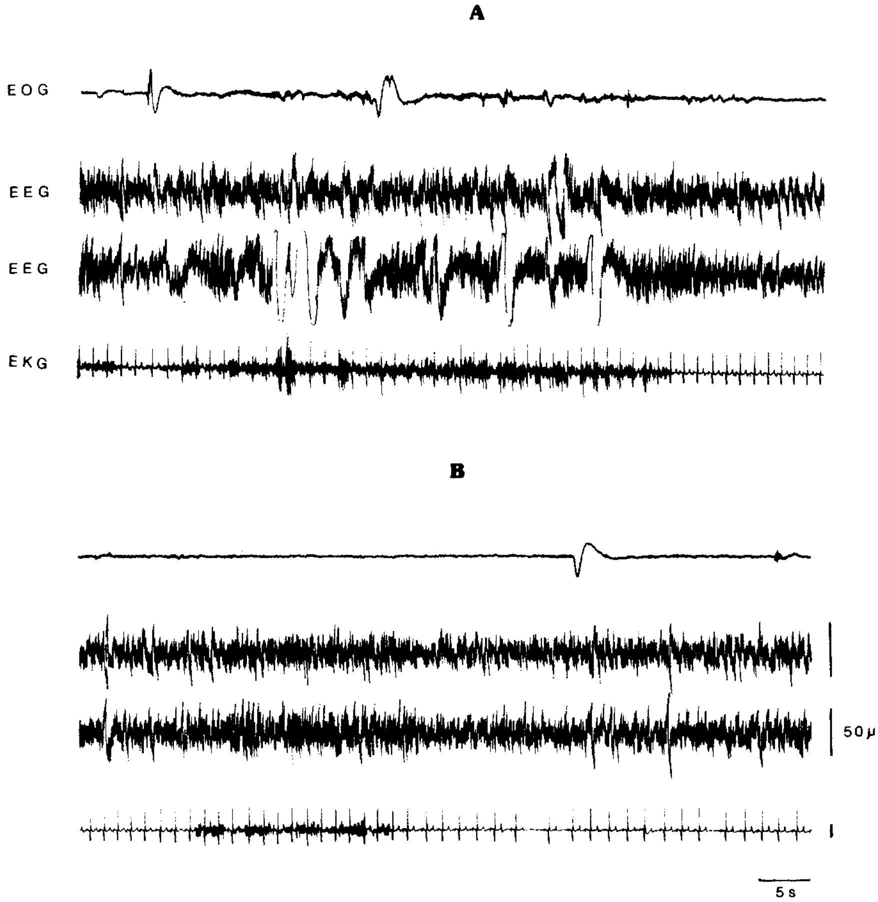

Figure 1. Polygraphic characteristics of active (A) and quiet (B) waking. During active waking, there are frequent eye movements; on the EEG some slow waves, produced by the animal's movements, can be observed; heart rate is elevated. During quiet waking, the eye movements become less frequent and heart rate decreases. EOG, electro-oculogram; EEG, left and right cerebral hemispheres respectively. Cal: 100 µv.