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Circadian pacemaker does not arrest in deep hibernation. Evidence for desynchronization from the light cycle

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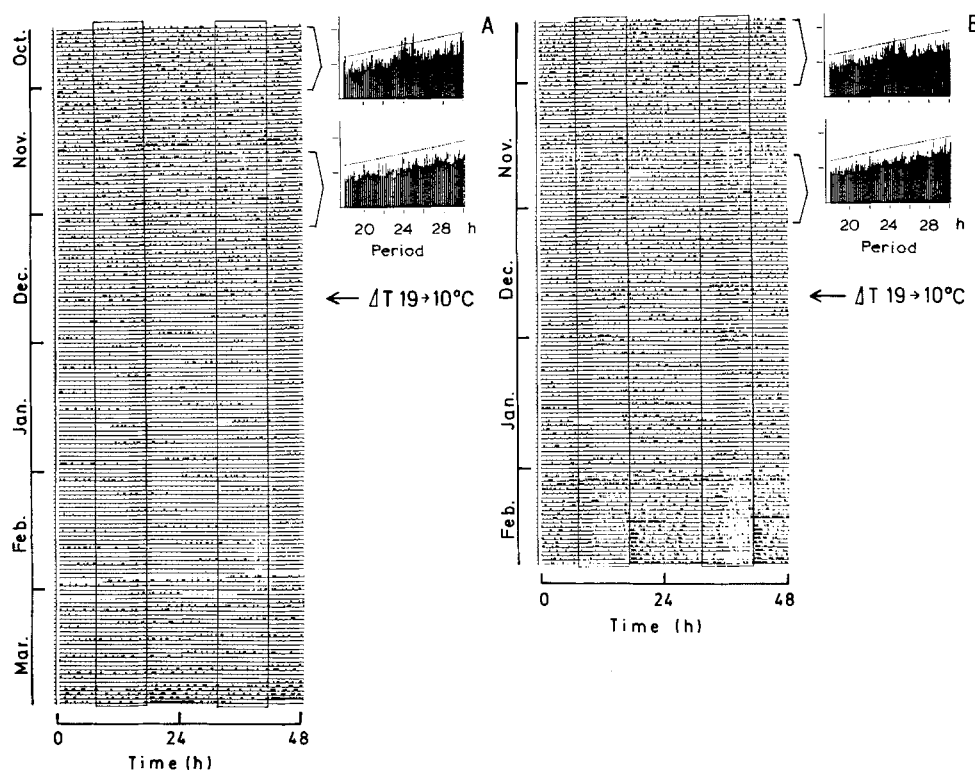
Summary. A freerunning rhythm of locomotor activity was observed between hibernation bouts in Turkish hamsters (*Mesocricetus brandti*) kept in 10L:14D light-dark cycles at $10 \pm 1^\circ\text{C}$. The data further indicate an influence of natural hypothermia upon the circadian system and its ability to entrain to light-dark cycles.

Key words. Hibernation; circadian rhythms; entrainment; light-dark cycle; desynchronization; Turkish hamster.

Twenty-five years ago evidence was presented that the circadian clock continues to run in hibernating mammals^{1,2}. In the common dormouse (*Glis glis*) a circadian rhythm of locomotor activity was shown to persist throughout the hibernation season (for about 280 days) in constant darkness and cold³. Freerunning rhythms of heterothermy were subsequently observed in the garden dormouse (*Eliomys quercinus*)⁴ and in the western jumping mouse (*Zapus princeps*)⁵. The ability of these rhythms to entrain to 24-h light-dark (LD) cycles was shown for both species of dormice^{3,4}. Recently, Vaněček and co-workers⁶ have presented data which suggest that the circadian pacemaker which drives the rhythm of melatonin formation in the pineal is arrested during hibernation bouts in the Syrian hamster (*Mesocricetus auratus*). New data from the closely related Turkish hamster (*M. brandti*), however, show that a circadian rhythm of

activity can persist through bouts of hibernation up to about 100 h.

The presented data derive from an experiment in which 7 Turkish hamsters (4 ♂; 3 ♀) were held under constant 10L:14D light-dark cycles (150:0.02 lx) for 18 months beginning from the middle of October 1984. The hamsters were born during the previous summer and were maintained under natural daylengths. Ambient temperature was $19 \pm 1^\circ\text{C}$ before 20 December and $10 \pm 1^\circ\text{C}$ thereafter. Activity was continuously recorded by a photocell and an infrared light source in the middle of the cage. Whenever the animal crossed the light beam, a contact was closed on an event-recorder channel. In addition, the sum of all impulses was recorded in 2-min intervals on magnetic disk (Kräussling system) for further computer processing. Food pellets (Altromin) and tap water were given ad libitum.



Original recordings of locomotor activity of 2 Turkish hamsters during the hibernation season. The animals were exposed to LD 10:14 (L indicated by frame). Records of successive days are plotted underneath each other on a 48-h scale. On 20 December, ambient temperature was changed

from 19 to 10°C . On the right margin of each record, chi-square periodograms are shown for sections indicated by brackets. Vertical lines reaching at or above the inclined line indicate significant values. White spaces on the records indicate recording failures.

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 τ s 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 τ s 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., Vančec̆ek 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 pooled⁹.

From the previously mentioned finding that the rhythm of melatonin formation in the pineal of the Syrian hamster is abolished during hibernation⁶, 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 hamsters¹⁰, 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 conditions¹

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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 rhythms². Temperature cycles can entrain freerunning rhythms not only in poikilothermic animals³, 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 shown⁶. 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 experi-

ment 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