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Seasonal aspects of sleep in the Djungarian hamster

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Abstract

Background: Changes in photoperiod and ambient temperature trigger seasonal adaptations in the physiology and behaviour of many species, including the Djungarian hamster. Exposure of the hamsters to a short photoperiod and low ambient temperature leads to a reduction of the polyphasic distribution of sleep and waking over the light and dark period. In contrast, a long photoperiod enhances the daily sleep-wake amplitude leading to a decline of slow-wave activity in NREM sleep within the light period. It is unknown whether these changes can be attributed specifically to photoperiod and/or ambient temperature, or whether endogenous components are contributing factors. The influence of endogenous factors was investigated by recording sleep in Djungarian hamsters invariably maintained at a low ambient temperature and fully adapted to a short photoperiod. The second recording was performed when they had returned to summer physiology, despite the maintenance of the 'winter' conditions.

Results: Clear winter-summer differences were seen in sleep distribution, while total sleep time was unchanged. A significantly higher light-dark cycle modulation in NREM sleep, REM sleep and waking was observed in hamsters in the summer physiological state compared to those in the winter state. Moreover, only in summer, REM sleep episodes were longer and waking bouts were shorter during the light period compared to the dark period. EEG power in the slow-wave range (0.75–4.0 Hz) in both NREM sleep and REM sleep was higher in animals in the summer physiological state than in those in the 'winter' state. In winter SWA in NREM sleep was evenly distributed over the 24 h, while in summer it decreased during the light period and increased during the dark period.

Conclusion: Endogenous changes in the organism underlie the differences in sleep-wake redistribution we have observed previously in hamsters recorded in a short and long photoperiod.

Background

Changes in photoperiod trigger seasonal adaptations in physiology and behaviour of many species [1]. The adaptations are manifold and include changes in body weight, pelage colour and density, altered social and sexual behaviors, in many rodents gonadal regression and sup-

pression of breeding, and in some species hibernation or episodes of daily torpor. In mammals, the main trigger for these changes is the shortening of the photoperiod that determines the duration of pineal melatonin secretion [1–11]. Seasonal changes in physiology can be facilitated by lowering of ambient temperature (T_A) [12–15]. The

encoding of seasonal time may involve clock genes, as suggested by the elevated expression of *Per1* and *Per2* genes in the SCN and pars tuberalis under a long photoperiod [16–19].

Few studies have addressed seasonal changes in sleep. Walker et al [20] reported annual changes in sleep in 4 golden mantled ground squirrels, with the largest amount of sleep in winter. Changes in sleep duration were found in 4 captive prosimians, *Microcebus murinus*, with major reductions of sleep in summer [21]. In humans, under natural conditions in winter and under controlled short photoperiod conditions in the laboratory, sleep duration is increased when nights are long [22–24], but also changes restricted to timing and not duration of sleep have been reported [25]. A behavioural study in elephants in captivity found an increase in sleep duration during the winter months [26]. In contrast, in small rodents, including the rat, Siberian chipmunk, and Djungarian hamster, sleep duration was not affected by a change in photoperiod [27–31]. However, a marked redistribution of sleep occurred across 24 h when the animals were recorded in a long and a short photoperiod.

The Djungarian hamster is a rodent that typically displays a large spectrum of behavioural and physiological adaptations to changes in photoperiod [2] (for references see [30]). The most prominent change in sleep was the enhancement of the light-dark amplitude in the amount of sleep when the hamsters were adapted to 'summer' conditions by a long photoperiod, after living in the 'winter' short photoperiod. Moreover, EEG power density in the slow-wave range was lower in the short photoperiod [32]. It is unknown whether the differences in sleep between the two photoperiods are a direct consequence of the change in the environment or if an endogenous component is involved. Syrian hamsters maintained in short days or in constant darkness do not sustain gonadal regression indefinitely, indicating that an endogenous component contributes to these changes [33,34]. In Djungarian hamsters the amplitude and duration of melatonin secretion returned to summer values despite the maintenance of the short photoperiod [8], (A. Stieglitz, PhD thesis, 1995), and we have frequently observed that the hamsters maintained in a short photoperiod and low T_A nevertheless gain weight and show the typical pelage change from white to dark brown (unpublished; Figure 1). It thus seems that the hamsters undergo a refractory period, despite the maintenance of 'winter' conditions in the environment. We investigated the endogenous nature of changes in sleep by comparing hamsters recorded in winter with animals recorded several months later, when they showed adaptations to summer, while they remained in a short photoperiod and low T_A throughout the experiment.

Results

In summer, when the hamster's pelage was dark brown (Figure 1), they showed a significant increase in the light-dark amplitude of total sleep time, NREM sleep and REM sleep compared to winter, when the fur was white with the typical dark band on the back (Figure 2). The total amount of sleep (TST) and the amounts of the single vigilance states remained at a similar level in winter and summer (Figure 2, Table 1). This result applied also to those hamsters which were recorded in both conditions ($n = 6$; TST: $58.4 \pm 2.1\%$ in winter physiology and $57.9 \pm 1.9\%$ in summer physiology; NREM sleep: $50.6 \pm 1.8\%$ and $49.6 \pm 1.6\%$; REM sleep: $8.5 \pm 0.4\%$ and $8.9 \pm 0.4\%$, paired *t*-test, n.s.). The increase in amplitude in summer was due to a significant increase of TST and a concomitant increase in REM sleep in the light period, while an opposite change occurred in the dark period (Table 1).

The changes in the vigilance states between the two conditions were reflected in the duration and frequency of episodes (Table 2). While in hamsters manifesting winter physiology, episode duration and episode frequency in NREM sleep and waking did not differ between the light and the dark period, and REM sleep episode frequency was larger in the light period compared to the dark period, when recorded in summer physiology, REM sleep episodes were longer, waking episodes shorter, and NREM and REM sleep episodes more frequent in the light period compared to the dark period. None of the 24-h values differed significantly between the hamsters in the winter or in the summer physiological state.

SWA in NREM sleep reflected the redistribution of TST in the light and dark period between the conditions. Thus, the LD amplitude increased significantly from winter to summer (Figure 2). No LD change in SWA in NREM sleep was observed in winter, while an increase of SWA was seen from the light to the dark period in summer. Within the SWA band, frequencies between 0.75–3.0 Hz increased significantly from winter to summer physiology (all hamsters: $378.07 \pm 34.89 \mu V^2$ in winter and $537.67 \pm 38.81 \mu V^2$ in summer, unpaired *t*-test, $p < 0.01$; $n = 6$; $386.05 \pm 26.93 \mu V^2$ in winter and $493.96 \pm 34.95 \mu V^2$ in summer, paired *t*-test, $p = 0.068$). An increase in EEG power was present in frequencies between 1.25 – 2.5 Hz also in REM sleep (not shown). Total EEG power (0.75–20.0 Hz) over all vigilance states did not differ between the hamsters in winter physiology and summer physiology ($1368.34 \pm 130.98 \mu V^2$ and $1650.48 \pm 119.51 \mu V^2$, $n = 10$ and 11 , respectively, unpaired *t*-test, $p = 0.13$; $1368.03 \pm 128.19 \mu V^2$ and $1513.63 \pm 90.26 \mu V^2$, $n = 6$, paired *t*-test, $p = 0.35$).

The comparison of the 24-h EEG power spectrum between the two cortical derivations showed a frontal



Figure 1
Djungarian hamsters displaying the typical winter and summer pelage.

predominance in NREM sleep in the low frequency range both in the hamsters in winter physiology (1.25–2.5 Hz) and summer physiology (1.25–4.0 Hz). The difference between the derivations remained the same in the winter and summer physiology hamsters.

To establish whether small differences in T_A or in brain temperature could have contributed to the differences in sleep, several correlations (Pearson product-moment correlation) were computed. No significant correlation was found between brain temperature and EEG parameters (total EEG power: $r^2 = 0.005$, $p = 0.77$, $n = 20$, brain temperature data of one hamster were lacking; $r^2 = 0.25$, $p = 0.10$, $n = 12$; LD SWA difference, $r^2 = 0.05$, $p = 0.34$, $n = 20$ and $r^2 = 0.28$, $p = 0.08$, $n = 12$; LD difference in the amount of NREM sleep, REM sleep and waking (n.s., not shown)). Also the correlations with T_A were not significant (total EEG power, $r^2 = 0.03$, $p = 0.50$, $n = 20$ and $r^2 = 0.02$, $p = 0.64$, $n = 12$; LD SWA difference, $r^2 = 0.12$, $p = 0.132$, $n = 20$ and $r^2 = 0.14$, $p = 0.24$, $n = 12$; LD difference in the

amount of NREM sleep, REM sleep and waking (n.s., not shown)).

Discussion

The main change in sleep observed in hamsters recorded in a physiological state typical for winter and for summer was an enhancement of the sleep-wake amplitude. The total amount of vigilance states remained unchanged, while the polyphasic sleep-wake pattern was redistributed. These summer-winter differences are similar to those observed in hamsters recorded after a prolonged adaptation to a short photoperiod at 16°C or after adaptation to a long photoperiod at 22°C [31] or in hamsters that remained always at 14.5°C but were adapted first to a short and then to a long photoperiod [32]. In the latter studies it remained open whether the changes were induced by the photoperiod or whether they have an endogenous component. Our results indicate that there is an endogenous component contributing to the seasonal changes in sleep.

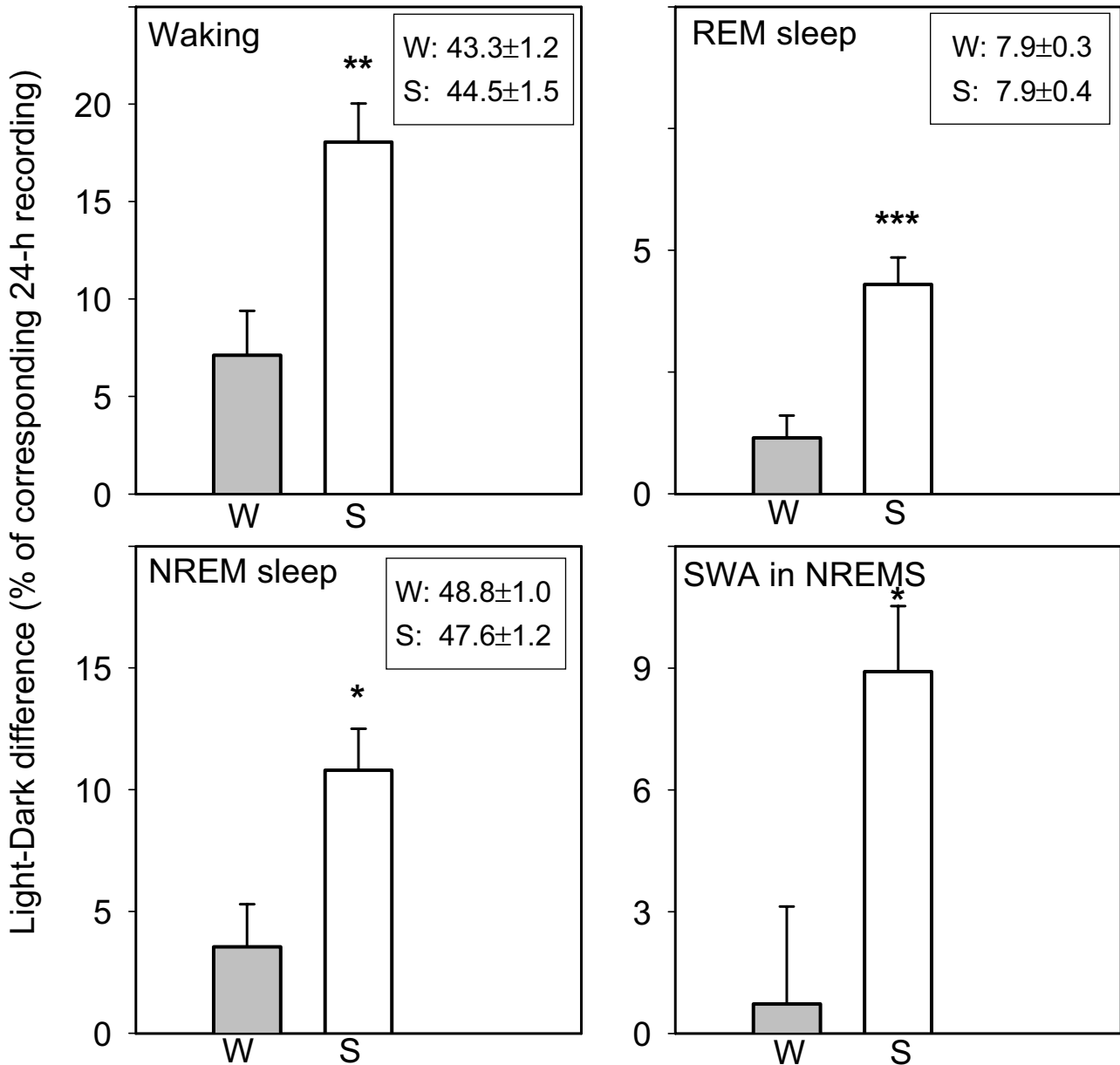


Figure 2

Winter-Summer difference in vigilance-state distribution. Light-dark differences in the vigilance states and slow-wave activity (SWA, mean EEG power density 0.75–4.0 Hz) in hamsters in physiological state belonging to winter and to summer. Mean 8-h and 16-h values (\pm SEM) expressed as percentage of the corresponding 24-h for waking, non-rapid eye movement (NREM) sleep and REM sleep. SWA in NREM sleep is expressed relative to the corresponding 24 h mean (= 100%). Numbers within panels represent total amount in % of 24 h (mean \pm SEM). Winter (W, n = 10) and summer (S, n = 11). Note different scales of panels. Winter vs. summer: *p < 0.01, **p < 0.005, ***p < 0.0005; unpaired t-test (for n = 6: waking p < 0.05, NREM sleep p = 0.065, REM sleep p < 0.01 and SWA p = 0.063, paired t-test).

The stability of sleep duration seems to be a feature of animals that exhibit a polyphasic sleep-wake pattern [27–

31], since humans that typically have a monophasic sleep pattern, did increase sleep duration during the winter

Table 1: Seasonal differences in the vigilance states.

	Hamsters in winter physiological state			Hamsters in summer physiological state		
	8-h L	16-h D	24 h	8-h L	16-h D	24 h
Waking	23.15 ± 0.94* °	27.43 ± 0.59°	624.03 ± 8.03	19.45 ± 0.90**	30.29 ± 0.81	640.16 ± 15.01
NREM sleep	31.30 ± 0.90	29.17 ± 0.57°	702.13 ± 9.99	33.69 ± 0.93**	27.21 ± 0.48	685.50 ± 14.80
REM sleep	5.70 ± 0.33* °	5.00 ± 0.18° °	113.35 ± 4.58	6.93 ± 0.31**	4.35 ± 0.11	114.34 ± 2.89

Mean values ± SEM in min/h in the light (L) and dark (D) period (LD 8:16 h) and 24-h values (minutes) for hamsters in winter physiological state (n = 10) and summer physiological state (n = 11). Differences between the corresponding periods in winter vs. summer: °p < 0.05, °°p < 0.005, two-tailed unpaired t-test. For n = 6, p < 0.05 for REM sleep in the light and dark period and waking in the light period; Differences L vs. D: *p < 0.05, **p < 0.0001, two-tailed paired t-test. For n = 6, L vs. D in summer, p < 0.001 for all vigilance states, two-tailed paired t-test.

Table 2: Seasonal differences in duration and frequency of vigilance state episodes.

	Hamsters in winter physiological state			Hamsters in summer physiological state		
	8-h L	16-h D	24 h	8-h L	16-h D	24 h
Episode duration (min)						
Waking	6.35 ± 0.72	6.27 ± 0.47	6.21 ± 0.42	5.26 ± 0.47**	7.57 ± 0.81	6.75 ± 0.62
NREM sleep	7.54 ± 0.31	7.39 ± 0.38	7.43 ± 0.35	7.94 ± 0.36	7.15 ± 0.31	7.40 ± 0.26
REM sleep	1.73 ± 0.07	1.67 ± 0.07	1.69 ± 0.06	2.08 ± 0.17***	1.64 ± 0.09	1.82 ± 0.12
Episode frequency (# per h)						
Waking	4.15 ± 0.40	4.29 ± 0.29	4.25 ± 0.30	3.98 ± 0.25	4.20 ± 0.41	4.13 ± 0.34
NREM sleep	4.48 ± 0.19	4.15 ± 0.23	4.26 ± 0.19	4.56 ± 0.19*	3.90 ± 0.23	4.12 ± 0.19
REM sleep	3.29 ± 0.20***	2.65 ± 0.15	2.86 ± 0.15	3.52 ± 0.27***	2.36 ± 0.14	2.75 ± 0.16

Mean values (± SEM) for duration (minutes) and frequency (number of episodes per hour) of vigilance state episodes for the light (L) and dark (D) period (LD 8:16 h), and for the entire 24 h recording in the winter physiological state (n = 10) and summer physiological state (n = 11). L vs. D: *p < 0.05, **p < 0.01, ***p < 0.005, ****p < 0.001, two-tailed paired t-test. For n = 6: 24-h REM sleep episode duration: winter vs. summer, p < 0.05, L vs. D in summer, p < 0.01; REM sleep episode frequency: L vs D p < 0.05 both in winter and summer.

months [22–24]. The changes in SWA in NREM sleep reflected the changes in the amount of sleep within the light or dark period. In winter, when sleep was more evenly distributed between the light and dark period, SWA showed only a minimal LD amplitude. In contrast, in summer when the hamsters were more awake during the dark period, SWA exhibited concomitantly higher values compared to the light period. Thus, hamsters in the summer physiological state sleep less but more intensively during the dark period compared to their sleep in winter. These data are in accordance with the two-process model of sleep regulation that predicts that the homeostatic Process S, quantified by SWA reflects the previous sleep-wake history [35].

The sleep-wake redistribution between the winter and summer physiology animals was reflected also in the frequency and duration of vigilance state episodes. Waking episode duration was lower and the frequency of NREM sleep episodes was higher during the light period in summer physiology, when the hamsters slept more. No

changes occurred in the hamsters in winter physiology when sleep was more evenly distributed over the 24 h.

Although day-length appears to be the primary environmental cue that the Djungarian hamster uses to initiate seasonally appropriate physiological and behavioural changes [2,8,14], ambient temperature and food restriction markedly affect the photoperiodic responses [14]. In order to make sure that the changes we observed were reflecting endogenous mechanisms, several correlations were computed. Not even a trend between any of the effects on sleep and T_A or brain temperature was observed. Also in a previous study, EEG power density in the slow-wave range had increased when hamsters were recorded first in a short photoperiod followed by a long photoperiod [32]. In both studies other EEG frequencies were not affected. We have repeatedly observed a decrease of EEG power density over time in rats and hamsters chronically implanted with EEG electrodes. It is therefore unlikely that the present increase in SWA from winter to summer was due to technical artifacts.

In a previous paper we concluded that when the Djungarian hamster prepares for the harsh environment it will encounter during winter, it dissociates sleep homeostasis from the circadian clock [32]. This was based on the data that showed that sleep homeostasis remained invariable in a long and short photoperiod, but the sleep-wake pattern had changed dramatically [31,36]. Nevertheless, it was evident that the circadian clock remained functional, because other behavioural and physiological rhythms remained in synchrony with the light-dark cycle [32,37], or free-ran in constant darkness [38]. The present data show that when the animal's physiology returns to its summer characteristics while the short photoperiod and low T_A are maintained, the circadian clock seems to regain control over the sleep-wake behaviour. This indicates that physiological changes occurring in the hamsters as they adapt to different photoperiods encompass also an interaction between the circadian clock and sleep homeostatic mechanisms.

Little is known about the mechanisms that underlie this interaction. Among the many adaptations to the short photoperiod, the most important advantage for survival the Djungarian hamster gains from the short photoperiod physiology is the change in metabolic rate [37]. Recent developments in narcolepsy research integrate sleep and metabolism and suggest that changes in metabolic rate do influence sleep regulation [39]. Also hormonal changes may be involved in the relation between sleep homeostasis and the circadian clock. For example it has been hypothesized that melatonin can serve both as a clock and as a calendar [1,9,40]. In the Djungarian hamster and the European hamster the duration and amplitude of melatonin secretion depends on photoperiod e.g. [6,11,41,54], (A. Stieglitz, PhD thesis, 1995). When the duration of darkness was increased the onset of melatonin synthesis was delayed in both species, while the end corresponded to lights on in the Djungarian hamster only when adaptation to the photoperiod was sufficiently long [6,11,42]. Thus, in the European hamster an endogenous, seasonal component became evident in the short photoperiod, where the end of melatonin secretion was unrelated to the time of lights on. The evidence that melatonin may have a direct effect on sleep in the Djungarian hamster [43,44] or in the rat [43,55] is inconclusive.

Previous comparisons of the EEG power spectra in NREM sleep have shown a frontal predominance of the low EEG frequencies in humans [45–47], rats [48,49], mice [50], and Djungarian hamsters [51]. Interestingly, the frontal predominance in EEG power density in NREM sleep was not affected by the seasonal changes in the animal's physiology, supporting the interpretation that frontal predominance may reflect a functional component that is related to previous waking activities.

Conclusions

Our data show that light-dark differences in sleep-wake behavior and the time-course of EEG SWA recover when the hamsters spontaneously exhibit changes related to long photoperiod physiology. The circadian clock seems to regain control of the circadian sleep-wake distribution.

Methods

Animals

Adult Djungarian hamsters (*Phodopus sungorus*) raised under a natural photoperiod in summer, were kept individually in Macrolon cages (36 × 20 × 35 cm) with food and water available ad libitum, and maintained in a short photoperiod with 8-h light – 16-h dark (LD, light from 09:00 – 17:00 h; 7 Watt OSRAM DULUX EL energy saving lamp, approximately 30 lux). Mean ambient temperature (T_A) was $15.5 \pm 0.2^\circ\text{C}$.

Surgery

When the weight reduction and the fur colour index (# 5–6 on the index scale 1–6, according to Figala et al [52]) as well as the gonadal regression indicated a strong adaptation to the short photoperiod (Figure 1), the 15 best adapted hamsters of a total of 32 were selected for i.p. implantation of temperature-sensitive transmitters (model X-M, Mini-mitter). At the age of 5.3 ± 0.4 months the hamsters (mean weight 26.6 ± 1.3 g, $n = 15$) were implanted under deep anaesthesia (Ketalar® 75 mg/kg, Parke-Davis; Rompun® 4 mg/kg, Bayer, i.p.) with gold-plated miniature screws (0.9 mm diameter) that served as EEG electrodes. Screws were placed epidurally over the right parietal cortex (2 mm lateral to midline and 2 mm posterior to bregma), right frontal cortex (2 mm lateral to midline and 2 mm anterior to bregma) and a reference electrode was placed over the cerebellum (2 mm posterior to lambda, on midline). A thermistor (Thermometrics, P20, R (25°C) = 1 k Ω , max. diam. = 0.5 mm, accuracy $\pm 0.05^\circ\text{C}$) was inserted horizontally between the skull and dura through a hole over the left frontal cortex (2–3 mm lateral to midline and 2 mm anterior to bregma) to measure cortical temperature (T_{CRT}). Two gold wires (diameter 0.2 mm) inserted into the neck muscles served to record the electromyogram (EMG). The electrodes and thermistor were soldered to stainless steel wires and to a plug that was fixed to the skull with dental cement [53]. Animals were connected to the cables and allowed to recover at least two weeks.

Experimental protocol

The two EEGs, EMG and T_{CRT} were continuously recorded for 24-h when the animal's physiology was in 'winter' conditions (January – February). After 'summer' physiology was manifest in all animals, i.e. fur colour changed from white-grey to brown-grey and regrowth of gonads was evident, a second 24-h record was obtained in March.

The short photoperiod and low T_A were maintained throughout the entire experiment. Six hamsters contributed to both days, whereas four and five hamsters contributed with a recording in winter or summer, respectively.

Data acquisition and analysis

The EEG and EMG signals were amplified (amplification factor approx. 2,000), conditioned by analogue filters (high-pass filter: -3 dB at 0.016 Hz; low-pass filter: -3 dB at 40 Hz, less than -35 dB at 128 Hz) sampled with 512 Hz, digitally filtered (EEG: low-pass FIR filter 25 Hz; EMG: band-pass FIR filter 20–50 Hz) and stored with a resolution of 128 Hz. EEG power spectra were computed for 4-s epochs by a Fast Fourier Transform (FFT) routine. Adjacent 0.25-Hz bins were averaged into 0.5-Hz (0.25 – 5.0 Hz) and 1.0-Hz (5.25–25.0 Hz) bins. The EMG was full-wave rectified and integrated over 4-s epochs, T_{CRT} and T_A inside the cage were sampled at 4-s intervals. Before each recording the EEG and EMG channels were calibrated with a 10 Hz sine wave, 300 μ V peak-to-peak signal.

The three vigilance states NREM sleep, REM sleep and waking were scored for 4-s epochs as in previous studies [30,53]. Vigilance states were determined off-line by visual inspection of the parietal and frontal EEG and EMG records and EEG power in the slow-wave range (0.75–4.0 Hz). Epochs containing EEG artifacts in both derivations or in a single derivation were excluded from spectral analyses of both EEG derivations (14.2 ± 0.9 SEM % of recording time. Artifacts occurred mainly during active waking: 24.4 ± 1.8 SEM % of waking). Vigilance states could always be determined.

The duration and frequency of vigilance state episodes were determined according to criteria described previously [30,53]. Differences in the EEG spectrum between the winter and summer recording were tested by ANOVA for repeated measures (rANOVA) or ANOVA. Whenever ANOVA reached significance, differences were evaluated by post hoc two-tailed paired *t*-tests within days or by unpaired *t*-test between two days. LD differences were tested with post hoc two-tailed paired *t*-tests within days or by unpaired *t*-test between two days.

All statistical comparisons of data from recordings performed in hamsters in winter and summer physiology were performed twice, once for the $n = 6$ hamsters which had been recorded both in winter and summer physiology (paired tests), and once for the entire group ($n = 10$ –11; unpaired tests).

Authors' contribution

All authors participated in the planning and execution of the study; all authors contributed to the draft and read and approved the manuscript.

Competing interests

None declared.

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