



Sex differences in Siberian hamster ultradian locomotor rhythms

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HIGHLIGHTS

- ▶ Sex and day length affect Siberian hamster ultradian (UR) and circadian (CR) rhythms.
- ▶ UR period was longer in females than in males in both long (LD) and short (SD) days.
- ▶ CRs were less prevalent, less robust and lower in amplitude in SDs than LDs.
- ▶ Neuroendocrine refractoriness to SD was compatible with persistent SD-like URs.

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ABSTRACT

Sex differences in ultradian activity rhythms (URs) and circadian rhythms (CRs) were assessed in Siberian hamsters kept in long day (LD) or short day (SD) photoperiods for 40 weeks. For both sexes URs of locomotor activity were more prevalent, greater in amplitude and more robust in SDs. The UR period was longer in females than males in both day lengths. The reproductive system underwent regression and body mass declined during the initial 10 weeks of SD treatment, and in both sexes these traits spontaneously reverted to the LD phenotype at or before 40 weeks in SD, reflecting the development of neuroendocrine refractoriness to SD patterns of melatonin secretion. Hamsters of both sexes, however, continued to display SD-like URs at the 40 weeks time point. CRs were less prevalent and the waveform less robust and lower in amplitude in SDs than LDs; the SD circadian waveform also did not revert to the long-day phenotype after 40 weeks of SD treatment. Short day lengths enhanced ultradian and diminished circadian rhythms in both sexes. Day length controls several UR characteristics via gonadal steroid and melatonin-independent mechanisms. Sex differences in ultradian timing may contribute to sex diphenisms in rhythms of sleep, food intake and exercise.

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1. Introduction

Despite well-established ultradian rhythms (URs) in sleep [1], food consumption [2,3], water intake [4], locomotor activity [5], heart rate [6] and body temperature [7], the substrates that mediate behavioral URs have rarely been investigated. A Web of Science search for the years 1990–2012, coupling the search terms “hormones” and “behavior” with either “ultradian” or “circadian”, yielded 52 and 5364 citations, respectively, evidence of the relative neglect of this class of biological rhythms. The neuroendocrine mechanisms that subserve URs are poorly understood and the existence and nature of sex differences in behavioral URs, if any, remain unspecified.

Robustness, amplitude, and presence of locomotor activity URs vary as a function of the stages of the Syrian hamster estrous cycle [8]. The

period (τ'), amplitude and complexity of male Siberian hamster locomotor URs increases when day lengths fall below 13 h light/day, which is associated with testicular regression [9] and marked reductions in blood androgen concentrations [10]. These observations raised the possibility that gonadal steroids influence ultradian behavior rhythms. However, gonadectomy alone did not alter the UR waveform of male hamsters housed in long days; testosterone and estradiol were likewise without effect on male locomotor URs [11], suggesting that the marked seasonal changes in the UR waveform occur largely independently of concurrent changes in gonadal hormones. It remains unknown, however, whether this conjecture applies to females; thus, a principal aim of this investigation was to evaluate URs in locomotor activity in intact female Siberian hamsters housed in long and short day lengths and to determine whether URs are similar or differ in females and males.

In Siberian hamsters, melatonin-dependent responses to short days (e.g., changes in body mass, pelage molt, reproductive and immune function) become refractory to extended (>20 weeks) short-day patterns of melatonin secretion, and exhibit ‘spontaneous’ reversion to the long-day phenotype. Despite the prominent role of melatonin in

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mediating mammalian physiological responses to changes in photoperiod [12], several aspects of the UR waveform response to short days are unaffected by extirpation of the pineal gland. UR τ' , for instance, increases from 2 h in long days to 4 h in short days, independent of pineal status [11]. In contrast, short-day induced decreases in UR mesor activity levels are counteracted by pinealectomy; short day modulation of the amplitude of the UR waveform is governed by both pineal-dependent and -independent mechanisms. These relations were established after 12 weeks of short day treatment of male Siberian hamsters [11]. It remains unknown whether the UR waveform eventually becomes refractory to short days. Short-day changes in UR τ' could spontaneously revert to the long day phenotype after 40 weeks of treatment, suggesting melatonin-dependent control of seasonal timing. Alternatively, failure of prolonged short-day exposure to trigger the long-day phenotype would establish that URs do not become refractory to short days, and imply that the prevailing photoperiod, rather than melatonin, controls seasonal changes in the UR waveform. The present study evaluated these hypotheses.

2. Materials and methods

2.1. Animals and housing

Siberian hamsters (*Phodopus sungorus*) from a breeding colony maintained at the University of Chicago on a light:dark cycle of 15L:9D (15L; lights off at 17:00 CST) were housed in polypropylene cages (28 × 17 × 12 cm) on wood shaving bedding (Harlan Sani-Chips, Harlan Inc., Indianapolis, IN, USA). Ambient temperature was 20 ± 0.5 °C, and relative humidity 53 ± 2%. Food (Teklad Rodent Diet 8604, Harlan Inc.), filtered tap water and cotton nesting material were continuously available in the cages. All procedures conformed to the USDA Guidelines for the Care and Use of Laboratory Animals and were approved by the Institutional Animal Care and Use Committee of the University of Chicago (Protocols 71383 and 71443). The experiments were conducted at the University of Chicago.

2.2. Photoperiods

Adult male and female hamsters, 60–90 days of age, from the 15L:9D breeding colony (n = 106) were housed singly. On week 0, hamsters were transferred to a short day (SD) photoperiod (9L:15D; lights off at 18:00 h CST), where they remained for the next 40 weeks (SD40 group); other groups remained in the 15L photoperiod for 40 weeks (LD group) or for 30 weeks, at which time they were transferred to SDs for the final 10 weeks of the experiment (SD10 group). Final sample sizes were: LD: n = 11 females, 13 males; SD40: n = 25 females, and 24 males; SD10: n = 12 females, and 16 males.

2.3. Somatic and reproductive measures

On weeks 10, 20, 28 and 40, hamsters were weighed (± 0.1 g) and reproductive status assessed under methoxyflurane anesthesia. These time points were selected so as to capture the temporal dynamics of somatic and behavioral changes during the development of refractoriness, and to allow sufficient time for refractoriness/recrudescence to manifest. The length and width of the left testis were measured (± 0.1 mm). The product of testis width squared times testis length provides a measure of estimated testis volume (ETV) highly correlated (R > 0.9) with testis weight [13]. Vaginal patency was determined using a blunt 2 mm stainless steel probe. Stage in the pelage color cycle was assessed using an integer scale of 1–4 (1 = dark 'summer' fur, 4 = white 'winter' fur; [14]) without knowledge of the animal's treatment condition.

Males that failed to exhibit gonadal regression (ETV > 400) and females with patent vaginas after 10 weeks of SD treatment (i.e., at week 10 for SD40 hamsters; at week 40 for SD10 hamsters), that also did not

exhibit a winter pelage (fur score = 1), were identified as photoperiod nonresponders (6 females and 6 males) and omitted from all subsequent analyses.

2.4. Activity measurements

We measured URs and CRs of spontaneous general locomotor activity — a non-food-specific behavior that correlates highly with daily rhythms of sleep-wakefulness, body temperature, and drinking behavior [15]. URs of locomotor activity correlate positively with feeding rhythms [5] and permit detailed analysis of underlying ultradian timing systems. Locomotor activity was monitored in the home cage between weeks 9–11 ("week 10"), weeks 23–27 ("week 25"), and weeks 38–40 ("week 40") for a minimum of 10 consecutive days with passive infrared motion detectors (Coral Plus, Visonic, Bloomfield, CT) positioned 22 cm above the cage floor that registered activity when 3 of 27 zones were crossed. Activity triggered closure of an electronic relay, recorded by a computer running ClockLab software (Actimetrics, Evanston, IL). Cumulative activity counts were collected at 6 min intervals.

2.5. Activity analyses

2.5.1. Ultradian rhythms (URs)

Activity data collected at 6 min intervals were parsed into light-phase only activity (150 or 90 data points/24 h) and dark-phase only activity (90 or 150 data points/24 h) files. The number of photophases and scotophases sampled was adjusted to provide 900 data points for each hamster to equalize statistical power in periodogram analyses from different photoperiods. For LD hamsters, 10 consecutive nights and 6 consecutive days generated dark-phase and light-phase activity files, each with 900 data points. For SD hamsters, 6 nights and 10 days were collated. Successive days of scotophase- and photophase-specific activity data were concatenated into separate files subjected to Lomb-Scargle periodogram (LSP) and cosinor periodogram analyses, as described in detail elsewhere [8].

2.5.2. Circadian rhythms (CRs)

Unparsed files (240 data points/24 h) 10 days in length were subjected to LSP and cosinor periodogram analyses.

2.6. Statistical analyses

Quantitative parameters of UR and CR waveforms were determined using LSP and cosinor analyses, as described previously [8]. LSP analyses [16] identified the statistical presence/absence of URs and CRs, and the number of significant peaks in the UR spectrum (range: 0.3–7.9 h). The level of statistical significance was set to 0.01. Cosinor analyses determined several quantitative measures of locomotor URs (range: 0.3–7.9 h) and CRs (range: 22–26 h): robustness (or 'prominence', the percent of variance accounted for by the best-fit cosine model, which corresponds to the coefficient of determination R^2 in regression analyses; [17]); mesor (rhythm-adjusted mean value around which the waveform oscillates); amplitude (the difference between the peak or trough value and the mesor), expressed as absolute values (activity counts) and relative values referenced to the photophase-specific mesor value to incorporate baseline activity levels during each photophase in determining rhythm amplitude. Acrophase was computed as the average time relative to the onset or offset of light at which the waveform peaks. The level of statistical significance was set to 0.05.

The LSP optimizes detection of URs by not displaying peaks at multiples of all rhythms detected [18,19]. Supplemental analyses after completion of LSP analysis [20] were adopted as recommended by Refinetti et al. [17], hence the cosinor periodogram [21], a preferred curve-fitting tool to quantify rhythm parameters [17], was used.

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