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Review

Adaptation to short photoperiods augments circadian food anticipatory activity in Siberian hamsters

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ABSTRACT

This article is part of a Special Issue "Energy Balance".

Both the light–dark cycle and the timing of food intake can entrain circadian rhythms. Entrainment to food is mediated by a food entrainable circadian oscillator (FEO) that is formally and mechanistically separable from the hypothalamic light-entrainable oscillator. This experiment examined whether seasonal changes in day length affect the function of the FEO in male Siberian hamsters (*Phodopus sungorus*). Hamsters housed in long (LD; 15 h light/day) or short (SD; 9 h light/day) photoperiods were subjected to a timed-feeding schedule for 10 days, during which food was available only during a 5 h interval of the light phase. Running wheel activity occurring within a 3 h window immediately prior to actual or anticipated food delivery was operationally-defined as food anticipatory activity (FAA). After the timed-feeding interval, hamsters were fed ad libitum, and FAA was assessed 2 and 7 days later via probe trials of total food deprivation. During timed-feeding, all hamsters exhibited increases FAA, but FAA emerged more rapidly in SD; in probe trials, FAA was greater in magnitude and persistence in SD. Gonadectomy in LD did not induce the SD-like FAA phenotype, indicating that withdrawal of gonadal hormones is not sufficient to mediate the effects of photoperiod on FAA. Entrainment of the circadian system to light markedly affects the functional output of the FEO via gonadal hormone-independent mechanisms. Rapid emergence and persistent expression of FAA in SD may reflect a seasonal adaptation that directs behavior toward sources of nutrition with high temporal precision at times of year when food is scarce.

Contents

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Introduction

Seasonal changes in physiology and behavior are ubiquitous in nature. Reproduction and immune function, ingestive and social behaviors, and scores of hormones exhibit seasonally-changing phenotypes (reviewed in Prendergast et al., 2009). Day length (photoperiod) figures prominently in the generation and/or entrainment of these seasonal physiological cycles (Goldman, 2001).

In mammals, accurate timing of seasonal phenotypic transitions is dependent on proper entrainment of the circadian system to seasonal changes in day length (Goldman, 2001; Hiebert et al., 2000); the entrained circadian pacemaker in the suprachiasmatic nucleus (SCN), in turn, drives a circadian rhythm in nocturnal pineal melatonin secretion (Borjigin et al., 2012). Thus, seasonal timing is dependent on feed-forward information from the circadian system. Seasonal physiological adaptations may also exert feedback effects on the circadian system. Following adaptation to short, winter-like day lengths (SDs), male Syrian hamsters exhibit larger light-induced phase shifts of the circadian clock as compared to hamsters housed under long day (LD) photoperiods (Pittendrigh and Daan, 1976; Pittendrigh et al., 1984). The photic thresholds for circadian phase-resetting are approximately 40 times greater in LD relative to SD hamsters (Glickman et al., 2012), suggesting that day length alters the sensitivity of the SCN to photic input, and consistent with a model in which the amplitude of the underlying circadian pacemaker is greater in LD relative to SD (Evans et al., 2004; Glickman et al., 2012). In addition to light, non-photic time cues (zeitgebers; e.g., temperature, social interactions, food availability) can also influence the circadian system (Mrosovsky, 1996; Mrosovsky and Salmon, 1987). However, the extent to which photoperiod alters circadian responses to non-photic zeitgebers has received limited study. In castrated male Syrian hamsters, the magnitude of circadian phase shifts induced by exposure to a novel running wheel was comparable under LD and SD photoperiods. Among the diverse non-photic zeitgebers, however, food is among the most potent (Mistlberger, 2011). The timing of food availability can set the phase of circadian activity and body temperature rhythms, even in the presence of a conflicting light–dark cycle (Coleman et al., 1982). Feeding manipulations that limit food access to a single, brief (3–5 h) timed daily meal yield robust food anticipatory activity (FAA), which stably precedes the timing of the meal (Mistlberger, 2011). Following the discontinuation of timed feeding, FAA persists for several cycles under conditions of total food deprivation, consistent with the conjecture that a self-sustained, but rapidly-dampening, food entrainable oscillator (FEO), or network of oscillators, including the SCN (Mistlberger, 2011), participates in the generation of circadian FAA. Whether, in common with other non-photic zeitgebers, entrainment to food is likewise unaffected by seasonal changes in day length remains largely unexamined. Food entrainment persists following SCN ablation (Stephan et al., 1979) indicating that photoperiod information is not required for entrainment to food; however, in addition to driving the timing of feeding behavior, the SCN exerts temporal gating of FAA and affects FAA amplitude (Acosta-Galvan et al., 2011), leaving open the possibility that photoperiod-driven changes in the amplitude of the circadian oscillation in the SCN may influence the expression of FAA.

Seasonal plasticity in the expression of FAA may afford hamsters additional mechanisms for maintaining energy balance. Enhancements in the expression of FAA in winter, for example, might direct temporally-precise behavior toward sources of nutrition at times of year when food is scarce. Thus, the present study tested the hypothesis that seasonal changes in photoperiod alter the ability of timed feeding to induce FAA. Experiments examined the rate of induction of FAA, FAA amplitude, and the persistence of FAA following the cessation of timed feeding schedules in adult male Siberian hamsters. FAA has not been directly examined in this species previously; however, Siberian hamsters are a canonical model for examining photoperiodism, and may prove useful in examinations of photoperiodic regulation of FAA. Hamsters exhibit robust photoperiodic changes in circadian entrainment (Prendergast and Pyter, 2009), food intake (Bartness, 1996), and, unlike Syrian hamsters, readily ingest food during the light phase (Paul et al., 2004). Because gonadal hormones affect food intake in this species (Bartness, 1996), a follow-up study was also performed to test the hypothesis that photoperiodic changes in FAA are mediated by the withdrawal of gonadal hormones that hamsters exhibit following phenotypic adaptation to short photoperiods.

Materials and methods

Animals and housing

Siberian hamsters (*Phodopus sungorus*) in all studies were derived from a breeding colony maintained at the University of Chicago on a long day (LD) photoperiod (15 h light, 9 h dark; lights off at 18:00 CST). Hamsters were housed in polypropylene cages ($28 \times 17 \times 12$ cm) containing wood shaving bedding (Sani-Chips, Harlan) along with cotton nesting material. Food (Teklad 8604, Harlan) and filtered tap water were provided ad libitum except during intervals of timed feeding, described below. In addition, during intervals of timed feeding, a nutritive supplement (Nutri-cal; Vetoquinol) was provided alongside the food. Ambient temperature was maintained at 20 ± 2 °C with relative humidity $50 \pm 5\%$. All treatments conformed to the USDA Guidelines for the Care and Use of Laboratory Animals and received prior approval by the local Animal Care and Use Committee.

Experiment 1: effects of photoperiod on entrainment to food

At the start of Experiment 1, adult (90–120 day old) male Siberian hamsters ($n = 72$) from the 15 L breeding colony were housed 1/cage and either transferred to a short day photoperiod (SD; 9 h light, 15 h dark; lights off at 18:00 h CST; $n = 36$) or remained in their natal LD ($n = 36$). After 12 weeks of exposure to photoperiods (week 12), reproductive condition in all hamsters was assessed under light isoflurane anesthesia, via a measure of estimated testis volume (ETV; testis length * testis width2), which correlates positively (R2>0.9) with testis weight (Gorman and Zucker, 1995). A minority of Siberian hamsters fails to undergo gonadal regression in SD ('non-responders'; Prendergast et al., 2001); thus only SD hamsters with ETV < 300 on week 12 ($n = 27$) were included in subsequent analyses. ETVs on week 12 were significantly greater in LD relative to SD hamsters (mean ± SEM; LD: 433 ± 12; SD: 96 ± 11; $p < 0.001$, data not illustrated).

Timed feeding procedure

On week 12, hamsters were transferred to larger polypropylene cages ($26 \times 48 \times 21$ cm) equipped with stainless steel running wheels (11.5 cm diameter) and allowed 7 days to acclimate. Running wheels were always present in the cage. The timing of events during timed feeding and control treatments are illustrated in Fig. 1.

Following running wheel acclimation for 7 days, experimental hamsters were trained on a timed feeding (TF) paradigm (LD: $n = 17$; SD: $n = 17$); control hamsters remained on ad libitum (AL) access to food (LD: $n = 18$; SD: $n = 17$; Fig. 1). During TF training, food was only available during a 5 h interval which began 6 h prior to lights off. TF training was maintained for 10 days, after which hamsters were subjected to 2 days of ad libitum feeding, followed by a 2 days of total food deprivation (TFD) to assess FAA (FAA early probe trial). Following the early probe trial, hamsters were returned to ad libitum food access for 7 days (AL interval), after which another 2 day interval of TFD occurred to assess FAA retention (FAA late probe trial).

Home cage locomotor activity collection

Running wheels were fitted with 2 small magnets that recorded half-wheel revolutions via a magnetic reed switch. Switch closures were