Brief communication

Body mass loss during adaptation to short winter-like days increases food foraging, but not food hoarding

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ABSTRACT

Siberian hamsters markedly reduce their body/lipid mass (~20–45%) in short 'winter-like' days (SD). Decreases in body/lipid mass associated with food deprivation or lipectomy result in increases in foraging and food hoarding. When at their SD-induced body/lipid mass nadir, food hoarding is not increased despite their decreases in body/lipid mass, but hoarding was not tested during the dynamic period of body/lipid mass loss (first 5–6 weeks of SDs). Therefore, we tested for changes in foraging/hoarding during this initial period in Siberian hamsters housed in a simulated burrow with a wheel running-based foraging system and exposed to either long 'summer-like' days (LD) or SDs. Two foraging effort conditions were used: 10 Revolutions/Pellet (pellet delivered after running 10 revolutions) and a Free Wheel/Free Food condition (wheel available, food pellets non-contingently available). Regardless of the foraging condition, body mass was significantly reduced across 8 weeks of SDs (~15%). Foraging increased after 7 weeks in SDs, but food hoarding did not increase compared to LDs. Instead food hoarding significantly decreased in SDs at Weeks 2–5 compared with Week 0 values, with the 10 Revolutions/Pellet foraging group returning to LD levels thereafter and the Free Wheel/Free Food group remaining reduced from Weeks 2–7. Collectively, we found that SDs decreased body mass, increased foraging after 7 weeks, and increased food hoarding, but only after an initial decrease and not above that seen in LDs. These data suggest that SD-induced body/lipid mass losses do not engender similar behavioral responses as seen with food deprivation or lipectomy.

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1. Introduction

Obtaining sufficient energy for the maintenance of life and re-production is essential for survival. For many animal species, especially those living in temperate climates, the presence and relative abundance of food is restricted annually and this seasonal variation has shaped seasonal cycles in animal physiology and behavior. For example, many animals exhibit seasonal cycles of breeding, adiposity, hibernation and immune responses (for review see: [1]). The most noise-free environmental cue [2] that synchronizes these physiological and behavioral cycles to the varying temperature, climate and food abundance is the daylength (for review see: [3,4]).

For seasonal mammals, as well as some species of birds, reptiles and amphibians, the daylength is encoded into a neuroendocrine signal through the synthesis and secretion of melatonin via a multisynaptic pathway beginning with the retina and ending in the pineal gland (for review see: [4]). Melatonin is synthesized and released only at night; thus, the peak nocturnal duration of melatonin secretion faithfully codes the daylength (nightlength; for review see: [5]). For Siberian hamsters

(*Phodopus sungorus*), long duration melatonin signals (>12 h) trigger short 'winter-like' day (SD) responses, whereas short duration melatonin signals (<8 h) trigger long 'summer-like' day (LD) responses (for review see: [5]). Thus, the nocturnal duration of melatonin release is able to transfer daylength information to many different physiological systems in photoperiodic seasonal animals and coordinate responses with annual changes in the environment (for review see: [4,5]).

Siberian hamsters are small (<50 g) photoperiod-responsive seasonal mammals that exhibit a broad suite of photoperiod-driven alterations in physiology and behavior [6]. Central to the work described here, Siberian hamsters decrease their body mass ~30% in SDs when food availability is lowest in nature [7], but also do so in the laboratory even when food is abundant (*e.g.*, [8–10]). In addition to the ability to cope with seasonal variation in food availability, Siberian hamsters can withstand energetic challenges that result in negative energy balance, such as food restriction/starvation, because they have ample lipid energy stores in body fat (white adipose tissue [WAT]; ~30–50% of total body mass [11]). In the laboratory, Siberian hamsters food deprived for 56 h lose ~20–30% of their body mass and, upon restoration of *ad libitum* feeding, they do not overeat [12,13]. Instead of overeating, Siberian hamsters [12,14] and other hamster species (*e.g.*, Syrian [*Mesocricetus auratus*] [14]) increase food hoarding. Pregnant and lactating Siberian hamsters experience decreases in body/lipid mass of up to ~50% [15,16] and, as with food deprivation-induced decreases in body/lipid mass, they show impressive

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increases in food hoarding upon refeeding [16]. Because large losses of body mass in adult mammals, including Siberian hamsters, are reflected primarily as decreases in body fat, it is not surprising that direct decreases in body fat, such as occur with surgical removal of WAT (partial lipectomy), trigger increases in food hoarding [17,18].

When Siberian hamsters are tested for their food hoarding after 11 weeks of SD exposure, a time after body mass/fat has reached its nadir, they do not hoard more than their LD counterparts despite these SD-induced body mass/fat losses [19]. From the above, it would be predicted that the SD-induced decreases in body and lipid mass of Siberian hamsters would markedly increase their food hoarding similarly to that occurring with food deprivation-induced losses [12,16,19–21] or with lipectomy [17,18]. It may be, however, that they only do so when their body and lipid mass are most dynamically decreasing during the initial 1 to 5 or 6 weeks of SD exposure. Therefore, we asked: Does the rapid body/lipid mass loss occurring during early SD exposure trigger increases in food foraging and hoarding? This was accomplished by using our foraging/hoarding system (described below and shown and described in: [22]) that allows the measurement of food foraging, hoarding and intake. Terminal measures of WAT and testes masses, as well as serum leptin concentration also were made.

2. Materials and methods

2.1. Animals and housing

Adult male Siberian hamsters, ~2.5–3 months old, weighing 32–50 g were obtained from our breeding colony; the colony was originally established in 1985, and has been outbred with wild caught individuals as previously described [23]. Hamsters were group housed in a LD photoperiod (16:8-h light–dark cycle [light onset at 2030]) from birth and weaned at 28 days of age. Room temperature was maintained at 21 ± 2 °C, with relative humidity at $\sim 50 \pm 10\%$. All procedures were approved by the Georgia State University Institutional Animal Care and Use Committee and were in compliance with the Public Health Service and United States Department of Agriculture guidelines.

At the start of the experiment, animals were transferred to the foraging/hoarding room and singly housed in polypropylene cages ($290 \times 180 \times 130$ mm) for two weeks to acclimate to the new light onset (0800) and single housing. The test diet (75 mg pellets, Dustless Precision Pellets (protein 18.8%, fat 5.0%, fiber 4.6%, ash 4.4%, moisture <5.0%, carbohydrate 61.5%, caloric value: 3.68 kcal/g; BioServ, French-town, NJ) and tap water were available *ad libitum* throughout unless otherwise noted. Siberian hamsters were then placed into the foraging/hoarding apparatuses for one week of acclimation as previously described [22]. Briefly, two cages were connected via polyvinyl-chloride tubing (38.1 mm in diameter and ~1.5 m long), with vertical and horizontal portions to facilitate movement between the top, or 'food cage', and the bottom, or 'burrow cage'. The top cage ($456 \times 234 \times 200$ mm) was equipped with a running wheel, food pellet dispenser and water bottle. The bottom cage ($290 \times 180 \times 130$ mm) contained Alpha-Dri bedding (Specialty Papers, Kalamazoo, MI) and one cotton nestlet (Ancare, Belmore, NY). The bottom cage was covered to simulate the darkness of a burrow. During the first two days of the acclimation period, the hamsters had free access to food and additionally, a pellet was dispensed for every 10 wheel revolutions. Wheel revolutions were counted using a magnetic detection system and a computer-based hardware/software package (Med Associates, Georgia, VT). On the third day, free food was removed and all animals were on a response-contingent condition for four days, where food was only obtained after 10 wheel revolutions. This 10 revolution/pellet condition was then maintained for 14 days when all three behavior measures had stabilized. At that time, animals were then assigned to one of four groups (2 foraging treatments × 2 daylength treatments). Groups were matched for average daily hoard and body mass change over the last 5 days of 10 revolutions/pellet period (baseline).

2.2. Foraging efforts and daylengths

Two foraging efforts used were: 1) 10 Revolutions/Pellet (10REV) and 2) Free Wheel/Free Food (FW, 300 pellets of food were available each day in a non-contingent manner with an active running wheel). The purpose of the 10REV group was to be able to measure food foraging. The purpose of the FW group was to test for *non-specific* alterations in locomotor activity that, without this group, would be interpreted as increases or decreases in the motivation to obtain food by the 10REV group and to be able to detect non-specific/malaise effects if FW wheel running is decreased from *bona fide* inhibition in the motivation to earn food. The two daylength treatments were: 1) LDs (16L:8D, light onset at 0800) and 2) SDs (8L:16D, light onset at 0700). The final number of animals per group was: a) LD/10REV ($n = 6$), b) SD/10REV ($n = 10$), c). LD/FW ($n = 7$) and d). SD/FW ($n = 11$). Animals remained in their respective treatment for 8 weeks. Body mass was recorded weekly to the nearest 0.01 g and wheel running, food foraging, hoarding and intake were recorded daily within one hour of light onset.

2.3. Measurements of food foraging, hoarding, and intake

Food foraged (pellets earned) was defined as the number of pellets delivered into the top cage of the 10REV group hamsters calculated as wheel revolutions ÷ 10. Hoarded food was removed each day and was defined as the number of pellets found in the bottom cage, as well as that removed from hamsters' check pouches. Surplus food was removed each day and defined as the food pellets that remained in the top cage that were neither ingested nor hoarded. Food intake in the 10REV group was determined by [pellets earned − (surplus food + food hoard)]. In the FW group, food intake was defined as [300 pellets − (surplus food + food hoard)]. An electronic balance was used to weigh the food pellets and set to "parts" measurement; thus, one 75-mg food pellet was equal to 1 pellet, with fractions of a pellet calculated as well. The wheel revolutions were recorded continuously in 5 minute bins of activity and analyzed as wheel revolutions per day.

2.4. Terminal measures

After 8 weeks of treatment, animals were lightly anesthetized with isoflurane and had ~400 µl of blood taken from the retro-orbital sinus. Blood was centrifuged at 4 °C for 30 min at 2500 rpm; serum was then collected, stored at −20 °C before leptin analysis (mouse leptin ELISA kit, Millipore, St. Charles, MO) and was performed according to the manufacturer's instructions. Pelage color was assessed using a four point scale 1 = summer and 4 = winter [24] and was recorded at the termination of the experiment (8 weeks). Animals were then killed by an overdose of pentobarbital sodium (300 mg/kg) and testes and epididymal-, inguinal-, and retroperitoneal WAT (EWAT, IWAT, and RWAT, respectively) were excised and weighed to the nearest 0.0001 g.

2.5. Statistical analyses

The repeated measures data (body mass and food foraging, hoarding and intake) were transformed into percent change from initial values ([[initial value − current value] / initial value] × 100) to control for unequal initial body mass and associated measures that that occurred between groups due to the loss of animals during the study.

Statistical analyses were conducted using NCSS version 2000 (Kaysville, UT) for all measures. Body mass, wheel activity and food hoarding and intake were analyzed using three-way repeated measures analysis of variance (ANOVA; Daylength × Foraging Effort × Time; 2 × 2 × 9). Food foraging was analyzed using a two-way repeated ANOVA (Daylength, × Time; 2 × 9). The terminal measures of serum leptin concentration, pelage color, paired testes mass and fat pad mass were analyzed using two-way ANOVA (Daylength × Foraging Effort; 2 × 2). Any SD animals with paired testes mass >250 mg were excluded