Physiology & Behavior 127 (2014) 8–12

Contents lists available at ScienceDirect

Physiology & Behavior

journal homepage: www.elsevier.com/locate/phb

Dynamic modification of hoarding in response to hoard size manipulation

John T. Garretson [a,c], Timothy J. Bartness [a,b,c,*]

[a] Neuroscience Institute, Georgia State University, 24 Peachtree Center Ave NE, Atlanta, GA 30302–4010, USA
[b] Department of Biology, Georgia State University, 24 Peachtree Center Ave NE, Atlanta, GA 30302–4010, USA
[c] Obesity Reversal Center, Georgia State University, 24 Peachtree Center Ave NE, Atlanta, GA 30302–4010, USA

HIGHLIGHTS

- Food hoard size rapidly affects hoarding.
- Hoard is decreased or increased when surreptitiously enlarged or diminished.
- Food deprivation does not increase hoarding for animals with enhanced food stores.

ARTICLE INFO

Article history:
Received 23 July 2013
Received in revised form 20 November 2013
Accepted 23 December 2013

Keywords:
Siberian hamster
Food deprivation
Hunger
Fasting

ABSTRACT

Food hoarding is an evolutionary adaptation whereby animals store food for later consumption when food is limited or when predation risk while foraging is high. It also occurs as part of normal appetitive behavior by humans and non-human animals when they are hungry. Contrary to popular belief, humans do not overeat after food restriction/fasting, rather they increase food hoarding, as do hamster species, but not in laboratory rats or mice. Thus, this aspect of human appetitive behavior is better modeled by hamsters than laboratory rats and mice. Here we tested whether male Siberian hamsters (*Phodopus sungorus*) modify their daily food hoard size under *ad libitum*-feeding and after food deprivation when we artificially increased or removed their food hoard. When the food hoard was completely removed, hamsters hoarded more food the next day than did animals where the hoard was surreptitiously increased. Hamsters that had alternating daily hoard increases/decreases rapidly adjusted their food hoarding inversely proportional to food hoard size. Similarly, after 48 h of food deprivation, a stimulus that initiates high levels of food hoarding upon refeeding in this species, hamsters with artificially increased food hoard size hoarded significantly less than did hamsters where we left the hoard unaltered additionally suggesting that food hoard size directly affects food hoarding. Collectively, as we previously found when the caloric value of the food offered was increased or decreased, food hoard size is in some sense 'regulated' and not simply a reflexive response triggered by inter-meal hunger or food deprivation.

1. Introduction

Food hoarding is achieved when animals forage for and store food for later consumption. Food hoarding is an appetitive ingestive behavior expressed across most animal species (for review see: [1]) including humans. Restricted food access, food deprivation/fasting and to a lesser extent the hunger that occurs between meals are the strongest stimuli that trigger food hoarding (for review see: [2]). Contrary to popular belief, humans exhibit essentially no or little post fast/food restriction-induced increases in eating (for review see: [2]). Rather, hungry humans 'overhoard' by bringing home more food even after mild periods of no food versus their fed counterparts [3–5]. Similarly, various hamster species including Siberian hamsters (*Phodopus sungorus*) studied here, markedly increase their food hoarding, but not food intake, with refeeding after food deprivation [6–9]. Thus, this appetitive ingestive behavior of food hoarding is more similar than different between humans and Siberian hamsters. Therefore, studies of food hoarding by Siberian hamsters appear to be an appropriate model for the study of the environmental and physiological controls of this appetitive ingestive behavior in humans (for review see: [2]).

We have identified several hormones and neuropeptides that are affected by food deprivation naturally such as ghrelin, agouti-related protein and neuropeptide Y and when given exogenously mimic in duration and magnitude the food deprivation-induced increases in food hoarding [10–12], but are not fully explored or understood. Of the many questions remaining to be answered, one that transcends both the environmental and physiological factors governing food hoarding is whether food hoard size is in some sense 'regulated'. That

* Corresponding author at: Department of Biology, 24 Peachtree Ctr Ave NE, Atlanta, GA, 30302–4010, USA. Tel.: +1 404 413 5334; fax: +1 404 413 5301.
E-mail address: bartness@gsu.edu (T.J. Bartness).

0031-9384/$ – see front matter © 2014 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.physbeh.2013.12.008

is, are there processes engaged when food hoarding is triggered that ultimately result in the maintenance of a relatively constant food hoard size, whether it is the physical size of the hoard (e.g., number of hoarded objects) or the overall caloric value of the hoard? We previously partially addressed this issue by challenging *ad libitum*-fed Siberian hamsters with food sources of varying caloric density relative to their standard chow-like food pellets [13]. Specifically, when caloric density was decreased by the addition of a cellulose diluent in the pellets, the number of food pellets hoarded increased proportionately to the decrease in caloric density such that the overall caloric value of the food was maintained, a feat accomplished within the first 24 h of the diet switch. Complementary to this, when the caloric density of the food was increased by adding dietary fat to the pellet composition, the number of food pellets was proportionately decreased such that overall caloric density was maintained — again accomplished within the first 24 h of the diet switch [13].

Collectively, the above data suggest caloric maintenance of food hoard size in *ad libitum*-fed hamsters. Untested, however, was whether food hoard size would be stable if food from the burrow was surreptitiously added or subtracted rather than altering caloric content or diet type thereby increasing or decreasing the size/caloric value of the food hoard. In addition, would any attempt to keep food hoard size constant be affected by food deprivation, the stimulus that most robustly naturally increases food hoarding? Another way of thinking about the possible maintenance of food hoard size tested here is whether the underlying mechanisms involved in daily food hoarding under *ad libitum* feeding conditions or following food deprivation trigger an inflexible almost 'fixed action pattern-like' amount of food hoarding or whether the hoarding is flexible responding to some characteristic of the food already cached. In nature, decreases in food hoard size could occur with food pilfering by conspecifics or heterospecifics and increases could occur via additions made by their pair-bonded mates or offspring as they communally burrow [14]. To accomplish this, we added or subtracted food from their hoard to test whether appropriate compensation occurred (decreased or increased food hoarding, respectively). We also challenged the hamsters with food deprivation to test their ability to adjust hoard size with surreptitious additions and subtractions from their food hoard.

2. Method

2.1. Animals

Three month old male Siberian hamsters ($n = 40$) from our breeding colony raised in a summer-like photoperiod (16:8 light:dark cycle; lights on at 19:00) were weaned at 18 days of age. Lineage of our breeding colony has been described previously [15]. Hamsters were assigned to individual polypropylene cages (456 × 234 × 200 mm) containing Alpha-Dri bedding (Specialty Papers, Kalamazoo, MI), one cotton Nestlet (Anacare, Belmore, NY) with both tap water and the test diet (Dustless Precision Pellets, Purified 75 mg pellets; Bio-Serv, Frenchtown, NJ) available *ad libitum*. Animals were then acclimated to a reverse 16:8 cycle light:dark cycle (lights on at 21:00) for 14 days before manipulations began to make data collection more convenient for the experimenters. We then assigned animals to experimental groups based on body mass and percent change in body mass over the 14-day diet and photoperiod acclimation. All procedures were approved by the Georgia State University Institutional Animal Care and Use Committee and were in accordance with Public Health Service and United States Department of Agriculture guidelines.

2.2. Materials and procedure

2.2.1. Foraging-hoarding apparatus

After the 14-day photoperiod acclimation, we transferred the hamsters to our simulated-burrow caging system where foraging, hoarding, and food intake were quantified daily (see [16] for detailed description of this apparatus). In brief, two cages were connected by a convoluted tunnel of polyvinyl chloride tubing (38.1 mm inner diameter and ~1.52 m in length) with the clear top cage (456 × 234 × 200 mm; 'foraging cage') containing tap water available *ad libitum*, a running wheel (584 mm diameter), and a hole through which food pellets were dispensed [food pellet dispenser (Med Associates, Georgia, VT)] when earned (described below). The opaque covered bottom cage (290 × 180 × 130 mm, 'burrow cage') contained Alpha Dri-bedding and one cotton Nestlet. A computer running MEDPC-IV software (Med Associates Inc., Georgia, VT) was connected to both the running wheel and food pellet dispenser of each simulated-borrow cage which recorded wheel revolutions and systematically triggered the food dispenser to deliver one food pellet into the foraging cage for every 10 wheel revolutions during the entire duration of the study across all animal treatment conditions, unless stated otherwise below. Each hamster was assigned to an individual simulated-burrow system, given constant access to their running wheel, and allowed to freely roam between the foraging and burrow cages through the convoluted PVC tubing. Note that Siberian hamsters earn pellets and hoard them in the burrow cage reliably and without training [16].

We defined food pellets stored in both the burrow cage and in hamster cheek pouches as hoarded food. Food pellets recovered from the foraging cage that were neither eaten nor hoarded were defined as surplus pellets. Food pellets earned (wheel revolutions divided by 10) were defined as 'pellets foraged' and 'food intake' was defined as the pellets foraged minus all pellets recovered. All food pellets and partial pellets were recovered 4 h prior to lights off. Food was assessed at this time because Siberian hamsters hoard food primarily at night and eat from the hoard during the day; therefore, collecting the food at this time assures that we are measuring at least the vast majority of their hoarded food (C. Klein and T. J. Bartness, unpublished observations). Food amounts were measured with a precision balance set to 'parts' measurement, resulting in one 75 mg food pellet = 1 with fractions of pellets computed by the balance. Surplus pellets and pellets hoarded were collected, weighed, and food intake calculated daily for all hamsters. All recovered pellets were discarded daily.

3. Experiment 1

3.1. Experimental groups

To assess the potential of Siberian hamsters to adjust their food hoarding based on food hoard size, we manipulated their hoard in three different daily conditions: 1) hoard was either removed, weighed, and discarded — the so-called '*removed group*' ($n = 10$), 2) removed, weighed, discarded and replaced with the same number of fresh pellets — the so-called '*replaced group*' ($n = 10$), a control for any disruption caused by food removal, 3) or removed, weighed, discarded then replaced with a fixed value of 100 fresh pellets — the so-called '*enhanced*' group ($n = 10$). To test if animals adjusted their hoarding acutely and in dynamic conditions, a fourth group of separate hamsters alternated between *removed*, *replaced*, and *enhanced* for 2 days each over a 6-day period '*alternated*' ($n = 10$). All food replacements were discreetly placed in a corner of the vacant burrow cage while the hamster was out of view in either the convoluted tubing connecting the burrow to the foraging cage, or in the foraging cage. All animals had continual access to all portions of their caging system, including the ability to earn food based on wheel revolutions, throughout Experiment 1.

3.2. Data analysis

Food hoarding, food intake and wheel running data were analyzed with one-way ANOVA. If hamsters hoard food based on the size of the