



Research report

Analyses of meal patterns across dietary shifts[☆]Yada Treesukosol^{*}, Timothy H. Moran

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ABSTRACT

The direct controls of meal size can be categorized into positive signals such as those from the oral cavity and negative signals such as postoral inhibitory cues. It follows that the relative contribution of these signals, and in turn meal pattern parameters, change across periods of high-energy diet exposure. Here, we compared daily intake and meal pattern analysis in male Sprague–Dawley rats presented a high-energy diet for 6 weeks then standard chow for ~1 week (HE), with those of standard chow fed controls (CHOW). These measures allow for evaluation of (1) whether there are distinct dynamic and static phases of DIO and if so, how they are characterized, (2) how meal patterns change across short and long term HE experience, and (3) ingestive behavioral changes when HE-fed animals are returned to standard chow. The HE animals showed significantly higher intake primarily driven by an increase in meal size compared to CHOW controls. This was most pronounced during the first several days of high-energy diet exposure thus characterizing the dynamic phase. Intake and meal size decreased with longer exposure to the diet but remained significantly higher than those of CHOW. Increased meal size could be driven by enhanced orosensory stimulation and/or reduced sensitivity to postoral inhibitory feedback. Distribution curves derived from histogram plots of meal size revealed both larger average meal size (right shift) and spread (standard deviation) thus it is tempting to speculate that more than one type of mechanism influences increased meal size. Meal number decreased suggesting post meal inhibitory signaling is relatively intact. However, this increase was insufficient to compensate for the increased meal size. When HE animals were switched to standard chow, daily intake and meal size decreased and eventually returned to values comparable to those of the CHOW rats. Meal number remained lower suggesting altered physiological mechanism(s) that underlie the control of ingestive behavior as a function of previous high-energy diet exposure.

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Introduction

In the diet induced obesity (DIO) model, animals are presented an energy-dense highly palatable diet and consequently overeat and gain weight. This animal model provides an experimental analogy for the overconsumption of high fat/high energy foods that contribute to the obesity observed in the human population. From studies in which rats became obese following hypothalamic lesions, the development of obesity can be characterized by a rapid rate of weight gain, which has been referred to as the dynamic phase, followed by a static phase characterized by a plateau in weight gain change (see Brobeck, 1946). In DIO models, caloric intake and rate of body weight gain decreases if animals are returned to standard chow over the recovery phase. It follows that the

changes in weight gain across the development of DIO may be mediated by changes in meal pattern attributes.

The direct controls of meal size can be categorized into positive and negative feedback that maintain and terminate eating behavior respectively (see Smith, 1996). Positive feedback is elicited by contact with gustatory, olfactory and somatosensory receptors in the oral cavity. Negative feedback is produced by contact with receptors in the oral cavity and postingestive receptors in the stomach and small intestine (Davis & Smith, 1990; Davis, Smith, & Miesner, 1993). Thus an increase in meal size may be attributed to increased orosensory stimulation and/or reduced sensitivity to postingestive inhibitory signals. For example, there is evidence of positive oral stimulation inducing an increase in meal size in human subjects (De Graaf, De Jong, & Lambers, 1999; Yeomans, 1996) and rats (Spector, Klumpp, & Kaplan, 1998; Warwick, Synowski, Rice, & Smart, 2003). Complementary to such findings, postoral inhibitory cues have also been shown to influence meal patterns (Lutz, Geary, Szabady, Del Prete, & Scharrer, 1995; Strohmayer & Greenberg, 1994; West, Fey, & Woods, 1984). It follows that the changes in weight gain across the development of DIO are driven by alterations in the relative contributions of these

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orosensory and postoral signals, yet these issues remain poorly understood.

In hypothalamic-lesioned obese rats, meal pattern analysis reveals increased meal size during the dynamic phase when body weight gain is most pronounced, but meal size returns back to baseline levels during the static phase when body weight plateaus. In contrast, the number of meals does not significantly change across the phases (Brooks, Lockwood, & Wiggins, 1946; Teitelbaum & Campbell, 1958). In general high-fat diet driven hyperphagia also appears to be influenced by an increase in meal size (Cottone et al., 2013; Farley, Cook, Spar, Austin, & Kowalski, 2003; Furnes, Zhao, & Chen, 2009; Melhorn et al., 2010). Collectively, evidence in the literature points to changes in meal pattern parameters across the development of DIO but there are some conflicting findings. Thus it is unclear as to when the “dynamic” and “static” phases occur and what meal pattern changes characterize these phases.

Furthermore, animals that are switched from a palatable or energy-dense diet to a standard chow diet generally reduce food intake (Rogers, 1985; Rolls, Rowe, & Turner, 1980) and body weight (Stephens, 1980; Wang et al., 2012). This has been reported to be accompanied by a number of changes including expression of genes associated with feeding and reward (Archer et al., 2005; Sharma, Fernandes, & Fulton, 2012) and hypothalamic inflammatory markers (Wang et al., 2012). Meal pattern analysis of this recovery period has been limited in the literature. One study in which rats were switched to standard chow following exposure to a cafeteria diet showed that animals initially reduced intake, meal size and meal frequency (Rogers, 1985). The manner in which meal patterns to standard chow alter as a function of previous exposure to a high-energy diet could be indicative of changes in the underlying physiological mechanisms of the behavior.

Here, meal patterns of rats switched to a high-energy diet were monitored across a period of several weeks and also after animals were returned to a standard chow diet. These meal pattern parameter values were compared to those of a control group that was maintained on standard chow throughout the study. These measures were systemically taken across consecutive daily sessions to evaluate first, whether there are distinct dynamic and static phases of DIO, and if so, how meal pattern parameters characterize them. Second, the study compared how meal pattern parameters change as a function of short- and long-term exposure to a high-energy diet. Finally, meal pattern analysis addressed how ingestive behavior changes when animals are returned to a standard chow diet following several weeks on a high-energy diet. An increase in meal size would be indicative of an increase in positive feedback (e.g. oral stimulation) and/or a decrease in negative feedback (e.g. postoral inhibitory signal). The relative contributions of these signals would possibly be most robust during the initial hyperphagia observed upon presentation of a high-energy diet, less evident with continual exposure to high-energy diet and return to control levels when HE animals are switched back to standard chow.

Methods

Subjects

Sixteen male Sprague Dawley rats (Harlan) ~275–300 g in body weight upon arrival were single-housed in DietMax System food intake monitoring cages (AccuScan Instruments, Inc., Columbus, OH) (length 32 cm, width 22 cm) that have stainless steel wire mesh bottoms in polycarbonate plastic cages. Animals were presented with ad libitum access to powdered chow (3.1 kcal/g, calories from protein 24%, calories from fat 18%, calories from carbohydrate 58%; 2018 Teklad, Harlan) and water, except where noted. Rats were housed in a room with automatically controlled

temperature (range 18–24 °C), humidity (range 18–53%) and a 12:12-h light–dark cycle. All experimental procedures were approved by the Institutional Animal Care and Use Committee at The Johns Hopkins University School of Medicine.

Behavioral procedure

Following 7 days of habituation to the laboratory environment and maintenance on chow diet, animals were assigned to the CHOW or HE groups such that the groups did not significantly differ in body weight, average daily intake, number of meals per day or average meal size. On Day 0, both groups were on standard chow. On Day 1, the HE animals were switched to ad libitum access to powdered high energy diet (4.73 kcal/g; calories from protein 20%, calories from fat 45%, calories from carbohydrate 35%; D12451, Research Diets). The diet has ~7% calories from corn starch, ~10% calories from maltodextrin and ~17% calories from sucrose that also promote intake. The CHOW controls remained on the powdered standard chow (3.1 kcal/g, calories from protein 24%, calories from fat 18%, calories from carbohydrate 58%; 2018 Teklad, Harlan). This continued for 42 consecutive days which will be referred to as the “experimental diet period”. Next, the animals that had been presented with the high-fat diet were returned to standard chow and measurements were taken across 6 consecutive days – what will be referred to as the “recovery period”. Meal pattern analysis data were lost for day 19 of the experimental diet period and day 4 of the recovery period due to computer issues, and thus are not included in the analysis.

Food intake was monitored continuously over 23-h daily test sessions. Powdered laboratory chow diet was provided ad libitum in a food jar placed on a scale in the feeding compartment of the cage. The animals had access to the food jar via an opening in the wall of the cage. A water bottle was mounted on an adjacent wall of the cage from which the rat had access to water via a spout through a hole in the cage wall.

Data analysis

A feeding bout was operationally defined as requiring ≥ 0.2 g food. An interval of ≥ 10 min without food intake defined the termination of a meal. This bout criterion has been used previously (Dailey, Tamashiro, Terrillion, & Moran, 2010; Dunn-Meynell et al., 2009) and on average accounted for ~95% of the feeding data in the current study. Meal size measured in grams or calories was divided by meal length in seconds to calculate eating rate values (g/s and kcal/s). Two-way ANOVAs were conducted to compare meal pattern parameter values across groups (group \times day) and for a given group across light–dark phases (phase \times day). Bonferroni-corrected post hoc *t*-tests were conducted at each day to compare values between the groups.

On a given behavioral test day, data of every meal was plotted to derive a histogram by meal size (bins of 1.0 kcal, *x*-axis) by the count (number of meals, *y*-axis). Values from each animal were accumulated across each group and the count was converted to a frequency value (count at each meal size bin divided by total count for data of a given group on a given day). Nonlinear regression was used to fit the following Gaussian equation to the data:

$$y = \frac{1}{\delta\sqrt{2\pi}} e^{-\frac{(x-\mu)^2}{2\delta^2}}$$

where *y* is the frequency calculated from meal number, *x* the meal size (kcal), μ the mean meal size and δ is the standard deviation. This allowed for comparisons of μ values (meal size) and δ (indication of the spread of the distribution) across behavioral testing days and groups.

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