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Characterization of attenuated food motivation in high-fat diet-induced obesity: Critical roles for time on diet and reinforcer familiarity

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HIGHLIGHTS

- Prior results on the role of obesigenic diets on food motivation have been inconsistent.
- Two factors appear critical: time consuming obesigenic diet and reinforcer familiarity.
- Increased time on obesigenic diet reduces food motivation, familiarity attenuates this.
- This helps reconcile prior results and contributes to an understanding of food motivation.
- Since prior food experience is critical, a varied diet would improve animal models of human obesity.

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ABSTRACT

Prior work using animal models to study the effects of obesogenic diets on food motivation have generated inconsistent results, with some reporting increases and others reporting decreases in responding on food-reinforced tasks. Here, we identified two specific variables that may account for these discrepant outcomes – the length of time on the obesigenic diet and the familiarity of the food reinforcer – and examined the independent roles of these factors. Time on diet was found to be inversely related to food motivation, as rats consuming a 40% high-fat diet (HFD) for only 3 weeks did not differ from chow-fed rats when responding for a sucrose reinforcer on a progressive ratio (PR) schedule, but responding was suppressed after 6 weeks of ad lib HFD consumption. Explicitly manipulating experience with the sucrose reinforcer by pre-exposing half the rats prior to 10 weeks of HFD consumption attenuated the motivational deficit seen in the absence of this familiarity, resulting in obese rats performing at the same level as lean rats. Finally, after 8 weeks on a HFD, rats did not express a conditioned place preference for sucrose, indicating a decrement in reward value independent of motivation. These findings are consistent with prior literature showing an increase in food motivation for rats with a shorter time consuming the obesigenic diet, and for those with more prior experience with the reinforcer. This account also helps reconcile these findings with increased food motivation in obese humans due to extensive experience with palatable food and suggests that researchers engaging in non-human animal studies of obesity would better model the conditions under which human obesity develops by using a varied, cafeteria-style diet to increase the breadth of food experiences.

1. Introduction

Motivation to obtain and consume palatable, energy dense foods is an important factor in the control of food intake and plays a key role in the development and maintenance of obesity. Obese individuals appear to be more highly motivated by palatable food than their lean counterparts [1,2]. This finding makes intuitive sense, but studies in human subjects are unable to clearly distinguish between motivational changes as a cause versus a consequence of obesity. Furthermore, there are a number of aspects that are difficult to probe in humans, such as the neural substrates of these changes and specific environmental factors that affect food-motivated behaviors.

However, the work to date on the effect of obesity on food-motivated behaviors in animal models has produced inconsistent outcomes. Studies in which high-fat diet (HFD) consumption occurs for a period of 12–15 weeks have shown reduced progressive ratio breakpoints for sucrose pellet reinforcers [3,4]. In contrast to these findings, la Fleur et al. [5] reported a significant increase PR responses for a sucrose reinforcer in rats on a high-fat, high-sugar choice diet, as did Figlewicz and colleagues [6,7] in both juvenile and adult rats on a commercial high-fat mixed diet.

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At first glance, it might appear that these discrepant outcomes represent a failure to replicate an effect across laboratories. We submit that this is not the only explanation; rather, differences in the methods and conditions used in these experiments may have contributed to the differences in the outcomes. Elucidating the role of key variables may yield insight into underlying mechanisms of food motivation as it relates to obesity.

We identified two primary factors that differed between the studies finding reductions in food-motivated behaviors and those finding increases in these same behaviors. First, these studies differed in the length of time that animals had subsisted on the high-fat diet prior to behavioral assays being carried out. Specifically, duration of high-fat diet consumption ranged from 3 weeks to 5 weeks in studies reporting increases in operant responding [5–7], while studies reporting decreases in responding were conducted after 12 weeks of diet exposure [3,4]. This suggests that the physiological and behavioral effects of these diets may shift as a result of persistent consumption and the corresponding gain in body weight and body fat. However plausible this seems, we can't conclusively attribute the differences in motivation across studies to the duration of diet consumption alone, as a number of other variables also differed between these experiments.

The second factor that we noted as a difference between these studies is the exposure to the taste of the reinforcer – sucrose – prior to any physiological changes induced by high-fat diet consumption or weight gain. This exposure is most apparent by contrasting the method of la Fleur et al. [5], in which rats tasted sucrose as a separate solution and consumed nearly 15% of their calories in this form, with that of Davis et al. [3], in which rats were given a commercial pre-mixed diet containing only 8% kcal from sucrose. This lead us to hypothesize that animals would show higher levels of motivation for a more familiar reinforcer.

The present studies aimed to provide an explanation for previously discrepant findings on the effect of high-fat diet consumption on food motivation by isolating and explicitly manipulating the duration of the ad lib diet consumption period and experience with the reinforcer, independent of diet composition and other factors. In Experiment 1, we tested PR responding for a sucrose reinforcer in the same group of rats following 3 and 6 weeks ad lib consumption of a HFD or chow, while Experiments 2 and 3 evaluated reinforcer familiarity by exposing half the rats to either the sucrose reinforcer or one of two specific reinforcer flavors prior to beginning a 10-week ad lib HFD consumption period. Finally, in order to assess the role of food reward in these processes, we tested the effect of diet-induced obesity on the development of conditioned place preference for a novel sucrose reinforcer (Experiment 4).

2. Methods

2.1. General methods

2.1.1. Subjects

Subjects for all experiments were male Long–Evans rats (Harlan Laboratories, Indianapolis, IN) approximately 60 days of age and weighing 225–250 g on arrival in the laboratory. All subjects were housed individually in Plexiglas “shoebox” style cages with wire lids. Room temperature was maintained at 20–23 °C with a 12 h:12 h light cycle. All handling and behavioral procedures occurred during the second half of the light period. Water was available ad libitum in the home cage. Food availability is described below. Animal care followed the Guide for Care and Use of Laboratory Animals and all procedures were approved by the Grinnell College Institutional Animal Care and Use Committee.

2.1.2. Diets

The standard chow diet contained 14% calories from fat with a caloric density of 3.0 kcal/g (Harlan Teklad Rodent Diet #8604, Indianapolis, IN). The high-fat diet (HFD) contained 40% calories from fat, almost entirely from a saturated fat source (butter), with a caloric density of 4.54 kcal/g (Research Diets, New Brunswick, NJ). Except where noted (Experiment 1), animals were maintained on these diets for 10 weeks prior to beginning food restriction and conditioning procedures. During the ad lib feeding periods, body weight and food intake was recorded weekly. All 45 mg pellets used in operant conditioning and conditioned place preference procedures were obtained from Test Diet (Richmond, IN).

2.1.3. Food restriction

For operant conditioning and conditioned place preference (CPP) procedures, all animals were reduced to 85% of their ad lib body weights prior to beginning training sessions and maintained at this weight throughout the experiment (except where noted). To achieve this weight, animals were given a small daily ration of their assigned food (i.e., animals consuming chow continued to receive chow and animals consuming HFD continued to receive HFD). Body weight was monitored and food rations were adjusted accordingly. Weight was reduced gradually over approximately 7 days and maintained throughout the experiment. Daily rations were given approximately 1 h before the onset of dark during the weight reduction phase and 30 min–1 h following the end of the behavioral session during the conditioning/testing phase.

2.1.4. Operant conditioning procedure

All operant conditioning was carried out in four identical chambers (Lafayette Instrument, Lafayette, IN). Each chamber had internal dimensions of approximately 12″ × 10″ × 8″ with two stainless steel end walls, Plexiglas sidewalls and top, and a stainless steel rod floor. On one end wall were two stainless steel levers, present during all sessions, and a single recessed food magazine with a Plexiglas entry flap positioned in the center between the two levers. Three infrared detectors were placed along the side walls of the chamber to detect activity. Each chamber was housed within a larger sound-attenuating chamber with a house light illuminated throughout each session and a ventilation fan, which served to provide a consistent auditory environment and minimize interference from outside noise. ABET II software (Lafayette Instrument, Lafayette, IN) was used to control, monitor and record from all chambers.

In all operant conditioning sessions, one lever was designated the active lever and remained active during all sessions, the second lever was designated inactive and presses on this lever never yielded any outcome. The reinforcer was one 45 mg pellet (pellet type specified for each experiment). All training sessions were 1 h in duration and one training session was conducted per day. The training schedule was as follows: two shaping sessions, two sessions of fixed ratio 1 (FR1), two sessions of FR3, two sessions of FR5. During shaping sessions, reinforcers were delivered on an FR1 schedule with additional reinforcer delivered at the end of every 5 min interval in which no reinforcers were earned via lever pressing, in order to familiarize the animals with the availability and delivery location of reinforcer pellets. During progressive ratio (PR) test sessions, the number of lever presses required to earn each reinforcer was determined according to the following schedule, which raised the response requirement by increasing increment for each subsequent reinforcer [8]: 1, 2, 4, 6, 9, 12, 15, 20, 25, 32, 40, 50, 62, 77, 95, 118, 145, 178, 219, 268, 328, 402, 492, 693, 737, 901. PR sessions were untimed and ended for each animal when 20 min elapsed without a reinforcer being earned. The final ratio completed prior to this was defined as the animal's “breakpoint”. Responses on both levers, magazine entries, and general activity were recorded for all training and testing sessions.

2.1.5. Conditioned place preference procedure

The conditioned place preference (CPP) procedure was conducted in a three compartment chamber (Med Associates, St. Albans, VT), comprising two 25 × 21 × 21 cm side chambers, one with black walls and a floor with a floor of smooth stainless steel parallel rods and one with white wall and a steel mesh grid floor, and a smaller center chamber (12 × 21 × 21 cm) with gray walls and a solid plastic floor. Motorized