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Obese and lean Zucker rats demonstrate differential sensitivity to rates of food reinforcement in a choice procedure

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HIGHLIGHTS

► Behavioral allocation to different densities and types of food reinforcement was compared in obese and lean Zucker rats.
► Allocation was characterized using the generalized matching equation.
► Obese Zucker rats were more sensitive to differing densities of food than lean Zucker rats.
► Obese Zucker rats did not demonstrate stronger preference for high-sucrose food options.

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ABSTRACT

The obese Zucker rat carries two recessive *fa* alleles that result in the expression of an obese phenotype. Obese Zuckers have higher food intake than lean controls in free-feed studies in which rats have ready access to a large amount of one type of food. The present study examined differences in obese and lean Zucker rats using concurrent schedules of reinforcement, which more ecologically models food selection using two food choices that have limited, but generally predictable availability. Lever-pressing of ten lean (*Fa/Fa* or *Fa/fa*) and ten obese (*fa/fa*) Zucker rats was placed under three concurrent variable interval variable interval (conc VI VI) schedules of sucrose and carrot reinforcement, in which the programmed reinforcer ratios for 45-mg food pellets were 5:1, 1:1, and 1:5. Allocation of responses to the two food alternatives was characterized using the generalized matching equation, which allows sensitivity to reinforcer rates (a) and bias toward one alternative ($\log k$) to be quantified. All rats showed a bias toward sucrose, though there were no differences between lean and obese Zucker rats. In addition, obese Zucker rats exhibited higher sensitivity to reinforcement rates than lean rats. This efficient pattern of responding was related to overall higher deliveries of food pellets. Effective matching for food, then, may be another behavioral pattern that contributes to an obese phenotype.

1. Introduction

1.1. Obese Zucker rats and free food intake

The obese Zucker rat, which has impaired leptin signaling, is a genetic model of obesity that has historically been used to determine behavioral and physiological mechanisms that contribute to obesity-related health problems (see [1,2] for reviews). However, much of the behavioral research on the Zucker strain is based on free food intake studies, in which obese Zuckers are found to have significantly higher caloric intake than their lean counterparts (e.g., [3–6]. In free food intake studies, a large amount of food is readily available with minimal effort required to gain access to it, and because obese Zuckers have a higher free-food intake, it is concluded that food is more rewarding to them.

When effort is required to procure food, however, the differences between lean and obese rats in food consumption patterns become smaller. Rasmussen and Huskinson [7], for example, placed lever-pressing for sucrose under a progressive ratio schedule of reinforcement, a well-established measure of food reinforcement [8,9]. The differences in breakpoints (the point at which lever-pressing ceases) between lean and obese rats were not statistically significant, thus providing no evidence of a difference in the value of sucrose between the two groups. In addition, larger differences in food consumption are found between lean and obese Zucker rats when the effort to obtain food is small (e.g., 1–50 lever-presses), but when the effort is larger (90–300 lever-presses), the differences become negligible [10,11]. Therefore, the large differences in food consumption observed between lean and obese Zucker rats may be limited to the free-feed environment.

Because small changes in the environmental arrangement of food lead to strong differences in food consumption patterns, an argument can be made for expanding the study of food intake beyond the

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free-feeding environment. For example, the use of a procedure that models choice, in which two or more food options vary in certain properties such as quality and availability, may extend our understanding of food consumption differences between lean and obese rats.

1.2. Concurrent schedules as a model of choice

A paradigm that more ecologically models environmental features of food procurement in the natural world is the concurrent schedule of reinforcement, a well-established model of choice (see [12–15] for reviews). Typically, reinforcers are made available for responding on two levers, and are delivered under independent variable interval (VI) schedules. In a single VI schedule, a reinforcer is delivered following the first response after a variable interval of time passes. A VI 12-s schedule, for example, delivers reinforcers after the first response is made after an average of 12-s elapses. Thus, it is possible to earn five reinforcers per minute at an overall predictable rate, but it is not predictable from moment to moment when those deliveries will occur.

Allocation of behavior to the two VI schedules is a measure of choice. Humans and non-humans have shown predictable patterns of responding under concurrent VI VI (conc VI VI) schedules, such that the allocation of their responses to each alternative is a linear function of the ratio of reinforcers earned on each side. This relationship is illustrated by Eq. (1), known as the generalized matching equation [16]:

$$\log\frac{B_1}{B_2} = a\log\frac{r_1}{r_2} + \log k \qquad (1)$$

in which B_1 and B_2 are the total number of responses to two alternatives (e.g., a left lever and a right lever, respectively), r_1 and r_2 are the total number of reinforcers earned on each respective alternative, and a and log k are free parameters that represent the slope and intercept of the line, respectively. This equation suggests that the log ratio of responses to the left lever (with respect to the number of responses made on the right lever) will equal, or "match" the log ratio of reinforcers earned on the left lever (with respect to the number of reinforcers earned on the right lever).

The free parameters, a and log k, are of interest in examining deviations from matching. The parameter, a, or slope of the matching line, refers to sensitivity of behavior (e.g., responses) to the differing reinforcer densities. A value of 1 means "perfect" matching, meaning that the organism is allocating behavior solely based on relative reinforcer rates. However, a pattern of responding that is more commonly found across species responding under conc VI VI schedules is "undermatching," and results in a value of $a<1$. This means that allocation of responses to the two food alternatives is less sensitive to richer sources of reinforcement. For example, if food is delivered at a ratio of 1:5, an organism that is less sensitive to the richer source of reinforcement will allocate its responses such that fewer responses are made to the richer alternative (the right lever in this case), resulting in a response ratio such as 1:4 or 1:3. A value of $a>1$ represents "overmatching," which suggests hypersensitivity to differences in reinforcer rates and results in more responses allocated to the richer alternative than would be predicted by perfect matching.

The log k parameter represents bias toward one alternative. When log $k=0$, no bias is evident. A log k value >0 suggests a bias toward the alternative represented in the numerator, here, the left alternative, and <0 suggests a bias toward the right alternative. Baum [16] asserted that bias can result from previous experience with one lever more than the other, or when one side offers a different amount or quality of reinforcers, such as when the reinforcers differ in palatability. One study [17], for example, assessed preference for hemp, buckwheat, and wheat in varying pairs using the bias parameter and found that buckwheat was preferred over hemp, wheat was preferred over buckwheat, and predicted that wheat would be preferred over hemp. Another study by Matthews and Temple also found, using the bias parameter, that dairy cows had a small preference for hay over dairy meal, though others had a small preference for dairy meal [18].

1.3. The present study

Sensitivities to amount of food or preference for different kinds of food (e.g., those high in fat or sugar content) may be behavioral patterns involved in obesity; therefore, it is important to understand these patterns in food selection. There have been no studies published (to our knowledge) in which obese Zucker rats respond for food in a choice procedure using concurrent schedules. In the present study, we exposed lean and obese Zuckers to three different concurrent schedules that differed in terms of programmed reinforcer ratios. Rats chose between allocating responses to two levers that differed only in relative amount of reinforcers delivered from each lever (phase 1). Then (in phase 2) a second pellet type was introduced on one of the levers that had a differing percentage of sucrose content, such that features of palatability could be examined in the context of choice. We hypothesized that all rats would display a bias toward the higher sucrose alternative, though obese Zuckers may have a stronger bias toward sucrose. We were also interested in whether lean and obese Zuckers would show differences in sensitivity to relative rates (amount) of reinforcement.

2. Materials and method

2.1. Subjects

Twenty experimentally naïve male Zucker rats (lean, $n=10$; obese, $n=10$) were acquired from a commercial breeder (Harlan; Livermore, CA) at approximately 21 days of age. They were housed in individual cages in a climate-controlled room, with a 12-h light/dark cycle (light beginning at 6:00 a.m.). Rats were given *ad libitum* access to standard rat chow and water until they were 10 weeks old, at which time they began lever-press training for operant sessions. At this time, lean rats weighed between 245 and 286 g and obese weighed 320–390 g. After this point, access to food was restricted to a daily 2-h free-feeding session, immediately following experimental sessions. This food restriction procedure has been shown to allow food to function as a reinforcer, but also keep deprivation levels similar between lean and obese rats while allowing minimal weight gain [10,11].

2.2. Apparatus

Seven Coulbourn® Habitest standard rat operant chambers were used for training and experimental sessions. Each chamber was placed inside a sound-attenuating cubicle, and contained a fan for air circulation and a speaker which provided white noise to reduce extra-chamber noise. Each chamber contained two levers, one on each side of a feeding trough, with a cue light above each lever. The depression of each lever controlled one of the two pellet feeders on the outside of the chamber, which delivered either a single 45-mg sucrose (3.4 kcal/g) or carrot-flavored (3.4 kcal/g) pellet (TestDiet®). Pellets were redirected from either side of the chamber to the feeding trough via a "Y" shaped tube. Following completion of the response criteria (as specified by the schedule), a light in the feeder area as well as a house light located 13 cm above the food dispenser was illuminated for 3 s during the delivery of the pellet. During this interval, lever-presses had no programmed consequences, though the individual VI timers continued to run. A Windows-based computer with Graphic State® software controlled reinforcer contingencies and collected data. All sessions were conducted in the morning at the same time (±15 min) from Monday to Friday.