Published in final edited form as:

Appetite. 2019 May 01; 136: 160–172. doi:10.1016/j.appet.2019.01.023.

Dietary effects on the determinants of food choice: Impulsive choice, discrimination, incentive motivation, preference, and liking in male rats

Catherine C. Steele^a, Jesseca R. A. Pirkle^a, Ian R. Davis^a, and Kimberly Kirkpatrick^a

^aDepartment of Psychological Sciences, Kansas State University, Manhattan, KS 66506

Abstract

The current study sought to understand how long-term exposure to diets high in saturated fat and refined sugar affected impulsive choice behavior, discrimination abilities, incentive motivation, food preferences, and liking of fat and sugar in male rats. The results showed that 8 weeks of dietary exposure impaired impulsive choice behavior; rats exposed to diets high in processed fat or sugar were more sensitive to changes in delay, a marker of impulsivity. For the high-fat group, these deficits in impulsive choice may stem from poor time discrimination, as their performance was impaired on a temporal discrimination task. The high-fat group also showed reduced magnitude sensitivity in the impulsive choice task, and they earned fewer rewards during lever press training indicating potentially reduced incentive motivation. The high-fat group also developed a preference for high-fat foods compared to the chow and high-sugar group who both preferred sugar. In contrast, dietary exposure did not alter the liking of fat or sugar as measured by a taste reactivity task. Together, the results suggest that the alterations in impulsive choice, time discrimination, incentive motivation, and food preferences induced by consumption of a high-fat diet could make individuals vulnerable to overeating, and thus obesity.

Keywords

impulsive choice; incentive motivation; preference; liking; diet; discrimination

1. Introduction

A large number of food choices made each day surround when, what, how much, and where to eat (Wansink & Sobal, 2007). Food choices are made by placing a subjective value on each outcome, and this value can be affected by a variety of factors including risk, delay, reward type, and amount (Fobbs & Mizumori, 2017). Individuals may consider how long it will take to get a food type, how much food they will get for the cost or effort, what kind of risk they might be taking (e.g. risk of heart attack or weight gain), and which food they

Corresponding Author: Catherine Steele, Department of Psychological Sciences, 492 Bluemont Hall, Kansas State University, Manhattan, KS 66506, USA, cchill1@ksu.edu.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

prefer. Low cost, ready to eat foods that comprise the Western Diet are tempting to many Americans likely because the food is highly palatable, relatively immediate, and cheap (Glanz, Basil, Maibach, Goldberg, & Snyder, 1998). As such, these energy dense, convenient foods constitute a large proportion of the American diet, and overconsumption of these foods can lead to obesity (Bowman & Vinyard, 2004).

Some have proposed that weight status affects food choice behaviors such as self-control and preference (van Meer, Charbonnier, & Smeets, 2016). Indeed, impulsive choice (Barlow, Reeves, McKee, Galea, & Stuckler, 2016; Bickel et al., 2014; Rasmussen, Lawyer, & Reilly, 2010; Schiff et al., 2015), incentive motivation (Singh & Sikes, 1974; Teitelbaum, 1957), liking for fat (Mela, 2001; Shin, Townsend, Patterson, & Berthoud, 2011), and fat and sugar preference (Cox, Hendrie, & Carty, 2016; Davis et al., 2007) are associated with obesity in rats and humans. While impulsive choice, characterized by an unwillingness to wait for a larger reward due to an increased rate of delay discounting, has been associated with obesity in humans, there is preliminary evidence that people who eat diets high in fat and sugar are more likely to be impulsive (Lumley, Stevenson, Oaten, Mahmut, & Yeomans, 2016). Indeed, male and female rats selectively bred for high-saccharine intake discounted delayed food rewards more than low saccharine rats (Perry, Nelson, Anderson, Morgan, & Carroll, 2007). Further, previous research from our laboratory found that high-fat and high-sugar diets increased impulsive choices by inducing a preference for the smaller reward available after a shorter delay and increasing sensitivity to delay in rats (Steele, Pirkle, & Kirkpatrick, 2017). While the high-fat diet resulted in moderate weight gain, weight gain in the high-sugar group was not significantly different from the control group, and body weight was not correlated with impulsive choice behavior. This indicates that the high-fat and high-sugar diets produced behavioral effects well before there were any overt signs of obesity. Therefore, it is critical to understand how diet affects behaviors that could drive food choice.

As such, the current study sought to understand how long-term exposure to diets high in saturated fat or refined sugar affects decision making using a rodent model with a focus on impulsive choice behavior, time and reward discrimination, incentive motivation, food preference, and liking. We hypothesized that exposure to diets high in saturated fat or refined sugar (rather than weight status) should lead to alterations in impulsive choice, time and reward discrimination, incentive motivation, food preference, and liking (Figure 1). These alterations in decision making processes are proposed to affect the food choices that determine dietary intake. Eventually, food choices may drive changes in weight status and/or body composition. Together, these aspects of choice behavior may elucidate how dietary factors could lead to deficits in decision making when confronted with daily food choices. Understanding how diet affects these factors is critical for delineating the determinants of food choice behavior.

2. Methods

2.1. Animals

Thirty-six male Sprague Dawley rats (Charles River, Portage, MI) arrived at Kansas State University at 21–25 days of age and weighing 34–50 g. Upon arrival, the rats were housed individually in a dimly-lit (red light) colony room that was set to a reverse 12-hr light:dark

schedule (lights off at approximately 7 am). The rats had *ad libitum* access to water in the home cages and during behavioral testing, and the rats were weighed at least five times per week throughout the experiment.

2.2. Apparatus

The behavioral tasks were conducted in 24 operant chambers (Med-Associates, St. Albans, VT), each housed within a sound-attenuating, ventilated box ($74 \times 38 \times 60$ cm). Each operant chamber ($25 \times 30 \times 30$) was equipped with a stainless steel grid floor; two stainless steel walls (front and back); and a transparent polycarbonate side wall, ceiling, and door. Two pellet dispensers (ENV-203), mounted on the outside of the front wall of the operant chamber, delivered 45-mg food pellets (Product #F0165, Bio-Serv, Flemington, NJ) to a food cup (ENV-200R7) that was centered on the lower section of the front wall. Head entries into the food cup were transduced by an infrared photobeam (ENV-254). Two retractable levers (ENV-112CM) were located on opposite sides of the food cup. The chamber was also equipped with a house light (ENV-215) that was centered at the top of the chamber's front wall, as well as two nose-poke key lights (ENV-119M-1) that were each located above the left and right levers. Water was always available from a sipper tube that protruded through the back wall of the chamber. Experimental events were controlled and recorded with 2-ms resolution by the software program MED-PC IV (Tatham & Zurn, 1989).

2.3. Procedure

Three days after arrival, rats were pseudo-randomly assigned into 3 groups matched for body weight (Group C: $M = 52.6$ g, $SE = 1.6$; Group HF: $M = 54.4$ g, $SE = 1.6$; Group HS: $M = 56.0$ g, $SE = 1.3$). Body composition was measured after 6 weeks and again after 9 months on their designated diets. After being on their diet for 8 weeks, rats received a series of tasks to determine how chronic exposure to a diet high in processed fat or sugar affected impulsive choice, time discrimination, reward magnitude discrimination, incentive motivation, food preference, and liking (Figure 2). Behavioral testing began with lever press training. Once lever pressing was acquired, an impulsive choice task was completed followed by the discrimination task that was most closely associated with the specific impulsive choice task (e.g. impulsive choice delay task followed by the time discrimination task or impulsive choice magnitude task followed by the reward magnitude discrimination task). Between the impulsive choice and the discrimination tasks, a buffer task was administered to reduce side biases and carry-over effects (Wang, Marshall, & Kirkpatrick, 2017). After the first set of impulsive choice and discrimination tasks, the rats completed another buffer task and the lever assignments were switched before beginning the next set of impulsive choice and discrimination tasks to minimize carryover effects. The order of the impulsive choice tasks was counterbalanced such that half of the rats received the delay manipulation of the impulsive choice task first and the other half of the rats received the magnitude manipulation of the impulsive choice task first. The impulsive choice tasks were counterbalanced because performance on one task can affect performance on the other task (Bailey, Peterson, Schnegelsiepen, Stuebing, & Kirkpatrick, 2018). Further, the discrimination tasks followed the impulsive choices tasks because training on these tasks could potentially alter performance on the impulsive choice task through improving time or reward magnitude discrimination (Marshall & Kirkpatrick, 2016; Smith, Marshall, &

Kirkpatrick, 2015). Following the measurement of impulsive choice and discrimination abilities, a preference test was conducted to determine how the dietary exposure affected food preference. Lastly, a taste reactivity task was conducted to assess the effect of long term dietary consumption on liking of fat and sugar. The impulsive choice and discrimination tasks were administered first to avoid any effects of exposure to fat and sugar during the preference and taste reactivity tasks in the control group.

2.3.1. Dietary manipulation

2.3.1.1. Initial dietary exposure.: The initial dietary exposure consisted of 8 weeks of exposure to the diets before behavioral testing began. This diet composition and duration was modeled after Jurdak, Lichtenstein, and Kanarek (2008). All rats received access to the same number of calories per day throughout the experiment regardless of group. The number of calories administered was matched to the number of calories consumed *ad libitum* during development such that rats received access to 50 calories during week 1, 60 calories during week 2, 80 calories during week 3, and 100 calories from week 4 until the end of experimentation (Leibowitz, Lucas, Leibowitz, & Jhanwar, 1991). However, the composition of calories differed between groups. The control group (Group C) received 100% of the calories from standard chow (LabDiet; 3.36 kcal/g). Rats in the high-sugar (Group HS) group received 60% of the calories from chow and 40% of the calories from a powdered sugar and water mixture (3.94 kcal/g), and rats in the high-fat (Group HF) group received 60% of the calories from chow and 40% of the calories from hydrogenated vegetable fat (9.3 kcal/g; Jurdak et al., 2008). The supplements (fat and sugar) were placed on the floor of the cage. The chow group received 40% of their chow on the floor of the cage to control for the experience of food delivery within the cage.

Three weeks before experimentation, the time allowed to eat the daily ration of supplement and chow was restricted to ensure the rats would be motivated to work for food in the experiment and to ensure that the chronic effects of the diet were tested. All rats continued to have access to 100 calories each day regardless of group, but the food remaining after the restriction period was removed. The rats were allowed 4 h to eat the first week of restriction, 3 h to eat in the second week of restriction, and 2 h to eat in the final week of restriction and continuing throughout experimentation. The gradual progression was used to reduce the time frame for eating to ensure good motivation to work for food in the experiments, while minimizing the impact on total consumption.

2.3.1.2. Dietary exposure during behavioral testing.: The rats received their diets throughout behavioral testing. During behavioral testing, part of the ration of chow was earned in the chambers through 45-mg grain-based pellets (Product #F0165, Bio-Serv, Flemington, NJ). The number of grams of pellets earned in the chambers was subtracted from the ration of chow. After the daily behavioral testing sessions, the remainder of the chow ration was placed on the top of the home cage and the dietary supplement (for Groups HF and HS) and equivalent chow (for Group C) was placed inside the cage.

2.3.1.3. Food consumption.: The bedding was scanned for spillage each day to determine the amount of supplement (chow, fat, or sugar) consumed. A formal analysis of spillage was

not conducted because the supplements were often mixed with bedding making it difficult to quantify. Generally, Group C and Group HF ate all their supplement, and Group HS ate a majority of the supplement.

All groups received 60% of their calories in chow placed in the food hopper on top of the cage each day, and chow leftover in the food hopper was measured to determine food intake. Food intake during behavioral testing was not analyzed because part of the daily food ration was received in the apparatus. This made it difficult to interpret consumption because some rats received more of their food in the experiment versus home cage and these foods were delivered under different conditions. One week prior to behavioral testing, the groups differed in their intake of chow received in the food hopper, which made up 60% of the calories from each diet, $F(2,270) = 22.44$, $p < .001$. Group HS ($M = 11.14$ g, $SE = 0.33$) and Group HF ($M = 9.31$ g, $SE = 0.34$) ate more chow than Group C ($M = 7.07$ g, $SE = 0.42$).

2.3.2. Body composition.—Body fat percentages were obtained as a measure of body composition using a Lunar PIXImus small animal densitometer (Lunar-General Electric, Madison, WI). A measurement of body fat percentage was obtained after 6 weeks on the diet and again following the food preference task, at which point the rats had experienced 9 months on the diet. The densitometer that was used for the measurements was specific for mice, so a smaller targeted region was examined. As such, the measurements focused on abdominal fat stores because visceral adipose tissue in the abdomen increases the risk of obesity-related diseases (Bjorndal, Burri, Staalesen, Skorve, & Berge, 2011). The region of interest spanned the abdomen from the 12th rib to the top of the pelvic girdle.

Anesthesia was used to ensure that the rats did not move during imaging. Isoflurane was administered in an induction chamber at a concentration of 3–5% and a flow rate of 500 ml/min. The rats were then transferred to a face mask with a concentration of 1–3% and a flow rate of 500 ml/min. An adequate level of anesthesia was confirmed by checking the pedal withdrawal reflex and mild tail pinch responses. Once the rat was anesthetized, they were placed on the platform of the densitometer and imaging began and continued for approximately 4–5 mins. As soon as the image was obtained, the rat was removed from anesthesia and placed in a recovery cage. Anesthesia was administered for 7–10 min for each imaging session.

2.3.3. Lever press training.—During the first training session, rats received magazine training and lever press training. The magazine training consisted of delivery of 60 food pellets into a food cup through a random time 60-s schedule. Following magazine training, lever press training rewarded lever presses with a fixed-ratio (FR) 1 schedule of reinforcement. Left and right levers were trained separately in 6 sub-blocks of 5 food deliveries per lever resulting in a total of 30 pellets per lever. Following the first training session, the rats continued lever press training during three sessions. First, lever pressing was rewarded on a FR1 schedule of reinforcement. Left and right levers were trained separately in four sub-blocks (two blocks per lever). Next, lever pressing was rewarded on a random ratio (RR) 3 schedule of reinforcement, followed by an RR5 schedule of reinforcement. For both the RR3 and RR5, each of the four sub-blocks consisted of 5 food deliveries per lever. In addition to serving to train the rats to reliably press both levers, total reinforcers earned

during the last session of lever press training were analyzed to assess incentive motivation to work for food.

2.3.4. Impulsive choice.—Two impulsive choice tasks were used to measure the rats' willingness to wait for a larger reward by presenting the rats with choices between a smaller-sooner (SS) reward and a larger-later (LL) reward. The tasks were a modification from Green and Estle (2003) and have been shown to produce stable and reliable choice behavior that correlates well with other choice tasks that use non-zero delays (Peterson, Hill, & Kirkpatrick, 2015). All rats completed two impulsive choice tasks, one that manipulated SS delay and one that manipulated LL magnitude, in a counterbalanced order. These have previously been shown to differentiate delay and magnitude sensitivity (Bailey et al., 2018; Garcia & Kirkpatrick, 2013). Each session consisted of a randomly intermixed series of free choice and forced choice trials. At the beginning of each session, there was a 10-s interval preceding the first trial. On free choice trials, both the left and right levers were inserted into the chamber, corresponding to smaller-sooner (SS) and larger-later (LL) outcomes, with lever assignments counterbalanced across rats. Upon selection of one of the outcomes via a lever press, the other lever was retracted. The choice initiated a delay until food was available to be delivered; the first lever press following this delay caused the lever to retract, food to be delivered, and a 60-s intertrial interval (ITI) to begin. Forced choice trials were identical to free choice trials, except that only one lever was inserted into the chamber. Lever presses were required at the end of the delay on both free and forced choice trials to promote the measurement of timing behavior. Other tasks that do not require explicit responses (i.e., that deliver fixed time schedules instead of fixed interval schedules) most likely will engender goal tracking and/or collateral behaviors during the delay (Staddon & Simmelhag, 1971) that have weaker experimental control compared to explicitly required lever pressing responses. Each session consisted of 54 free choice trials, 14 SS forced choice trials, and 14 LL forced choice trials, and lasted until all 82 trials have been completed or approximately 2 hr had elapsed.

For the delay manipulation, the SS choice always delivered 1 pellet and the LL reward always delivered 2 pellets. There were 45 sessions. The LL delay was 30 s and the SS delay increased every 15 sessions: 5, 10, and 20 s. For the magnitude manipulation, the SS delay was always 10 s and the LL delay was always 30 s. There were 45 sessions. The SS reward was 1 pellet and the LL reward increased every 15 sessions: 1, 2, and 4 pellet(s).

2.3.5. Buffer task.—A modification of the lever press training was used in between each task to minimize side biases and the carryover effects from one task to another. Wang et al. (2017) found that the buffer task minimized cross-task interference and eliminated side biases. The first session delivered FR1 → RR3 → RR5 schedules from lever press training where each schedule was trained for one block with 20 reinforcers earned on each lever, constituting three blocks in total. The second and third session consisted of three blocks of RR5 with 20 reinforcers on each lever per block. A 5-min inter-block interval (IBI) was delivered in all sessions.

2.3.6. Time discrimination.—A time discrimination task, adapted from Church and Deluty (1977), was used to test the rats' ability to discriminate different signal durations.

This task was used to determine whether rats may have deficits in discrimination abilities that may directly affect food choices. In addition, poorer ability to discriminate delays predicts more impulsive behavior (Marshall, Smith, & Kirkpatrick, 2014), which could indirectly affect food choices. Rats completed training sessions where the levers were associated with a long or a short duration. After learning the association, rats received 10 testing sessions where intermediate delays were presented, and the rats classified the delay as short or long.

2.3.6.1. Training.: Rats received training with a 4-s short and a 12-s long houselight signal, where responding on the short lever would be considered a correct response for the 4-s signal and the long lever would be considered a correct response for the 12-s signal. Each trial began with the onset of the houselight that lasted for either the short or long duration. Following the signal, both levers were inserted and a discriminative response was collected. Correct responses were followed by a 1-pellet food delivery and then a 15-s ITI. Incorrect responses were followed by a correction trial that was composed of a 5-s ITI and a repeat of the previous trial until a correct response was made and food was delivered. Sessions lasted for a maximum of 2 hr. Each session delivered 160 trials in four blocks of 40 trials each. Each block consisted of 20 long and 20 short trials. Training continued until the rats achieved a group criterion of at least 80% correct on two consecutive sessions, which took 11 sessions for rats that received this task first and 13 sessions for rats that received this task second. The correct response for the short 4-s duration was the same lever as the SS lever and the correct response for the 12-s duration was the same lever as the LL lever in the delay impulsive choice task.

2.3.6.2. Testing.: Once training was completed, the rats received a series of test sessions with non-reinforced durations following a geometric progression intermixed with normal training trials: 4, 5.26, 6.04, 6.93, 7.94, 9.12, and 12 s signals. Therefore, the middle duration was the geometric mean of the shortest and longest signal duration, which has been found to be the point of subjective equality between the two durations (Church & Deluty, 1977). Test trials were administered in the same fashion as normal training trials, except that responses were not followed by reinforcement and there were no correction trials. The subjective perception of the length of the signal duration was tested, so there were no correct responses to test trials. Each of the four blocks consisted of 1 test of each duration intermixed among the 40 training trials so that each duration was administered 4 times in a session. There were 10 test sessions. The tests yielded a psychophysical function relating the signal duration to the proportion of long responses.

2.3.7. Reward magnitude discrimination.—The reward magnitude discrimination task involved the simultaneous presentation of both levers, for which lever pressing was reinforced on variable-interval (VI) schedules of reinforcement. Following the magnitude manipulation of the impulsive choice task, rats completed the buffer task and then began the reward magnitude discrimination task. The reward magnitude discrimination task consisted of a concurrent VI-VI task with two VI 30 s schedules of reinforcement, in which food became available to be delivered t s following lever insertion. The values of t were drawn from independent negative exponential distributions with means and variances of 30 s to

promote constant rates of responding. Food was delivered following the first lever press after t s had elapsed on that lever. The schedule of food deliveries on the two levers were independent.

The primary manipulation within the concurrent VI-VI task was the reward magnitude on the VI 30-s schedule; with the “large” lever on the same side as the LL outcome in the magnitude impulsive choice task. On the “small” lever, one pellet of food was delivered following completion of the VI 30. Alternatively, on the “large” lever, the reward magnitude increased across phases: 1, 2, and 4 pellet(s). Each session lasted until approximately 200 food pellets were delivered or until 2 hr had elapsed. Rats were trained until they exhibited stable behavior. Phase 1 lasted for 11 sessions for rats who received this test first and 13 sessions for rats who received this test second. Subsequently, Phases 2–3 lasted for 5 sessions.

2.3.8. Food preference.—A restricted access consumption test was used to determine how dietary history affected food preferences. Following the impulsive choice and discrimination tasks, each rat completed the preference test which consisted of three days of testing: an exposure period and two preference tests. For the exposure period, the rats were placed in a breeder cage (18.25 in $\times$ 12 in $\times$ 6.25 in) with two bowls, randomly assigned to a corner of the cage. There was 1 g of each supplement (fat and sugar) placed in each bowl. The rats were given an opportunity to explore the cage and consume both supplements. The rats were removed after they consumed all the supplements or after 10 min had elapsed. On the second and third day of testing, each rat went through a preference test, where rats were given the choice between the two supplements (fat and sugar). The location of the bowls was switched each day to control for any potential side biases. They were given 1 min to eat from the two bowls, which contained 3 g of each supplement. Once 1 min had elapsed, the rat was removed from the cage, and any remaining supplement was weighed.

2.3.9. Liking.—A taste reactivity task was used to investigate the rat’s liking of fat and sugar. This task measured rat’s hedonic responses (i.e., facial expressions) to various concentrations of fat and sugar solutions that were administered via an oral fistula. The rats underwent surgery before beginning testing.

2.3.9.1. Surgery. This experiment used a fistula implantation technique similar to the procedure used in Kiefer, Hill, and Kaczmarek (1998). Rats were anesthetized with intraperitoneal injections of ketamine (80 mg/kg) and diazepam (5 mg/kg). Supplemental doses were given as needed. All animals were implanted with an intraoral fistula made of 160-gauge polyethylene tubing. The oral end of the fistula was flared with heat to create a flat edge that was approximately .6 cm in diameter. Teflon sheeting was used to create a ring with an outer diameter of .7 cm. The Teflon ring was placed between the flared end of the fistula and the rat’s cheek to serve as a washer. A 19-g hypodermic needle was used to insert a PE-160 polyethylene tube (Fisher, 1417012E) lateral to the rat’s first maxillary molar. The plastic tube was then threaded subcutaneously, around the zygomatic arch, and exited the top of the rat’s head between the ears. The tubing was secured with another Teflon washer similar in size and a 22-g, 1.5-cm metal piece was inserted into the tubing that was later used to connect to the infusion pump tubing. After surgery, all rats received a subcutaneous

injection of Meloxicam (2.0 mg/kg). Rats were given a minimum of 4 days to recover, during which they were monitored closely, weighed, handled daily, and had their fistulas flushed daily to prevent closing. Two rats were removed before testing due to incorrect tubing placement.

2.3.9.2. Testing.: During testing, rats were placed in a plexiglass cylinder that was 10 cm tall and 20 cm in diameter. A 1.5-mm hole was drilled in the lid of the cylinder through which one end of PE-160 polyethylene tubing was woven through and could be attached to the fistula tubing on top of the rat's head. Prior to being attached, the tubing was filled with the appropriate solution. The other side of the tubing was connected to a 10-ml glass syringe that was mounted in an infusion pump (Sage, M361, Vernon Hills, IL). This allowed for direct infusion of solution into the rodent's mouth. The plexiglass chamber was placed on a piece of glass that covered a 61 × 61 cm wooden table top. The table top had a 25-cm diameter circle cut in the center of the table. A black and white 0.33-in camera (Product number: T3z2910CS-IR, Torrance, CA) was placed directly underneath the open circle to record taste reactivity behaviors. To acclimate the rats to the chamber, the rats were placed in the chamber for 5 min. The following day, all rats receive a 1-ml infusion of tap water for one minute to acclimate them to the infusion procedure. The behaviors during the water trial were recorded.

Rats completed a single 60-s infusion trial each day. The video recording and infusion pump were turned on to start the trial, and the trial ended 60 s after the first reactivity response. During this time, rats had 1 ml of solution infused through an intraoral fistula directly into their mouth. All rats were exposed to fat and sugar solutions in a counterbalanced order. Both solutions were infused with the concentrations delivered in an ascending order. The concentrations from this experiment were taken from Shin et al. (2011). The fat solution consisted of corn oil (Mazola corn oil) mixed with distilled water and tween 80 (.375ml/50mL solution; Sigma-Aldrich, St. Louis, MO) with concentrations of .06%, 1%, and 32%. The sugar solutions consist of sugar cane mixed with distilled water with concentrations of 0.01, 0.10 M, and 1.0 M.

2.3.9.3. Scoring.: All taste reactivity testing videos were recorded using Limelight (version 4). The videos were scored by a single, blind scorer on a preset frame by frame (.065 s per frame) duration. This procedure relied on established operational definitions found in Berridge and Grill (1984) and scoring criteria found in Berridge (2000). A subset of the videos (4%) were validated by another blind scorer. The videos were scored measuring the number of hedonic response (Reynolds & Berridge, 2002). Hedonic responses consisted of tongue protrusions, lateral tongue protrusions, and mouth movements. Tongue protrusions were classified as rhythmic extensions of the tongue displayed through the midline of the mouth. Lateral tongue protrusions were classified as non-rhythmic extensions of the tongue in which the tongue emerges on either side of the mouth. Mouth movements were classified as small, rhythmic openings of the mouth. Paw-licking, large, rhythmic, extensions of the tongue directed at the paw, was only considered a hedonic response if it was not associated with grooming responses for .13 s. The video scoring also recorded when the rat was out-of-scope which was defined as when the scorer could not see the mouth.

2.4. Data analysis

The raw data were imported into MATLAB 2016a (The MathWorks, Natick, MA). Repeated measures mixed effects regressions were conducted for each task (see Results for details). Mixed effects models are the recommended analytical approach in the fields of Psychology and Neuroscience (Boisgontier & Cheval, 2016) because they increase generalizability to the population and reduce Type I error rates (Boisgontier & Cheval, 2016; Moscatelli, Mezzetti, & Lacquanti, 2012). Further, the regressions included all individual observations (e.g., all choices) as the mixed effects regressions treat individual observations as correlated observations within subjects (Cnaan, Laird, & Slasor, 1997) to further reduce Type I error rates. The mixed effects regression models estimate fixed effects (group level variables) and random effects (individual differences). The hypothesized effects were tested as fixed effects, and the Akaike Information Criterion (AIC) was used to determine the best random effects structure. When the random effects were highly correlated, a more parsimonious random effects model was selected to avoid overparameterization (Baayen, Davidson, & Bates, 2008; Bates, Kliegl, Vasishth, & Baayen, 2015). Any transformation of variables is described in the corresponding results section. All categorical variables were effect-coded so that the coefficients summed to 0, with the chow group as the reference group. Post-hoc analyses were conducted on significant effects to compare the high-fat and high-sugar groups to the chow group using the coefficient test function in MATLAB. As a measure of effect size, the unstandardized regression weights (b) and the associated 95% confidence intervals are reported.

3. Results

3.1. Body weight

A repeated measures linear regression was used to predict body weight (g) as a function of age in post-natal days (PND) across the whole study. The best fitting model included Group $\times$ Age and both main effects as fixed effects. Intercept and age were included as random effects. Group was a categorical predictor (effect coded) and age was a continuous predictor (mean centered and log transformed to correct for violations of normality). There was a significant main effect of group, such that Group HF ($b = 360.79$) weighed more than Group C at the mean age (PND 138; $b = 330.23$), $t(7460) = 2.58$, $p = .010$. Group HS ($b = 343.59$) did not significantly differ from Group C at the intercept, $t(7460) = 1.13$, $p = .259$. Rats gained weight as they aged, $t(7460) = 44.28$, $p < .001$, $b = 154.37$ [147.54, 161.21], and there was a significant Group $\times$ Age interaction (Figure 3). Post-hoc analyses indicated that Group HF ($b = 168.06$) gained weight at a faster rate than Group C ($b = 141.70$), $t(7460) = 3.09$, $p = .002$. However, Group HS ($b = 153.36$) did not significantly differ from Group C, $t(7460) = 1.37$, $p = .172$.

3.2. Body composition

A repeated measures linear regression was used to predict the percent body fat in the abdomen (log transformed to normalize the data) obtained through the Lunar PIXImus densitometer scan. The best fitting model included the Group $\times$ Time interaction and both main effects. Intercept was included as a random effect. Group was a categorical predictor

(effect coded) and time was a continuous predictor. Intercept tests were performed at each of the time points to test group differences in percent body fat at 1.5 and 9 months.

There was a significant main effect of group at 1.5 months (see Figure 4), such that Group HF ($b = 2.86$) had a higher percent of body fat than Group C ($b = 2.36$), $t(66) = 6.70$, $p < .001$. Group HS also had higher percent body fat ($b = 2.69$) compared to Group C, $t(66) = 4.34$, $p < .001$. There was also a significant main effect of group at 9 months, such that Group HF ($b = 3.28$) had a higher percent of body fat than Group C ($b = 2.64$), $t(66) = 8.50$, $p < .001$. Group HS also had higher percent body fat ($b = 2.85$) compared to Group C, $t(66) = 2.76$, $p = .007$. There was also a significant Group $\times$ Time interaction. However, post-hoc tests indicated that the change in percent body fat in Group HF ($b = 0.42$) did not differ from Group C ($b = 0.28$), $t(66) = 1.73$, $p = .089$, nor did Group HS ($b = 0.16$) differ from Group C, $t(66) = 1.51$, $p = .136$. Overall, the high-fat and the high-sugar groups had higher body fat percentages than the chow group.

3.3. Impulsive choice

A repeated measures logistic regression was used to predict the proportion of LL choices made during each phase (delay or magnitude) of the impulsive choice tasks. The primary dependent measure was the individual choices for the SS and LL outcomes (SS = 0, LL = 1). The approach used by Wileyto, Audrain-McGovern, Epstein, and Lerman (2004) was adapted to help parse out bias versus sensitivity to better isolate the mechanisms of dietary effects on choice behavior. As such, the slope for each task represented the sensitivity to the manipulated parameter (magnitude or delay), and the intercept represented a preference in choice behavior. The slope of the function is most closely related to the delay discounting rate, which has been implicated as a predictor of obesity. The SS delay was scaled so that the intercept represented a 5-s delay for the SS reward (SS/LL-minimum SS/LL). Therefore, the intercept represents a preference for the SS reward. The LL magnitude was scaled so that the intercept represented a preference for the large magnitude reward (SS/LL – SS/maximum LL). The model for both tasks included Group $\times$ LL magnitude (or SS delay) as a fixed effect and intercept as a random effect.

3.3.1. Delay manipulation.—Overall, rats showed a preference for the SS reward, $t(72572) = -8.48$, $p < .001$, $b = -1.75$ [$-2.16, -1.35$] at the intercept (5 s). Note that the b -values are expressed in log odds so that negative values indicate an SS preference, positive indicate an LL preference, and 0 indicates indifference. Although there was a trend for more SS choices in the two dietary conditions, there was no significant main effect of group, indicating that Group HS ($b = -3.31$) and Group HF ($b = -1.86$) did not differ from Group C ($b = -1.25$) in their preference for the SS reward, $p > .07$. All groups showed a positive slope with changes in the SS delay, such that as the SS delay increased, the rats made more LL choices, $t(72572) = 115.73$, $p < .001$, $b = 6.33$ [$6.22, 6.43$]. The groups differed in their sensitivity to delay as evidenced by a significant Group $\times$ Delay interaction (see Figure 5A). Post-hoc tests indicated that Group HF ($b = 6.26$) had a steeper slope than Group C ($b = 5.76$), $t(72572) = 3.70$, $p < .001$, indicating greater delay sensitivity. Similarly, Group HS ($b = 6.96$) had a steeper slope than Group C, $t(72572) = 8.91$, $p < .001$. Overall, Group HS and

Group HF displayed a greater sensitivity to delay than Group C, but they did not differ in their preference for the SS reward at the 5-s delay.

3.3.2. Magnitude manipulation.—Overall, rats showed a preference for the large magnitude LL reward, $t(70423) = 4.48$, $p < .001$, $b = 0.59$ [0.33, 0.85] at the intercept. There was no main effect of group. All groups showed a positive slope with changes in the LL magnitude, such that as the LL magnitude increased, the rats made more LL choices, $t(70423) = 111.32$, $p < .001$, $b = 5.21$ [5.12, 5.30]. The groups differed in their sensitivity to the changes in the magnitude of the large reward as evidenced by a significant Group $\times$ Magnitude interaction (see Figure 5B). Post-hoc tests indicated that Group HF ($b = 4.52$) had a shallower slope than Group C ($b = 5.54$), indicating reduced sensitivity to magnitude, $t(70423) = 8.87$, $p < .001$. However, Group HS ($b = 5.55$) did not differ in their sensitivity to magnitude, compared to Group C, $t(70423) = .10$, $p = .923$. Overall, Group HF was less sensitive to magnitude than Groups HS and C.

3.4. Discrimination

3.4.1. Temporal Discrimination.—A repeated measures logistic regression was used to predict the proportion of long responses during the testing sessions within the temporal discrimination task (short = 0, long = 1). The best fitting model included Group $\times$ Signal Duration and both main effects as fixed effects. Random effects included intercept and signal duration. Group was a categorical predictor (effect coded). Signal duration was continuous and was mean centered at the geometric mean because it is the typical point of bisection (Church & Deluty, 1977). Two additional tests were performed with signal duration centered on each of the anchors to test discrimination of the short and long signals. Signal duration was scaled in proportion to the long signal duration (Duration/Maximum Duration).

There was a significant tendency to report the middle duration (the geometric mean) as short, $t(7632) = -6.29$, $p < .001$, $b = -0.29$ [-0.38, -0.20], but there were no group differences at the geometric mean. There was a strong tendency to report the 4-s anchor as short, $t(7632) = -13.06$, $p < .001$, $b = -1.26$ [-1.45, -1.07]. In addition, Group HF ($b = -0.97$) reported the 4-s duration as longer in comparison to Group C ($b = -1.62$) at the 4-s anchor duration, $t(7632) = 2.77$, $p = .006$. Group HS ($b = -1.19$) did not differ from Group C at the 4-s duration, $t(7632) = 1.86$, $p = .06$. There was a strong tendency to report the 12-s anchor as long, $t(7632) = 11.84$, $p < .001$, $b = 1.38$ [1.15, 1.61], but there were no group differences. There was a significant main effect of signal duration, such that as the signal duration increased the rats increasingly reported that the signal was long, $t(7632) = 13.62$, $p < .001$, $b = 3.96$ [3.39, 4.53]. There was also a significant Group $\times$ Signal Duration interaction (see Figure 6). Post-hoc tests indicated that the change in proportion of long responses made by Group HF ($b = 3.13$) across signal durations had a flatter slope than Group C ($b = 4.91$), $t(7632) = 2.48$, $p = .013$. The change in proportion of long responses for Group HS ($b = 3.83$) did not significantly differ from Group C, $t(7632) = 1.52$, $p = .128$. Overall, Group HF showed a shallower slope and reported the 4-s duration as longer than Group C.

3.4.2. Reward magnitude discrimination.—A repeated measures logistic regression was used to predict the proportion of large responses during each phase of the reward magnitude discrimination task (small = 0, large = 1). The best fitting model included Group $\times$ Magnitude and both main effects as fixed effects. Random effects included intercept and magnitude. Group was a categorical predictor (effect coded) and magnitude was a continuous predictor. Magnitude was scaled so that the intercept predicted choice when the large magnitude was 4 pellets to assess magnitude discrimination at the largest magnitude value.

There was no significant main effect of group indicating that the groups did not differ in their ability to discriminate between 1 and 4 pellets. There was a significant main effect of magnitude, such that as the magnitude of the large lever increased, the rats pressed the large lever more often, $\chi^2(107624) = 8.30, p < .001, b = .39 [.29, .48]$. There was no significant Group $\times$ Magnitude interaction as depicted in Figure 7.

3.5. Incentive motivation

A repeated measures linear regression was used to analyze the number of reinforcers earned during the last session of the lever press training task, which included FR1, RR3, and RR5, to obtain a measure of incentive motivation to press for food prior to any experience in the other tasks that could have altered responding. The best fitting model included Group as a fixed effect and the intercept as a random effect. There was a significant main effect of group. Post-hoc analyses indicated that Group HF ($b = 165.84$) earned significantly fewer reinforcers than Group C ($b = 238.92$), $\chi^2(33) = 5.39, p < .001$. The number of reinforcers earned by Group HS ($b = 223.50$) did not significantly differ from Group C, $\chi^2(33) = 1.14, p = .264$ (see Figure 8). Overall, Group HF earned fewer reinforcers, suggesting a decreased incentive motivation to work for food.

To investigate whether differences in incentive motivation to respond may be playing a critical role in impulsive choices, we also assessed responding on forced choice trials during the choice task. We observed the same patterns as in Figure 8 in that the high-fat group responded less on forced choice trials and the high-sugar group responded similarly to the chow group. To assess whether the differences were related to choice behavior, we correlated the responses during the LL forced choice trials with their overall LL choices. The number of responses did not correlate with their choice behavior, $r = .11, p = .28$.

3.6. Preference test

A repeated measures linear regression was used to predict preference for fat or sugar during the exposure and consumption tests. The dependent variable was the log odds of preference for fat (versus sugar) to correct for deviations from normality. The preference score was computed by taking the natural logarithm of the grams of fat consumed divided by the grams of sugar consumed. A value of .5 was added to each amount to account of exclusive consumption (Garcia & Kirkpatrick, 2013). Therefore, a preference score of 0 indicated no preference, positive preference scores indicated a preference for fat and negative a preference for sugar.

For the exposure period (test number 1), the best fitting model included Group as a fixed effect and intercept as a random effect. Group was a categorical predictor (effect coded) and test number was a continuous predictor. There were no significant differences in consumption between Group HF ($b = .08$) and Group C ($b = -0.26$), $t(33) = 1.52$, $p = .138$, nor between Group HS ($b = -0.33$) and Group C, $t(33) = 0.33$, $p = .745$.

For the consumption test, the best fitting model included Group $\times$ Test Number and both main effects as fixed effects. Intercept was included as a random effect. Test number was scaled so that the intercept represented preference during the second test. There was a significant main effect of group, such that Group HF ($b = 0.83$) consumed more fat than Group C ($b = -0.83$), $t(66) = 4.09$, $p < .001$ during the second test. Group HF showed a preference for fat as indicated by an estimate above 0, while Group C showed a preference for sugar. Group HS also showed a preference for sugar ($b = -1.55$), and this preference did not significantly differ from Group C, $t(66) = 1.78$, $p = .079$. There was no significant Group $\times$ Test Number interaction (see Figure 9). Overall, Group HS and C showed a preference for sugar, while Group HF showed a preference for fat.

3.7. Taste reactivity

A repeated measures linear regression was conducted to predict the number of hedonic responses during the 60-s trials that comprised the taste reactivity task. The total number of hedonic responses was log-transformed to address issues of normality. The categorical variables of solution (fat and sugar) and group (HF, HS, and C) were effect coded. Sugar was the reference condition for solution. Intercept was included as a random effect for all models. Concentration was scaled so that the relative concentration was calculated for both Fat and Sugar solutions to allow for comparison (relative concentration = $1 - \frac{\text{concentration}}{\text{max concentration}}$). The intercept represented the maximum concentration. The best fitting model included Group $\times$ Solution $\times$ Concentration and all lower effects. Intercept was included as a random effect. Overall, the hedonic responses significantly increased with increases in the concentration of the solution for both fat and sugar, $t(165) = 6.40$, $p < .001$, $b = 0.07$ [0.05, 0.10] (Figure 10). There were no other significant effects, indicating that the dietary groups did not differ in their liking of fat and sugar.

4. Discussion

Given that people make approximately 200 food choices a day (Wansink & Sobal, 2007) and obesity is thought to affect behaviors related to food choice (van Meer et al., 2016), the goal of the current study was to determine how long-term diet exposure affected body weight, body composition, and different aspects of behaviors related to food choice. The key determinants of food choice that were investigated included impulsive choice behavior, time and reward discrimination, incentive motivation, food preference, and liking. The results indicated that a high-fat diet significantly altered food preference and led to greater delay sensitivity in impulsive choice behavior in both the delay and magnitude tasks, as well as impairments in time discrimination and incentive motivation. The high-sugar diet increased delay sensitivity in the impulsive choice task, while leaving the other behaviors intact. The

results have implications for the development of obesity given that these factors can affect food choice behavior.

4.1. Body weight and composition

The behaviors measured in the current study have been linked to obesity (Bickel et al., 2014; Cox et al., 2016; Davis et al., 2007; Horstmann et al., 2015; Jarmolowicz et al., 2014; Mela, 2001; Rasmussen, Reilly, & Hillman, 2010; Shin et al., 2011; Singh & Sikes, 1974; Teitelbaum, 1957). Body weight is a common measure of obesity in rodent models (Novelli et al., 2007). While the high-fat group in this study weighed significantly more than the chow group, differences in weight were not detected for the high-sugar group, and even the high-fat group were far from obese. There are inconsistent results surrounding the effect of diet on body weight, where some studies find that both high-fat and high-sugar diets lead to weight gain, while others find that only high-fat diets lead to weight gain (Jurdak & Kanarek, 2009; Jurdak et al., 2008; Steele et al., 2017).

There also were differences in body fat percentage in the abdomen, such that the high-fat and high-sugar groups had higher body fat percentages than the chow group. Body fat percentages were altered by the diets in the present study. Schemmel, Mickelsen, and Gill (1970) proposed that body composition is under greater dietary control compared to body weight, which may explain the greater changes in body composition resulting from diet exposure in the present experiment. The results suggest that high-fat and high-sugar diets can lead to higher percentages of body fat, even when controlling for the number of calories received, indicating that diet composition has significant effects on body composition (Miller, Lindeman, Wallace, & Niederpruem, 1990). Thus, body composition (e.g., body fat percentage) may be a better measure of obesity. In addition, the relationship with impulsive choice is more robust when using body fat percentage as a measure instead of Body Mass Index (BMI; Nederkoorn, Smulders, Havermans, Roefs, & Jansen, 2006; Rasmussen et al., 2010), suggesting that body composition may be a better measure for predicting behavioral changes.

4.2. Impulsive choice

Impulsive choice behavior was investigated through impulsive choice tasks with delay and magnitude manipulations to determine how dietary exposure affected delay and magnitude sensitivity and preferences for shorter delays or larger magnitudes. In the delay manipulation, rats exposed to diets high in saturated fat and refined sugar increased delay sensitivity, replicating Steele et al. (2017). Delay sensitivity, or an increased slope of the choice function, is an indicator of increased delay discounting rate, a marker of impulsivity (Odum, 2011). Delay discounting is the rate of decay of reward value when rewards are delayed and has been proposed to predict a susceptibility to a wide range of diseases including obesity (Barlow et al., 2016; Bickel et al., 2014; Rasmussen et al., 2010; Schiff et al., 2015). While the diets affected delay sensitivity/delay discounting, there were no differences in preference for the SS reward at the 5-s delay. This is in contrast to Steele et al. (2017) who found that both the high-fat and high-sugar diets resulted in a preference for the SS reward when extrapolating the data to the 0-s SS delay. Overall, the results from the delay manipulation of the impulsive choice task suggest that diets high in saturated fat and

refined sugar led to increased delay discounting rates. Results from the magnitude manipulation of the impulsive choice task suggest that there were no differences in the preference for the large reward, but the rats fed a high-fat diet displayed a shallower slope suggesting they were not as sensitive to changes in reward magnitude. Therefore, rats fed a high-fat diet had to be offered a larger LL reward before switching from SS to LL choices. Together, these results suggest that rats fed a high-fat diet display deficits on both the delay and magnitude manipulation task whereas rats fed a high-sugar diet only display deficits on the delay manipulation task. The pattern of results in the high-fat group suggests a combination of reduced value for larger magnitudes coupled with increased discounting rates for delayed rewards.

One possible reason for the different patterns in the delay and magnitude tasks is that there may have been carryover effects despite the use of the buffer task. This can be seen in comparing the results when given the choice between 1 pellet after 10-s versus 2 pellets after 30-s (the 10-s SS delay condition in the delay task and the 2 pellet condition in the magnitude task). While Group HF and HS appear to produce similar results across tasks, Group C did not display a strong preference for either reward during the delay manipulation yet displayed a preference for the SS reward during the magnitude manipulation. The results could potentially be due to a magnitude contrast effect in the chow condition (Smith, Peterson, & Kirkpatrick, 2016), or possibly to the effect of previous experience on the delay task. Further study will be required to discern the nature of these effects in the chow group.

In addition to contrast effects, another aspect of the choice task that could affect behavior is the absence of a 0-s delay condition. There are a number of ways to measure impulsive choice, with the most important aspect being the choice between a smaller-sooner (SS) and larger-later (LL) reward (Odum, 2011). However, one key feature of the current study compared to a number of other studies is that the present impulsive choice task did not use a 0-s delay. The current task should be most relevant to decisions where both the SS and LL are delayed, such as food decisions. Food rewards usually involve delays associated with procurement, delivery, and/or handling (e.g. unwrapping) time and would therefore rarely be immediately delivered.

A 0-s delay, which is likely to be a few milliseconds in practice, would most likely involve the sub-second cerebellar motor timing system, whereas the delays in seconds range used for the other choice parameters would most likely rely on the interval timing system which involves the frontal-striatal loops (Allman, Teki, Griffiths, & Meck, 2014; Buhusi & Meck, 2005; Droit-Volet, 2013). Because interval timing has been implicated as a potentially key factor in impulsive choices (Baumann & Odum, 2012; Marshall, Smith, & Kirkpatrick, 2014; McClure, Podos, & Richardson, 2014; Wittmann & Paulus, 2008), we opted to focus on parameters that would maximize the reliance on the interval timing system. Indeed, there is evidence that 0-s delays have different impacts on choice compared to short delays. Indifference points from a paradigm with a 0-s SS do not predict indifference points when the SS is delayed (Mitchell & Wilson, 2012). In addition, exposure to delayed rewards prior to choice testing promotes LL choices, but exposure to 0-s delays have little to no effect (Renda, Rung, Hinnenkamp, Lenzini, & Madden, 2018). Altogether, these results suggest that 0-s delay paradigms may invoke different processes from paradigms when both rewards

are delayed. However, it does appear that the two types of paradigms may both be sensitive to group-level effects on choice as smokers show steeper discounting with both 0-s and delayed SS paradigms compared to non-smokers (Mitchell & Wilson, 2012). This suggests that there may be some common factors at work in the two paradigms. Further research is needed to understand how these task differences can impact behavior.

Overall, the results provide evidence that high-fat and high-sugar diets increased sensitivity to delay that could affect food choice and eventually lead to obesity or other disorders characterized by impulsive choice. Diet-induced impulsivity may be a causal pathway to obesity as impulsivity is proposed to serve as a pre-cursor to a wide range of diseases and disorders (Bickel, Jarmolowicz, Mueller, Koffarnus, & Gatchalian, 2012). Further, these results may explain the relationship between obesity and impulsive choice that is often seen in humans (Bickel et al., 2014; Fields, Sabet, & Reynolds, 2013; Jarmolowicz et al., 2014; Rasmussen et al., 2010).

4.3. Discrimination Abilities

The results from the time discrimination task indicated that the increased sensitivity to delay exhibited by the high-fat group may be related to poor time discrimination abilities, as the high-fat group displayed deficits in discriminating signal durations. Specifically, they had poorer time discrimination evidenced by a shallower slope of their bisection function. Poor time discrimination predicts increased impulsive choice behavior (Marshall et al., 2014). In addition, time-based behavioral interventions improve both time discrimination and impulsive choice (Smith et al., 2015). Therefore, the deficits in timing may be a key factor in the impulsive behavior exhibited by the high-fat group in this study and in Steele et al. (2017). In addition, time discrimination abilities could be a determinant of food choice behavior as some aspects of food choices are time-based such as when to eat and how long to spend eating.

In contrast, the high-sugar group did not show significant deficits in time discrimination, suggesting an alternative mechanism for the alterations in choice behavior. One possibility is that the high-sugar group may instead exhibit delay aversion, which is a predictor of impulsive choice (Marshall et al., 2014) and is seen in individuals with ADHD (Bitsakou, Psychogiou, Thompson, & Sonuga-Barke, 2009; Karalunas & Huang-Pollock, 2011). The high-sugar group did show a greater sensitivity to delay which may be a marker of delay aversion. Future research should investigate delay aversion as a potential mechanism of impulsive choice for the high-sugar group.

The reward magnitude discrimination task found no differences, so deficits in reward discrimination may not be responsible for the results of the HF condition in the magnitude manipulation of the impulsive choice task, as the high-fat diet did not affect reward magnitude discrimination but did affect sensitivity to magnitude. The relationship between reward discrimination and impulsive choice may not be as robust as the relationship between temporal discrimination and choice, as indicated by mixed results in previous studies (Marshall & Kirkpatrick, 2016; Marshall et al., 2014). However, it is possible that the mixed results are due to the nature of the tasks used to measure reward magnitude discrimination. It has been proposed that a task where the individual's behavior determines reward instead of

experimental manipulations may be more sensitive to the effects of reward magnitude on behavior (Marshall & Kirkpatrick, 2016). In this study, the set experimental manipulations determined the reward (Marshall et al., 2014). It is possible that the high-fat group may have alterations in reward magnitude discrimination that a more sensitive task could elucidate. Further work is needed to gain a better understanding of the high-fat diet effects on choices in the reward magnitude impulsive choice task.

4.4. Food preference, liking, and wanting

Food preference and liking are similar in nature, but there are key distinctions between the two that help create a better understanding of determinants of food choice. Liking is a hedonic reaction to a particular substance, while food preference is a choice between two options (Finlayson, King, & Blundell, 2007). In this experiment, the high-fat and high-sugar groups did not significantly differ in hedonic responding (i.e., liking) to fat or sugar. These results suggest that long-term exposure to a high-fat or high-sugar diet does not change liking of these substances (see also Lesser, Arroyo-Ramirez, Mi, & Robinson, 2017). However, other experiments have found blunted responses to fat and sugar after developing obesity from high-fat consumption (Shin et al., 2011). This could be due to differences in methodology; the taste reactivity task used in this experiment directly infused the solutions into the mouth instead of studying voluntary ingestion by placing the substance on the surface of the apparatus (Berridge, 2000). The taste reactivity task, therefore, allowed for more controlled measurement parameters as all rats received the same amount of solution during each trial. The conflicting results could also be a result of the long-term exposure of the diet. It is possible that the dietary effects caused an increased liking of fat and sugar early in the diet exposure phase, but these effects could have reduced after prolonged exposure to the diet, with a transition occurring from increased liking to increased wanting (see Robinson, Robinson, & Berridge, 2013). These results suggest that long-term consumption of diets composed of high-fat and high-sugar do not alter liking. As a result, liking may not be a main contributor to food choices, at least not with long-term diet exposure.

While the present study did not find differences in liking, the rats fed a high-fat diet showed an increased preference for fat. Exposure to a particular diet can lead to strong and persistent changes in preference (Sclafani, 1995). On the other hand, the high-sugar and chow group showed a preference for sugar. The sugar preference displayed by the chow group is likely due to an innate preference for sugar (Sclafani, 1995). The results from the preference test suggest that long-term exposure to a high-fat diet overrode innate preferences. This has implications for humans as consumption of unhealthy fatty foods could increase preference for those foods.

As food preference and liking are only two aspects of food choice (Mela, 2001), it is also important to examine incentive motivation which may assess wanting of foods. While there were no differences in liking of fat and sugar resulting from dietary exposure, the high-fat diet altered incentive motivation and preference. Indeed, Group HF responded less during the final session of lever press training and during forced choice trials in the impulsive choice task suggesting they did not value the reinforcers as much as the control or high-sugar group, illustrating potential deficits in incentive motivation potentially caused by the

high-fat diet. This is consistent with the magnitude choice task where the rats did not switch to the larger LL as readily, and is also consistent with previous literature that has found that people and rats with obesity are less willing to work for food (Singh & Sikes, 1974; Teitelbaum, 1957). In addition, responding during forced choice trials did not correlate with choice behavior, so this suggests that the deficits in choice behavior were not due to effort motivation, but more likely were due to outcome-oriented motivational processes, such as altering the demand for the food rewards. Therefore, diets high in processed fats affect incentive motivation, and further research is needed to better identify the potential motivational effects of the diet. Together, these results are consistent with studies in humans implying that liking is more resistant to change, but wanting can be altered (Mela, 2006). Indeed, alterations of preference and incentive motivation were found, and these two behaviors could drive food choice behavior.

4.5. Conclusions

Food choices are complex and can be influenced by impulsive choice, time or reward magnitude discrimination, food preferences, incentive motivation to work for food, and liking. Ultimately, a high-fat diet increased sensitivity to delay and decreased sensitivity to magnitude in the impulsive choice tasks, impaired time discrimination, decreased incentive motivation, and altered food preferences towards greater preference for fats. While, the high-sugar diet increased sensitivity to delay in the impulsive choice task, there were no other deficits as measured by the other tasks. All these factors could influence food choice, and food choices determine one's diet. Finally, food choices could contribute to changes in body composition and eventually weight status, as overconsumption of high-fat and high-sugar foods can lead to obesity. Figure 1 had proposed a preliminary model for understanding these relationships. This model has been revised based on the current results and is diagrammed in Figure 11. The present results suggest that liking is not affected by long-term dietary exposure, so this factor has been removed. However, because the high-fat diet impaired time discrimination, this is an important predictor. Time discrimination could directly alter food choices as many food choices involve timing information such as when to eat and how long to eat for. Further, diet can affect time discrimination, and time discrimination is thought to affect impulsive choice (Marshall et al., 2014). Finally, it appears that body composition changes occur in advance of changes in body weight under the current dietary conditions, and this may explain the weaker relationship between impulsive choice and BMI (Barlow et al., 2016; Bickel et al., 2014; Rasmussen et al., 2010; Schiff et al., 2015).

This current study provides evidence that these factors can be affected by diet. Future research should investigate how these factors could influence each other. For example, food preference may be related to impulsive choice. A preference for a particular food should lead to increased consumption (Mela, 2001), which is a more natural condition for dietary exposure, in comparison to the caloric restriction used here. As consumption for foods high in fat and sugar increases with increased preference (Mela, 2001), those foods could then induce impulsive behavior (diet-induced impulsivity), which was shown in this study and in Steele et al. (2017).

The combined results suggest that it may be necessary to target decision making skills and related cognitive processes to help individuals combat the deficits in impulsive choice behavior and incentive motivation induced by diet, and potentially avoid the development of obesity or other maladaptive behaviors that can result from long-term consumption of foods high in processed fat and sugar. One potential avenue to improve impulsive choice behavior may be through a time-based behavioral intervention, particularly in the high-fat group which showed clear timing deficits. The high-fat diet-induced impulsivity appeared to result in poor time discrimination, and time-based interventions have successfully promoted self-controlled behavior and improved timing in rats (Smith et al., 2015). The high-sugar group may require a different intervention, as their time discrimination abilities were relatively intact. It is possible that an intervention for delay tolerance could help the high-sugar group, and this could be an additional target for the high-fat group as well. Further research will be needed to determine whether delay tolerance is affected by high-fat and/or high-sugar diets. In addition, targeting poor incentive motivation could be a possibility for improving food choices in rats fed a high-fat diet. Future research should investigate the efficacy of interventions to determine if they could be used to promote healthy food choices in conjunction with treatment programs for diet-related illnesses such as obesity.

Acknowledgements

This research was supported by the National Science Foundation Graduate Research Fellowship Program awarded to Catherine Steele and R01 grant MH085739 from the National Institutes of Health awarded to Kimberly Kirkpatrick and Kansas State University. CCS, KK, and JRAP designed research; CCS, JRAP, and IRD performed research; CCS and KK analyzed the data, and CCS, JRAP, IRD, and KK wrote the paper. Thanks to Cassi Friday, Carrie Bailey, and Jeremy Lott for their assistance with the conduct of the experiment, and to Dr. Stephen Kiefer for conducting the training for the taste reactivity surgeries. Parts of this experiment were presented at the Society for Neuroscience meeting in 2016, the Society for the Quantitative Analyses of Behavior meeting in 2017, and the Pavlovian Society meeting in 2017.

References

- Allman MJ, Teki S, Griffiths TD, & Meck WH (2014). Properties of the internal clock: first- and second-order principles of subjective time. *Annu Rev Psychol*, 65, 743–771. doi:10.1146/annurev-psych-010213-115117 [PubMed: 24050187]
- Baayen RH, Davidson DJ, & Bates DM (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language*, 59, 390–412. doi:10.1016/j.jml.2007.12.005
- Bailey C, Peterson JR, Schnegelsiepen A, Stuebing SL, & Kirkpatrick K (2018). Durability and generalizability of time-based intervention effects on impulsive choice in rats. *Behavioural Processes*, 152, 54–62. [PubMed: 29544866]
- Barlow P, Reeves A, McKee M, Galea G, & Stuckler D (2016). Unhealthy diets, obesity and time discounting: a systematic literature review and network analysis. *Obesity Reviews*, 17, 810–819. doi:10.1111/obr.12431 [PubMed: 27256685]
- Bates D, Kliegl R, Vasishth S, & Baayen H (2015). Parsimonious mixed models. *arXiv preprint arXiv:1506.04967*.
- Baumann AA, & Odum AL (2012). Impulsivity, risk taking, and timing. *Behavioural Processes*, 90, 408–414. doi:10.1016/j.beproc.2012.04.005 [PubMed: 22542458]
- Berridge KC (2000). Measuring hedonic impact in animals and infants: Microstructure of affective taste reactivity patterns. *Neurosci Biobehav Rev*, 24, 173–198. doi:10.1016/S0149-7634(99)00072-X [PubMed: 10714382]
- Berridge KC, & Grill HJ (1984). Isohedonic tastes support a two-dimensional hypothesis of palatability. *Appetite*, 5, 221–231. [PubMed: 6524918]

- Bickel WK, George Wilson A, Franck CT, Terry Mueller E, Jarmolowicz DP, Koffarnus MN, & Fede SJ (2014). Using crowdsourcing to compare temporal, social temporal, and probability discounting among obese and non-obese individuals. *Appetite*, 75, 82–89. doi:10.1016/j.appet.2013.12.018 [PubMed: 24380883]
- Bickel WK, Jarmolowicz DP, Mueller WT, Koffarnus MN, & Gatchalian KM (2012). Excessive discounting of delayed reinforcers as a trans-disease process contributing to addiction and other disease-related vulnerabilities: Emerging evidence. *Pharmacology & Therapeutics*, 134(3), 287–297. doi:10.1016/j.pharmthera.2012.02.004 [PubMed: 22387232]
- Bitsakou P, Psychogiou L, Thompson M, & Sonuga-Barke EJ (2009). Delay Aversion in Attention Deficit/Hyperactivity Disorder: an empirical investigation of the broader phenotype. *Neuropsychologia*, 47(2), 446–456. doi:10.1016/j.neuropsychologia.2008.09.015 [PubMed: 18929587]
- Bjorndal B, Burri L, Staalesen V, Skorve J, & Berge RK (2011). Different adipose depots: their role in the development of metabolic syndrome and mitochondrial response to hypolipidemic agents. *Journal of Obesity*, 2011, 490650. doi:10.1155/2011/490650 [PubMed: 21403826]
- Boisgontier MP, & Cheval B (2016). The anova to mixed model transition. *Neuroscience & Biobehavioral Reviews*, 12–14. doi:10.1016/j.neubiorev.2016.05.034
- Bowman SA, & Vinyard BT (2004). Fast food consumption of U.S. Adults: Impact on energy and nutrient intakes and overweight status. 23, 2(163–168). doi:10.1080/07315724.2004.10719357
- Buhusi CV, & Meck WH (2005). What makes us tick? Functional and neural mechanisms of interval timing. *Nature Reviews Neuroscience*, 6, 755–765. doi:10.1038/nrn1764 [PubMed: 16163383]
- Church RM, & Deluty MZ (1977). Bisection of temporal intervals. *Journal of Experimental Psychology: Animal Behavior Processes*, 3(3), 216–228. doi:10.1037/0097-7403.3.3.216 [PubMed: 881613]
- Cnaan A, Laird N, & Slator P (1997). Tutorial in biostatistics: using the general linear mixed model to analyse unbalanced repeated measures and longitudinal data. *Stat Med*, 16(2349), 80.
- Cox DN, Hendrie GA, & Carty D (2016). Sensitivity, hedonics and preferences for basic tastes and fat amongst adults and children of differing weight status: A comprehensive review. *Food Quality and Preference*, 48, 359–367. doi:10.1016/j.foodqual.2015.01.006
- Davis C, Patte K, Levitan R, Reid C, Tweed S, & Curtis C (2007). From motivation to behaviour: A model of reward sensitivity, overeating, and food preferences in the risk profile for obesity. *Appetite*, 48, 12–19. doi:10.1016/j.appet.2006.05.016 [PubMed: 16875757]
- Droit-Volet S (2013). Time perception in children: A neurodevelopmental approach. *Neuropsychologia*, 51(2), 220–234. doi:10.1016/j.neuropsychologia.2012.09.023 [PubMed: 22999968]
- Fields SA, Sabet M, & Reynolds B (2013). Dimensions of impulsive behavior in obese, overweight, and healthy-weight adolescents. *Appetite*, 70, 60–66. doi:10.1016/j.appet.2013.06.089 [PubMed: 23831015]
- Finlayson G, King N, & Blundell JE (2007). Liking vs. wanting food: Importance for human appetite control and weight regulation. *Neurosci Biobehav Rev*, 31, 987–1002. doi:10.1016/j.neubiorev.2007.03.004 [PubMed: 17559933]
- Fobbs WC, & Mizumori SJY (2017). A framework for understanding and advancing intertemporal choice research using rodent models. *Neurobiol Learn Mem*, 139, 89–97. [PubMed: 28065715]
- Garcia A, & Kirkpatrick K (2013). Impulsive choice behavior in four strains of rats: Evaluation of possible models of Attention-Deficit/Hyperactivity Disorder. *Behavioural Brain Research*, 238, 10–22. doi:10.1016/j.bbr.2012.10.017 [PubMed: 23085479]
- Glanz K, Basil M, Maibach E, Goldberg J, & Snyder D (1998). Why Americans eat what they do: Taste, nutrition, cost, convenience, and weight control concerns as influences on food consumption. *J Am Diet Assoc*, 98, 1118–1126. [PubMed: 9787717]
- Horstmann A, Dietrich A, Mathar D, Possel M, Villringer A, & Neumann J (2015). Slave to habit? Obesity is associated with decreased behavioural sensitivity to reward devaluation. *Appetite*, 87, 175–183. doi:10.1016/j.appet.2014.12.212 [PubMed: 25543077]

- Jarmolowicz DP, Cherry JB, Reed DD, Bruce JM, Crespi JM, Lusk JL, & Bruce AS (2014). Robust relation between temporal discounting rates and body mass. *Appetite*, 78, 63–67. doi:10.1016/j.appet.2014.02.013 [PubMed: 24650831]
- Jurdak N, & Kanarek RB (2009). Sucrose-induced obesity impairs novel object recognition learning in young rats. *Physiology & Behavior*, 96(1), 1–5. doi:10.1016/j.physbeh.2008.07.023 [PubMed: 18718844]
- Jurdak N, Lichtenstein AH, & Kanarek RB (2008). Diet-induced obesity and spatial cognition in young male rats. *Nutritional Neuroscience*, 11(2), 48–54. doi:10.1179/147683008x301333 [PubMed: 18510803]
- Karalunas SL, & Huang-Pollock CL (2011). Examining relationships between executive functioning and delay aversion in attention deficit hyperactivity disorder. *Journal of Clinical Child & Adolescent Psychology*, 40(6), 837–847. doi:10.1080/15374416.2011.614578
- Kiefer SW, Hill KG, & Kaczmarek HJ (1998). Taste reactivity to alcohol and basic tastes in outbred mice. *Alcoholism: Clinical and Experimental Research*, 22, 1146–1151. doi:10.1111/j.1530-0277.1998.tb03714.x
- Leibowitz SF, Lucas DJ, Leibowitz KL, & Jhanwar YS (1991). Developmental patterns of macronutrient intake in female and male rats from weaning to maturity. *Physiology and Behavior*, 50(6), 1167–1174. [PubMed: 1798771]
- Lesser EN, Arroyo-Ramirez A, Mi SJ, & Robinson MJF (2017). The impact of a junk-food diet during development on ‘wanting’ and ‘liking’. *Behav Brain Res*, 317, 163–178. doi:10.1016/j.bbr.2016.09.041 [PubMed: 27650100]
- Lumley J, Stevenson RJ, Oaten MJ, Mahmut M, & Yeomans MR (2016). Individual differences in impulsivity and their relationship to a Western-style diet. *Personality and Individual Differences*, 97, 178–185. doi:10.1016/j.paid.2016.03.055
- Marshall AT, & Kirkpatrick K (2016). Mechanisms of impulsive choice: III. The role of reward processes. *Behavioural Processes*, 123, 134–148. [PubMed: 26506254]
- Marshall AT, Smith AP, & Kirkpatrick K (2014). Mechanisms of impulsive choice: I. Individual differences in interval timing and reward processing. *Journal of Experimental Analysis of Behavior*, 102(1), 86–101.
- Marshall AT, Smith AP, & Kirkpatrick K (2014). Mechanisms of impulsive choice: I. Individual differences in interval timing and reward processing. *Journal of the Experimental Analysis of Behavior*, 102(1), 86–101. doi:10.1002/jeab.88 [PubMed: 24965705]
- McClure J, Podos J, & Richardson HN (2014). Isolating the delay component of impulsive choice in adolescent rats. *Frontiers in Integrative Neuroscience*, 8(3), 1–9. doi:10.3389/fnint.2014.00003 [PubMed: 24474908]
- Mela DJ (2001). Determinants of food choice: Relationships with Obesity and Weight Control. *Obesity Research*, 9(4), 249S–255S. [PubMed: 11707550]
- Mela DJ (2006). Eating for pleasure or just wanting to eat? Reconsidering sensory hedonic responses as a driver of obesity. *Appetite*, 47, 10–17. doi:10.1016/j.appet.2006.02.006 [PubMed: 16647788]
- Miller WC, Lindeman AK, Wallace J, & Niederpruem M (1990). Diet composition, energy intake, and exercise in relation to body fat in men and women. *Am J Clin Nutr*, 52, 426–430. [PubMed: 2393005]
- Mitchell SH, & Wilson VB (2012). Differences in delay discounting between smokers and nonsmokers remain when both rewards are delayed. *Psychopharmacology (Berlin)*, 219, 549–562. [PubMed: 21983917]
- Moscattelli A, Mezzetti M, & Lacquanti F (2012). Modeling psychophysical data at the population-level: the generalized linear mixed model. *Journal of Vision*, 12(11), 26. doi:10.1167/12.11.26
- Nederkoorn C, Smulders FT, Havermans RC, Roefs A, & Jansen A (2006). Impulsivity in obese women. *Appetite*, 47(2), 253–256. doi:10.1016/j.appet.2006.05.008 [PubMed: 16782231]
- Novelli ELB, Diniz YS, Galhardi CM, Ebaid GMX, Rodrigues HG, Mani F, ... Novelli Filho JLVB (2007). Anthropometrical parameters and markers of obesity in rats. *Laboratory Animals*, 41, 111–119. [PubMed: 17234057]
- Odum AL (2011). Delay discounting: I’m a k, you’re a k. *Journal of Experimental Analysis of Behavior*, 96(3), 427–439. doi:10.1901/jeab.2011.96-423

- Perry JL, Nelson SE, Anderson MM, Morgan AD, & Carroll ME (2007). Impulsivity (delay discounting) for food and cocaine in male and female rats selectively bred for high and low saccharin intake. *Pharmacology Biochemistry and Behavior*, 86(4), 822–837. doi:10.1016/j.pbb.2007.03.012
- Peterson JR, Hill CC, & Kirkpatrick K (2015). Measurement of impulsive choice in rats: Same- and alternate-form test-retest reliability and temporal tracking. *Journal of the Experimental Analysis of Behavior*, 103, 166–179. doi:10.1002/jeab.124 [PubMed: 25490901]
- Rasmussen EB, Lawyer SR, & Reilly W (2010). Percent body fat is related to delay and probability discounting for food in humans. *Behav Processes*, 83(1), 23–30. doi:10.1016/j.beproc.2009.09.001 [PubMed: 19744547]
- Rasmussen EB, Reilly W, & Hillman C (2010). Demand for sucrose in the genetically obese Zucker (fa/fa) rat. *Behavioural Processes*, 85(2), 191–197. doi:10.1016/j.beproc.2010.07.008 [PubMed: 20674704]
- Renda CR, Rung JM, Hinnenkamp JE, Lenzini SN, & Madden GJ (2018). Impulsive choice and pre-exposure to delays: iv. effects of delay- and immediacy-exposure training relative to maturational changes in impulsivity. *Journal of the Experimental Analysis of Behavior*, 109(3), 587–599. doi:doi:10.1002/jeab.432 [PubMed: 29683190]
- Reynolds SM, & Berridge KC (2002). Positive and negative motivation in nucleus accumbens shell: Bivalent rostrocaudal gradients for GABA-elicited eating, taste “liking”/ “disliking” reactions, place preference/avoidance, and fear. *The Journal of Neuroscience*, 22, 7308–7320. [PubMed: 12177226]
- Incentive Salience and the Transition to Addiction 391–399 (2013).
- Schemmel R, Mickelsen O, & Gill JL (1970). Dietary obesity in rats: body weight and body fat accretion in seven strains of rats. *The Journal of Nutrition*, 100, 1041–1048. [PubMed: 5456549]
- Schiff S, Amodio P, Testa G, Nardi M, Montagnese S, Caregaro L, & Sellitto M (2015). Brain and Cognition Impulsivity toward food reward is related to BMI: Evidence from intertemporal choice in obese and normal-weight individuals. *Brain and Cognition*, 1–8. doi:10.1016/j.bandc.2015.10.001
- Scalafani A (1995). How food preferences are learned: laboratory animal models. *Proceedings of the Nutrition Society*, 54, 419–427. doi:10.1079/pns19950011 [PubMed: 8524889]
- Shin AC, Townsend RL, Patterson LM, & Berthoud H. r. (2011). “Liking” and “wanting” of sweet and oily food stimuli as affected by high-fat diet-induced obesity, weight loss, leptin, and genetic predisposition. *Am J Physiol Regul Integr Comp Physiol*, 301, R1267–1280. doi:10.1152/ajpregu.00314.2011. [PubMed: 21849633]
- Singh D, & Sikes S (1974). Role of past experience of food-motivated behavior of obese humans. *Journal of Comparative and Physiological Psychology*, 86, 503–508. doi:10.1037/h0036247 [PubMed: 4814766]
- Smith AP, Marshall AT, & Kirkpatrick K (2015). Mechanisms of impulsive choice: II. Time-based interventions to improve self-control. *Behavioural Processes*, 112, 29–42. doi:10.1016/j.beproc.2014.10.010 [PubMed: 25444771]
- Smith AP, Peterson JR, & Kirkpatrick K (2016). Reward contrast effects on impulsive choice and timing behavior in rats. *Timing & Time Perception*, 4, 147–166. doi:10.1163/22134468-00002059 [PubMed: 27867839]
- Staddon JER, & Simmelhag VL (1971). The “superstition” experiment: A reexamination of its implications for the principles of adaptive behavior. *Psychological review*, 71(1), 3–43.
- Steele CC, Pirkle JRA, & Kirkpatrick K (2017). Diet-induced impulsivity: Effects of a high-fat and a high-sugar diet on impulsive choice in rats. *PLoS One*, 12(6), e0180510. doi:10.1371/journal.pone.0180510 [PubMed: 28662133]
- Tatham TA, & Zurn KR (1989). The MED-PC experimental apparatus programming system. *Behavior Research Methods, Instruments, & Computers*, 21(2), 294–302. doi:10.3758/BF03205598
- Teitelbaum P (1957). Random and food-directed activity in hyperhagic and normal rats. *Journal of Comparative and Physiological Psychology*, 50, 486–490. [PubMed: 13481188]
- van Meer F, Charbonnier L, & Smeets PA (2016). Food Decision-Making: Effects of Weight Status and Age. *Curr Diab Rep*, 16(84), 1–8. doi:10.1007/s11892-016-0773-z [PubMed: 26699764]

- Wang MZ, Marshall AT, & Kirkpatrick K (2017). Differential effects of social and novelty enrichment on individual differences in impulsivity and behavioral flexibility. *Behavioural Brain Research* SreeTestContent1, 327, 54–64. doi:10.1016/j.bbr.2017.03.028
- Wansink B, & Sobal J (2007). Mindless eating: The 200 daily food decisions we overlook. *Environment and Behavior*, 39(1), 106–123.
- Wileyto EP, Audrain-McGover J, Epstein LH, & Lerman C (2004). Using logistic regression to estimate delay-discounting functions. *Behavior Research Methods, Instruments, & Computers*, 36(1), 41–51.
- Wittmann M, & Paulus MP (2008). Decision making, impulsivity and time perception. *Trends in Cognitive Sciences*, 12(1), 7–12. doi:10.1016/j.tics.2007.10.004 [PubMed: 18042423]

Figure 1.

Proposed effects of diet on impulsive choice, discrimination abilities, incentive motivation, food preference, and liking. Diet exposure is proposed to alter all these processes which in turn affect food choice. Changes in food choices affect dietary exposure, creating a feedback loop which can in turn exacerbate the effects of impulsive choice, incentive motivation, discrimination abilities, food preferences, and/or liking in future food choices. The ultimate effects of changes in food choices are to alter weight status and/or body composition.

Figure 2.

Order of procedures experienced by sub-groups of rats within each dietary condition. Following the dietary manipulation, behavioral testing began with lever press training. Then, rats received the impulsive choice and discrimination tasks in a counterbalanced order separated with a buffer task. All rats then experienced food preference testing and taste reactivity testing at the end of the experiment. The line types around the group names correspond to the line types in subsequent graphs.

Figure 3.

Mean body weight (g) for each group as a function of age. PND = postnatal day. HF = high-fat; HS = high-sugar; C = chow.

Figure 4. Mean percent body fat in the abdomen for each group as a function of time on the diet. HF = high-fat; HS = high-sugar; C = chow. Error bars ($\pm$ SEM) were computed with respect to the estimated marginal means of the fitted generalized linear mixed-effects model. The secondary axis is included for interpretation of the b -values, which are log-transformed.

Figure 5.

Mean proportion of larger-later (LL) choices for each group as a function of SS delay or LL magnitude. Left: Impulsive choice: delay task performance. Right: Impulsive choice: magnitude task performance. HF = high-fat; HS = high-sugar; C = chow; SS = smaller-sooner. Error bars (+/- SEM) were computed with respect to the estimated marginal means of the fitted generalized linear mixed-effects model. The secondary axis is included for interpretation of the b -values, which are in log odds.

Figure 6.

Mean proportion of long responses on the temporal bisection task for each group as a function of signal duration. HF = high-fat; HS = high-sugar; C = chow. Error bars ($\pm$ SEM) were computed with respect to the estimated marginal means of the fitted generalized linear mixed-effects model. The secondary axis is included for interpretation of the b -values, which are in log odds.

Figure 7.

Mean proportion of large responses for each group as a function of the large magnitude. HF = high-fat; HS = high-sugar; C = chow. Error bars (+/- SEM) were computed with respect to the estimated marginal means of the fitted generalized linear mixed-effects model. The secondary axis is included for interpretation of the b -values, which are in log odds.

Figure 8.

Mean reinforcers earned during the last lever press training session. HF = high-fat; HS = high-sugar; C = chow. Error bars ($\pm$ SEM) were computed with respect to the estimated marginal means of the fitted generalized linear mixed-effects model.

Figure 9.

Mean preference score for each group as a function of test number, where test 1 represents the exposure period and tests 2 and 3 were the subsequent consumption tests. The horizontal line at 0 represents indifference. HF = high-fat; HS = high-sugar; C = chow. Error bars ($\pm$ SEM) were computed with respect to the estimated marginal means of the fitted generalized linear mixed-effects model. The secondary axis is included for interpretation of the b -values, which are in log odds.

Figure 10.

A) Mean numbers of hedonic responses (log transformed) for each group as a function of relative concentration of fat. B) Mean numbers of hedonic responses (log transformed) for each group as a function of relative concentration of sugar. HF = high-fat; HS = high-sugar; C = chow. Error bars ($\pm$ SEM) were computed with respect to the estimated marginal means of the fitted generalized linear mixed-effects model.

Figure 11.

Diet exposure altered impulsive choice, time discrimination, incentive motivation, and food preference, which in turn could affect food choice. Changes in food choices affect dietary exposure, creating a feedback loop which can in turn exacerbate the effects of impulsive choice, time discrimination, incentive motivation, and food preferences in future food choices. The ultimate effects of changes in food choices can alter body composition and eventually weight.