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Intermittent feeding alters sensitivity to changes in reward value

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ABSTRACT

The influence of binge-like feeding schedules on subsequent food-related behavior is not well understood. We investigated the effect of repeated cycles of restriction and refeeding on two food-related behaviors; goal-directed responding for a palatable food reward and sensory-specific satiety. Hungry rats were trained to perform two instrumental actions for two distinct food outcomes and were then subjected to repeated cycles of restricted and unrestricted access to their maintenance chow for 30-days or were maintained on food restriction. Goal-directed control was then assessed using specific satiety-induced outcome devaluation. Rats were given 1 h access to one of theoutcomes and were then immediately given a choice between the two actions. Rats maintained on restriction responded more for the valued than the devalued reward but rats with a history of restriction and refeeding failed to show this effect. Importantly, all rats showed sensory-specific satiety when offered a choice between the two foods, indicating that pre-feeding selectively reduced the value of the pre-fed food. By contrast, sensory-specific satiety was not observed in rats with a history of intermittent feeding when the foods were offered sequentially. These results indicate that, similar to calorically dense diets, intermittent feeding patterns can impair the performance of goal-directed actions as well as the ability to reject a pre-fed food when it is offered alone.

1. Introduction

To optimize food-related behavior, both animals and humans must integrate knowledge regarding food expectation (that is, which actions lead to which food outcomes) with the current desirability or motivational value of those foods (Balleine & Dickinson, 1998; Balleine, 1992; Dickinson & Balleine, 1994). Successful integration of these elements ensures that food-seeking behaviors are goal-directed, thereby allowing the subject to flexibly adapt their behavior according to changes in their motivational state as well as environmental fluctuations.

An obesogenic diet can lead to a range of cognitive impairments, including deficits in food-related behaviors (Furlong, Jayaweera, Balleine, & Corbit, 2014; Kendig, Boakes, Rooney, & Corbit, 2013; Morris, Beilharz, Maniam, Reichelt, & Westbrook, 2015; Reichelt, Abbott, Westbrook, & Morris, 2016; Reichelt, Morris, & Westbrook, 2014; Reichelt, Westbrook, & Morris, 2015). For example, the consumption of palatable foods is associated with the loss of goal-directed control over food-seeking behavior (Furlong et al., 2014; Kendig et al., 2013). Corbit and colleagues have demonstrated that rats given long-term, intermittent access to a 10% sucrose solution (Kendig et al., 2013) or sweetened condensed milk (Furlong et al., 2014) fail to selectively reduce their responding for a food reward following outcome devaluation. Sensory-specific satiety (Rolls, 1986; Rolls, Rolls, Rowe, & Sweeney, 1981), an important factor in food choice and meal duration (Hetherington & Rolls, 1996), is also disrupted in rats fed a high fat, high sugar diet (Reichelt et al., 2014). In the latter study, following ad libitum consumption of one food, rats fed a control diet showed sensory-specific satiety and rejected the pre-fed food while readily consuming a second food with distinct sensory properties. In contrast, rats fed a high fat, high sugar diet did not reject the pre-fed food and consumption of this food was similar to that of a non pre-fed food (Reichelt et al., 2014).

In addition to the consumption of high fat, high sugar diets, eating patterns alone can have a considerable impact on food-

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related behavior. Animal models of binge-like eating in humans show that intermittent feeding causes a range of abnormalities in consummatory behavior. For example, repeated cycles of restriction and refeeding of maintenance chow promote binge-like eating that persists after the cessation of restriction-refeeding cycles (Hagan & Moss, 1997) and, moreover, binge-eating prone rats subjected to restriction-refeeding cycles of chow and palatable food are more likely to tolerate foot-shock in order to gain access to palatable foods than non-cycled rats (Oswald, Murdaugh, King, & Boggiano, 2011). Sensory-specific satiety is also disrupted following binge-like feeding in rats (Ahn & Phillips, 2012). That is, rats exposed to a 30-day restriction-refeeding cycle, consisting in four days of restricted access followed by two days of ad libitum food, failed to reject a food recently eaten to satiety whereas rats maintained on food restriction consumed less of the prefed food compared to a novel food (Ahn & Phillips, 2012). Taken together, these studies provide clear evidence that intermittent feeding patterns can have dramatic effects on subsequent consummatory behavior. However, it remains to be determined if binge feeding, like high fat or high sugar diets, also promotes habitual food-seeking actions, which could have important consequences for food choices and decision making in general.

Following the work of Ahn and Phillips (2012), we assessed the impact of repeated cycles of restricted and unrestricted chow intake on sensory-specific satiety and goal-directed behavior in rats. Moderately food deprived rats were first trained to perform two actions for two different food rewards. Then, rats were either maintained on chow restriction or they were switched to an intermittent chow feeding schedule for one month. All rats were then food restricted prior to behavioral testing. We assessed goal-directed control, using specific satiety-induced outcome devaluation, followed by a simultaneous or sequential test of sensory-specific satiety.

2. Materials and methods

2.1. Subjects

Forty-six experimentally naïve male outbred Long Evans rats (320–400 g) obtained from Monash University Animal Research Platform served as subjects. They were housed in plastic boxes (2–3 rats per box) located in a climate controlled colony room and were maintained on a 12 h light/dark cycle. Five days before the start of the behavioral procedures, the rats were handled daily and put on a food restriction schedule to maintain them at 85–90% of their ad libitum feeding weight. All experimental procedures were approved by the Animal Ethics Committee at the University of Sydney.

2.2. Apparatus

Training and testing took place in 16 MED Associates operant chambers enclosed in sound- and light-resistant shells. Each chamber was equipped with two pellet dispensers that delivered one of two food pellets (Bioserv Biotechnologies) into a recessed magazine when activated. Pellets were a 45 mg grain food pellet offering 3.35 kcal/gm (consisting in 21.3% protein, 3.8% fat and 54% carbohydrate; ingredients: Ground Corn, Banana Flakes, Dehulled Soybean Meal, Corn Gluten Meal, Ground Wheat, Corn Gluten Feed, Fish Meal, Dehydrated Alfalfa Meal, Casein, Dried Whey, Sucrose, Fructose, Dextrose, Dried Beet Pulp, Soybean Oil, Porcine Animal Fat, Dried Brewers Yeast, Mineral Mix, Vitamin Mix, Magnesium Stearate, DL-Methionine, Choline Chloride, Sodium Propionate, Ascorbic Acid, Kaolin) or a 45 mg purified food pellet offering 3.6 kcal/gm (consisting in 18.7% protein, 5.6% fat and 59.1% carbohydrate; ingredients: Sucrose, Dextrose, Casein, Corn Oil, Mineral Mix, Cellulose, Corn Syrup, Calcium Silicate, Vitamin Mix, Magnesium Stearate, Choline Bitartrate, DL-Methionine, L-Cystine, Ascorbic Acid, Vitamin E Acetate and tBHQ). The chambers contained two retractable levers that could be inserted to the left and the right of the magazine. An infrared photo beam crossed the magazine opening, allowing for the detection of head entries. A house light (3 W, 24 V) provided illumination of the operant chamber. A set of two microcomputers running MED Associates proprietary software (Med-PC) controlled all experimental events and recorded lever presses.

2.3. Procedures

2.3.1. Instrumental training

After 5 d of food restriction, rats were given two sessions of magazine training. Rats were placed in the operant chamber and given access to 45 mg grain and purified pellets delivered on a random time 60 s schedule. Forty outcomes were delivered per session, 20 of each pellet. Rats then received 8 d of instrumental training during which two instrumental actions (i.e., presses on two retractable levers positioned to the left and to the right of the magazine) were trained with the two different outcomes (grain and purified pellets) in the same session. During the session, each lever was presented twice for a maximum of 10 min each or until 20 outcomes were earned, i.e., rats could earn a maximum of 40 grain and 40 purified pellets within the session. The inter-trial interval between lever presentations was 2.5 min. The order of the lever presentation was alternated and counterbalanced across rats and days. Response-outcome relationships were also counterbalanced across rats. For the first 2 d, lever pressing was continuously reinforced after which the reinforcement schedule was increased using random ratio (RR) schedules. A RR5 schedule was used on days 3–5 and a RR10 schedule was used on days 6–8.

2.3.2. Restriction-refeeding cycles

Following instrumental training, rats were allocated to either an Intermittent group ($n = 23$) or a Control group ($n = 23$). Similar to previous studies (Ahn & Phillips, 2012; Hagan & Moss, 1997; Oswald et al., 2011), rats in group Intermittent received four days of restricted access (10 g per day) to their home-cage chow followed by two days of unrestricted chow. This pattern repeated for five cycles. Rats in the control group were maintained on chow restriction for the first 20 days followed by 10 days of unrestricted access to chow. Both groups were therefore equated for the number of days on restricted and unrestricted food intake; that is, the groups only differed in the pattern of the availability of the food. At the end of restriction-refeeding cycles, both groups were given unrestricted access to chow for 14 days to ensure that the percent weight change was similar for both groups prior to behavioral testing (Ahn & Phillips, 2012). Finally, all rats were food restricted three days prior to testing and remained food restricted until the end of the behavioral procedures (Ahn & Phillips, 2012).

2.3.3. Instrumental outcome devaluation test

Rats were given 1 h access to one of the two outcomes (grain or purified pellets; 20 g) in clear plastic feeding chambers (clear plastic tubs located in a different room to that used for training). Immediately after devaluation they received a 3 min instrumental choice extinction test, in which both levers were available but no outcome was delivered. Forty-eight hours after the first outcome devaluation test, rats were given a second test with the other outcome. That is, rats that were pre-fed on grain pellets in the first devaluation test were now pre-fed with purified pellets and vice versa.