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Sensory-specific satiety is intact in rats made obese on a high-fat high-sugar choice diet

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ABSTRACT

Sensory-specific satiety (SSS) is the temporary decreased pleasantness of a recently eaten food, which inhibits further eating. Evidence is currently mixed whether SSS is weaker in obese people, and whether such difference precedes or follows from the obese state. Animal models allow testing whether diet-induced obesity causes SSS impairment. Female rats (n = 24) were randomly assigned to an obesogenic high-fat, high-sugar choice diet or chow-only control. Tests of SSS involved pre-feeding a single palatable, distinctively-flavored food (cheese- or cocoa-flavored) prior to free choice between both foods. Rats were tested for short-term SSS (2 h pre-feeding immediately followed by 2 h choice) and long-term SSS (3 day pre-feeding prior to choice on day 4). In both short- and long-term tests rats exhibited SSS by shifting preference towards the food not recently eaten. SSS was not impaired in obese rats. On the contrary, in the long-term tests they showed stronger SSS than controls. This demonstrates that neither the obese state nor a history of excess energy consumption fundamentally causes impaired SSS in rats. The putative impaired SSS in obese people may instead reflect a specific predisposition, properties of the obesogenic diet, or history of restrictive dieting and bingeing.

1. Introduction

Food choice and amount consumed are both strongly influenced by the sensory properties of available foods. Obviously, good-tasting foods are preferred and more likely to be overconsumed, but even the most palatable food can become progressively less pleasurable throughout a meal. *Sensory-specific-satiety* (SSS) refers to the declining pleasure and attraction to the sensory attributes of the specific foods eaten in the meal relative to other foods (Hetherington&Rolls, 1996, p. p267; Rolls, 1986; Rolls, Rolls, Rowe, & Sweeney, 1981). Though eating to satiety generally suppresses appetite, the foods eaten in the meal become much less attractive than others. Hence, varied meals with multiple courses can often be quite large, and even after a large meal the pleasure of eating can rapidly return when dessert arrives. SSS is an immediate effect of the sensory attributes of the eaten food independent of its post-ingestive consequences. It contributes to meal termination and then gradually decays in the post-meal interval, and thus impaired SSS would promote overeating by permitting larger meals or more rapid resumption of eating.

Some evidence suggests humans who are obese may show a weaker or slower decline in hedonics during a meal. The clearest evidence comes from studies of habituation of automatic responses (e.g., salivation) or motivational impact (i.e., willingness to work for more) of a stimulus as a result of repetitive, monotonous exposure to it. Since eating inherently involves repetitive exposure, habituation of responses to initially-pleasurable sensations may explain loss of interest and enjoyment of the food which promotes meal termination (Epstein, Temple, Roemmich, & Bouton, 2009). Indeed, reflexive salivation habituates over a series of small exposures to a palatable flavor and dishabituates with introduction of a new flavor (Epstein, Rodefer, Wisniewski, & Caggiula, 1992; Temple et al., 2006), but individuals with obesity show much less decline (Bond et al., 2009; Epstein, Paluch, & Coleman, 1996). Similarly, hedonic ratings of a sweet taste decrease more slowly over repeated tasting for individuals with obesity (Pepino & Mennella, 2012). Compared to lean children, overweight children exhibit slower decline in motivation to persist at a task to earn small tastes of a food (Temple, Giacomelli, Roemmich, & Epstein, 2007).

However, overall the evidence for SSS impairment in obesity is mixed. Studies relying on hedonic ratings of foods before and after a meal have generally not found lean-obese differences on these

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measures (Brondel et al., 2007; Snoek, Huntjens, Van Gemert, De Graaf, & Weenen, 2004). Nor do individuals with obesity show more rapid return of hedonic evaluation of a recently eaten food in the post-meal interval (Havermans, Roefs, Nederkoorn, & Jansen, 2012). Thus additional research on this topic is necessary to resolve these discrepancies and determine if and under what circumstances SSS impairments may occur, and further, the direction of causation. A difference in SSS could be a preexisting causal factor in overeating, or could emerge as a consequence of chronic overeating or positive energy balance. Thus controlled studies in an animal model of diet-induced obesity would be valuable for dissociating these possibilities.

Studies of these effects in animal models are few but do provide clear evidence for sensory-specific decreases in food motivation following recent consumption. Work based on the habituation paradigm has shown in both infant and adult rats that a series of brief, small intra-oral infusions of a palatable flavored solution causes gradual decrease in the automatic mouthing and licking responses that indicate hedonic evaluation, and temporarily suppresses voluntary intake of that flavor (Swithers & Martinson, 1998; Swithers-Mulvey & Hall, 1992). The hedonic response immediately returns when the flavor is changed, demonstrating it is a sensory-specific effect. In monkeys, neural responses to the sight or taste of a food in several ventral forebrain areas are suppressed more for a recently-eaten food than for a non-eaten food (Rolls, Murzi, Yaxley, Thorpe, & Simpson, 1986). In experiments directly analogous to the SSS paradigm, rats fed a distinctive sweet or savory snack food in one meal consume substantially less in a second meal when offered the same food than if given the opposite food, and this effect is paralleled by shifting dopamine responses in prefrontal cortex and nucleus accumbens (Ahn & Phillips, 1999).

There is, however, little animal work specifically investigating diet-induced obesity (DIO) and SSS. The most relevant study does show that prior history with a palatable, varied cafeteria diet impairs SSS in rats (Reichelt, Morris, & Westbrook, 2014). But additional work would be necessary to determine if that impairment is attributable to weight gain itself, or specific macronutrients, or to the history of sensory variety, palatability, or some other aspect of the cafeteria diet. The purpose of the present experiment was to directly compare SSS in lean control rats versus rats with DIO induced by a high-fat, high sugar (HFHS) choice protocol. This protocol produces dramatic weight gain, and effectively models many physiological and behavioral aspects of human diet-induced obesity. Rats fed a HFHS choice diet persistently increase calorie intake and fat stores, adopt a pattern of "snacking" between meals, develop peripheral leptin resistance and impaired glucose metabolism, and show dysregulated food motivation (la Fleur, Luijendijk, van der Zwaal, Brans, & Adan, 2014; La Fleur, Luijendijk, Van Rozen, Kalsbeek, & Adan, 2011; La Fleur et al., 2007; Wald & Myers, 2015).

In this experiment SSS was measured by feeding rats a palatable snack food with distinctive sensory properties (either Cheese-flavored corn snacks or chocolate-flavored breakfast cereal) for some time prior to offering a free choice between both of those foods. SSS would shift preference away from the food that had recently been eaten. In humans SSS acts in the short term to promote cessation of a meal, and also in the longer term when the same food is eaten repeatedly over days (Raynor & Wing, 2006; Rolls & De Waal, 1985; Weenen, Stafleu, & De Graaf, 2005). As these may represent separate processes, the present study included both a short-term and long-term tests.

2. Methods

2.1. Subjects

All procedures were approved by the Bucknell University IACUC. Subjects were 24 experimentally naive female Sprague Dawley rats from our breeding colony. At the start rats were 125–140 days old and weighed 303.6 ± 21.0 (Mean ± SD). Rats were housed in 8 × 16 × 10.5″ plastic tub cages with corncob bedding, in a colony room maintained at approximately 21 °C and 40% humidity, with a 12:12 h light:dark cycle (lights on at 0800).

2.2. Diet-induced obesity

Two groups matched for initial body weight were created by random assignment. The control group (CON, n = 12) was maintained on an ordinary, cereal-based lab chow (Mazuri 5663) ad libitum, whereas the diet-induced obesity (DIO) group (n = 12) was fed the same chow plus ad libitum access to both lard (Armour Star, ConAgra Foods) and 30% sucrose solution. Lard was provided in a cup hung inside the cage and sucrose was in a 200 ml bottle on the cage lid. Both were provided in ample amounts and replenished daily. All CON and DIO rats also had ad libitum drinking water. Rats were maintained on these diets for 6 months prior to beginning the behavioral measurements.

2.3. Test foods

Sensory-specific satiety tests involved two palatable snack foods: Cheese Balls (Utz brand, Hanover, PA) and Cocoa Puffs (General Mills, Golden Valley, MN). Both have corn flour as the chief ingredient but are distinct in taste and flavor. Cheese Balls are savory and high fat, and Cocoa Puffs are chocolate flavored, sweet, and lower in fat. Rats were familiarized with 5 g of each in the home cage prior to a preliminary preference measurement conducted approximately one week before the main experiment. In this initial preference test rats were given ad lib overnight (18 h) access to both foods in the absence of chow. All rats moderately preferred Cocoa over Cheese, but CON and DIO rats consumed similar amounts and had similar preference (Mean ± SD intakes, CON: 15.1 ± 2.5 g cocoa and 7.9 ± 3.0 g cheese; DIO: 17.7 ± 3.8 g cocoa and 5.9 ± 3.0 g cheese. CON and DIO values are not significantly different.)

2.4. Long-term sensory-specific satiety

This test was conducted to determine if rats' relative preference for the two snack foods shifted after consuming one of them repeatedly over several days. During this testing the HFHS diet was discontinued for DIO rats. Each rat was provided 20 g/day of only one of the snack foods for three consecutive days, plus ad libitum chow. Half the rats in CON and DIO received Cheese and the other half Cocoa. On the fourth day, all food was removed for 6 h prior to a free choice between Cheese vs. Cocoa. Ample pre-weighed amounts of both foods were provided in adjacent feeders, and overnight (18 h) intake was measured by weighing the remainders the following day. Care was taken to collect any spilled food from the bedding for measurements. Rats were then given ad libitum chow for 6 days before the cycle was repeated, with each rat receiving the opposite initial food for three days prior to a second choice test. Thus all rats were tested for their preference for Cheese vs. Cocoa after three days of eating Cocoa, and after three days of eating Cheese, but the order of those tests was counterbalanced. After this testing, DIO rats were returned to the HFHS diet for two weeks before proceeding.