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Research report

The effects of energy balance, obesity-proneness and sex on the neuronal response to sweet taste

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HIGHLIGHTS

- One day of over- or under-feeding does not impact the neuronal response to sucrose.
- Obesity-resistance was associated with greater neuronal responses to sucrose expectation.
- Men had significantly greater neuronal response to sucrose receipt than women.

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ABSTRACT

We have previously shown that propensity for weight gain, energy balance state and sex are important determinants of the neuronal response to visual food cues. It is not clear, though, whether these factors also impact the neuronal response to taste. The objective of this study was to examine the neuronal response to sweet taste during energy imbalance in men and women recruited to be obesity-prone (OP) or obesity-resistant (OR). OP (13 men and 12 women) and OR (12 men and 12 women) subjects were studied after 1 day of eucaloric, overfed and underfed conditions in a randomized crossover design. On each test day, fMRI was performed in the respective acute fed state while subjects received in random order 60 trials each of 1 M sucrose solution (SU), or artificial saliva (AS) following a visual cue predicting the taste. The neuronal response to SU versus AS expectation was significantly greater in the amygdala, orbitofrontal cortex, putamen and insula in OR versus OP; SU receipt was not different between groups. There were also sex-based differences with men having greater neuronal response to SU versus AS receipt in the caudate than women. The results, however, were not impacted by the state of energy balance. In summary, response to expectation but not receipt of basic sweet taste was different in OR compared to OP, highlighting the importance of learning and conditioning in the propensity to gain weight. Response to sucrose taste receipt was stronger in men than women, raising questions about the effect of sex hormones on brain response to food.

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1. Introduction

Obesity continues to be a significant global public health problem despite efforts to promote healthy eating and physical activity behaviors. An important percentage of the population, however, remains normal weight despite being subjected to the same environmental forces that promote excess food intake and reduced physical activity. Understanding how these obesity-resistant (OR) individuals adapt to the obesogenic environment could lead to important advances in developing better treatment interventions for those who are prone to weight gain and obesity.

The regulation of food intake involves complex interactions between physiologic signals such as peripheral adiposity-related and meal-related hormones and higher brain circuitry important

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in reward, motivation, and integration of environmental cues [1]. We and others have used neuroimaging methods such as functional magnetic resonance imaging (fMRI) to study the neurocircuitry associated with energy intake regulation and the mechanisms associated with excess food intake. Obesity appears to be associated with abnormal responses to visual, gustatory and olfactory cues in brain regions known to be important in appetitive behaviors such as the hypothalamus, amygdala, hippocampus, orbitofrontal and prefrontal cortex, and insula [2–8]. We have previously found that reduced-obese and obesity-prone (OP) individuals have altered neuronal responses to visual food cues associated with altered eating-related behavior states as compared to normal weight OR individuals and that these differences in responses are impacted by the baseline state of energy balance [9–12]. While visual food-related stimuli are very important in the process of food intake, taste is also a very potent and important stimulus. Pleasant and sweet taste is associated with significant activation of brain regions important in the rewarding and hedonic properties of food and has been shown to be altered in obesity [13,14]. Studies examining the neuronal response to sweet taste stimuli in individuals prone to weight gain and/or obesity, however, have not been well examined. We designed the present study to examine the neuronal response to sweet taste (sucrose) in individuals who self-identified themselves as being resistant to weight gain and obesity, i.e. OR, as compared to individuals who self-identified themselves as being at risk for weight gain and obesity, i.e. OP, as previously defined. Classification was based on personal and family weight history with a key feature being the reliance on self-perception of the tendency to gain weight or not [11,12,15–18]. Previous research suggests that overconsumption of food leads to addiction-like dopamine D2 receptor down-regulation in the striatum [19]. Human functional imaging studies are in support indicating a reduction in brain response to food receipt in OFC and striatum in obesity [20]. In addition, individuals with obesity display diminished brain response during a dopamine-related taste reward learning task in ventral striatum and insula [14]. It is uncertain whether brain function differences between obese and normal weight individuals are premorbid or whether they develop in response to overconsumption of food. In this study we examined individuals not obese, but prone or resistant to developing obesity. We hypothesized that brain function could distinguish those groups and provide information on how brain function could be involved in promoting obesity. We expected that the OP group would show decreased brain response in brain regions that process food reward with the hypothesis that lower activation in those regions would indicate the need for more food stimulation compared to OR for a similar reward system stimulation. Such a mechanism could promote overeating and obesity.

2. Methods and procedures

2.1. Ethics statement

All research participants provided written informed consent prior to enrolling in this study, according to the principles expressed in the Declaration of Helsinki. This study was approved by the Colorado Multiple Institutional Review Board.

2.2. Research participants

Research participants were adults aged 25–40 years (mean 30.8 ± 3.6 years) who were free of significant medical and psychiatric disease, including eating disorders as assessed by a screening medical history and physical examination, laboratory testing and questionnaires (Eating Attitudes Test [21] and Center for Epidemiologic Studies Depression Scale [22]). Research participants were recruited to have a propensity to be resistant to weight gain and obesity (obesity-resistant – OR) or to be prone to weight gain and obesity (obesity-prone – OP) as previously defined [11,12,15–18]. In brief, OR participants had a BMI of 17–25 kg/m^2 and reported no obese first degree relatives, never being overweight, weight stability, few to no attempts to lose weight, and no excessive levels of physical activity. OP participants had a BMI of 20–30 kg/m^2 and reported at least one obese first degree relative, a history of past weight fluctuations, putting effort into weight regulation, but were weight stable for at least 3 months before being enrolled. Research participants were right-handed and were without MRI exclusions. A total of 49 participants, 24 OR (12 men and 12 women) and 25 OP individuals (13 men and 12 women), were studied and included in the current analyses.

2.3. Study design and measurements

Baseline assessments were first completed and included: anthropometric measurements (body weight, height), Three Factor Eating Questionnaire (TEFQ) [23], taste perception test (described below), and body composition (lean body mass, fat mass) measurement by dual-energy X-ray absorptiometry (DPX whole-body scanner, Lunar Radiation Corp., Madison, WI, USA). Each research participant then underwent three study phases in a randomized counterbalanced manner, with each phase consisting of: (1) a 3-day baseline eucaloric diet period to ensure energy and macronutrient balance; (2) an intervention diet on day 4; and (3) a study day on day 5. The three study phases consisted of one of the following intervention diets on day 4: eucaloric (EU) diet, overfeeding (OF) by 40% above estimated energy needs, or underfeeding (UF) by 40% of baseline caloric intake. During all three study phases, the diets were made up of the same macronutrient composition: 50% carbohydrate, 30% fat, and 20% protein. Estimates of daily energy needs were made using lean body mass (as determined by DEXA) in the following equation: Resting Metabolic Rate (RMR) = (fat free mass $\times$ 23.9) + 372. The estimates were confirmed using RMR as assessed by indirect calorimetry, multiplied by an activity factor of 1.3. This method has been used successfully by our group in a number of prior studies [9,10,24–27]. All the food was prepared and provided by the Clinical Translational Research Center (CTRC) metabolic kitchen. Research participants presented to the CTRC each morning to be weighed, eat breakfast, and pick up the remainder of their daily meals which were packed in coolers. Research participants were asked to maintain their usual physical activity patterns and were questioned regarding activity and compliance. Research participants were asked to refrain from consuming any alcoholic or calorie-containing beverages during the study phases. Study days were scheduled during the follicular phase of their menstrual cycle in women.

2.4. Study day

Research participants presented to the CTRC after an overnight fast of at least 10 h. They first completed baseline (fasting) hunger and satiety ratings by visual analog scale (VAS) [10]. Hunger was rated by VAS on a line preceded by the question, “How hungry are you right now?” and anchored on the left by “not at all hungry” and by “extremely hungry” on the right. Satiety was rated by the question, “How full do you feel right now?” with the anchors “not at all” and “extremely.” Subjects were then escorted to the Brain Imaging Center at the University of Colorado where they consumed a liquid breakfast meal over 20 min. The caloric content of the liquid breakfast was equal to 25% of the energy provided during the intervention diet (EU, OF, or UF) and had an identical macronutrient composition (50% carbohydrate, 30% fat, and 20% protein). fMRI measures were then performed 60 min after the start of the meal

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