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Energy density and macronutrient composition determine flavor preference conditioned by intragastric infusions of mixed diets

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Abstract

In prior studies rats preferred a flavor (CS+HF) paired with intragastric (IG) infusions of a high-fat diet to a flavor (CS+HC) paired with a high-carbohydrate diet, yet just the opposite preference was observed with pure-nutrient infusions. The present study tested the hypothesis that variations in nutrient density as well as composition influence flavor learning. Animals were trained (22 h/day) with IG infusion of milk-based high-fat and high-carbohydrate liquid diets paired with intakes of flavored, noncaloric CS+ solutions. A third flavor, the CS−, was paired with water infusion. Standard chow was available ad libitum. The rats preferred both CS+ flavors to the CS−, whether the infused diets were dense (HF and HC, 2.1 kcal/ml) or dilute (hf and hc, 0.5 kcal/ml), indicating that all diet infusions were reinforcing. They consumed the CS+hc and CS+hf equally in training, and preferred the CS+hc, showing that at low-energy density carbohydrate was more reinforcing than fat. In contrast, CS+HF intake exceeded that of CS+HC in training, and the rats preferred the CS+HF to the CS+HC. In further tests the rats preferred the CS+HF to the CS+hc, the CS+HF to the CS+hf, and the CS+HC to the CS+hc; i.e., when the diets differed in energy density the flavors associated with the more concentrated infusions were preferred. In the absence of influence by flavor cues from the nutrients themselves, rats' preferences for flavors associated with diets high in fat or carbohydrate are dependent on energy density. The differential satiating effects of fat and carbohydrate may contribute to these density-dependent preferences.

Keywords: Flavor preference conditioning; Intragastric feeding; Reinforcement; Satiety; Energy density; Bout patterns

1. Introduction

Much attention has focused on the potential negative effects of consuming a high-fat diet, which include excess energy intake and obesity. The role of dietary fat in human obesity has been debated, but there is extensive evidence that high-fat foods promote overeating and adiposity in laboratory animals [2,21]. Relative to a high-carbohydrate diet, a high-fat diet is typically, but not always, overeaten [21], with high-fat fed rats gaining more weight. Three characteristics of high-fat foods are implicated in their hyperphagia-promoting effects: strong orosensory attractiveness, high energy density, and low satiating effects.

In a series of studies, Warwick and colleagues [22,25,27–29] used liquid diets varying in fat and carbohydrate composition to "dissect" the factors contributing to the overconsumption of high-fat foods. In one experiment, orosensory and density factors were controlled using a self-regulated intragastric feeding procedure in which rats drank a saccharin solution which was paired with isocaloric infusions of a high-fat or high-carbohydrate liquid diet. Over the course of the 16-day experiment, the rats in the high-fat group self-infused more liquid diet and gained more weight than did the rats in the high-carbohydrate group. The authors proposed that the high-fat diet stimulated greater intake because, compared to the high-carbohydrate diet, it produced less satiation during the meal and shorter satiety after the meal (that is, high-fat meals were larger and more frequent, respectively). Subsequent studies from the same laboratory reported that the high-fat diet generated larger meal sizes when orally consumed or intragastrically infused, and also suppressed chow intake less than did the high-carbohydrate diet [19,30].

Reduced satiation and satiety may not be the only reason why high-fat foods are overconsumed relative to high-carbohydrate foods. There is now extensive evidence that nutrients can have

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positive postingestive actions that reinforce food preferences and actually stimulate intake in some cases (reviewed in [17]). Thus, increased positive feedback, in addition to reduced negative feedback, may contribute to high-fat induced overeating. To investigate the interaction of positive and negative feedback in the preference for high-fat vs. high-carbohydrate foods, our laboratory used Warwick's liquid diets as intragastric infusates in a flavor preference conditioning procedure [7]. The rats were trained to drink distinctly flavored solutions that were paired with intragastric infusions of the isocaloric diets, so that the animals were exposed only to the post-oral effects of the diets. When trained with intragastric infusions of energy-dense liquid diets, the rats consumed more of, and later preferred, the flavor paired with the high-fat diet relative to the flavor paired with the isocaloric diet rich in carbohydrates.

The preference for the high-fat over the high-carbohydrate-paired flavor contrasts with the opposite flavor preferences observed in conditioning studies using infusions of pure nutrients: the carbohydrate-paired flavor is generally preferred to the fat-paired flavor [9,11,20]. Taken together, the available data indicate that the post-oral reinforcing effect of carbohydrate (specifically, glucose and glucose-containing saccharides) is more pronounced than that of fat when pure nutrients are used, but with mixed diets, the high-carbohydrate source is less reinforcing than the high-fat source. There are several procedural differences in the experiments conducted with the mixed diet and pure-nutrient infusions which could account for the discrepant findings (see [10]). Of interest here are differences in caloric density: the conditioning studies conducted with pure nutrients involved relatively dilute infusates (0.64 kcal/ml) whereas the experiments using the high-carbohydrate and high-fat diets used more energy-dense infusates (2.1 kcal/ml).

Although it would be logical to assume that the post-oral reinforcing effects of nutrients should increase with energy density, this is not always the case. Rats may actually prefer a flavor paired with a less dense nutrient over a flavor paired with a denser nutrient (e.g., [16,23]). One explanation for this energy-density effect is that the enhanced satiating actions of calorically-rich nutrient solutions reduce their net reinforcing effect [17]. The high-carbohydrate and high-fat diet infusions used in prior conditioning studies, although equal in energy density, differed in their satiating action. This is indicated by the findings that the high-carbohydrate infusions produced smaller and/or less frequent ingestive bouts than did the high-fat infusions [7,10,22,30]. Therefore, the flavor paired with the high-carbohydrate infusions may have been less preferred than the high-fat-paired flavor because the more pronounced satiating action of carbohydrate, relative to fat, counteracted its otherwise stronger post-oral reinforcing effect. Lucas et al. [7] investigated this possibility by training rats with a dilute form of the high-carbohydrate diet (1.4 kcal/ml) that was matched to the high-fat diet (2.1 kcal/ml) in its satiating action. This was demonstrated by the fact that the rats self-infused the diets in similar patterns (numbers and volumes of bouts) during training. In the subsequent choice test, the flavor paired with the high-fat diet was not preferred to the flavor paired with the diluted high-carbohydrate diet.

An implication of the above findings is that the post-oral reinforcing effects of mixed diets vary not only as a function of macronutrient composition but also as a function of energy density. In particular, whereas rats prefer a flavor paired with an energy-dense high-fat diet over that of an isocaloric high-carbohydrate diet, in a comparison of isocaloric dilute diets they may prefer the high-carbohydrate-paired flavor. There is an accumulating evidence that the energy density of foods influences energy intake, satiety, and adiposity [14]. The present study investigated the possibility that energy density also determines the relative post-oral reinforcing actions of foods that differ in carbohydrate and fat content. Rats were trained with novel flavors paired with intragastric infusions of high-fat and high-carbohydrate diets that varied in energy density (0.5 or 2.1 kcal/ml). Intakes and preferences were evaluated when the animals had the choice between flavors associated with isocaloric diets differing in composition, with diets of fixed composition but varying in caloric density, or with diets varying in both composition and caloric density. In addition to measuring daily fluid and energy intakes, bout patterns were analyzed to evaluate the relative satiation and satiety effects of the various diets.

2. Experiment 1. Low-density (0.5 kcal/ml) high-fat and high-carbohydrate diets

When prepared at a 2.1 kcal/ml energy density, the flavor associated with a high-fat liquid diet infusion was preferred to the flavor paired with a high-carbohydrate diet infusion [7]. In contrast, flavors paired with lower-density carbohydrate infusions were preferred over isocaloric fat-paired flavors in several studies of pure-nutrient infusion effects [9,11,20]. The first experiment tested the hypothesis that reducing the energy density of the mixed diets to 0.5 kcal/ml would alter their relative flavor-conditioning effectiveness to resemble those of pure-nutrient infusates. The 0.5 kcal/ml density was intermediate in energy to the 8% and 16% carbohydrate concentrations we have commonly used as our pure-nutrient infusates, so it maintained an energy content that was expected to support flavor preference learning.

2.1. Subjects

Adult female Sprague–Dawley rats ($n=16$) bred from stock obtained from Charles River Laboratories, Wilmington, MA) were used. The animals weighed 244 to 350 g and were housed in individual wire-mesh cages in a room maintained at 21 °C and under a 12:12 h light–dark cycle (lights on at 08:00). They were 15 weeks old at the time of surgery.

2.2. Surgery

The rats were anesthetized with an ip administration of ketamine (63 mg/kg) and xylazine (9.4 mg/kg) and a stainless-steel intragastric cannula was surgically implanted at the fundus of the stomach as previously described [3]. After the surgery, animals were given two weeks to recover in their home cages. During this time their gastric cannulas were closed with stainless-