

Brief Communication

Meal size of high-fat food is reliably greater than high-carbohydrate food across externally-evoked single-meal tests and long-term spontaneous feeding in rat

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Abstract

A series of studies in rat using isoenergetic (kcal/ml) liquid diets differing in fat content has previously found dietary fat to dose-dependently increase daily caloric intake. In single-meal tests in which meal initiation was externally evoked in feeding-associated environments, the behavioral expression of this overeating was found to be larger meal intake. The present studies confirmed the ecological validity of this larger meal size of high-fat diet (HF) relative to high-carbohydrate diet (HC): meal size of HF > HC in home-cage testing (Experiment 1), and during undisturbed, spontaneous feeding in which ingestive behavior was continuously monitored (Experiments 2 and 3). These findings demonstrate that single-meal paradigms yield results consistent with spontaneous feeding of high-fat and high-carbohydrate liquid diets, thus supporting the use of single-meal studies to better understand the physiological bases of elevated caloric intake associated with chronic consumption of a high-fat diet.

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Consumption of a diet high in fat is typically associated with greater intake and weight gain than consumption of a high-carbohydrate, lower fat diet in laboratory animals (reviewed in Warwick and Schiffman (1992)). In humans, epidemiological data provide evidence of this link, although the numerous confounds of dietary fat content with other dietary and lifestyle factors prevents inference of causality. Experimental research in humans has yielded mixed results: an intake-stimulatory effect of increased dietary fat has been noted by some but not all investigators, probably due to methodological variations and the confounding of fat content with palatability and/or caloric density (reviewed in Rolls and Hammer (1995) and Warwick (1996)). The existence of a causal link between dietary fat content and energy intake in humans is controversial (e.g. Bray & Popkin, 1998; Willett, 1998), but given the escalating rate of obesity in Western society, ongoing research into dietary

factors that may contribute to excessive intake and weight gain is essential.

To dissociate the influences of palatability, energy density, and macronutrient-specific postingestive effects on high-fat diet hyperphagia, isoenergetic (both 2.3 kcal/ml; 9.62 MJ/ml) liquid diets differing in fat:carbohydrate ratio were developed (Warwick & Weingarten, 1995). Reliably, the high-fat (HF) diet elicited greater daily energy intake and weight gain than the high-carbohydrate (HC) diet across a variety of paradigms, including oral feeding both with ad lib chow (Warwick, 2003; Warwick, Synowski, & Bell, 2002) and without chow (Warwick & Weingarten, 1995); self-regulated intragastric feeding both with chow (Lucas, Ackroff, & Sclafani, 1998; Warwick, Synowski, Rice, & Smart, 2003) and without chow (Warwick et al., 2003; Warwick & Weingarten, 1995); when diets were gelled to semi-solid form, and when energy density was halved by addition of water (Warwick et al., 2002). A linear dose-response relationship between dietary fat content (ranging from 17 to 60% of energy) and daily energy intake has also been demonstrated (Warwick, 2003).

Behaviorally, the greater daily energy intake associated with HF must reflect larger and/or more frequent meals

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relative to HC. To investigate the behavioral expression of high-fat diet hyperphagia, HF and HC were compared in single-meal tests and in preloading paradigms. Reliably, meal size (energy) of HF exceeded that of HC (Warwick, McGuire, Bowen, & Synowski, 2000; Warwick & Synowski, 1999), indicating that meal-terminating mechanisms are less potently engaged by fat than by carbohydrate. In addition, preloading studies have demonstrated that HF elicits less postprandial satiety per kcal than HC (Warwick, 2003; Warwick et al., 2000).

The present studies sought to determine the ecological validity of the larger meal size of HF relative to HC that has been observed in single-meal, exogenously-driven feeding tests. This was achieved by determining meal size of HF and HC in the home cage (Experiment 1), and during undisturbed, spontaneous feeding behavior (Experiments 2 and 3).

Experiment 1: meal size in home cage

A larger meal size of HF relative to HC has been observed in paradigms in which animals were removed from the home cage, placed in an experimental chamber, and offered food shortly thereafter (Warwick et al., 2000; Warwick & Synowski, 1999). After a few repetitions of this ritual, rats clearly associate the chamber with eating as evidenced by nose-pokes and licks in the food area prior to food presentation. The present study investigated whether differential meal size of HF and HC would still be observed when appetitive expectations were minimized by testing in the home cage.

Twelve male Long-Evans rats were housed singly in wire-mesh hanging cages, in a colony room was maintained at 26 °C and illuminated on a 12:12-h light–dark cycle with lights out at 1800 h. Tap water was available ad libitum. High fat (HF) and high-carbohydrate (HC) diets were prepared as described previously (Warwick et al., 2002). Briefly, these diets were prepared from evaporated milk, sucrose, corn oil and micronutrients, contained equivalent protein (7% of energy), and were isocaloric at 2.3 kcal/ml (9.62 MJ/ml). The HF diet provided 60% energy from fat and 33% energy from carbohydrate, while in the HC diet the proportions were 16% energy from fat, 77% from carbohydrate. Rats were given a bottle of either HF or HC in their home cage for 30 min (intake measured to the nearest gram), approximately mid-way through the light phase. This was repeated for 5 days, until intake stabilized, and then repeated with the alternate diet. Presentation order was counterbalanced across rats.

Intake of HF (mean 37.4 s.e. 1.9 kcal; 156.5 s.e. 7.7 MJ) was greater than intake of HC (mean 24.4 s.e. 2.0 kcal; 102.1 s.e. 8.4 MJ), $t(11)=4.97$, $p<0.001$. This larger meal size of HF relative to HC in home-cage testing is consistent with previous observations in which intake was measured in experimental environments specifically designed to elicit

ingestive responding (Warwick et al., 2000; Warwick & Synowski, 1999). To further confirm the greater intake of HF relative to HC across testing paradigms, sixteen additional rats were first trained to initiate feeding in response to a buzzer-light conditioned stimulus (CS) in experimental chambers (see Weingarten, 1985). When the CS reliably elicited feeding, meal size was then assessed under two conditions: (1) in the chambers following presentation of the CS, and (2) in the home cage, with conditions alternated until intake stabilized. Half of the animals consumed HC while half consumed HF. Two-way ANOVA indicated no significant effect of test condition, $F(1,15)=0.05$, n.s., but the expected significant effect of diet, $F(1,15)=23.8$, $p<0.001$, with meal size of HF (mean 32.6 s.e. 2.3 kcal; 136.4 s.e. 9.5 MJ) again larger than HC (mean 23.2 s.e. 2.1 kcal; 97.1 s.e. 8.7 MJ).

The robust finding of greater meal size of HF relative to HC when appetitive expectancies were both maximized (distinctive environment coupled with feeding-associated CS) and minimized (home cage testing) is encouraging. However, even home cage testing includes rituals (e.g. bottle preparation and placement) that are predictors of impending food availability and could thus become conditioned appetitive cues (see Weingarten, 1985 for discussion). To determine whether HF elicited a relatively larger meal size during natural feeding, the next study compared uncued, spontaneous meal size of HF and HC.

Experiment 2: meal size during spontaneous feeding

When consumed ad libitum, HF elicits greater daily energy intake than HC; however, there is an initial period of hypophagia and weight loss probably attributable to neophobia (Warwick & Weingarten, 1995). Since atypical meal patterning would be expected during this initial phase, a period of diet acclimation took place prior measurement of spontaneous intake of HF and HC. Twenty-three new rats were housed in Plexiglas experimental chambers (Med-Associates, Inc., St Albans VT) equipped with contact lickmeters. They were divided into two weight-matched groups and allowed to acclimate to either HF or HC ad lib for 8 days; intake data were not recorded during this phase. Following the acclimation period, ad lib intake continued for an additional 8 days during which lick data (resolution 0.1 s) were collected and daily intake measured. Lick data were stored in an array for computerized analysis to determine the number of meals consumed per day, with a meal defined as a period of licking behavior composed of at least 10 licks with interlick intervals (ILIs) no longer than 10 min. Average meal size (energy) was calculated daily for each rat by dividing daily diet intake, in kcal (MJ), by the number of meals consumed (Lucas et al., 1998; Warwick et al., 2003).

Daily intake by rats fed HF was greater than rats fed HC, $t(21)=3.24$, $p<0.05$, consistent with previous findings

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