Citation:
Hopkins, M and Gibbons, C and Caudwell, P and Blundell, JE and Finlayson, G (2016) Differing effects of high-fat or high-carbohydrate meals on food hedonics in overweight and obese individuals. British Journal of Nutrition, 115 (10). pp. 1875-1884. ISSN 1475-2662 DOI: https://doi.org/10.1017/S0007114516000775

Link to Leeds Beckett Repository record:
https://eprints.leedsbeckett.ac.uk/id/eprint/3082/

Document Version:
Article (Accepted Version)

Differing Effects of High Fat or High Carbohydrate Meals on Appetite and Food Hedonics in Overweight and Obese Individuals.

Mark Hopkins[1, 2], Catherine Gibbons[2], Phillipa Caudwell[2, 3], John E. Blundell[2] & Graham Finlayson[2].

[1]Academy of Sport and Physical Activity, Faculty of Health and Wellbeing, Sheffield Hallam University, Sheffield, S10 2BP, UK. [2]Institute of Psychological Sciences, Faculty of Medicine and Health, University of Leeds, Leeds, LS2 9JT, UK. [3]Medical and Healthcare Affairs, AstraZeneca, Horizon Place, 600 Capability Green, Luton, LU1 3LU, UK.

Corresponding author:

Dr Mark Hopkins,
Academy of Sport and Physical Activity,
Faculty of Health and Wellbeing,
Sheffield Hallam University,
Sheffield,
United Kindom.

Tel: +44 (0) 1142 255368.
Email: M.Hopkins@shu.ac.uk.

Running title:

Macronutrient composition & food hedonics

Key Words:

Macronutrient composition: Energy intake: Satiation: Satiety: Food hedonics

Abbreviations:

HFLC, high fat/low carbohydrate foods; LFHC, low fat/high carbohydrate foods; SQ, satiety quotient; LFPQ, Leeds Food Preference Questionnaire.

ABSTRACT

While the effects of dietary fat and carbohydrate on satiety are well documented, little is known about the impact of these macronutrients on food hedonics. We examined the effects of *ad libitum* and isoenergetic meals varying in fat and carbohydrate on satiety, energy intake and food hedonics. In all, sixty-five overweight and obese individuals (BMI = 30.9 ± 3.8 kg/m^2) completed two separate test meal days in a randomised order in which they consumed high-fat/low-carbohydrate (HFLC) or low-fat/high-carbohydrate (LFHC) foods. Satiety was measured using subjective appetite ratings to calculate the satiety quotient. Satiation was assessed by intake at *ad libitum* meals. Hedonic measures of explicit liking (subjective ratings) and implicit wanting (speed of forced-choice) for an array of HFLC and LFHC foods were also tested before and after isoenergetic HFLC and LFHC meals. The satiety quotient was greater after *ad libitum* and isoenergetic meals during the LFHC condition compared to the HFLC condition ($P = 0.006$ and $P = 0.001$, respectively), while *ad libitum* energy intake was lower in the LFHC condition ($P < 0.001$). Importantly, the LFHC meal also reduced explicit liking ($P < 0.001$) and implicit wanting ($P = 0.013$) for HFLC foods compared to the isoenergetic HFLC meal, which failed to suppress the hedonic appeal of subsequent HFLC foods. Therefore, when coupled with increased satiety and lower energy intake, the greater suppression of hedonic appeal for high-fat food seen with LFHC foods provides a further mechanism for why these foods promote better short-term appetite control than HFLC foods.

INTRODUCTION

The role of dietary carbohydrate in the etiology and treatment of obesity is controversial, with some arguing that carbohydrate intake plays a more prominent role in promoting overconsumption and weight gain than dietary fat (1, 2). While this view has been strongly debated(3), it has long been established that dietary macronutrients exert a hierarchical effect on appetite-related processes such as satiety and short-term food intake(4). When expressed relative to energy content rather than weight of food, protein exerts the strongest effect on satiety, followed by carbohydrate, whilst fat exerts the weakest effect(5). This hierarchical effect has been demonstrated under a variety of laboratory and free-living conditions using subjective measures of appetite, biomarkers of satiety and food intake(6-11). However, the underlying metabolic, and in particular, behavioural mechanisms that promote overconsumption following the consumption of energy dense, high-fat foods are not well understood.

The differential effects of dietary macronutrients on satiety may relate to differences in pre-ingestive cognitive and sensory signals generated at the time of consumption(12) and/or the post-ingestive metabolic effects of these foods(13-15). However, recent evidence suggests that the hedonic value of foods encountered following consumption (e.g. food liking and wanting), which is closely linked to the perceived taste and energy content of food, can also influence appetite and energy intake(16). For example, a heightened liking (the perceived pleasurable sensory properties of food) and wanting (the attraction towards a specific food over available alternatives(17)) for high fat, high sweet foods has been noted in overweight and obese individuals(18) and those who demonstrate binge eating(19). Despite this, the effect of macronutrient composition on food hedonics has received little attention and existing data are contradictory.

While high protein meals (25% of total energy) have been shown not to effect food hedonics compared to isoenergetic low protein meals (7% of total energy)(20), Lemmens et al.(21) reported that a meal containing 65% of its total energy from protein reduced ‘wanting’ to a greater extent than an isoenergetic high carbohydrate meal (65% of total energy). Furthermore, a 14 day low protein diet (0.5 g protein·kg body weight^{-1}·d^{-1}) was found to increase protein intake, wanting, preference for savoury high protein foods(22) and the neural activation to savoury food cues in brain reward regions(23) compared to a high protein diet (2.0 g protein·kg body weight^{-1}·d^{-1}).

While these data suggest that dietary macronutrients may also differentially effect food hedonics, the acute effects of macronutrient composition, and in particular, dietary fat, on food hedonics has yet to be examined. Given the controversy over the relative contribution of dietary fat and carbohydrate in promoting overconsumption and weight gain, this warrants further attention. Therefore, the aim of the present study was to examine the effects of *ad libitum* and isoenergetic meals varying in dietary fat and carbohydrate on energy intake, satiety and food hedonics in overweight and obese individuals.

METHODS

Participants

In all, sixty-five overweight and obese males (N = 26) and females (N = 39) were recruited onto this randomised, crossover design study. Descriptive characteristics of participants are displayed in Table 1. All participants were non-smokers, physically inactive (≤ 2 hrs·wk^{-1} of exercise over the previous six months), weight stable (± 2 kg for the previous three months) and not taking medication known to affect metabolism or appetite. This study was conducted according to the guidelines laid down in the Declaration of Helsinki, and ethical approval was granted by the Leeds West National Health Service Research Ethics Committee (09/H1307/7). All participants provided written informed consent before taking part. The project was registered under international standard identification for controlled trials ISRCTN47291569.

Table 1 here.....

Study Design

Participants completed two separate probe test meal days in a randomised order in which they consumed either high fat/low carbohydrate (HFLC) or low fat/high carbohydrate (LFHC) meals across the day that were matched for sensory properties and taste. Total daily energy intake was measured using a laboratory-based test meal design that included fixed energy and *ad libitum* meals, while satiation (energy intake during a single meal) was measured during *ad libitum* meal consumption only. Satiety was measured using subjective appetite ratings adjusted for energy intake from the breakfast and lunch meals to calculate the satiety quotient (SQ) (24). Hedonic measures of explicit liking (subjective ratings) and implicit wanting (speed of forced-choice) for an array of HFLC and LFHC foods were also tested before and after the isoenergetic lunch meal using the Leeds Food Preference Questionnaire (LFPQ)(25).

Procedures

Total Daily Energy Intake and Satiation

Total daily energy intake and satiation (measured via energy intake during a single meal) were measured using a laboratory-based test meal protocol in which participants consumed either HFLC or LFHC foods across the whole day. Test days were separated by at least two days, and the order in which participants performed the HFLC and LFHC days was randomized and counter-balanced. The form of the meals on each test day was identical, with foods similar in appearance and taste acceptability so participants could not detect the nutritional manipulation. The mean proportion of energy contributed by fat, protein, and carbohydrate to total daily energy intake on the HFLC and LFHC test days was 56.0 ± 3.2%, 13.9 ± 2.1%, and 30.1 ± 3.9%, and 23.0 ± 3.3%, 13.5 ± 1.5%, and 63.5 ± 4.4%, respectively. Mean taste acceptability for the HFLC and LFHC conditions was assessed using visual analogue scales in a sub-sample of participants ($N = 16$) who took part in the wider study, and no differences existed between the HFLC (62.3 ± 7.2 mm) and LFHC conditions (56.9 ± 6.1 mm; $P = 0.242$). Similarly, mean food satisfaction was also assessed using visual analogue scales following the HFLC (63.8 ± 7.9 mm) and LFHC (62.2 ± 6.6 mm) conditions, and again, did not differ between conditions ($P = 0.724$).

During the test days, participants consumed an *ad libitum* breakfast meal, a fixed energy lunch (800 kcals) and an *ad libitum* dinner meal (four hours apart). After the dinner meal, participants were free to leave the research laboratory but were given an *ad libitum* snack box of foods to consume if desired during the evening. All meals provided on the test day were either HFLC or LFHC, and participants were required to consume only the foods and drinks provided on these test days. Details of the individual food items, macronutrient composition and weight of food consumed can be found in Supplementary Table S1 and elsewhere(26).

All meals consumed in the research unit were eaten in isolation, with participants instructed to eat as much or as little as they wanted until comfortably full during *ad libitum* meal consumption. Food was provided in excess of expected consumption, with participants able to request further food or water if required. Prior to participation individuals completed a food preference questionnaire, and if they strongly disliked any of the test foods, participants were excluded if a suitable alternative (matched for macronutrient composition) could not be found. Energy intake was calculated by weighing the food before and after consumption (to the nearest 0.1 g), and with reference to the manufacturers' energy values. To calculate test meal energy intake, the energy equivalences used for protein, fat and carbohydrate were 4, 9 and 3.75 $\text{kcal}\cdot\text{g}^{-1}$, respectively. Total daily energy intake was taken as the energy consumed during the breakfast, lunch and dinner meals, and intake from the snack box. Energy intake during the *ad libitum* breakfast and dinner meals was used to represent satiation in the present paper.

Subjective Appetite Ratings

Subjective ratings of appetite were measured during test meal probe days using visual analogue scales presented on a validated hand-held electronic appetite rating system (EARS II)(27). On each day, ratings were recorded immediately before and after a meal, and at hourly intervals throughout the day (from 0800 to 1800 hours). The use of visual analogue scales for the measurement of subjective appetite has previously been shown to be valid and reproducible(28). Furthermore, visual analogue scales have been used to detect changes in appetite following manipulations of energy intake(29, 30) and diet composition(31), while the EARS II electronic rating system has been validated against the traditional pen and paper technique(27).

Satiety

The suppression of hunger per calorie of intake for the *ad libitum* breakfast meal and fixed energy lunch meals was assessed by calculating the satiety quotient (SQ). The SQ was developed by Green et al.(24), and expresses changes in post-prandial appetite ratings relative to the energy content of a meal. As such, it reflects the capacity of a meal to modulate the strength of post-prandial satiety sensations. The SQ of a meal was calculated using the following formula using subjective hunger ratings(24), with a higher SQ indicative of a greater satiating efficiency:

$$\text{Satiety Quotient} = \frac{\text{rating pre-eating episode} - \text{rating post-eating episode}}{\text{intake of eating episode}} \text{ X } 100$$

It has been suggested that the SQ provides a better marker of satiety than post-prandial hunger ratings, as it takes into account both the pre-meal appetite sensations and the energy content of the meal consumed(32). The SQ has also been shown to be associated with *ad libitum* food intake following a variety of nutritional interventions(32, 33).

Hedonic Assessment of HFLC and LFHC Foods

Immediately prior to and following the fixed energy lunch meal, the hedonic profile of an array of foods was assessed using the Leeds Food Preference Questionnaire(25). The LFPQ provides measures of different components of food preference and hedonics. Participants are presented with an array of pictures of individual food items common in the diet. Foods in the array are chosen by the experimenter from a validated database to be either predominantly high (> 45% energy) or low (< 20% energy) in fat but similar in familiarity, protein content, sweet or non-sweet taste and acceptability. Each food category was represented by eight photographs of ready-to-eat foods. Details of the mean energy density, serving and macronutrient composition of food items and categories' used in the LFPQ can be found in Table 2. The LFPQ has been validated against physiological and behavioural endpoints in a range of research(34-36). The specific endpoints examined from the LFPQ were explicit liking, implicit wanting and food preference for HFLC relative to LFHC foods, as described below. The LFPQ has been shown to demonstrate reliable immediate and post-meal changes(37), and is a good predictor of food choice and intake in laboratory and community-based samples(22, 38).

Table 2 here....

Explicit Liking and Implicit Wanting

To measure explicit liking, participants rated the extent to which they liked each food (e.g. how pleasant would it be to taste this food now?). The food images were presented individually in a randomised order and participants made their ratings using a 100 mm visual analogue scale.

Implicit wanting was assessed using a forced choice methodology in which the food images were paired so that every image from each food category was compared to every other type over 96 trials (food pairs). Participants were instructed to respond as quickly and accurately as they could, indicating the food they want to eat the most at that time (e.g. which food do you most want to eat now?). Following Dalton et al.(39), the food pair trials were presented in three blocks, with each stimulus appearing eight times. Stimuli were presented until a valid response was detected up to a maximum of 4000 ms with a variable 500-1000 ms washout between presentations in which a central fixation cross was displayed. To measure Implicit Wanting, reaction times for all responses were covertly recorded and used to compute mean response times for each food type after adjusting for frequency of selection. Therefore, a positive score indicates a more rapid preference for high fat foods over low fat foods and a negative score indicates the opposite. A score of zero indicates that high fat and low fat foods are equally preferred. A frequency-weighted algorithm was used so the Implicit Wanting score could be influenced by both selection (positively contributing to the score) and non-selection (negatively contributing to the score) of food type.

Statistical Analysis

Data are reported as mean ± SEM throughout unless otherwise stated. Statistical analyses were performed using IBM SPSS for Windows (Chicago, Illinois, Version 21). Where appropriate, Greenhouse-Geisser probability levels were used to adjust for sphericity, and Bonferroni adjustments were applied to control for multiple *post-hoc* comparisons. Our sample size of $N = 65$ was assessed for adequate power by a posteriori power analysis using G*Power(40) to find an effect of macronutrient composition on implicit wanting for HFLC food, based on data from Griffioen-Roose et al.(35), and expected correlation of 0.5, $\beta = 0.8$ and $\alpha = 0.05$. A paired t-test was used to examine differences between pre-meal subjective appetite ratings (hunger and fullness) and total daily energy intake during the HFLC and LFHC conditions. To examine the effects of macronutrient composition on satiation (i.e. energy intake during breakfast and lunch meals) was examined using a two-way ANOVA (meal*macronutrient composition) with repeated measures. Similarly, the effect of macronutrient composition on satiety (SQ) was examined following the *ad libitum* breakfast and fixed energy lunch meals using separate two-way ANOVAs (time*macronutrient composition) with repeated measures.

For LFPQ measures, mean scores for HFLC and LFHC categories were computed for implicit wanting and explicit liking outcomes. Mean LFHC scores were then subtracted from the mean for HFLC scores to provide a composite score representing hedonic value for HFLC relative to LFHC food for liking and wanting. Using this approach a positive score indicated greater liking or wanting for HFLC foods over LFHC foods; a negative score indicated greater liking or wanting for LFHC foods over HFLC foods; and a score of zero indicated an equal liking or wanting for HFLC and LFHC foods. The explicit liking and implicit wanting appeal bias scores were examined separately using a two-way ANOVA (macronutrient composition*hunger state) with repeated measures. Interactions were explored further using simple post hoc comparisons. To test whether hedonic endpoints were associated with food intake, simple linear regression was used to examine the relationships between explicit liking and implicit wanting and *ad libitum* dinner meal intake.

RESULTS

The Effect of Macronutrient Composition on Appetite, Satiation and Total Daily Energy Intake

No differences existed between the pre-breakfast ratings of subjective hunger (63.3 ± 2.9 vs. 60.8 ± 3.1 mm; $P = 0.509$) or fullness (19.9 ± 2.34 vs. 24.4 ± 2.8 mm; $P = 0.138$) during HFLC and LFHC conditions, respectively. Similarly, no differences existed in ratings of hunger (62.3 ± 3.0 vs. 63.7 ± 3.0 mm; $P = 0.592$) or fullness (30.1 ± 2.6 vs. 27.3 ± 2.6 mm; $P = 0.320$) immediately before the lunch meal during HFLC and LFHC conditions, respectively.

Total daily energy intake was significantly greater during the HFLC condition compared to the LFHC condition (990.4 ± 81.0 kcal; $P < 0.001$). As expected, no differences existed in energy intake during the fixed energy HFLC (799.9 ± 2.3 kcal) and LFHC (785.8 ± 2.9 kcal; $P > 0.05$) lunch meals. In order to examine the effects of macronutrient composition on satiation (i.e. energy intake during a single meal) during the *ad libitum* breakfast and dinner meals, energy intake during the separate test meals was examined. A two-way ANOVA (meal*macronutrient composition) with repeated measures indicated a significant main effect of meal ($F_{(2.54,\ 162.81)} = 35.926$; $P < 0.001$; $\eta^2 = 0.360$) and macronutrient composition ($F_{(1,\ 64)} = 156.953$; $P < 0.001$; $\eta^2 = 0.710$). There was also a significant meal*macronutrient composition interaction ($F_{(2.10,\ 134.64)} = 36.045$; $P < 0.001$; $\eta^2 = 0.360$), such that energy intake was significantly higher at breakfast (337.2 ± 44.2 kcal; $P < 0.001$) and dinner (531.8 ± 35.2 kcal; $P < 0.001$) during the HFLC condition compared to the LFHC condition (Figure 1).

Figure 1 here....

The Effect of Macronutrient Composition on Satiety Following *Ad Libitum* Breakfast Meal Consumption

There was a significant effect of macronutrient composition on SQ following the consumption of the *ad libitum* breakfast meal, with a two-way ANOVA (time*macronutrient composition) with repeated measures indicating a significant main effect of time ($F_{(1.49,\ 95.49)} = 97.024$; $P < 0.001$; $\eta^2 = 0.603$) and macronutrient composition ($F_{(1,\ 64)} = 8.072$; $P = 0.006$; $\eta^2 = 0.112$). Furthermore, there was a significant time*macronutrient composition interaction ($F_{(2.27,\ 143.20)} = 19.687$; $P < 0.001$; $\eta^2 = 0.235$), such that the LFHC breakfast SQ was significantly higher than the HFLC breakfast SQ immediately after ($P < 0.001$) and at 60 ($P < 0.001$) and 120 minutes post meal consumption ($P = 0.001$; Figure 2).

Figure 2 here.....

The Effect of Macronutrient Composition on Satiety Following Consumption of the Isoenergetic Lunch Meal

There was also an effect of macronutrient composition on SQ following consumption of the fixed energy lunch meal (Figure 2), with a two-way ANOVA (time*macronutrient composition) with repeated measures indicating a significant main effect of time ($F_{(2.56,\ 164.38)} = 109.980$; $P < 0.001$; $\eta^2 = 0.632$). There was also a significant main effect of macronutrient composition ($F_{(1,\ 64)} = 11.314$; $P = 0.001$; $\eta^2 = 0.150$), such that SQ was significantly higher following consumption of the LFHC meal compared to the HFLC meal ($P = 0.001$). However, there was no time*macronutrient composition interaction ($F_{(2.96,\ 189.57)} = 0.187$; $P = 0.945$; $\eta^2 = 0.003$).

The Effect of Macronutrient Composition on the Hedonic Assessment of Food Following Isoenergetic Meal Consumption

When the explicit liking score for HFLC relative to LFHC foods was examined, a two-way ANOVA with repeated measures indicated a significant main effect of macronutrient composition ($F_{(1,\ 64)} = 8.432$; $P = 0.005$; $\eta^2 = 0.116$), such that explicit liking for HFLC foods was greater during the HFLC condition. There was also a significant macronutrient composition*hunger state interaction ($F_{(1,\ 64)} = 5.993$; $P = 0.017$; $\eta^2 = 0.086$). While explicit liking did not differ between conditions in the hungry state i.e. pre-meal ($P = 0.519$), explicit liking for HFLC foods was significantly lower in the fed state following the consumption of the LFHC meal compared to the HFLC meal ($P < 0.001$; Figure 3).

Figure 3 here...

When the implicit wanting score for HFLC relative to LFHC foods was examined, a significant main effect of macronutrient composition was seen ($F_{(1,\ 64)} = 4.846$; $P = 0.031$; $\eta^2 = 0.070$), such that implicit wanting was higher during the HFLC condition. There was no main effect of hunger state ($F_{(1,\ 64)} = 0.205$; $P = 0.652$; $\eta^2 = 0.001$), and the macronutrient composition*hunger state interaction approached significance ($F_{(1,\ 64)} = 2.851$; $P = 0.096$; $\eta^2 = 0.043$). As can be seen in Figure 3, consumption of the HFLC meal increased wanting (1.00 ± 2.92) while LFHC foods decreased wanting (-3.57 ± 3.35). Post hoc comparisons indicated that implicit wanting for HFLC foods did not differ between conditions in the hungry state (i.e. pre-meal; $P = 0.427$), but was significantly lower in the fed state following the consumption of the LFHC meal compared to the HFLC meal ($P = 0.011$; Figure 3).

Association between the Hedonic Assessment of HFLC and LFHC Food and *Ad Libitum* Food Intake

To examine whether the hedonic assessment of food was associated with food intake, simple linear regression was used to examine the relationships between explicit liking, implicit wanting and *ad libitum* dinner intake. As can be seen in Table 3, positive associations were seen between explicit liking and implicit wanting (in the hungry and fed states) and *ad libitum* dinner intake during the HFLC and LFHC conditions.

Table 3 here....

DISCUSSION

The aim of the present study was to examine the effects of macronutrient composition on energy intake, satiety and the post-ingestive hedonic assessment of subsequent foods. When participants were allowed to eat *ad libitum*, consumption of LFHC foods resulted in greater post-prandial satiety (higher SQ values), greater satiation (lower self-selected meal intake) and lower total daily energy intake compared to the consumption of HFLC foods. Importantly, despite controlling for energy content, weight and palatability, the explicit liking and implicit wanting for high fat foods were also suppressed to a greater extent following consumption of the LFHC lunch meal compared to the HFLC meal. As such, these data indicate that changing the composition of meals from HFLC to LFHC not only reduces energy intake and increases satiety, but also reduces the relative hedonic value of other high fat/low carbohydrate food options. Taken together, these findings suggest that LFHC foods may promote better short-term appetite control than HFLC foods via both hedonic and appetite-based mechanisms.

The Effects of Macronutrient Composition on Satiety and Food Intake

A clear effect of macronutrient composition on energy intake was observed in the present study, with total daily energy intake and self-selected intake (satiation) during the *ad libitum* breakfast and dinner meals significantly lower during the LFHC condition compared to the HFLC condition. There was also a strong effect of macronutrient composition on satiety, with the *ad libitum* LFHC breakfast found to be more satiating than the equivalent HFLC breakfast (as indicated by higher post-prandial SQ scores). Indeed, the consumption the LFHC breakfast increased satiety despite the lower energy content of the LFHC breakfast meal (and no differences in fasting hunger or fullness between conditions). This effect was transient however, with no differences in SQ noted between conditions 180 minutes post consumption. The effect of macronutrient composition was also apparent under isoenergetic feeding conditions (albeit to a lesser extent), with greater SQ again seen following the LFHC lunch meal. In line with previous findings(5, 8), these data indicate that switching from HFLC to LFHC foods not only reduces energy intake, but also increases the potency of postprandial satiety under *ad libitum* and isoenergetic feeding conditions.

Alterations in the physiological signals arising from the fat and carbohydrate content of the meals may underlie the differences in satiety seen in the present study, with the macronutrient composition of meals mediating the secretion of post-prandial satiety hormones such as glucagon-like peptide-1 and peptide YY(13-15). Mixed macronutrient meals representative of the natural local eating habits of the participants were used in the present study. The mean carbohydrate content during the HFLC was 30.1 ± 3.9% (as opposed to 63.5 ± 4.4% in the LFHC condition), similar to that recommended by the recent Scientific Advisory Committee on Nutrition recommendations on carbohydrates(41). As such, the carbohydrate content of the HFLC meals would have still stimulated the release/suppression of post-prandial satiety hormones, but to a lesser extent than the LFHC meal. This may help account for why the differences in SQ between conditions were smaller under isoenergetic feeding condition, a finding that has been previously reported(42).

The Effect of Macronutrient Composition on Food Hedonics

Although differences in the hedonic assessment of food is increasingly being recognised as a risk factor for overconsumption and weight gain(25), the effect of macronutrient composition on the liking and wanting for subsequent foods has received little attention. Importantly, the present study demonstrated that explicit liking for high fat foods was reduced to a greater extent following consumption of a LFHC test meal compared to a HFLC meal (despite controlling for the energy, weight and palatability of food). Furthermore, similar trend effects were observed for implicit wanting, with the LFHC meal decreasing wanting for high fat foods while the HFLC meal increased wanting for high fat foods. These findings are interesting given that pre-meal appetite sensations (hunger and fullness) did not differ between conditions. It is also interesting to note that when hungry, individuals preferred HFLC foods relative to LFHC foods to a similar degree during both conditions. This preference changed away from HFLC foods in the fed state during the LFHC condition, but remained during the HFLC condition. While this apparent dissociation during the fed state might counter-intuitively suggest that individuals increased their preference for the more satiating LFHC foods in the fed state during the LFHC condition (despite already being more satiated), the decreased appeal bias scores in the fed state during the LFHC condition are more likely to reflect a reduced preference for HFLC, rather than an increased preference for LFHC foods *per se*. Indeed, previous studies have shown that when satiated, individuals tend to experience a reduced preference for HFLC compared to LFHC under *ad libitum* feeding conditions(25, 37). As such, it was interesting to observe in the present study that the consumption of HFLC food did not reduce liking or wanting for HFLC foods to the same extent as consumption of LFHC food under isoenergetic conditions. Therefore, a sustained liking and wanting for high energy foods when satiated may throw new light on how high fat diets lead to overconsumption.

The underlying mechanisms behind this macronutrient derived effect on food hedonics are unknown, but may again be linked to the metabolic consequences of food ingestion. Leptin and insulin, which are both thought to tonically inhibit brain reward pathways(43), are known to exhibit differential responses to dietary fat and carbohydrate ingestion(44-46). While pre-breakfast ratings of hunger and fullness did not differ between conditions (indicating that participants started each condition with the same motivation to eat), it is possible that the response to breakfast may have also influenced the subsequent responses to lunch. However, no differences existed between conditions for pre-lunch subjective hunger, fullness or SQ, suggesting the observed differences in post-meal liking and wanting were due to differences in the meal characteristics rather than a 'carryover' effect from breakfast.

These novel findings, found using a robust sample size (N = 65) and a validated measure of food liking and wanting(34-36), suggest a role for macronutrient composition in mediating the perceived hedonic value of food during the fed state. This is of importance as the attenuated post-meal suppression of food liking and wanting following HFLC food consumption may pose as a risk factor for later snacking or larger subsequent meal intake. Indeed, in the present study explicit liking and implicit wanting were positively associated with energy intake during the *ad libitum* dinner meal, indicating that the changes in food hedonics were expressed behaviourally through subsequent food intake (although differences in breakfast intake and satiety would have also influenced dinner intake). It is interesting to note that Lemmens et al.(21) reported that the consumption of a high protein, but not carbohydrate, meal reduced wanting. These data are in contrast to the current findings in which the LFHC meal actually suppressed liking and wanting for high fat foods. However, while hedonic reward was measured using behaviourally relevant tasks during the present study using a large sample (N = 65), Lemmens et al.(21) measured wanting via engagement with memory games in a small sample of individuals (N = 16) characterised by disinhibited eating behaviour (defined as a score > 5 on the Three Factor Eating Questionnaire(47)).

It should be noted that while the present study indicates that LFHC foods dampen the hedonic appeal of high fat foods to a greater extent than HFLC foods (while also resulting in greater satiety and lower energy intake), eating behaviour was only measured across a single day. As such, inferences about the long-term effects of a habitual LFHC diet on food hedonics cannot be made in the present study. However, Martin et al.(48) has reported that individuals (N = 134) following a two year low carbohydrate diet were ‘less bothered by hunger’ and demonstrated decreased cravings for carbohydrates and preferences for high carbohydrate and sugar foods compared to those following a low fat diet (N = 136). Furthermore, protein status following a 14 day high protein diet has been shown to affect subsequent protein intake, wanting and preference for savoury, high protein foods(22) and neural activation in brain reward regions in response to savoury food cues(23). However, further research is needed to examine the long-term effects of diets varying in macronutrient composition on food hedonics.

The need to for long-term studies examining the effects of macronutrient composition on food hedonics is emphasised by the on-going debate regarding the effectiveness of diets differing in macronutrient composition on weight loss(49). The present findings suggest that LFHC foods promote reduced energy intake, and are in line with previous studies demonstrating low fat diets are effective for long-term weight loss(50). However, inferences made about changes in body composition from studies that manipulate dietary intake acutely should be made cautiously. Indeed, recent findings have questioned whether low-fat diets are more effective than other isoenergetic dietary interventions for weight loss (i.e. low carbohydrate or high protein diets)(51). It should also be noted that no control was made for menstrual cycle phase in female participants. This may have contributed to the variability seen in food hedonics, as studies have previously shown that eating behaviour and food hedonics are influenced to a small extent by the phases of the menstrual cycle(52, 53). Furthermore, this study only included overweight and obese individuals, and therefore, no inferences can be made as to whether macronutrient composition also mediates food hedonics in lean individuals.

Conclusions

When consumed under *ad libitum* and isoenergetic feeding conditions, HFLC foods have a weaker action on satiety and promote greater energy intake than compared to LFHC foods. Importantly, HFLC foods also failed to dampen the subsequent appeal bias for high fat foods compared to energy, weight and palatability matched LFHC foods. Therefore, these data demonstrate the acute impact of dietary fat and carbohydrate in moderating energy intake, and suggest that HFLC foods not only promote subsequent energy intake via effects on satiation and satiety, but also through an effect on the subsequent hedonic value of food. Taken together, these data suggest that LFHC foods may help promote better short-term appetite control than HFLC foods.

FINANCIAL SUPPORT:

Research relating to this study was funded by BBSRC (DRINC) grant BB/G005524/1 and European Union Seventh Framework Programme (FP7/2007-2013) under grant agreement number 266408 ‘Full4Health’. Neither funding body had a role in the design, analysis or writing of this article. The project was registered under international standard identification for controlled trials ISRCTN47291569.

CONFLICT OF INTEREST:

The authors declare no conflict of interest.

AUTHORSHIP:

The authors’ contributions are as follows: MH contributed to the data collection, data analyses and wrote the manuscript. CG and PC contributed to the study design and data collection. JEB contributed to the study design, interpretation of data and writing of the manuscript. GF contributed to the study design, data analyses, interpretation of data and writing of the manuscript. All authors read and approved the final version of the manuscript.

REFERENCES

1. Taubes G. Good Calories, Bad Calories: Challenging the Conventional Wisdom on Diet, Weight Control, and Disease. Alfred A. Knopf, New York; 2007.
2. Taubes G. Why We Get Fat: And What to Do About It: New York, Random House, Inc.; 2011.
3. Hall KD, Bemis T, Brychta R, Chen KY, Courville A, Crayner EJ, et al. Calorie for Calorie, Dietary Fat Restriction Results in More Body Fat Loss than Carbohydrate Restriction in People with Obesity. Cell Metab. 2015; **22**(3):427-436
4. Blundell J, Lawton C, Cotton J, Macdiarmid J. Control of human appetite: implications for the intake of dietary fat. Annu Rev Nutr. 1996;**16**(1):285-319.
5. Blundell JE, Burley V, Cotton J, Lawton C. Dietary fat and the control of energy intake: evaluating the effects of fat on meal size and postmeal satiety. Am J Clin Nutr. 1993;**57**(5):772S-7S.
6. Cotton JR, Burley VJ, Weststrate JA, Bhmdell JE. Dietary fat and appetite: similarities and differences in the satiating effect of meals supplemented with either fat or carbohydrate. J Hum Nutr Diet. 1994;**7**(1):11-24.
7. Robinson TM, Gray RW, Yeomans MR, French SJ. Test-meal palatability alters the effects of intragastric fat but not carbohydrate preloads on intake and rated appetite in healthy volunteers. Physiol Behav. 2005;**84**(2):193-203.
8. Lawton C, Burley V, Wales J, Blundell J. Dietary fat and appetite control in obese subjects: weak effects on satiation and satiety. Int J Obes. 1993;**17**:409-16.
9. Westerterp-Plantenga M, Rolland V, Wilson S, Westerterp K. Satiety related to 24 h diet-induced thermogenesis during high protein/carbohydrate vs high fat diets measured in a respiration chamber. Eur J Clin Nutr. 1999;**53**(6):495-502.
10. Astbury NM, Stevenson EJ, Morris P, Taylor MA, Macdonald IA. Dose–response effect of a whey protein preload on within-day energy intake in lean subjects. Brit J Nutr. 2010;**104**(12):1858-67.
11. Holt S. The effects of high-carbohydrate vs high-fat breakfasts on feelings of fullness and alertness, and subsequent food intake. Int J Food Sci. 1999;**50**(1):13-28.
12. Cecil J, Francis J, Read N. Comparison of the effects of a high-fat and high-carbohydrate soup delivered orally and intragastrically on gastric emptying, appetite, and eating behaviour. Physiol Behav. 1999;**67**(2):299-306.

13. Gibbons C, Caudwell P, Finlayson G, Webb D-L, Hellström PM, Näslund E, et al. Comparison of postprandial profiles of ghrelin, active GLP-1, and total PYY to meals varying in fat and carbohydrate and their association with hunger and the phases of satiety. J Clin Endocrinol Metab. 2013;**98**(5):E847-E55.

14. Essah PA, Levy JR, Sistrun SN, Kelly SM, Nestler JE. Effect of macronutrient composition on postprandial peptide YY levels. J Clin Endocrinol Metab. 2007;**92**(10):4052-5.

15. Bowen J, Noakes M, Trenerry C, Clifton P. Energy intake, ghrelin, and cholecystokinin after different carbohydrate and protein preloads in overweight men. J Clin Endocrinol Metab. 2006;**91**(4):1477.

16. Berthoud HR. Homeostatic and non-homeostatic pathways involved in the control of food intake and energy balance. Obesity. 2006;**14**(S8):197S-200S.

17. Finlayson G, King N, Blundell J. Liking vs. wanting food: importance for human appetite control and weight regulation. Neurosci Biobehav Rev. 2007;**31**(7):987-1002.

18. Nijs IM, Muris P, Euser AS, Franken IH. Differences in attention to food and food intake between overweight/obese and normal-weight females under conditions of hunger and satiety. Appetite. 2010;**54**(2):243-54.

19. Davis CA, Levitan RD, Reid C, Carter JC, Kaplan AS, Patte KA, et al. Dopamine for 'wanting' and opioids for 'liking': a comparison of obese adults with and without binge eating. Obesity. 2009;**17**(6):1220-5.

20. Griffioen-Roose S, Mars M, Finlayson G, Blundell JE, de Graaf C. The effect of within-meal protein content and taste on subsequent food choice and satiety. Brit J Nutr. 2011;**106**(05):779-88.

21. Lemmens SG, Martens EA, Born JM, Martens MJ, Westerterp-Plantenga MS. Lack of effect of high-protein vs. high-carbohydrate meal intake on stress-related mood and eating behavior. Nutr J. 2011;**10**(136):22152216.

22. Griffioen-Roose S, Mars M, Siebelink E, Finlayson G, Tomé D, de Graaf C. Protein status elicits compensatory changes in food intake and food preferences. Am J Clin Nutr. 2012;**95**(1):32-8.

23. Griffioen-Roose S, Smeets PA, van den Heuvel E, Boesveldt S, Finlayson G, de Graaf C. Human protein status modulates brain reward responses to food cues. The Am J Clin Nutr. 2014;**100**(1):113-22.

24. Green S, Delargy H, Joanes D, Blundell J. A Satiety Quotient: A Formulation to Assess the Satiating Effect of Food. Appetite. 1997;**29**(3):291-304.

25. Finlayson G, King N, Blundell J. The role of implicit wanting in relation to explicit liking and wanting for food: Implications for appetite control. Appetite. 2008;**50**(1):120-7.

26. Caudwell P, Finlayson G, Gibbons C, Hopkins M, King N, Naslund E, et al. Resting metabolic rate is associated with hunger, self-determined meal size, and daily energy intake and may represent a marker for appetite. Am J Clin Nutr. 2013;**97**(1):7-14.

27. Gibbons C, Caudwell P, Finlayson G, King N, Blundell J. Validation of a new hand-held electronic data capture method for continuous monitoring of subjective appetite sensations. Int J Behav Nutr Phys Act. 2011;**8**(1):57-64.

28. Flint A, Raben A, Blundell J, Astrup A. Reproducibility, power and validity of visual analogue scales in assessment of appetite sensations in single test meal studies. Int J Obes. 2000;**24**(1):38-48.

29. de Graaf C, Schreurs A, Blauw YH. Short-term effects of different amounts of sweet and nonsweet carbohydrates on satiety and energy intake. Physiol Behav. 1993;**54**(5):833-43.

30. Stubbs J, Rowley E, Hughes D, Johnstone A, Reid C, King N, et al. Evaluating a new electronic appetite rating system (EARS). Int J Obes. 1997;**21**:405-15.

31. Johnstone A, Stubbs R, Harbron C. Effect of overfeeding macronutrients on day-to-day food intake in man. Euro J Clin Nutr. 1996;**50**(7):418.

32. Drapeau V, King N, Hetherington M, Doucet E, Blundell J, Tremblay A. Appetite sensations and satiety quotient: predictors of energy intake and weight loss. Appetite. 2007;**48**(2):159-66.

33. Drapeau V, Blundell J, Therrien F, Lawton C, Richard D, Tremblay A. Appetite sensations as a marker of overall intake. Br J Nutr. 2005;**93**(2):273-80.

34. Finlayson G, Arlotti A, Dalton M, King N, Blundell JE. Implicit wanting and explicit liking are markers for trait binge eating. A susceptible phenotype for overeating. Appetite. 2011;**57**(3):722-8.

35. Griffioen-Roose S, Finlayson G, Mars M, Blundell JE, de Graaf C. Measuring food reward and the transfer effect of sensory specific satiety. Appetite. 2010;**55**(3):648-55.

36. Verschoor E, Finlayson G, Blundell J, Markus CR, King NA. Effects of an acute α-lactalbumin manipulation on mood and food hedonics in high-and low-trait anxiety individuals. Brit J Nutr. 2010;**104**(04):595-602.

37. Finlayson G, King N, Blundell J. Is it possible to dissociate liking'and wanting'for foods in humans? A novel experimental procedure. Physiol Behav. 2007;**90**(1):36-42.

38. French SA, Mitchell NR, Finlayson G, Blundell JE, Jeffery RW. Questionnaire and laboratory measures of eating behavior. Associations with energy intake and BMI in a community sample of working adults. Appetite. 2013;**72**:50-8.

39. Dalton M, Blundell J, Finlayson GS. Examination of food reward and energy intake under laboratory and free-living conditions in a trait binge eating subtype of obesity. Front Psychol. 2013;**4**:757.

40. Faul F, Erdfelder E, Lang A-G, Buchner A. G* Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. Behav Res Methods. 2007;**39**(2):175-91.

41. Raben A, Agerholm-Larsen L, Flint A, Holst JJ, Astrup A. Meals with similar energy densities but rich in protein, fat, carbohydrate, or alcohol have different effects on energy expenditure and substrate metabolism but not on appetite and energy intake. Am J Clin Nutr. 2003;**77**(1):91-100.

42. Nutrition TSACo. The Scientific Advisory Committee on Nutrition recommendations on carbohydrates, including sugars and fibre. 2015.

43. Morton G, Cummings D, Baskin D, Barsh G, Schwartz M. Central nervous system control of food intake and body weight. Nature. 2006;**443**(7109):289-95.

44. Havel PJ, Townsend R, Chaump L, Teff K. High-fat meals reduce 24-h circulating leptin concentrations in women. Diabetes. 1999;**48**(2):334-41.

45. Romon M, Lebel P, Velly C, Marecaux N, Fruchart J, Dallongeville J. Leptin response to carbohydrate or fat meal and association with subsequent satiety and energy intake. Am J Physiol Endocrinol Metab. 1999;**277**(5):E855-E61.

46. Romon M, Lebel P, Fruchart J-C, Dallongeville J. Postprandial leptin response to carbohydrate and fat meals in obese women. J Am Coll Nutr . 2003;**22**(3):247-51.

47. Stunkard A, Messick S. The three-factor eating questionnaire to measure dietary restraint, disinhibition and hunger. J Psychosom Res. 1985;**29**(1):71-83.

48. Martin CK, Rosenbaum D, Han H, Geiselman PJ, Wyatt HR, Hill JO, et al. Change in Food Cravings, Food Preferences, and Appetite During a Low Carbohydrate and Low Fat Diet. Obesity. 2011;**19**(10):1963-70.

49. McNeil J, Doucet É. Possible factors for altered energy balance across the menstrual cycle: a closer look at the severity of PMS, reward driven behaviors and leptin variations. Eur J Obstet Gynecol Reprod Biol. 2012;**163**(1):5-10.

50. McNeil J, Cameron JD, Finlayson G, Blundell JE, Doucet E. Greater overall olfactory performance, explicit wanting for high fat foods and lipid intake during the mid-luteal phase of the menstrual cycle. Physiol Behav. 2013;**112-113**:84-9.

49. Pagoto SL, Appelhans BM. A call for an end to the diet debates. Jama. 2013;**310**(7):687-8.

50. Lissner L, Levitsky DA, Strupp BJ, Kalkwarf HJ, Roe DA. Dietary fat and the regulation of energy intake in human subjects. Am J Clin Nutr. 1987;**46**(6):886-92.

51. Tobias DK, Chen M, Manson JE, Ludwig DS, Willett W, Hu FB. Effect of low-fat diet interventions versus other diet interventions on long-term weight change in adults: a systematic review and meta-analysis. Lancet Diabetes Endocrinol. 2015; **3**, 12, 968–979.

52. McNeil J, Doucet É. Possible factors for altered energy balance across the menstrual cycle: a closer look at the severity of PMS, reward driven behaviors and leptin variations. Eur J Obstet Gynecol Reprod Biol. 2012;**163**(1):5-10.

53. McNeil J, Cameron JD, Finlayson G, Blundell JE, Doucet E. Greater overall olfactory performance, explicit wanting for high fat foods and lipid intake during the mid-luteal phase of the menstrual cycle. Physiol Behav. 2013;**112-113**:84-9.

FIGURE LEGENDS

FIGURE 1:

Figure 1: Mean (SEM) total daily energy intake and energy intake during separate meals during the high fat/low carbohydrate and low fat/high carbohydrate conditions. HFLC, high fat, low carbohydrate; LFHC, low fat, high carbohydrate. *Significant difference in breakfast intakes ($P < 0.05$). **Significant difference in dinner intakes ($P < 0.05$). ***Significant difference in total daily energy intake as indicated by a two-way ANOVA with repeated measures ($P < 0.05$).

FIGURE 2:

Figure 2: Mean (SEM) post-prandial changes in the satiety quotient following the consumption of *ad libitum* high fat/low carbohydrate and low fat/high carbohydrate breakfast (Panel A) and fixed energy lunch meals (Panel B). HFLC, high fat, low carbohydrate; LFHC, low fat, high carbohydrate. *Significant difference in the satiety quotient between conditions as indicated by a two-way ANOVA with repeated measures ($P < 0.01$).

FIGURE 3:

Figure 3: Mean (SEM) explicit liking (Panel A) and implicit wanting (Panel B) appeal bias scores for high fat foods relative to low fat foods before and after consumption of isoenergetic high fat/low carbohydrate and low fat/high carbohydrate meals. HFLC, high fat, low carbohydrate; LFHC, low fat, high carbohydrate. *Significant difference in energy intake between conditions as indicated by a two-way ANOVA with repeated measures ($P < 0.05$).

TABLE 1

Table 1: Mean (± SD) descriptive characteristics for participants (n = 65).

	Whole Group	**Males**	**Females**
Age (yrs)	41.3 ± 8.7	41.5 ± 7.7	41.3 ± 9.3
BMI (kg/m^2)	30.9 ± 3.8	30.6 ± 4.4	31.0 ± 3.5
Body Fat (%)	39.3 ± 7.5	32.8 ± 5.9	43.6 ± 5.2
Fat Mass (kg)	35.4 ± 9.3	32.8 ±10.8	37.2 ± 7.9
Fat-Free Mass (kg)	54.5 ± 10.4	64.8 ± 6.8	47.7 ± 5.9
RMR (kcal$\cdot$day^{-1})	1756.5 ± 340.7	2037.0 ± 283.4	1558.3 ± 197.9

BMI, body mass index; RMR, resting metabolic rate. Body composition was measured using air displacement plethysmography while resting metabolic rate was measured using indirect calorimetry. Details of the procedures used can be found elsewhere(26).

TABLE 2

Table 2. Nutritional characteristics for food images and food categories used in the Leeds Food Preference Questionnaire.

High Fat / Low Carbohydrate	**% CHO**	**% Protein**	**% Fat**	**Kcal/serving**	**Low Fat / High Carbohydrate**	**% CHO**	**% Protein**	**% Fat**	**Kcal/serving**
Salted peanuts	6.5	18	73.8	364	**Savoury biscuits**	64.2	12.4	19.4	**480**
Crisps	37.9	3.6	58.4	336	**Pilau rice**	86.6	10.3	3.1	**145**
Swiss cheese	0.1	24.4	75.5	250	**New potatoes**	90.8	8.4	0.8	**150**
Chips	48	4	48	361	**Bread roll**	73.0	14.0	13.0	**265**
Milk chocolate with nuts (Galaxy)	32.5	5.2	62.3	469	**Marshmallows**	94.1	4.9	0.7	**384**
Jam doughnut	44.9	6.6	48.5	380	**Popcorn**	89.0	3.0	7.0	**390**
Cream cake	42.1	6.1	49.7	198	**Jelly babies**	91.0	6.7	2.0	**344**
Shortbread	47.1	5.1	47.7	102	**Fruit salad**	84.0	4.0	12.0	**130**
Mean HFLC	**32.4**	**9.1**	**58.0**	**307**	**Mean LFHC**	**84.1**	**8.0**	**7.3**	**286**

CHO, carbohydrate; HFLC, high fat, low carbohydrate; LFHC, low fat, high carbohydrate.

TABLE 3

Table 3: Correlation coefficients between measures of explicit liking and implicit wanting and *ad libitum* dinner intake during the HFLC and LFHC conditions ($N = 65$).

	Explicit Liking: Hungry State	**Explicit Liking: Fed State**	**Implicit Wanting: Hungry State**	**Implicit Wanting: Fed State**
HFLC Dinner Intake (kcal)	r = 0.313*, R^2 = 0.098	r = 0.302*, R^2 = 0.091	r = 0.271*, R^2 = 0.074	r = 0.408**, R^2 = 0.167
LFHC Dinner Intake (kcal)	r = 0.342*, R^2 = 0.117	r = 0.369*, R^2 = 0.136	r = 0.315*, R^2 = 0.099	r = 0.453**, R^2 = 0.206

HFLC, high fat, low carbohydrate; LFHC, low fat, high carbohydrate. *$P < 0.05$; **$P < 0.001$. Simple linear regression was used to examine the relationships between explicit liking and implicit wanting and *ad libitum* dinner meal intake.