1 **Differing Effects of High Fat or High Carbohydrate Meals on Appetite and Food**

2 **Hedonics in Overweight and Obese Individuals.**

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35 HFLC, high fat/low carbohydrate foods; LFHC, low fat/high carbohydrate foods; SQ,
36 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

92 high protein foods[22] and the neural activation to savoury food cues in brain reward

93 regions[23] compared to a high protein diet (2.0 g protein·kg body weight^{-1}·d^{-1}).

94 While these data suggest that dietary macronutrients may also differentially effect

95 food hedonics, the acute effects of macronutrient composition, and in particular,

96 dietary fat, on food hedonics has yet to be examined. Given the controversy over the

97 relative contribution of dietary fat and carbohydrate in promoting overconsumption

98 and weight gain, this warrants further attention. Therefore, the aim of the present

99 study was to examine the effects of *ad libitum* and isoenergetic meals varying in

100 dietary fat and carbohydrate on energy intake, satiety and food hedonics in

101 overweight and obese individuals.

102 **METHODS**

103 **Participants**

104 In all, sixty-five overweight and obese males (*N* = 26) and females (*N* = 39) were

105 recruited onto this randomised, crossover design study. Descriptive characteristics of

106 participants are displayed in Table 1. All participants were non-smokers, physically

107 inactive (≤ 2 hrs·wk^{-1} of exercise over the previous six months), weight stable (± 2 kg

108 for the previous three months) and not taking medication known to affect metabolism

109 or appetite. This study was conducted according to the guidelines laid down in the

110 Declaration of Helsinki, and ethical approval was granted by the Leeds West National

111 Health Service Research Ethics Committee (09/H1307/7). All participants provided

112 written informed consent before taking part. The project was registered under

113 international standard identification for controlled trials ISRCTN47291569.

114

115 *Table 1 here.....*

116 **Study Design**

117 Participants completed two separate probe test meal days in a randomised order in

118 which they consumed either high fat/low carbohydrate (HFLC) or low fat/high

119 carbohydrate (LFHC) meals across the day that were matched for sensory properties

120 and taste. Total daily energy intake was measured using a laboratory-based test meal

121 design that included fixed energy and *ad libitum* meals, while satiation (energy intake

122 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 $56.0 \pm 3.2\%$, $13.9 \pm 2.1\%$, and $30.1 \pm 3.9\%$, and $23.0 \pm 3.3\%$, $13.5 \pm 1.5\%$, and $63.5 \pm 4.4\%$, 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

154 individual food items, macronutrient composition and weight of food consumed can

155 be found in Supplementary Table S1 and elsewhere[26].

156 All meals consumed in the research unit were eaten in isolation, with participants

157 instructed to eat as much or as little as they wanted until comfortably full during *ad*

158 *libitum* meal consumption. Food was provided in excess of expected consumption,

159 with participants able to request further food or water if required. Prior to

160 participation individuals completed a food preference questionnaire, and if they

161 strongly disliked any of the test foods, participants were excluded if a suitable

162 alternative (matched for macronutrient composition) could not be found. Energy

163 intake was calculated by weighing the food before and after consumption (to the

164 nearest 0.1 g), and with reference to the manufacturers' energy values. To calculate

165 test meal energy intake, the energy equivalences used for protein, fat and

166 carbohydrate were 4, 9 and 3.75 kcal·g^{-1}, respectively. Total daily energy intake was

167 taken as the energy consumed during the breakfast, lunch and dinner meals, and

168 intake from the snack box. Energy intake during the *ad libitum* breakfast and dinner

169 meals was used to represent satiation in the present paper.

170 **Subjective Appetite Ratings**

171 Subjective ratings of appetite were measured during test meal probe days using visual

172 analogue scales presented on a validated hand-held electronic appetite rating system

173 (EARS II)[27]. On each day, ratings were recorded immediately before and after a

174 meal, and at hourly intervals throughout the day (from 0800 to 1800 hours). The use

175 of visual analogue scales for the measurement of subjective appetite has previously

176 been shown to be valid and reproducible[28]. Furthermore, visual analogue scales have

177 been used to detect changes in appetite following manipulations of energy intake[29, 30]

178 and diet composition[31], while the EARS II electronic rating system has been

179 validated against the traditional pen and paper technique[27].

180 **Satiety**

181 The suppression of hunger per calorie of intake for the *ad libitum* breakfast meal and

182 fixed energy lunch meals was assessed by calculating the satiety quotient (SQ). The

183 SQ was developed by Green et al.[24], and expresses changes in post-prandial appetite

184 ratings relative to the energy content of a meal. As such, it reflects the capacity of a

185   meal to modulate the strength of post-prandial satiety sensations. The SQ of a meal

186   was calculated using the following formula using subjective hunger ratings[24], with a

187   higher SQ indicative of a greater satiating efficiency:

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

188

189   It has been suggested that the SQ provides a better marker of satiety than post-

190   prandial hunger ratings, as it takes into account both the pre-meal appetite sensations

191   and the energy content of the meal consumed[32]. The SQ has also been shown to be

192   associated with *ad libitum* food intake following a variety of nutritional

193   interventions[32, 33].

Hedonic Assessment of HFLC and LFHC Foods

195   Immediately prior to and following the fixed energy lunch meal, the hedonic profile

196   of an array of foods was assessed using the Leeds Food Preference Questionnaire[25].

197   The LFPQ provides measures of different components of food preference and

198   hedonics. Participants are presented with an array of pictures of individual food items

199   common in the diet. Foods in the array are chosen by the experimenter from a

200   validated database to be either predominantly high (> 45% energy) or low (< 20%

201   energy) in fat but similar in familiarity, protein content, sweet or non-sweet taste and

202   acceptability. Each food category was represented by eight photographs of ready-to-

203   eat foods. Details of the mean energy density, serving and macronutrient composition

204   of food items and categories' used in the LFPQ can be found in Table 2. The LFPQ

205   has been validated against physiological and behavioural endpoints in a range of

206   research[34-36]. The specific endpoints examined from the LFPQ were explicit liking,

207   implicit wanting and food preference for HFLC relative to LFHC foods, as described

208   below. The LFPQ has been shown to demonstrate reliable immediate and post-meal

209   changes[37], and is a good predictor of food choice and intake in laboratory and

210   community-based samples[22, 38].

211   *Table 2 here....*

212   **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)

279 and LFHC (785.8 ± 2.9 kcal; $P > 0.05$) lunch meals. In order to examine the effects of

280 macronutrient composition on satiation (i.e. energy intake during a single meal)

281 during the *ad libitum* breakfast and dinner meals, energy intake during the separate

282 test meals was examined. A two-way ANOVA (meal*macronutrient composition)

283 with repeated measures indicated a significant main effect of meal ($F_{(2.54, 162.81)}$ =

284 35.926; $P < 0.001$; $\eta^2 = 0.360$) and macronutrient composition ($F_{(1, 64)}$ = 156.953; $P <$

285 0.001; $\eta^2 = 0.710$). There was also a significant meal*macronutrient composition

286 interaction ($F_{(2.10, 134.64)}$ = 36.045; $P < 0.001$; $\eta^2 = 0.360$), such that energy intake was

287 significantly higher at breakfast (337.2 ± 44.2 kcal; $P < 0.001$) and dinner (531.8 ±

288 35.2 kcal; $P < 0.001$) during the HFLC condition compared to the LFHC condition

289 (Figure 1).

290

291 *Figure 1 here....*

292

293 **The Effect of Macronutrient Composition on Satiety Following *Ad Libitum***

294 **Breakfast Meal Consumption**

295

296 There was a significant effect of macronutrient composition on SQ following the

297 consumption of the *ad libitum* breakfast meal, with a two-way ANOVA

298 (time*macronutrient composition) with repeated measures indicating a significant

299 main effect of time ($F_{(1.49, 95.49)}$ = 97.024; $P < 0.001$; $\eta^2 = 0.603$) and macronutrient

300 composition ($F_{(1, 64)}$ = 8.072; $P = 0.006$; $\eta^2 = 0.112$). Furthermore, there was a

301 significant time*macronutrient composition interaction ($F_{(2.27, 143.20)}$ = 19.687; $P <$

302 0.001; $\eta^2 = 0.235$), such that the LFHC breakfast SQ was significantly higher than the

303 HFLC breakfast SQ immediately after ($P < 0.001$) and at 60 ($P < 0.001$) and 120

304 minutes post meal consumption ($P = 0.001$; Figure 2).

305

306 *Figure 2 here.....*

307

308 **The Effect of Macronutrient Composition on Satiety Following Consumption of**

309 **the Isoenergetic Lunch Meal**

310

311 There was also an effect of macronutrient composition on SQ following consumption

312 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; $P < 0.001$; η^2 = 0.632). There was also a significant main effect of macronutrient composition ($F_{(1, 64)}$ = 11.314; $P = 0.001$; η^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; $P = 0.945$; η^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; $P = 0.005$; η^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; $P = 0.017$; η^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; $P = 0.031$; η^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; $P = 0.652$; η^2 = 0.001), and the macronutrient composition*hunger state interaction approached significance ($F_{(1, 64)}$ = 2.851; $P = 0.096$; η^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).

347

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

350

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

357

358 *Table 3 here....*

359

360 **DISCUSSION**

361

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

376

The Effects of Macronutrient Composition on Satiety and Food Intake

378 A clear effect of macronutrient composition on energy intake was observed in the
379 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 $30.1 \pm 3.9\%$ (as opposed to $63.5 \pm 4.4\%$ 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

446 observed differences in post-meal liking and wanting were due to differences in the
447 meal characteristics rather than a 'carryover' effect from breakfast.

448

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

467

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

480 further research is needed to examine the long-term effects of diets varying in
481 macronutrient composition on food hedonics.

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

498 **Conclusions**

499

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

510 **FINANCIAL SUPPORT:**

511

517

518 **CONFLICT OF INTEREST:**

519

520 The authors declare no conflict of interest.

521

522 **AUTHORSHIP:**

523 The authors' contributions are as follows: MH contributed to the data collection, data

524 analyses and wrote the manuscript. CG and PC contributed to the study design and

525 data collection. JEB contributed to the study design, interpretation of data and writing

526 of the manuscript. GF contributed to the study design, data analyses, interpretation of

527 data and writing of the manuscript. All authors read and approved the final version of

528 the manuscript.

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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 ($P < 0.05$).

711 **TABLE 1**

712 **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·day^{-1})	1756.5 ± 340.7	2037.0 ± 283.4	1558.3 ± 197.9

713 BMI, body mass index; RMR, resting metabolic rate. Body composition was

714 measured using air displacement plethysmography while resting metabolic rate was

715 measured using indirect calorimetry. Details of the procedures used can be found

716 elsewhere[26].

717 **TABLE 2**

718 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**

719 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.