Food reward in active compared to inactive men: Roles for gastric emptying and body fat

Horner, Katy M.; Finlayson, Graham S; Byrne, Nuala M.; King, Neil A.

Published in:
Physiology and Behavior

DOI:
10.1016/j.physbeh.2016.04.009

Title 1: Food reward in active compared to inactive men: Roles for gastric emptying and body fat

Authors: Katy M Horner[1,2], Graham Finlayson[3], Nuala M Byrne[1,4] , Neil A King[1]

Departmental and Institutional Affiliations:

[1]School of Exercise and Nutrition Sciences and Institute of Health and Biomedical Innovation, Queensland University of Technology, Brisbane, Australia

[2]Institute of Food and Health, University College Dublin, Dublin 4, Ireland

[3]School of Psychology, Faculty of Medicine and Health, University of Leeds, UK

[4]Bond Institute of Health and Sport, Faculty of Health Sciences and Medicine, Bond University, Gold Coast, Australia

Running Head: Food Hedonics, Gastric Emptying, Activity

Corresponding Author:

Katy Horner,
Institute of Food and Health,
University College Dublin,
Dublin 4,
Ireland.
Email: katyhorner@gmail.com

Abstract

Habitual exercise could contribute to weight management by altering processes of food reward via the gut-brain axis. We investigated hedonic processes of food reward in active and inactive men and characterised relationships with gastric emptying and body fat. Forty-four men (Active: n=22; Inactive: n=22, BMI range 21-36 kg/m^2; percent fat mass range 9-42%) were studied. Participants were provided with a standardised fixed breakfast and an ad libitum lunch meal 5h later. Explicit liking, implicit wanting and preference among high-fat, low-fat, sweet and savoury food items were assessed immediately post-breakfast (fed state) and again pre-lunch (hungry state) using the Leeds Food Preference Questionnaire. Gastric emptying was assessed by ^{13}C-octanoic acid breath test. Active individuals exhibited a lower liking for foods overall and a greater implicit wanting for low-fat savoury foods in the fed state, compared to inactive men. Differences in the fed state remained significant after adjusting for percent fat mass. Active men also had a greater increase in liking for savoury foods in the interval between breakfast and lunch. Faster gastric emptying was associated with liking for savoury foods and with an increase in liking for savoury foods in the postprandial interval. In contrast, greater implicit wanting for high-fat foods was associated with slower gastric emptying. These associations were independent of each other, activity status and body fat. In conclusion, active and inactive men differ in processes of food reward. The rate of gastric emptying may play a role in the association between physical activity status and food reward, via the gut-brain axis.

Keywords: liking; wanting; gastric emptying; physical activity.

Introduction

Epidemiological studies consistently show that individuals who are physically active are less likely to gain weight over time [1]. One hypothesis to explain why physical activity is crucial for weight maintenance is that human physiology is biased towards maintaining energy balance at a high energy flux (i.e. a high level of energy intake and energy expenditure) [2]. In support of this hypothesis, in an early study of 213 workers with varying occupations in West Bengal (India), Mayer [3] demonstrated that energy intake was more closely matched to energy expenditure in physically active compared to sedentary workers. More recent evidence from both cross-sectional and longitudinal studies further supports a role for physical activity in improved short-term appetite control [4], [5], [6], [7], [8]. Blundell [9] termed the sedentary range ‘ the zone of dysregulation’ and proposed that people living in this zone are at a greater risk of overeating due to the lack of physiological regulation that occurs within this range. The underlying mechanisms however remain to be fully determined.

Day-to-day food intake involves the coordination of both non-homeostatic and homeostatic signals, including psychological, physiological, behavioural and neural events [10] which interact to form part of a ‘psychobiological system’ controlling appetite [11]. Food preferences and reward pathways can exert a strong influence on food intake. Weight control can be enhanced or undermined by the influence of exercise on hedonic processes of ‘liking’ and ‘wanting’ for food which in turn alter food preference [12], [13]. For example, the impact of exercise on fat mass loss has been shown to be diminished in some overweight and obese individuals who exhibit increased explicit liking and wanting for food (particularly, high fat sweet foods) post-exercise [13]. However, whether food hedonics differ between habitually active versus inactive individuals has not been examined.

Physiological signals arising from the gastrointestinal (GI) tract could also have a mechanistic role in the influence of physical activity on appetite control [7], [14]. Gut peptides released from the GI tract and gastric emptying (the rate at which food empties from the stomach) play an important integrative relationship in the short-term control of food intake [15], and are altered by physical activity level [16], [17]. We recently observed gastric emptying was faster in habitually active compared to inactive men and was associated with activity energy expenditure [17]. A growing body of work has demonstrated interactions between the food reward system and signals from the GI tract [10], [18], [19], [20], [21]. Therefore, it is possible that signals from the GI tract could interact with reward signals to influence food intake with habitual physical activity.

However, to the best of our knowledge, associations between hedonic processes of food reward and gastric emptying have not been previously investigated in humans.

Examining the relationships between gastrointestinal signalling and psychological processes involved in the control of food intake could improve the understanding of mechanisms involved in the impact of habitual physical activity on energy balance. In the current study, we aimed to 1) examine whether food preferences and implicit and explicit hedonic processes of ‘liking’ and ‘wanting’ differ between active and inactive men, and 2) determine whether gastric emptying predicts differences in food hedonics, with and without adjusting for body fat. As fat mass has been shown to correlate with eating behaviour and hedonic processes in overweight and obese individuals [22], [23], differences in body composition could be a confounding factor when comparing food reward between active and inactive individuals. Adjusting for body fat will allow effects of physical activity to be explored while controlling for fat mass.

Materials and Methods

Design

Participants in this between groups design study undertook two separate test mornings one week apart: (1) body composition and energy expenditure assessment and 2) appetite behaviour/gastric emptying assessment. Measures including body composition (assessed by air displacement plethysmography), energy expenditure (activity energy expenditure assessed by accelerometery, resting energy expenditure by indirect calorimetry) and gastric emptying (assessed by ^{13}C-octanoic acid breath test) were taken as previously reported [17].

Participants

Forty-four men were studied. The sample size (n=22 Active and n=22 Inactive) was selected to detect a minimum 10% difference between groups for the main GE outcome measure [24]. Inclusion criteria were: male, aged 18-55 yrs, BMI 18-40 kg/m^2, weight stable (< ±4 kg change over last 6 months), no history of GI surgery or disorder, non-diabetic, no medical conditions and not taking medication known to influence gastric emptying or appetite, willing to consume study test breakfast and lunch meals and not a heavy smoker (<10 per day). Participants were classified based on their self-reported physical activity patterns over the last 6 months as either inactive (undertaking ≤1 structured exercise session per week and not engaged in strenuous work) or active (undertaking ≥4 structured exercise sessions per week). Individuals who did not fit either category were excluded. One exercise session was defined as at least 40 minutes of moderate to high intensity activity [4]. The study was conducted according to the guidelines laid down in the Declaration of Helsinki and ethical approval was granted by Queensland University of Technology Research Ethics Committee. All participants provided written informed consent.

Appetite Behaviour and Gastric Emptying Assessment Day Protocol

Participants attended the laboratory after a 12-hour overnight fast, and having avoided alcohol and strenuous exercise for 24 hours. Participants were provided with a fixed pancake breakfast labelled with 100mg ^{13}C-octanoic acid (Cambridge Isotope Laboratories, Andover, USA), and spread with butter and strawberry jam [1676 kJ (400 kcal); 15g (15%) PRO, 17g (37%) Fat, 48g (48%) CHO)],and a 250ml drink of water. The test meal and drink were consumed within 10 minutes. Gastric emptying of the meal was assessed by ^{13}C-Octanoic acid breath test as described [24]. Breath samples were collected in 10ml glass Exetainer tubes (Labco, Buckinghamshire, UK) prior to the breakfast, immediately after, and subsequently every 15 minutes for 5 hours [24]. Data were analysed according to Ghoos et al. [25] as described [24] and the two main parameters lag time (t_{lag}), reflecting the initial emptying rate, and half time ($t_{1/2}$) were used in the present analyses. Participants remained in the laboratory in sedentary activities throughout the test morning. A lunch meal was served 5h after breakfast in the laboratory.

Subjective Appetite Sensations and Test Meal Palatability

Subjective appetite sensations were measured immediately before and after breakfast, and periodically during the postprandial period using an electronic appetite rating system [26]. Participants were asked to rate feelings of hunger, fullness and desire to eat on 100 mm visual analogue scales, anchored at each end with the statements “not at all” and “extremely”. Five hour postprandial area under the curve (AUC) was calculated using the trapezoidal rule.

To assess palatability of the test meal, six questions concerning sweet, savoury, tasty, pleasant, filling and satisfying ratings were assessed on a 100mm scale using an identical electronic appetite rating system [26] immediately post consumption of the fixed breakfast meal.

Food Reward Assessment; Preferences, ‘Liking’ and ‘Wanting’

Our operational definition of reward-value is through explicit liking and implicit wanting responses to high fat versus low fat and sweet versus savoury images of food. Food preferences and ‘liking’ and ‘wanting’ were examined immediately after breakfast consumption (fed state) which was repeated 5h later prior to lunch (hungry state) using a computer-based procedure - the Leeds Food Preference Questionnaire (LFPQ, for a detailed description see [27]). The LFPQ has been shown to demonstrate reliable immediate post-meal changes [27], is sensitive to changes in sensory specific satiation [28] and is a good predictor of food choice and intake in both laboratory and community settings [29], [30].

The LFPQ included 16 photographic food images administered using experiment software (E-prime v.1.2, Psychology Software Tools, ND). The foods were organised into separate categories of high fat savoury (HFSA), low fat savoury (LFSA), high fat sweet (HFSW) and low fat sweet (LFSW) (**Table 1**).

[Table 1 About Here]

Using the LFPQ, explicit ‘liking’ (the conscious feeling of pleasure expected from tasting each food [27]) was measured by presenting each food image one at a time on the computer screen and participants were asked to rate their perceived pleasantness of that food on a 100mm visual analogue scale, anchored at each end with ‘not at all’ and ‘extremely’. Mean ratings for each category were calculated. A higher score indicates a higher explicit ‘liking’ for that category. Implicit wanting was assessed according to each participant’s reaction time in selecting a type of food during each forced choice trial, adjusting for the frequency of selection and overall mean response time.

Preference for fat and sweet/savoury taste were evaluated by computing the fat bias (high fat > low fat) and the taste bias (sweet > savoury) scores for explicit liking and implicit wanting. The fat bias was calculated as the mean score for high fat foods minus the mean score for low fat foods. Thus a positive number indicates a high fat food bias and a negative number a low fat food bias. The taste bias was calculated as the mean score for sweet foods minus the mean score for savoury foods. Thus, a positive number indicates a sweet taste bias and a negative number a savoury taste bias.

Statistical Analysis

Data are expressed as mean ± SEM unless otherwise stated. Differences between active and inactive groups were assessed by t test. To assess whether differences in percent fat mass (FM) contributed to these findings, the data were further analysed using ANCOVA, with percent FM as a covariate and activity status (active or inactive) as the independent factor. Changes from post-breakfast to pre-lunch were assessed by Repeated Measures ANOVA. Pearson correlation coefficients and multiple regression analyses were used to determine relationships between gastric emptying lag and half times, and process of food reward. To examine any influence of percent FM on the relationships observed, partial correlations were also undertaken controlling for percent FM. Statistical analysis was performed using PASW Statistics 18.0 (SPSS Inc., Chicago, IL) and Graph Pad Prism version 6.0 for Mac (GraphPad Software, San Diego, CA, USA). Statistical significance was set at $P < 0.05$ unless otherwise stated.

Results

Participant Characteristics

Mean anthropometric, body composition, energy expenditure and physical activity characteristics were reported previously [17]. Key anthropometric, body composition and energy expenditure characteristics are summarised in **Table 2.** No participants were elite athletes. Gastric emptying was significantly faster in the active compared to inactive group (lag time (t_{lag}): active: 95±13 and inactive: 110±16 min, $P < 0.001$; half time ($t_{1/2}$): active: 157±18 and inactive, 179±21 min, $P < 0.001$).

Both active and inactive groups displayed meal-related oscillations in subjective sensations of hunger, fullness and desire to eat, but ratings did not differ significantly between active and inactive groups ($p > 0.05$, **Supplementary Figure 1**). Palatability ratings (tasty, savoury, sweet, pleasant) of the fixed breakfast test meal did not significantly differ between the two groups ($P > 0.05$ for all, **Supplementary Table 1**).

[Table 2 About Here]

Food Reward; Explicit Liking and Implicit Wanting

Comparison of Active and Inactive men in fed and hungry states

Active men showed a lower 'liking' for HFSA, HFSW, LFSW and for foods overall when fed compared to inactive men (**Table 3**). The lower 'liking' for LFSW and for foods overall remained significant after adjusting for percent FM (**Table 3**). In the hungry state, there were no significant differences in 'liking' between active and inactive men. However, active men had a greater implicit wanting for LFSA foods in both the fed and hungry states compared to inactive men (**Table 3**). This remained significant after adjusting for percent FM in the fed but not hungry state (**Table 3**).

[Tables 3 and 4 About Here]

Changes over time during the post prandial interval

As expected, ratings of liking and wanting assessed by the LFPQ changed over time during the test morning from breakfast (i.e. fed state) to lunch 5h later (i.e. hungry state). Changes in explicit liking for all foods and separate food categories from breakfast to lunch are shown in **Figure 1**. Active men had a greater increase in explicit liking for all food categories combined (assessed by LFPQ) between breakfast and lunch compared to inactive men ($F(1, 42) = 4.13$, $P = 0.048$), and particularly for savoury foods (**Figure 1**). Trends in the differences observed between active and inactive men remained after adjusting for percent FM (Liking All: $P = 0.05$; Liking LFSA: $P = 0.05$; Liking HFSA: $P = 0.07$).

[Figure 1 About Here]

No significant differences in changes in implicit wanting over the postprandial interval were observed between active and inactive men (**Table 4**).

Relationship of Food Reward Profiles with Gastric Emptying

Gastric emptying was negatively correlated with the increase in liking for LFSA foods ($t_{1/2}$: $r=-0.34$, $P = 0.02$) and increase in liking taste bias towards savoury foods (t_{lag}: $r = -0.30$, $P = 0.048$; $t_{1/2}$: $r = -0.30$, $P = 0.045$) in the post prandial interval between breakfast and lunch. In addition, gastric emptying was positively correlated with the liking taste bias for savoury foods when hungry (t_{lag}: $r = 0.48$, $P < 0.01$; $t_{1/2,}$ **Figure 2a**) and the average (average of fed and hungry states) liking taste bias (t_{lag}: $r = 0.44$, $P < 0.01$; $t_{1/2}$: $r = 0.36$, $P = 0.02$). These correlations indicate faster gastric emptying was associated with greater liking for savoury foods. Liking fat bias was not significantly correlated with gastric emptying ($P > 0.05$ for all).

Implicit wanting taste bias was not associated with gastric emptying ($P > 0.05$ for all). However, implicit wanting fat bias was positively correlated with gastric emptying when fed ($t_{1/2}$: $r = 0.37$, $P = 0.01$), and 5-hours later when hungry (t_{lag}: $r = 0.31$, $P = 0.04$; $t_{1/2}$: **Figure 2b**) and the average implicit wanting fat bias ($t_{1/2}$: $r = 0.40$, $P < 0.01$). These findings collectively indicate slower gastric emptying was associated with greater implicit wanting for high fat foods.

To examine any influence of body composition on the relationships observed, partial correlations were also undertaken. The significant correlations reported between food reward profiles and gastric emptying remained significant after controlling for body composition (BMI or percent FM) ($P < 0.05$ for all).

[Figure 2 About Here]

Regression analysis revealed associations of gastric emptying $t_{1/2}$ with liking taste bias and implicit wanting fat bias were independent of each other and activity status (gastric emptying $t_{1/2}$ Model Adjusted $R^2 = 0.37$, $p < 0.01$; activity status $\beta = 0.37$, $P < 0.01$; liking taste bias $\beta = 0.30$, $P = 0.02$; wanting fat bias $\beta = 0.28$, $P = 0.03$). When BMI or percent FM were included in the same model, they did not contribute to any of the variance (BMI $\beta = 0.01$, $P = 0.99$; percent FM $\beta = 0.00$, $P = 0.99$) and the observed associations remained significant, indicating they were independent of body fat.

Discussion

This is the first study to compare measures of food reward and gastric emptying between active versus inactive individuals. Our results demonstrate that food reward differs between active versus inactive men and suggests that gastric emptying could have a mechanistic role in 'liking' and 'wanting' processes of food reward.

Using a computer based assessment procedure, we observed that both explicit 'liking' and implicit 'wanting' differed between active and inactive men. Firstly, active men displayed a lower explicit liking for HFSA, LFSW and foods overall and showed a greater implicit wanting for LFSA in the fed state, compared to inactive men. Elevated 'liking' and 'wanting' for energy dense foods are considered psychological markers in individuals who are susceptible to overconsumption [31] and involve both conscious (subjective, explicit) and subconscious (automatic, implicit) processes [27], [32]. Indeed, one salient characteristic of individuals who binge eat appears to be the persistent preference for sweet foods in the presence and absence of hunger, which has been demonstrated under both laboratory and free-living conditions [33], using identical methodology as the present study. Dalton et al. [34] reported that binge eaters had a greater explicit 'liking' for HFSW foods and a greater implicit wanting for sweet foods in the fed state compared to non-binge eaters, suggesting these characteristics may represent a marker for susceptibility to overeat. The hedonic characteristics observed in binge-eaters are in contrast to the active individuals in our study. The hedonic characteristics observed in the active individuals including lower liking for foods and a greater implicit wanting for LFSA foods in the fed state could be one potential factor contributing to improved appetite and body weight regulation that has previously been documented in more active individuals [1], [3], [4], [6], [9].

We further observed that active men had a greater increase in 'liking' for all foods, in particular savoury foods between breakfast (fed state) and lunch (hungry state - 5h after breakfast) This is suggestive of a more sensitised appetite system in active compared to inactive men. 'Liking' for food has previously been shown to be greater when individuals are in a hungry (3-4 hours postprandial) versus fed state [27], whereas this effect is reduced in individuals with higher binge eating scores [35]. The greater increase in liking of savoury foods observed between the fed and hungry states in active individuals may indicate that hedonic responses function more in response to nutritional need-state in habitual exercisers compared to inactive individuals.

Interestingly, when compared to savoury foods, liking for sweet foods increased to a lesser extent between the fed (post-breakfast) and hungry (pre-lunch) state and this was apparent in both active and inactive men. It has previously been shown that 'liking' for sweet foods does not increase to the same extent as fatty foods in hungry compared to fed conditions [27]. Moreover, following a 24h fast, Cameron et al. [36] reported that 'liking' for savoury foods was greater in the hungry versus fed state, whereas 'liking' for sweet foods was unchanged. While historically, hedonic processes have been viewed as a function of nutritional need-state [27] - whereby in a state of depletion, the hedonic response (experienced palatability or pleasure) to foods is enhanced and when replete, the hedonic effect is reduced [37] - it is increasingly recognised that palatable sugar- and fat-rich foods can override satiation and promote overeating [38]. Hedonic responses to palatable sweet foods may therefore be less dependent on sensations of satiation and satiety than savoury foods. This may in part explain the blunted change in liking for sweet foods between the fed (post-breakfast) and hungry (pre-lunch) state that we and others [27], [36] have reported.

As could be expected, body composition differed significantly between active and inactive men and therefore could provide one plausible mechanism for the differences in food reward observed. Indeed, after adjusting for body fat, no significant differences in hedonic processes were observed in the hungry state between active and inactive groups, while in the fed state the higher liking for HFSA foods observed in inactive individuals no longer remained significant. This suggests that factors other than physical activity status, including body fat may contribute to hedonic processes in the hungry state and liking for high-fat foods in the fed state. Others have recently reported positive relationships between fat mass and wanting for high fat foods in particular, in overweight and obese individuals [22]. Nevertheless, the majority of differences observed between active and inactive men in the present study including liking for foods overall, liking for LFSW foods and implicit wanting for LFSA foods in the fed state, along with increases in liking for foods overall and LFSA foods in the postprandial interval, remained significant after adjusting for differences in body fat. These findings suggest physical activity status influences these hedonic processes, independent of body fat.

Differences in gut physiology could be one potential mechanism contributing to the differences in food reward we observed between active and inactive individuals in the present study. The inactive individuals had a slower gastric emptying and slower gastric emptying was associated with a higher fat mass as we recently reported [17]. A major aim of the present investigation was to examine potential associations between hedonic processes and gastric emptying. The phenomenon that information from the gut during a meal leads not only to decreased hunger and satiation but also to a feeling of reward is certainly not new [39], [40]. However, the signals and mechanisms involved remain to be fully elucidated. In our cross-sectional analyses of active and inactive men, we found that faster gastric emptying was associated with greater liking of savoury food whereas slower gastric emptying was associated with greater implicit wanting for high fat food. These relationships were independent of each other activity status and body fat and suggest that gastric emptying may have a mechanistic role in food reward. Our finding that faster gastric emptying was associated with enhanced ‘explicit’ liking for savoury foods and with an increase in liking for savoury foods between the fed and hungry state is consistent with the view that hedonic responses to savoury foods may be associated with nutritional-need state i.e. the less food remaining in the stomach the greater the ‘liking’ for (savoury) foods.

Interestingly, in contrast to ‘liking’ for savoury foods and to this view, greater implicit ‘wanting’ for high fat foods was associated with slower gastric emptying. To the best of our knowledge relationships between ‘liking’ and ‘wanting’ and gastric emptying have not been previously documented in humans. However, Miras et al. [41] demonstrated that gastric bypass altered the reinforcing effects of sweet and fatty candy but not of vegetables, suggesting that gastric bypass results in the selective reduction of the reward value of a sweet/fat taste [42]. A reduced hedonic response and preference for high energy/fat foods has been increasingly documented in animal models and humans after gastric bypass [41], [43], [44] - a procedure which significantly accelerates the delivery of nutrients to the distal small intestine and alters gut hormone responses, but this has not been observed after gastric banding [43], [44] - a procedure which does not change the emptying rate or gut hormonal responses [15]. These alterations in gut physiology specific to gastric bypass may have a mechanistic role in the reduced hedonic response to high fat foods - findings which highlight the importance of the gut-brain axis in reward-based eating behaviour [43].

Our findings of a faster emptying rate being associated with a reduced implicit wanting for high fat foods are consistent with these observations after gastric bypass. One explanation may be that a slower gastric emptying would mean a reduced homeostatic drive and this could provide more opportunity for hedonic motivation to influence behavior, especially responses to high fat palatable foods. Additionally, the observed associations could be mediated by changes in gut hormones or dopamine release, both of which have been associated with the rate of gastric emptying [19], [45], [46], [47], [48], [49] and also linked to food reward [21]. The rate of gastric emptying plays an important role in the release of intestinal satiation peptides [49], [50], [51]. Moreover, in animals differences in gastric emptying rate are comparable to differences in dopamine efflux [45] and evidence suggests that stimulation of the GI tract with nutrients is sufficient to stimulate the release of dopamine in brain circuits controlling food intake [19]. A slower emptying rate could contribute to a blunted gut hormone or dopamine release and impairments in these pathways associated with food reward and control. As such the hedonic response to food could disrupt or override homeostatic signals of satiety.

The limitations of the present study should be considered. Given the cross-sectional nature of the study, causal relationships between gastric and hedonic responses are not possible to establish and this is an area that requires further investigation. Moreover, it is important to acknowledge that a wide range of genetic, environmental, psychological, and physiological factors contribute to the short and long term control of food intake [52]. Gastric emptying and gut hormones have an integrative relationship in appetite control and gut hormones in turn may influence fatty acid detection or perception [44]. Characterising a combination of GI factors may therefore provide further mechanistic insight into differences in food reward with physical activity level. Furthermore, whether food reward differs between active and inactive men in response to other types of test meal as a result of sensory-specific satiety or if measured earlier in the postprandial period (e.g. at 3h) when hunger ratings are lower, is of interest. Findings may also be different in females and this is another area that requires further study.

In conclusion, these data demonstrate that in addition to differences in gastric emptying, habitual exercisers are characterised by different hedonic responses for high fat or low fat and sweet or savoury foods, compared to inactive individuals. These processes do not appear to operate independently. Interactions between the gut and hedonic aspects of appetite control could play a key role in the impact of habitual exercise on energy balance.

Acknowledgements

We are grateful to the participants in the study. This study was supported by a Queensland University of Technology Postgraduate Research Award (QUTPRA).

Financial Support

This study was supported by a Queensland University of Technology Postgraduate Research Award (QUTPRA).

Conflicts of Interest

The authors have no conflicts of interest to disclose.

Authorship

KMH, GF, NMB and NAK contributed to the design of the study; KMH collected the data, contributed to data analysis and drafted the manuscript; GF provided the experimental task, performed data and statistical analysis and contributed to critical revision of the manuscript. NMB and NAK provided critical revision of the manuscript. All authors read and approved the final manuscript.

References

[1] Hill JO, Wyatt HR (2005) Role of physical activity in preventing and treating obesity. J Appl Physiol **99**, 765-770.

[2] Hill JO (2006) Understanding and Addressing the Epidemic of Obesity: An Energy Balance Perspective. Endocr Rev **27**, 750-761.

[3] Mayer J, Roy P, Mitra KP (1956) Relation between caloric intake, body weight, and physical work: studies in an industrial male population in West Bengal. Am J Clin Nutr **4**, 169-175.

[4] Long SJ, Hart K, Morgan LM (2002) The ability of habitual exercise to influence appetite and food intake in response to high- and low-energy preloads in man. Br J Nutr **87**, 517-523.

[5] Martins C, Truby H, Morgan LM (2007) Short-term appetite control in response to a 6-week exercise programme in sedentary volunteers. Br J Nutr **98**, 834-842.

[6] Van Walleghen EL, Orr JS, Gentile CL et al. (2007) Habitual physical activity differentially affects acute and short-term energy intake regulation in young and older adults. Int J Obes **31**, 1277-1285.

[7] Martins C, Kulseng B, Rehfeld JF et al. (2012) Impact of Chronic Exercise on Appetite Control in Overweight and Obese Individuals. Med Sci Sports Exerc **45**, 805-812.

[8] Beaulieu K, Hopkins M, Blundell J et al. (2016) Does Habitual Physical Activity Increase the Sensitivity of the Appetite Control System? A Systematic Review. Sports Med, [In Press].

[9] Blundell JE (2011) Physical activity and appetite control: can we close the energy gap? Nutr Bull **36**, 356-366.

[10] Blundell J (1991) Pharmacological approaches to appetite suppression. Trends Pharmacol Sci **12**, 147-157.

[11] Blundell JE, King NA (1996) Overconsumption as a cause of weight gain: Behavioural-physiological interactions in the control of food intake (appetite). CIBA Foundation Symposia, 138-158.

[12] Finlayson G, Bryant E, Blundell JE et al. (2009) Acute compensatory eating following exercise is associated with implicit hedonic wanting for food. Physiol Behav **97**, 62-67.

[13] Finlayson G, Caudwell P, Gibbons C et al. (2011) Low Fat Loss Response after Medium-Term Supervised Exercise in Obese Is Associated with Exercise-Induced Increase in Food Reward. J Obes, pii: 615624.

[14] Blundell JE, Caudwell P, Gibbons C et al. (2012) Role of resting metabolic rate and energy expenditure in hunger and appetite control: a new formulation. Dis Model Mech **5**, 608-613.

[15] Horner KM, Byrne NM, Cleghorn GJ et al. (2011) The effects of weight loss strategies on gastric emptying and appetite control. Obes Rev **12**, 935-951.

[16] Martins C, Kulseng B, King NA et al. (2010) The Effects of Exercise-Induced Weight Loss on Appetite-Related Peptides and Motivation to Eat. J Clin Endocrinol Metab **95**, 1609-1616.

[17] Horner KM, Byrne NM, Cleghorn GJ et al. (2015) Influence of Habitual Physical Activity on Gastric Emptying in Healthy Males and Relationships with Body Composition and Energy Expenditure. Br J Nutr **3**, 489–96 .

[18] Ren X, Ferreira JG, Zhou L et al. (2010) Nutrient Selection in the Absence of Taste Receptor Signaling. J Neurosci **30**, 8012-8023.

[19] de Araujo IE, Ferreira JG, Tellez LA et al. (2012) The gut–brain dopamine axis: A regulatory system for caloric intake. Physiol Behav **106**, 394-399.

[20] Tellez LA, Medina S, Han W et al. (2013) A Gut Lipid Messenger Links Excess Dietary Fat to Dopamine Deficiency. Science **341**, 800-802.

[21] Sun X, Veldhuizen MG, Wray AE et al. (2014) The neural signature of satiation is associated with ghrelin response and triglyceride metabolism. Physiol Behav **136**, 63-73.

[22] Hopkins M, Gibbons C, Caudwell P et al. (2014) Fasting Leptin Is a Metabolic Determinant of Food Reward in Overweight and Obese Individuals during Chronic Aerobic Exercise Training. Int J Endocrinol, Article ID 323728, 8 pages, 2014.

[23] O’Neill BV, Bullmore ET, Miller S et al. (2012) The relationship between fat mass, eating behaviour and obesity-related psychological traits in overweight and obese individuals. Appetite **59**, 656-661.

[24] Horner KM, Byrne NM, Cleghorn GJ et al. (2013) Reproducibility of gastric emptying in overweight and obese males. Clin Nutr, **33**, 684-688.

[25] Ghoos YF, Maes BD, Geypens BJ et al. (1993) Measurement of gastric emptying rate of solids by means of a carbon-labeled octanoic acid breath test. Gastroenterology **104**, 1640-1647.

[26] Gibbons C, Caudwell P, Finlayson G et al. (2011) Validation of a new hand-held electronic data capture method for continuous monitoring of subjective appetite sensations. Int J Behav Nutr Phys Act **8**, 57.

[27] Finlayson G, King N, Blundell J (2008) The role of implicit wanting in relation to explicit liking and wanting for food: Implications for appetite control. Appetite **50**, 120-127.

[28] Griffioen-Roose S, Finlayson G, Mars M et al. (2010) Measuring food reward and the transfer effect of sensory specific satiety. Appetite **55**, 648-655.

[29] Griffioen-Roose S, Mars M, Finlayson G et al. (2011) The effect of within-meal protein content and taste on subsequent food choice and satiety. Br J Nutr **106**, 779-788.

[30] French SA, Mitchell NR, Finlayson G et al. (2014) Questionnaire and laboratory measures of eating behavior. Associations with energy intake and BMI in a community sample of working adults. Appetite **72**, 50-58.

[31] Finlayson G, Dalton M (2012) Hedonics of Food Consumption: Are Food Liking and Wanting Viable Targets for Appetite Control in the Obese? Current Obesity Reports **1**, 42-49.

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

[33] Dalton M, Finlayson G (2014) Psychobiological examination of liking and wanting for fat and sweet taste in trait binge eating females. Physiol Behav **136**, 128-134.

[34] Dalton M, Blundell J, Finlayson G (2013) Effect of BMI and binge eating on food reward and energy intake: further evidence for a binge eating subtype of obesity. Obes Facts **6**, 348-359.

[35] Dalton M (2013) Biopsychological investigation of hedonic processes in individuals susceptible to overeating: role of liking and wanting in trait binge eating. University of Leeds.

[36] Cameron JD, Goldfield GS, Finlayson G et al. (2014) Fasting for 24 Hours Heightens Reward from Food and Food-Related Cues. PLoS ONE **9**, e85970.

[37] Cabanac M (1989) Maximization of pleasure, the answer to a conflict of motivations. Comptes Rendus de l Academics des Sciences Serie III **409**, 397-402.

[38] Sclafani A (2013) Gut-brain nutrient signaling. Appetition vs. satiation. Appetite **71**, 454-458.

[39] Berthoud HR (2008) Vagal and hormonal gut-brain communication: from satiation to satisfaction. Neurogastroenterol Motil **20**, 64-72.

[40] Sclafani A (2004) Oral and postoral determinants of food reward. Physiol Behav **81**, 773-779.

[41] Miras AD, Jackson RN, Jackson SN et al. (2012) Gastric bypass surgery for obesity decreases the reward value of a sweet-fat stimulus as assessed in a progressive ratio task. Am J Clin Nutr **96**, 467-473.

[42] Astrup A (2012) Weight loss produced by gastric bypass surgery: more gut feelings hit the brain. Am J Clin Nutr **96**, 457-458.

[43] Scholtz S, Miras AD, Chhina N et al. (2013) Obese patients after gastric bypass surgery have lower brain-hedonic responses to food than after gastric banding. Gut. **6**, 891-902.

[44] le Roux CW, Bueter M, Theis N et al. (2011) Gastric bypass reduces fat intake and preference. Am J Physiol Regul Integr Comp Physiol **301**, R1057-R1066.

[45] Ferreira JlG, Tellez LA, Ren X et al. (2012) Regulation of fat intake in the absence of flavour signalling. J Physiol **590**, 953-972.

[46] Vazquez Roque MI, Camilleri M, Stephens DA et al. (2006) Gastric sensorimotor functions and hormone profile in normal weight, overweight, and obese people. Gastroenterology **131**, 1717-1724.

[47] Schirra J, Katschinski M, Weidmann C et al. (1996) Gastric emptying and release of incretin hormones after glucose ingestion in humans. J Clin Invest **97**, 92-103.

[48] French SJ, Murray B, Rumsey RDE et al. (1993) Is cholecystokinin a satiety hormone? Correlations of plasma cholecystokinin with hunger, satiety and gastric emptying in normal volunteers. Appetite **21**, 95-104.

[49] Meyer-Gerspach AC, Wolnerhanssen B, Beglinger B et al. (2014) Gastric and intestinal satiation in obese and normal weight healthy people. Physiol Behav **129**, 265-271.

[50] Steinert RE, Meyer-Gerspach AC, Beglinger C (2012) The role of the stomach in the control of appetite and the secretion of satiation peptides. Am J Physiol Endocrinol Metab **302**, E666-E673.

[51] Pilichiewicz AN, Chaikomin R, Brennan IM et al. (2007) Load-dependent effects of duodenal glucose on glycemia, gastrointestinal hormones,

antropyloroduodenal motility, and energy intake in healthy men. Am J Physiol Endocrinol Metab **293**, 743-753.

[52] de Castro JM (2004) Genes, the environment and the control of food intake. Br J Nutr **92**, S59-S62.

Table 1. Photographic food stimuli used in the food preference and 'liking' and 'wanting' computer task (grouped by food category)

HFSA	LFSA	HFSW	LFSW
Chips (fries)	Tomatoes	Doughnuts	Jelly beans
Pizza	Chicken	Chocolate	Juice
Meat pie	Rice	Milkshake	Mixed fruits
Swiss cheese	Boiled potatoes	Ice-cream	Apple

HFSA, high fat savoury; LFSA, low fat savoury; HFSW, high fat sweet; LFSW, low fat sweet.

Table 2. Participants' anthropometric, body composition and energy expenditure characteristics

	Inactive (n=22)		Active (n=22)		P-value
	Mean	SEM	Mean	SEM	
Age (years)	30.5	1.82	29.4	1.67	0.56
Height (m)	1.78	0.02	1.80	0.02	0.55
Weight (kg)	87.1	3.36	79.2	2.50	0.07
BMI (kg/m^2)	27.4	0.89	24.5	0.55	**0.02**
Body Composition					
FM (%)	26.2	1.85	14.3	1.24	**<0.001**
FFM (kg)	63.3	1.74	67.7	1.90	0.10
Activity EE (kcal/day)[1]	525	42	709	51	**<0.01**
Total EE (kcal/day)[1]	2665	95	2890	92	0.09

Values are means (± SEM).
[1]Energy expenditure data refers to n =19 in Inactive group.
BMI, body mass index; FM, fat mass; FFM, fat free mass, EE, energy expenditure.

Table 3. Mean (±SEM) explicit liking and implicit wanting in fed (post-breakfast) and hungry (pre-lunch 5h later) states for different food categories in active (n = 22) compared to inactive (n = 22) men.

	Inactive (n = 22)	**Active (n = 22)**	**Effect of Activity P-value** (without adj.)	**Main Effect %FM P-value**	**Effect of Activity after adjustment for %FM P-value**
Fed state					
Liking HFSA	35.66 (4.65)	21.86 (4.05)	**0.03**	0.98	0.09
Liking HFSW	45.51 (4.64)	32.32 (5.03)	**0.06**	0.99	0.15

Liking LFSA	30.98 (4.05)	25.57 (4.42)	0.37	0.75	0.38
Liking LFSW	55.68 (3.65)	40.61 (4.37)	**0.01**	0.26	**<0.01**
Liking All	41.96 (3.34)	30.10 (3.67)	**0.02**	0.67	**0.04**
Wanting HFSA	-7.14 (7.05)	-5.47 (7.04)	0.87	0.68	0.70
Wanting HFSW	10.03 (5.34)	-4.30 (7.86)	0.14	0.87	0.22
Wanting LFSA	-27.42 (5.88)	-5.61 (6.33)	**0.02**	0.35	**0.02**
Wanting LFSW	24.52 (6.49)	15.38 (6.33)	0.32	0.24	0.13
Hungry state					
Liking HFSA	62.01 (4.14)	62.5 (4.93)	0.94	0.75	0.79
Liking HFSW	59.72 (4.08)	50.35 (6.42)	0.23	0.39	0.70
Liking LFSA	52.53 (3.65)	60.09 (4.11)	0.18	0.91	0.34
Liking LFSW	56.26 (3.54)	48.95 (3.67)	0.16	0.57	0.15
Liking All	57.63 (2.86)	55.47 (3.48)	0.63	0.78	0.75
Wanting HFSA	27.39 (6.00)	26.79 (7.17)	0.95	0.58	0.69
Wanting HFSW	-9.30 (5.14)	-21.18 (6.85)	0.17	0.19	0.82
Wanting LFSA	-4.06 (3.77)	12.24 (5.99)	**0.03**	0.51	0.19
Wanting LFSW	-14.03 (4.51)	-17.85 (5.15)	0.58	0.85	0.59

All, all categories of food combined; LFSA, low fat savoury; HFSA, high fat savoury, LFSW, low fat sweet; HFSW, high fat sweet.

Table 4. Mean (±SEM) changes in explicit liking and implicit wanting for different food categories from fed (post-breakfast) to hungry (pre-lunch 5h later) states in active (n = 22) compared to inactive (n = 22) men.

	Inactive (n = 22)	**Active (n = 22)**	**Effect of Activity P-value** (without adj.)	**Main Effect %FM P-value**	**Effect of Activity after adjustment for %FM P-value**
Change from fed to hungry state					
Liking HFSA	26.35 (4.11)	40.64 (5.13)	**0.04**	0.73	0.07
Liking HFSW	14.22 (4.36)	18.00 (5.26)	0.58	0.33	0.30
Liking LFSA	21.56 (2.87)	34.52 (4.49)	**0.02**	0.81	**0.05**
Liking LFSW	0.58 (2.99)	8.34 (5.03)	0.19	0.56	0.17
Liking All	15.68 (2.58)	25.38 (4.02)	**0.05**	0.48	**0.05**
Wanting HFSA	34.53 (7.31)	32.27 (5.65)	0.81	0.31	0.41
Wanting HFSW	-19.33 (6.19)	-16.88 (5.18)	0.76	0.11	0.21
Wanting LFSA	23.36 (5.47)	17.85 (5.23)	0.47	0.09	0.10
Wanting LFSW	-38.56 (7.49)	-33.24 (6.15)	0.59	0.31	0.34

All, all categories of food combined; LFSA, low fat savoury; HFSA, high fat savoury, LFSW, low fat sweet; HFSW, high fat sweet.

Figure Legends

Figure 1. Mean changes in explicit liking from breakfast to lunch (5h later) in active (n = 22) compared to inactive (n = 22) men, as assessed using the LFPQ.
All, all categories of food combined; LFSA, low fat savoury; HFSA, high fat savoury, LFSW, low fat sweet; HFSW, high fat sweet.
Error bars indicate SEM. * $p < 0.05$.

Figure 2. (a) Scatter plot illustrating slower gastric emptying (i.e. longer gastric emptying $t_{1/2}$) is associated with greater liking for sweet compared to savoury foods at pre-lunch. A positive taste bias score = liking for sweet foods > savoury foods. A negative taste bias score = liking for savoury foods > sweet foods. Partial correlations showed the relationship remained significant after adjusting for BMI ($r = 0.43$, $P < 0.01$) or percent FM ($r = 0.38$, $P = 0.01$). Removal of the extreme individual point for gastric emptying $t_{1/2}$ (value: 231min) reduced r from 0.43 to $r = 0.30$, $P = 0.04$. **(b)** Scatter plot illustrating slower gastric emptying ($t_{1/2}$) is associated with greater implicit wanting for high fat compared to low fat foods at pre-lunch. A positive fat bias score = wanting for high fat foods > low fat foods. A negative fat bias score = wanting for low fat foods > high fat foods. Partial correlations showed the relationship remained significant after adjusting for BMI ($r = 0.37$, $P = 0.01$) or percent FM ($r = 0.32$, $P = 0.04$). Removal of the extreme individual point for gastric emptying $t_{1/2}$ (value: 231min) increased r from 0.36 to $r = 0.43$, $P < 0.01$.
n = 44 for both.