UNIVERSITY OF LEEDS

This is a repository copy of *High Habitual Physical Activity Improves Acute Energy Compensation in Nonobese Adults*.

White Rose Research Online URL for this paper:
http://eprints.whiterose.ac.uk/119079/

Article:

Beaulieu, K orcid.org/0000-0001-8926-6953, Hopkins, M orcid.org/0000-0002-7655-0215, Long, C et al. (2 more authors) (2017) High Habitual Physical Activity Improves Acute Energy Compensation in Nonobese Adults. Medicine & Science in Sports & Exercise, 49 (11). pp. 2268-2275. ISSN 0195-9131

https://doi.org/10.1249/MSS.0000000000001368

(c) 2017, Lippincott, Williams & Wilkins. This is an author produced version of a paper published in Medicine & Science in Sports & Exercise. Uploaded in accordance with the publisher's self-archiving policy.

Reuse

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.

White Rose university consortium
Universities of Leeds, Sheffield & York

eprints@whiterose.ac.uk
https://eprints.whiterose.ac.uk/

High habitual physical activity improves acute energy compensation in nonobese adults

Kristine Beaulieu[1*], Mark Hopkins[2], Cecilia Long[1], John Blundell[1], Graham Finlayson[1]

1. School of Psychology, University of Leeds, Leeds, LS2 9JT, United Kingdom
2. School of Food Science & Nutrition, University of Leeds, Leeds, LS2 9JT, United Kingdom

*Corresponding author:
Kristine Beaulieu
School of Psychology
University of Leeds
Leeds, LS2 9JT
United Kingdom
Email: k.beaulieu14@leeds.ac.uk
Phone: +44 (0) 113 343 5753
Fax: +44 (0) 113 343 5749

ABSTRACT

Purpose: Evidence suggests that homeostatic satiety signalling is enhanced with higher levels of physical activity (PA), with active individuals demonstrating an improved ability to compensate for previous energy intake (EI). However, prior studies lacked objective assessment of both PA level and EI. This study examined the effect of objectively-measured PA level on homeostatic (energy compensation) and hedonic (liking and wanting) responses to high-energy (HEP), low-energy (LEP) and control preloads.

Methods: Thirty-four nonobese individuals were grouped by tertiles of accelerometry-measured habitual moderate-to-vigorous PA (low: LoMVPA; moderate: ModMVPA; high: HiMVPA), similar in age, sex and BMI. Following a preliminary assessment, EI (fixed-energy breakfast and ad libitum lunch, dinner and evening snack box meals) was determined during three probe meal days in which preloads varying in energy content (HEP: 699 kcal, LEP: 258 kcal, control: 0 kcal) were consumed prior to the lunch meal. Liking and wanting were assessed pre- and post-preload consumption (Leeds Food Preference Questionnaire) and appetite ratings were taken throughout the day.

Results: Relative to control, EI at lunch was reduced to a greater extent after consumption of HEP compared to LEP in ModMVPA ($p<.01$) and HiMVPA ($p=.01$), but not LoMVPA ($p=.59$), reflecting more accurate energy compensation in HiMVPA and ModMVPA. There were no effects on cumulative EI post-preload (lunch, dinner and snack box combined). HEP led to a greater suppression of hunger, liking and wanting compared to LEP in all MVPA tertiles.

Conclusion: Nonobese individuals with lower levels of measured PA were insensitive to the nutritional manipulation of the preloads, suggesting a weaker satiety response to food. This study provides objective evidence that higher habitual PA improves acute homeostatic appetite control.

Keywords: appetite control; satiety; preloads; energy intake; food hedonics

BACKGROUND

The role of physical activity (PA) in homeostatic appetite control and body weight regulation is gaining more attention within the scientific community. Earlier reports have proposed an enhancement in the sensitivity of appetite control with increasing levels of PA (6, 26), and the J-shape relationship between PA level and energy intake initially observed by Mayer et al. (30) has been recently confirmed by Shook et al. (36) and a systematic review (4). To better understand the effect of PA on food intake, it is important that distinct appetite processes such as satiation and satiety are examined. Satiation leads to meal termination, whereas satiety is the post-meal suppression of hunger and inhibition of further eating (9).

Recent evidence shows that satiation, measured with a passive overconsumption paradigm comparing energy intake at high-fat and high-carbohydrate meals, is not influenced by PA level in nonobese individuals matched for body mass index (BMI) (5). Satiety, however, has been shown to be improved in physically active individuals. Using a preload-test meal paradigm, studies have found that physically active individuals show better energy compensation than inactive individuals such that they reduce energy intake to offset the difference in energy consumed in the preload (23, 25, 28, 39). Moreover, measuring the satiety quotient (SQ; change in appetite scores relative to the energy content of a meal) in the hours following a fixed meal, studies have showed that satiety increases after 12 weeks of exercise training in previously inactive overweight and obese individuals (10, 22). These improvements in satiety signalling may relate to exercise-induced changes in postprandial satiety hormones such as leptin (19, 25), insulin (19, 24), and GLP-1 (24).

However, the beneficial effects of PA on satiety were based mainly on food diaries and all on self-reported habitual PA (23, 39). Test meals for the assessment of energy intake under controlled laboratory conditions are preferred over food diaries as self-report measures are subject to bias and misreporting, and cannot be relied upon to provide a veridical account of food actually consumed (13). Additionally, with wearable technologies being more available, objective assessment of habitual PA via accelerometry can now readily be used, reducing bias from participants overestimating their PA (13, 34). Furthermore, the preloads used in previous studies were liquid-based and not matched for macronutrient composition, which may affect individuals' compensatory response (2, 29).

In addition to an action on homeostatic mechanisms (satiation and satiety), other mechanisms in which habitual PA may affect appetite control is the rewarding value of foods (liking and wanting) and hedonic preference for high-fat foods (21). These can override physiological satiety signals and lead to overconsumption (14). Therefore, the objective of this study was to investigate the homeostatic (energy compensation) and hedonic (liking and wanting for high-fat foods) responses to high-energy (HEP), low-energy (LEP) and control preloads in nonobese individuals differing in objectively-measured PA using an experimental system assessing several dimensions of appetite control (11). We hypothesised that more active individuals would have a greater reduction of energy after the HEP relative to LEP compared to their less active counterparts.

METHODS

Participants. Thirty-four participants aged 18-55 years were included based on the following criteria: BMI between 20.0-29.9 kg/m^2, non-smoker, weight stable (±2 kg for previous 3 months), no change in PA over the previous 6 months, not currently dieting, no history of eating disorders, not taking any medication known to affect metabolism or appetite, and acceptance of the study foods. In order to recruit three groups of participants that differed in PA level (i.e. low: ≤1 day/week, moderate: 2-3 days/week or high: ≥4 days/week), the short-form of the validated International Physical Activity Questionnaire (12) was used as part of the screening process to estimate habitual moderate-to-vigorous PA (MVPA). Age, sex and BMI were also monitored throughout screening to ensure the groups were similar in these characteristics. Following initial screening, habitual MVPA was then measured and confirmed using a multi-sensor device (SenseWear Armband (SWA); BodyMedia, Inc; Pittsburgh, USA) and used to group participants into a posteriori sex-specific tertiles of daily MVPA (low: LoMVPA, moderate: ModMVPA, or high: HiMVPA). Approximately half of the participants remained in their original self-report PA group estimated by the IPAQ (45%, 45% and 58%, in the LoMVPA, ModMVPA and HiMVPA tertiles, respectively). For males, LoMVPA corresponded to <112 min MVPA/day and HiMVPA to >148 min MVPA/day, while for females, LoMVPA corresponded to <90 min MVPA/day and HiMVPA to >143 min MVPA/day. This study was approved by the School of Psychology Ethical Committee at the University of Leeds, and participants provided written informed consent prior to taking part and were remunerated upon completing the study.

Study protocol. Following preliminary assessments, LoMVPA (82.7 ± 16.2 min MVPA/day), ModMVPA (120.7 ± 14.8 min MVPA/day) and HiMVPA (174.0 ± 38.6 min MVPA/day) underwent 3 laboratory probe days, in a Latin square crossover design, that included a fixed breakfast followed by a HEP, LEP or control, and ad libitum lunch, dinner and snack box meals to examine the 24-h energy intake response to preloads varying in energy content relative to no-energy control (Figure 1).

For the 24 h prior to the testing sessions, the participants refrained from exercise, and did not consume caffeine or alcohol. On each test day, the participants arrived at the research unit between 07:00-09:00 following a 10-h fast (no food or drink except water). Prior to the first meal day, the participants consumed their habitual diet but were required to record their food intake for 24 h in a diary that was provided to them during the preliminary assessment, and replicated their food intake prior to the subsequent meal days. Compliance with these guidelines was verified upon arrival at the laboratory for each testing session.

During the meal days, participants restricted their PA (i.e. were not allowed to exercise) and at each meal day, upon arrival at the laboratory, participants were fitted with the SWA and wore the monitor until the following morning (~24 h) to assess energy expenditure. Subjective appetite ratings were measured using visual analogue scales (VAS) before and after each meal and at hourly intervals throughout the day, and the hedonic preference for high-fat foods was measured with the Leeds Food Preference Questionnaire (LFPQ; (16)) before and after consumption of the preload. Energy intake at individual meals was measured (described below), and subsequently used to calculate 24-h energy intake. After a fixed energy breakfast, participants returned 3 h later for the consumption of the preloads, 1 h after which they consumed an ad libitum lunch. Dinner was consumed 4 h after lunch and participants were given an ad libitum snack box for the remainder of the evening. Each meal day was separated by at least seven days.

Preliminary assessment and habitual physical activity. At least 8 days before the meal days, resting metabolic rate (RMR; indirect calorimetry), body composition (fat mass, fat-free mass; BodPod), maximal aerobic capacity (VO_{2max}; modified Balke protocol), and eating behaviour traits (restraint, disinhibition, binge eating, craving control) were assessed as previously described (5). Upon completion, participants were fitted with a SWA and were instructed to wear the armband on their non-dominant arm over 7 days for at least 23 h/day (awake and asleep, except for the time around showering, bathing or swimming). Compliance was defined as 5 days of wear (including one weekend day) with at least 22 h/day. Proprietary algorithms available in the accompanying software (version 8.0 professional) were used to calculate total daily energy expenditure (TDEE), PA level (PAL; TDEE/basal metabolic rate), and minutes spent sleeping, sedentary (<1.5 METs) or in light intensity (1.5-2.9 METs) or moderate and higher intensity (≥ 3.0 METs) PA (1).

Fixed energy and ad libitum meals. Participants consumed a fixed-energy breakfast that provided 25% of individual RMR. Upon consumption, participants were free to leave the research unit but were instructed not to eat or drink any food (except water). Three hours after breakfast, participants returned to the laboratory and consumed either a porridge HEP (699 kcal) or LEP (258 kcal) with 150g of water or 495.5g of water (control). HEP and LEP were of similar macronutrient composition (39% energy from carbohydrates, 46% energy from fat and 15% energy from protein; see Table 1 in Supplemental Digital Content 1 for ingredients of the preloads), weight, volume and palatability. Pilot testing (n=9) showed no difference in sweetness, liking, pleasantness, and desire to eat between preloads ($p \geq .41$). Participants had 15 minutes to consume the fixed-energy meals, and food items were weighed before and after consumption to ensure compliance.

One hour after the start of the preload, an ad libitum lunch consisting of risotto (1.99 kcal/g, 53.3% carbohydrate, 39.9% fat, 6.8% protein) with a side of cucumber and tomatoes was provided, and four hours after lunch, an ad libitum dinner was provided, consisting of vegetarian chilli (1.30 kcal/g, 49.8% carbohydrate, 37.4% fat, 12.8% protein) with a side of pineapple. For these meals, food was provided in excess of expected consumption, and the participants were instructed to eat as much or as little as they liked until comfortably full. Following dinner, participants were given a snack box containing a selection of foods (strawberry yoghurt, apples, tangerines, cheese crackers, almonds, popcorn, and granola bars) and were instructed to eat only from this snack box until they went to bed that evening. Food items were weighed before and after consumption and energy intake was calculated using energy equivalents for protein, fat and carbohydrate of 4, 9 and 3.75 kcal/g, respectively, from the manufacturers' food labels. Cumulative energy intake was calculated as energy intake at lunch, dinner and evening snack box.

Appetite ratings. Appetite ratings were assessed before and after each meal, and at hourly intervals throughout the meal day via VAS for hunger, fullness, desire to eat and prospective food consumption (PFC) using an electronic system (17). To specifically examine the effect of the preloads on satiety, area under the curve (AUC) was calculated using the trapezoid rule for the 1-h period following preload consumption (post-preload, VAS 5-7 in Figure 1) and the 2-h period following lunch consumption (post-preload and lunch, VAS 7-10 in Figure 1).

Hedonic preference for high-fat foods. The LFPQ (16) was administered pre- and post-preload consumption to determine scores of implicit wanting and explicit liking for high-fat (>50% energy) and low-fat (<20% energy) foods matched for familiarity, sweetness, protein, and acceptability, and has been validated in a wide range of research (15, 18, 40). Implicit wanting was assessed by asking the participants to select as fast as possible which food from specific categories "they most want to eat". Scores for implicit wanting were computed from mean response times adjusted for frequency. To measure explicit liking, the participant rated the extent to which they liked each food ("How pleasant would it be to taste this food now?") using a 100-mm VAS. Low-fat scores were subtracted from high-fat scores to obtain the fat appeal bias score; a positive score indicates greater liking or wanting towards high-fat compared to low-fat foods.

Statistical analysis. The sample size was based after the study by Long et al. (23) who demonstrated that nonobese high active individuals consumed less after a HEP relative to a LEP (d=0.88). A similar effect size in the present study was estimated and it was calculated that n=10 per group would be sufficient to detect a difference in intake between HEP and LEP within groups with $1-\beta=0.8$ and $\alpha=0.05$, one-tailed.

Differences in characteristics of the MVPA tertiles were determined via one-way ANOVAs. Pearson's correlations were conducted to examine associations between fat-free mass, RMR and daily energy intake. To examine the effect of the preloads, energy intake, appetite sensations and food hedonics (liking and wanting) in HEP and LEP relative to control were computed. Differences in relative energy intake and appetite AUC were determined via two-way mixed model ANOVA with condition (HEP, LEP) as the within-subject factor and MVPA tertile as the between-subject factor. Changes in relative liking and wanting were assessed with three-way mixed-model ANOVAs with condition and time (pre- and post-preload consumption) as the within-subject factors and MVPA tertile as the between-subject factor. Bonferroni post hoc analyses adjusted for multiple comparisons were used when significance was achieved. Significance was established at $p<.05$.

RESULTS

Participant characteristics and habitual PA. The characteristics of the 3 MVPA tertiles are presented in Table 1. The tertiles did not significantly differ in age, BMI, body composition, resting metabolic rate or eating behaviour traits, but by design, differed in terms of VO_{2max}, habitual PA and sedentary behaviour. Because SWA wear time differed significantly between tertiles (LoMVPA: 1415.8 ± 13.5 min/day, ModMVPA: 1420.6 ± 8.4 min/day, HiMVPA: 1406.7 ± 13.8 min/day; p=.03), one-way ANCOVAs controlling for SWA wear time were conducted on habitual free-living total daily energy expenditure, light PA, MVPA, sedentary time and physical activity level (PAL).

Ad libitum energy intake. In the control condition, there were no significant differences between tertiles in energy intake at lunch, dinner, evening snack box, or daily 24-h energy intake (all p≥.16; see Table in Supplemental Digital Content 2 for values). Daily energy intake was associated with fat-free mass (r(32)= .51, p=.002) and RMR (r(32)= .53, p=.001).

For energy intake at lunch following HEP and LEP relative to control, there was a significant effect of condition, as expected, with HEP suppressing subsequent energy intake to a greater degree than LEP overall (p=.01). Furthermore, there was a significant condition and MVPA tertile interaction (p=.03), revealing that ModMVPA (p<.01) and HiMVPA (p=.01) had a greater reduction in intake after HEP compared to LEP, but no differences existed for LoMVPA (p=.59; Figure 2 and Figure in Supplemental Digital Content 3 for individual response). There were no main effects or interaction for cumulative energy intake relative to control (lunch, dinner and evening snack box combined; all p>.10; Table 2 and Figure in Supplemental Digital Content 3 for individual response). Daily energy intake (including breakfast and preload) was greater in HEP compared to LEP in all tertiles (p<.001; Table 2).

Appetite ratings. Following preload consumption, hunger AUC relative to control was more suppressed in HEP compared to LEP, with no differences between tertiles (p=.03; Figure 3a). There were no condition effects for fullness, desire to eat and PFC (Figure 3c-d). Following both preload and lunch consumption, AUC for hunger, desire to eat and PFC relative to control were all more suppressed and fullness was greater in HEP compared to LEP, again with no differences between tertiles (all $p \leq .03$; Figure 3).

Food hedonics. Two participants in HiMVPA did not have complete LFPQ data. In the control condition, there were no differences in liking and wanting fat appeal bias from pre- to post-water consumption or between tertiles (all $p \geq .26$; see Table Supplemental Digital Content 4 for values). For both liking and wanting pre- to post-preload relative to control, a 3-way ANOVA revealed a main effect of preload consumption ($p \leq .01$) and condition and preload consumption interaction ($p \leq .05$), revealing a greater reduction in liking and wanting for high-fat foods after HEP compared to LEP, but no differences relating to MVPA tertile (Figure 4).

Meal day energy expenditure. Four participants (2 ModMVPA and 2 HiMVPA) did not have valid SWA meal day data as they removed the sensor before going to bed. In the control condition, there were no significant differences between tertiles in meal day energy expenditure (LoMVPA: 1964.6 ± 341.4 kcal; ModMVPA: 2077.0 ± 309.4 kcal; HiMVPA: 2270.4 ± 394.3 kcal; $p=.15$). In response to the HEP and LEP, there was no main effect of condition ($p=.76$), MVPA tertile ($p=.21$) or interaction between condition and MVPA tertile ($p=.38$) on meal day energy expenditure (Table 2). However, overall, meal day energy expenditure was lower than habitual TDEE as measured by the SWA over 7 days by 238 ± 232 kcal ($p<.001$).

DISCUSSION

This study examined the strength of satiety, energy compensation and 24-h energy intake in individuals varying in PA levels using objective assessment of energy intake and habitual PA. Including the measurement of other biopsychological determinants of appetite control such as food hedonics allowed inferences about their impact on PA level and satiety to be drawn. In the entire sample, as expected, 24-h energy intake was positively associated with fat-free mass and RMR, and HEP gave rise to greater suppression of subsequent food intake than LEP, confirming functional appetite control (7, 8). Additionally, the HEP also led to a greater suppression of hunger and reduction in food hedonics (liking and wanting for high-fat foods) compared to the LEP across all MVPA tertiles. However, an examination of the different PA levels showed that ModMVPA and HiMVPA had a greater reduction of ad libitum energy intake at lunch following consumption of the HEP compared to the LEP, whereas LoMVPA did not, supporting a role for habitual PA in the sensitivity of appetite control.

Habitual physical activity and energy compensation

Unlike previous studies examining the impact of PA level on energy compensation, this study classified groups on objective and quantified habitual MVPA. Furthermore, to reduce the likelihood of confounding effects on the compensatory response, the preloads were matched for macronutrient composition and consisted of a semi-solid food (rather than a liquid), and the MVPA tertiles were similar in terms of participant age, sex and BMI. The results show that the LoMVPA tertile were less sensitive to the nutritional manipulation of the preload, compared to the ModMVPA and HiMVPA groups who showed a greater reduction in subsequent intake in response to HEP. This is consistent with previous studies in which low levels of PA were found to be detrimental to homeostatic appetite control (23, 25, 28, 39). In contrast, previous studies have reported that the physiological processes that signal satiety appear to be enhanced with habitual PA or exercise-training, with changes seen in postprandial appetite-related peptides favouring satiety (19, 24, 25). Interestingly, Sim et al. (37) observed a tendency towards a reduction in energy intake following intake of a HEP with a concomitant improvement in insulin sensitivity after 12 weeks of high-intensity intermittent exercise training but not moderate-intensity continuous exercise training. This supports the thought that insulin sensitivity mediates the strength of satiety peptides such as GLP-1 and CCK (31, 35). Another process that could mediate the release of appetite-related peptides to signal satiety is gastric emptying, which was found to be faster in active compared to inactive males (20).

The inter-relationships that exist between PA, sedentary behaviour, body composition, and TDEE make it difficult to isolate which specific component associated with PA is contributing to the sensitivity of appetite control. Nonetheless, long-term habitual PA may lead to chronic physiological adaptations involved in satiety signalling, including reduced fat mass and enhanced insulin sensitivity, fine-tuning the appetite control system in its ability to detect adjustments in energy intake (over- or under-consumption) and to compensate appropriately at a subsequent meal. In line with these findings, the present study found intake to be reduced in the ModMVPA and HiMVPA groups in response to HEP. While improved post-meal satiety has been noted in physically active individuals, studies have reported that satiation does not differ between active and inactive individuals, as these distinct appetite processes may have differing underlying mechanisms (5).

The acute preload response at the ad libitum lunch meal in ModMVPA and HiMVPA was similar to that previously observed; however, previous evidence on daily (cumulative) energy compensation is conflicting. Some studies have demonstrated improvements in daily energy compensation with greater PA (25, 28), whereas another study, in line with the current results, suggests no improvements (37). Of note, assessment of daily energy intake in the aforementioned studies was done via food diaries which are prone to bias and misreporting, but in the current study, energy intake was objectively-assessed over 24 h. Furthermore, there was a large variability in the individual response in terms of cumulative EI, which may have contributed to the non-significant results. Other methodological factors may also explain these inconsistent findings, such as the different designs (exercise-training vs. cross-sectional), or physical characteristics (liquid vs. semi-solid) and macronutrient composition (matched vs. unmatched) of the preloads used between studies (3). Nevertheless, total daily energy intake was greater following HEP compared to LEP in all MVPA tertiles. This highlights the importance of promoting the consumption of foods lower in energy density to avoid a passive overconsumption of energy (33), irrespective of PA level (5).

Impact of HEP and LEP on appetite sensations and food hedonics

In all MVPA tertiles, compared to LEP, HEP led to a greater suppression of hunger, and after lunch, greater fullness and suppression of hunger, desire to eat and prospective food consumption. Changes in appetite sensations following consumption of liquid preloads varying in energy content in inactive and active individuals have been inconsistent across studies, with one showing greater fullness after HEP compared to LEP (27), while others showing no differences in appetite sensations (23, 25). In the current study, a semi-solid preload was preferred over a liquid preload to elicit a strong impact on appetite and in the following compensatory response in energy intake within the time frame allocated between preload consumption and ad libitum meal (2). Interestingly, all tertiles showed a greater suppression of hunger following HEP but only the more active tertiles reduced energy intake at lunch after its consumption. The effects observed on appetite sensations are difficult to translate into clinical significance and may depend on PA level.

The consumption of the HEP was reflected by a greater reduction in both liking and wanting fat appeal bias relative to LEP, without any differences between tertiles. This reduction in the hedonic preference for high-fat foods was likely mediated by the greater energy content of the HEP (~400 kcal) and subsequent greater suppression of hunger following its consumption. In contrast, we have recently observed no differences in liking and wanting fat appeal bias following ad libitum consumption of a high-fat/high-energy-dense meal compared to a low-fat/low-energy-dense meal (to a similar level of fullness) despite a greater energy intake of just below 400 kcal at the high-fat meal (5). Thus, it appears that an individual's hunger/satiety state may mediate the hedonic response to meals to a greater extent than energy intake or macronutrient composition, with greater suppression of hunger and/or perceived fullness leading to a greater reduction in liking and wanting for high-fat relative to low-fat foods. Alternatively, consumption of fixed (i.e. preload) and ad libitum meals may produce distinct hedonic responses. As with the appetite sensations, considering all tertiles responded similarly in their liking and wanting response, but differently in terms of energy intake, the effects observed on food hedonics were likely small. The mechanisms responsible for the blunted compensatory response in energy intake in LoMVPA remain to be fully elucidated, and in the current study, seem not to be related to the subjective appetite or hedonic response to the preloads.

In terms of the influence of PA level on the hedonic preference for high-fat foods, in the current nonobese sample, no differences in liking and wanting among MVPA tertiles were observed. These findings corroborate our previous findings where similarities in food hedonics in nonobese individuals differing in PA levels were also found (5). Heightened rewarding value of foods may be dependent upon a greater accumulation of body fat, as greater liking and wanting for high-fat foods have been observed in overweight inactive males compared to their leaner active counterparts (21) and also in overweight/obese females compared to healthy-weight females (32).

Limitations

Strengths of this study include robust measurements of objective PA to classify groups according to MVPA tertiles and probe meal days to quantify 24-h energy intake within a multi-level experimental platform to assess various components of appetite control and eating behaviour. However, this enhanced control did not allow for a very large sample size and may not have reflected real-world or long-term effects. Furthermore, a standardised diet on the days prior to the meal days was not provided, which may have strengthened the results. Assessment of postprandial appetite-related peptides following the preloads could also have provided a better depiction of satiety signalling differences between the MVPA tertiles, and should be addressed in future studies. It should also be acknowledged that the study only included nonobese individuals and this did not allow for the inclusion of very inactive and sedentary individuals; therefore, the individuals in the LoMVPA tertile were relatively active (~80 min/day of total MVPA). Although, according to a recent analysis comparing data obtained from PA sensors (as in the present study) with current PA guidelines, the amount of total daily MVPA (through structured PA and non-structured daily activities) to achieve PA guidelines (PAL of 1.75) is approximately 140 min/day of total MVPA (38). Nevertheless, this study was conducted in lean individuals and the findings may not be applicable to individuals who are obese and/or very inactive. Indeed it is now our view that PA will exert differing effects on appetite control according to the amount of fat mass and the proportion of truly sedentary behaviour. There is not one general rule that covers the relationship of PA and appetite control across the entire population.

Conclusions

Consumption of a HEP reduced energy intake at the following meal in nonobese individuals with moderate to high levels of MVPA compared to a LEP; however, this effect was absent in individuals with lower levels of MVPA. This suggests individuals with low levels of PA have a weaker satiety response to food. On the other hand, individuals who are more physically active are sensitive to the energy content of foods and have better ability to adjust intake at a subsequent meal. The mechanisms underlying this process remains to be fully elucidated, but could be linked to physiological satiety signalling rather than hedonic factors. Using objective measures of PA and energy intake, these data support previous evidence that lower levels of PA in nonobese individuals are detrimental to acute homeostatic appetite control.

Acknowledgements

No external funding was received to conduct this study.

Conflicts of Interest

The authors have no conflicts of interest to declare. The results of the present study do not constitute endorsement by ACSM and are presented clearly, honestly, and without fabrication, falsification, or inappropriate data manipulation.

REFERENCES

1. Ainsworth BE, Haskell WL, Herrmann SD, Meckes N, Bassett DR, Jr., Tudor-Locke C, Greer JL, Vezina J, Whitt-Glover MC, and Leon AS. 2011 Compendium of Physical

Activities: a second update of codes and MET values. Med Sci Sports Exerc. 2011;43(8):1575-81.

2. Almiron-Roig E, Chen Y, and Drewnowski A. Liquid calories and the failure of satiety: how good is the evidence? Obes Rev. 2003;4(4):201-12.

3. Almiron-Roig E, Palla L, Guest K, Ricchiuti C, Vint N, Jebb SA, and Drewnowski A. Factors that determine energy compensation: a systematic review of preload studies. Nutr Rev. 2013;71(7):458-73.

4. Beaulieu K, Hopkins M, Blundell JE, and Finlayson G. Does Habitual Physical Activity Increase the Sensitivity of the Appetite Control System? A Systematic Review. Sports Med. 2016;46(12):1897-919.

5. Beaulieu K, Hopkins M, Blundell JE, and Finlayson G. Impact of physical activity level and dietary fat content on passive overconsumption of energy in non-obese adults. Int J Behav Nutr Phys Act. 2017;14(1):14.

6. Blundell JE. Physical activity and appetite control: can we close the energy gap? Nutrition Bulletin. 2011;36(3):356-66.

7. Blundell JE, de Graaf C, Hulshof T, Jebb S, Livingstone B, Lluch A, Mela D, Salah S, Schuring E, van der Knaap H, and Westerterp M. Appetite control: methodological aspects of the evaluation of foods. Obes Rev. 2010;11(3):251-70.

8. Blundell JE, Finlayson G, Gibbons C, Caudwell P, and Hopkins M. The biology of appetite control: Do resting metabolic rate and fat-free mass drive energy intake? Physiol Behav. 2015;152(Pt B):473-8.

9. Blundell JE, Rogers PJ, and Hill A. Evaluating the satiating power of food: implications for acceptance and consumption. In: JEA Solms editor. Food Acceptance and Nutrition. London: Academic Press; 1987, pp. 205-19.

10. Caudwell P, Gibbons C, Hopkins M, King N, Finlayson G, and Blundell J. No sex difference in body fat in response to supervised and measured exercise. Med Sci Sports Exerc. 2013;45(2):351-8.

11. Caudwell P, Gibbons C, Hopkins M, Naslund E, King N, Finlayson G, and Blundell J. The influence of physical activity on appetite control: an experimental system to understand the relationship between exercise-induced energy expenditure and energy intake. Proc Nutr Soc. 2011;70(2):171-80.

12. Craig CL, Marshall AL, Sjostrom M, Bauman AE, Booth ML, Ainsworth BE, Pratt M, Ekelund U, Yngve A, Sallis JF, and Oja P. International physical activity questionnaire: 12-country reliability and validity. Med Sci Sports Exerc. 2003;35(8):1381-95.

13. Dhurandhar NV, Schoeller D, Brown AW, Heymsfield SB, Thomas D, Sorensen TI, Speakman JR, Jeansonne M, Allison DB, and the Energy Balance Measurement Working G. Energy balance measurement: when something is not better than nothing. Int J Obes (Lond). 2014.

14. Erlanson-Albertsson C. How palatable food disrupts appetite regulation. Basic Clin Pharmacol Toxicol. 2005;97(2):61-73.

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

16. Finlayson G, King N, and 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.

17. Gibbons C, Caudwell P, Finlayson G, King N, and Blundell J. Validation of a new hand-held electronic data capture method for continuous monitoring of subjective appetite sensations. The international journal of behavioral nutrition and physical activity. 2011;8:57.

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

19. Guelfi KJ, Donges CE, and Duffield R. Beneficial effects of 12 weeks of aerobic compared with resistance exercise training on perceived appetite in previously sedentary overweight and obese men. Metabolism. 2013;62(2):235-43.

20. Horner KM, Byrne NM, Cleghorn GJ, and King NA. Influence of habitual physical activity on gastric emptying in healthy males and relationships with body composition and energy expenditure. Br J Nutr. 2015:1-8.

21. Horner KM, Finlayson G, Byrne NM, and King NA. Food reward in active compared to inactive men: Roles for gastric emptying and body fat. Physiol Behav. 2016;160:43-9.

22. King NA, Caudwell PP, Hopkins M, Stubbs RJ, Naslund E, and Blundell JE. Dual-process action of exercise on appetite control: Increase in orexigenic drive but improvement in meal-induced satiety. Am J Clin Nutr. 2009;90(4):921-7.

23. Long SJ, Hart K, and Morgan LM. The ability of habitual exercise to influence appetite and food intake in response to high- and low-energy preloads in man. Br J Nutr. 2002;87(5):517-23.

24. Martins C, Kulseng B, King NA, Holst JJ, and Blundell JE. The effects of exercise-induced weight loss on appetite-related peptides and motivation to eat. J Clin Endocrinol Metab. 2010;95(4):1609-16.

25. Martins C, Kulseng B, Rehfeld JF, King NA, and Blundell JE. Effect of chronic exercise on appetite control in overweight and obese individuals. Med Sci Sports Exerc. 2013;45(5):805-12.

26. Martins C, Morgan L, and Truby H. A review of the effects of exercise on appetite regulation: an obesity perspective. Int J Obes. 2008;32(9):1337-47.

27. Martins C, Morgan LM, Bloom SR, and Robertson MD. Effects of exercise on gut peptides, energy intake and appetite. J Endocrinol. 2007;193(2):251-8.

28. Martins C, Truby H, and Morgan LM. Short-term appetite control in response to a 6-week exercise programme in sedentary volunteers. Br J Nutr. 2007;98(4):834-42.

29. Mattes R. Fluid calories and energy balance: the good, the bad, and the uncertain. Physiol Behav. 2006;89(1):66-70.

30. Mayer J, Roy P, and Mitra KP. Relation between caloric intake, body weight, and physical work: studies in an industrial male population in West Bengal. Am J Clin Nutr. 1956;4(2):169-75.

31. Morton GJ, Cummings DE, Baskin DG, Barsh GS, and Schwartz MW. Central nervous system control of food intake and body weight. Nature. 2006;443(7109):289-95.

32. Nijs IM, Muris P, Euser AS, and 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.

33. Rolls BJ. The role of energy density in the overconsumption of fat. J Nutr. 2000;130(2S Suppl):268S-71S.

34. Sallis JF, and Saelens BE. Assessment of Physical Activity by Self-Report: Status, Limitations, and Future Directions. Res Q Exerc Sport. 2000;71(sup2):1-14.

35. Schwartz MW, Woods SC, Porte D, Jr., Seeley RJ, and Baskin DG. Central nervous system control of food intake. Nature. 2000;404(6778):661-71.

36. Shook RP, Hand GA, Drenowatz C, Hebert JR, Paluch AE, Blundell JE, Hill JO, Katzmarzyk PT, Church TS, and Blair SN. Low levels of physical activity are associated with dysregulation of energy intake and fat mass gain over 1 year. Am J Clin Nutr. 2015;102(6):1332-8.

37. Sim AY, Wallman KE, Fairchild TJ, and Guelfi KJ. Effects of High-Intensity Intermittent Exercise Training on Appetite Regulation. Med Sci Sports Exerc. 2015;47(11):2441-9.

38. Thompson D, Batterham AM, Peacock OJ, Western MJ, and Booso R. Feedback from physical activity monitors is not compatible with current recommendations: A recalibration study. Prev Med. 2016;91:389-94.

39. Van Walleghen EL, Orr JS, Gentile CL, Davy KP, and Davy BM. Habitual physical activity differentially affects acute and short-term energy intake regulation in young and older adults. Int J Obes. 2007;31(8):1277-85.

40. Verschoor E, Finlayson G, Blundell J, Markus CR, and King NA. Effects of an acute alpha-lactalbumin manipulation on mood and food hedonics in high- and low-trait anxiety individuals. Br J Nutr. 2010;104(4):595-602.

List of Supplemental Digital Content

Supplemental Digital Content 1 (docx): Table 1 Ingredients and macronutrient composition of the high-energy preload (HEP) and low-energy preload (LEP)

Supplemental Digital Content 2 (docx): Table 1 Absolute energy intake in the control, low-energy preload (LEP) and high-energy preload (HEP) conditions across tertiles of MVPA

Supplemental Digital Content 3 (tiff): Figure 1 Individual response in lunch and cumulative EI relative to control in the low-energy preload (LEP) and high-energy preload (HEP) conditions across tertiles of MVPA

Supplemental Digital Content 4 (docx): Table 1 Absolute liking and wanting fat appeal bias scores pre- and post-preload consumption in the control, low-energy preload (LEP) and high-energy preload (HEP) conditions across tertiles of MVPA

Figure captions

Figure 1 Experimental protocol. RMR resting metabolic rate; VO_{2max} maximal aerobic capacity; VAS appetite visual analogue scales; LFPQ Leeds Food Preference Questionnaire; HEP high-energy preload; LEP low-energy preload; CON no-energy control.

Figure 2 Energy intake at lunch after the high-energy (HEP) and low-energy (LEP) preloads relative to control. Significant condition and MVPA tertile interaction, with post hoc analyses revealing that ModMVPA and HiMVPA had a greater reduction in intake after HEP compared to LEP *$p \leq .01$. LoMVPA, low moderate-to-vigorous physical activity tertile; ModMVPA, moderate moderate-to-vigorous physical activity tertile; HiMVPA, high moderate-to-vigorous physical activity tertile. Error bars indicate standard error of the mean.

Figure 3 Area under the curve (AUC) for ratings hunger (A), fullness (B), desire to eat (C) and prospective food consumption (PFC; D) following consumption of the high-energy (HEP) and low-energy (LEP) preloads relative to control (post-preload, VAS 5-7 over 1h; post-preload & lunch, VAS 7-10 over 2h). For clarity, group means are shown, demonstrating a main effect of condition *$p<.05$. Positive values indicate greater appetite scores relative to control and negative values indicate lower appetite scores relative to control. Error bars indicate standard error of the mean.

Figure 4 Liking (A) and wanting (B) pre- and post-consumption of the low-energy (LEP) and high-energy (HEP) preloads relative to control. For clarity, group means are shown, demonstrating a significant interactions between condition and preload consumption, with post hoc analyses showing a greater reduction in liking and wanting for high-fat foods pre- to post-preload in HEP compared to LEP †$p<.01$ *$p=.001$ **$p<.001$. Positive scores indicate greater liking or wanting towards high-fat compared to low-fat foods, whereas negative scores indicate greater liking or wanting towards low-fat compared to high-fat foods. Error bars indicate standard error of the mean.