



The complex pattern of the effects of prolonged frequent exercise on appetite control, and implications for obesity

John E. Blundell^{*}, Kristine Beaulieu

Appetite Control and Energy Balance Research Group (ACEB), School of Psychology, Faculty of Medicine and Health, University of Leeds, Leeds, UK

ARTICLE INFO

Handling Editor: M.M. Hetherington

Keywords:

Physical activity
Exercise
Appetite control
Energy balance
Obesity

ABSTRACT

From a public health perspective, much of the interest in the relationship between exercise and appetite rests on the implications for energy balance and obesity. Energy balance reflects a dynamic 2-way interaction between energy expenditure (EE) and energy intake (EI). Physical activity and exercise, and appetite are the behavioural components of EE and EI, respectively. Beyond EE, exercise is a powerful and complex physiological stimulus acting on several bodily systems. There are multiple effects of frequent and prolonged exercise on appetite which include *inter alia* an increase in fasting hunger, an enhancement of post-prandial satiety, a modulation of the hedonic responses to food and improvements in eating behaviour traits. These lead to variable adjustments in EI and in a reduction in the susceptibility to overconsumption. Frequent and prolonged physical activity and exercise behaviour can strengthen and sensitise the appetite control system, whilst physical inactivity and sedentariness (low level of EE) fails to downregulate EI and can permit overconsumption. Not all of the effects of exercise operate uniformly to drive appetite in the same direction. The complexity of the interaction between EE and EI means that the effects of prolonged exercise are characterised by substantial individual heterogeneity. This leads to variable effects on energy balance and body mass.

1. Orientation

The late Henry Taylor proposed that 'energy intake is in exact homeostasis with energy expenditure under conditions of high energy expenditure ... (but) ... there is a failure of homeostasis in a sedentary lifestyle because of its accompanying low energy expenditure'. He postulated that 'body signals go awry in sedentary lifestyles; when a person does no physical work, the body will not recognise that it is being overfed. Sedentary persons may lose their innate ability to compensate for inactivity by reducing their eating' (cited by Jacobs, 2006).

2. What is the issue?

The brief for this commentary is to present a critique of the effect of prolonged periods of physical activity (exercise) on the expression of human appetite. This requires a few words to define the scope and nature of the work, and to anticipate what can and cannot be concluded from such bio-behavioural and cultural complexity. From a public health perspective, much of the interest in the relationship between exercise and appetite rests on the implications for energy balance and

obesity. Therefore, to be meaningful, we include in our task situations in which physical activity is naturally incorporated into habitual daily routines (leading to changes in total EE) and where it is deliberately imposed for a specific experimental purpose (to test a hypothesis, for example).

The task also requires entering the debate about the value of exercise for the control of body mass and obesity. This commentary therefore goes beyond the reporting of experimental studies of exercise and will examine in addition the habitual or long-term relationship between physical activity and body mass. For clarity, we use the term appetite to include the totality of processes that influence food consumption, and which therefore includes sensations of hunger, fullness and a desire to eat, eating patterns, food selection, food hedonics and satiety. Appetite is therefore a complex phenomenon that is best regarded as an emergent property of a complex system (UK Government's Foresight Programme, 2007). EI is one quantifiable component of appetite which is 100% behaviour but with very variable topography (humans are omnivores and eating varies markedly between different cultures on the planet).

Exercise is also a multifaceted form of behaviour and varies in intensity and duration as well as in its modality (running, walking, cycling,

^{*} Corresponding author.

E-mail address: j.e.blundell@leeds.ac.uk (J.E. Blundell).

<https://doi.org/10.1016/j.appet.2023.106482>

Received 24 January 2023; Accepted 1 February 2023

Available online 6 February 2023

0195-6663/© 2023 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

swimming for example) and the manner in which it is performed in different human groups varying in ethnicity and culture. Given the complexity of this field of enquiry, it is unlikely that there will be a single statement that can describe the interrelationships between prolonged exercise and appetite, and it would be wise to avoid trying to reach all-embracing conclusions. Limited, specific, and modest conclusions may be possible; and, of course, people are most interested in an answer to the limited question of the impact of exercise on food (energy) intake. This question can be most clearly addressed through a planned and controlled experimental study. However, what people really want to know is: what happens under free-living real-world situations? For this, the outcomes of studies need to be interpreted in the light of additional information.

The importance of this area of research is given relevance and urgency by the worldwide pandemic of obesity, and the potential role that exercise can play in the management of a person's body mass (and more particularly, body fat). For this reason, we can translate the brief of this commentary into an enquiry about the effect of chronic exercise, or prolonged frequent periods of habitual physical activity, on the management of body mass. Given that a definition of physical activity is a behaviour that is accompanied by the expenditure of energy and a stimulation of skeletal musculature, it is reasonable to expect that prolonged frequent exercise will have beneficial effects on body composition and the management of obesity. This supposition is often viewed negatively and has become a controversial issue.

3. What is the controversy?

First, it should be recognised that prolonged and habitual physical activity is undertaken by various types of people and for a variety of reasons. For example, lean individuals do exercise to maintain general health and to retain leanness, athletes for fitness and performance and to keep body fat low (but not desirable in all cases), people with overweight to prevent their BMI reaching and exceeding a value of 30 kg/m², people with obesity endeavouring to lose body fat, and people who have lost body fat intending to prevent body fat regain. In all of these cases, there is inevitably a relationship between the amount and intensity of exercise carried out and body composition. It may be that the most powerful effect of frequent and prolonged exercise is to allow people (of whatever body mass) to maintain weight and therefore to prevent weight gain (e.g. Jakicic, Marcus, Lang, & Janney, 2008), or to mitigate weight gain in the face of weight-inducing dietary habits which promote overconsumption. For example, in the UK, there is a calculated excess daily intake of 195–320 kcal/day (Public Health England, 2018) which contributes to the inexorable rise in the prevalence of adult overweight and obesity in the country reaching 68% of men and 60% of women in 2019 (NHS Digital, 2019). This occurs simultaneously with an estimated 70% of the population of England being sedentary for at least 7 h per day (Office for Health Improvement and Disparities, 2022) and some studies showing that people spend approximately 11 h per day in sedentary behaviour (67% of waking time) (Myers, Gibbons, Finlayson, & Blundell, 2017). Under these circumstances, it is very difficult to detect whether or not, in those individuals with a high physical activity behaviour (but with an associated pattern of overconsumption), the positive effect of exercise on body mass is being overridden by excessive food consumption.

Although the maintenance of body mass or the prevention of body mass gain are likely to be the most important ways in which physical activity can influence the state of obesity, these are difficult to measure and are not a main focus of attention. What people really want to know is whether exercise training can produce body mass loss in people living with obesity. Over the years, various journalists in the print media have derided this possibility with headlines such as 'Health warning: exercise makes you fat' (Telegraph, 2009), and 'The myth about exercise: why exercise won't make you slim' (Time Magazine, 2009). Academics have also expressed negative views such as 'Physical activity does little to

control weight' (Pontzer, 2017). Are these views based on a fair and objective analysis of the evidence?

4. Prolonged exercise and body mass

For years, one of the most respected scientific investigations remains a position paper for the American College of Sports Medicine entitled 'Appropriate physical activity interventions for weight loss and prevention of weight regain for adults' (Donnelly et al., 2009). This report showed a clear dose-response relationship between the amount of exercise performed (minutes per week or energy expended per week) and the reduction of body mass and the resistance to body mass regain after loss. In 2003, a consensus meeting of physical activity experts published an expert review of evidence with the conclusion that 'moderate intensity activity of 45–60 min per day is required to prevent the transition to overweight and obesity' (Saris et al., 2003). For individuals previously living with obesity, 60–90 min would be required. Later, a Cochrane review concluded that 'exercise has a positive effect on body mass and cardiovascular risk factors in people with overweight and obesity, particularly when combined with a diet' (Shaw, Gennat, O'Rourke, & Del Mar 2006). A further report concluded that 'for people starting an exercise programme, this leads to a negative energy balance and a remarkably consistent loss of body fat in relation to the net cost of exercise training' (Elder & Roberts, 2007). Although these outcomes may have been modest, they certainly did not support the view that exercise interventions are futile for weight management. In addition, the report of Public Health England (2013) has accepted the findings of the Foresight Report (2007) that physical activity is a key contributor to energy balance, helping to prevent obesity and excess body mass gain. Moreover, in a study of obesity, physical activity and EI in US adults between 1988 and 2010, the proportion of adults who reported no leisure time physical activity increased from 19.1% to 51.7% and this was associated with upward trends in BMI and waist circumference (Ladabaum, Mannalithara, Myer, & Singh, 2014). Consequently, there is considerable empirical evidence and opinion about an established link between physical (in-)activity and obesity. However, we recognise the possibility of reverse causality operating in some cases (e.g. Carrasquilla, García-Ureña, Fall, Sørensen, & Kilpeläinen, 2022).

However, until recently there was no comprehensive and objective overview of all available reviews and studies in individuals with overweight or obesity. This has now been remedied with a series of seven systematic reviews and meta-analyses on the impact of exercise training interventions on body mass, body fat, and other variables of interest conducted under the auspices of the European Association for the Study of Obesity (EASO) Physical Activity Working Group in order to produce guidelines for the obesity community (Oppert et al., 2021). These analyses have shown clearly that aerobic exercise training at moderate intensity leads to loss of body mass, total fat, visceral fat, intra-hepatic fat, and improvements in blood pressure, with an expected average body mass loss of 2–3 kg. Resistance training at moderate-to-vigorous intensity is recommended for preservation of lean mass during body mass loss. Any type of exercise training is recommended for improvements in metabolic and cardiorespiratory fitness.

Specifically, the overview of 12 systematic reviews and 149 studies by Bellicha et al. (2021) of exercise training on body mass loss and changes in body composition shows conclusively that exercise can produce a reduction in the amount of body mass and body fat. However, the reductions are quite modest (although this is partly a function of the limited time periods of the training and low doses of exercise employed), ranging from 1.5 to 3.5 kg body mass loss and 1.3–2.6 kg fat loss over a period of 2 weeks–12 months. This outcome reflects a common view that exercise alone appears to be less effective than theoretically expected on the basis of the energy expended (Martin et al., 2019; Myers, Dalton, Gibbons, Finlayson, & Blundell, 2019; Thomas et al., 2012). In turn, this raises the possibility that effects of exercise on EI may offset the negative energy balance brought about by physical activity EE. What is the

evidence?

5. Exercise training and appetite control

In one of the EASO systematic reviews (Beaulieu et al., 2021), meta-analysis highlighted that among 25 exercise groups, exercise training (ranging 2–72 weeks; median 12 weeks) did not lead to a significant post-intervention difference in EI compared to non-exercise control groups. Meta-regression showed this was not affected by intervention duration. However, due to the high number of poor-quality studies (i.e. using self-reported food intake measures), sensitivity analyses were conducted in only fair/good quality studies (reduced to 5 exercise groups). This resulted in a 102-kcal post-exercise difference between exercisers relative to controls. It is important to note that this equated to a negligible effect size, and is an effect based on the average which does not reflect inter-individual variability (discussed below). Therefore, over time, on average, there may be small compensatory increases in EI in response to the increased energy demands from greater physical activity behaviour. Indeed, the review also found a small increase in fasting hunger after exercise training (Beaulieu et al., 2021) as demonstrated previously in a medium term (12-week) study (King et al., 2009).

Nevertheless, as can be calculated from the energy expended during exercise, this should still lead to a negative energy balance, some degree of body mass loss, and favourable changes in body composition with sufficient EE. Small positive changes were also observed in relation to eating behaviour traits, with a reduction in disinhibition and an increase in restraint (Beaulieu et al., 2021). Overall, the outcome of this systematic review shows that periods of exercise training give rise to quite small average changes in EI. However, the average change in EI (a single number) does not disclose the various components of the appetite system that may be modulated by the powerful impact of prolonged exercise on different physiological processes.

6. Prolonged frequent exercise and appetite control

There is a number of research strategies to examine the effect of frequent exercise on food consumption. Firstly, it is possible to examine simultaneously the physical activity habits and the dietary intake patterns of a specified and rather homogenous group of participants. Over half a century ago, this type of study was conducted by Edholm, Widdowson and colleagues on army cadets (Edholm, 1977; Edholm et al., 1970; Edholm, Fletcher, Widdowson, & McCance, 1955). As the authors reported, ‘the differences in the intakes of food (between individuals) must originate in the differences in energy expenditure’ (Edholm et al., 1955). The authors concluded that there was a relationship between EE and EI, and this formed the basis for appetite control itself. However, the authors did not describe the nature of the mechanisms underlying the relationship.

A similar research strategy had also been used on a randomly selected group of individuals. This is the method employed in the now classic work of Jean Mayer in the study of jute mill workers in Calcutta (Mayer, Roy, & Mitra, 1956). The outcome of the study was that food intake varied according to the degree of physical activity of the workers. However, the relationship was not linear: daily occupational physical activity and EI were closely matched in those performing physically demanding jobs, whereas in those performing light or sedentary occupational roles, this coupling was lost such that daily EI exceeded EE. This prompted the interpretation that the level of EE (associated with different degrees of labour at work) caused changes in the control of food intake, illustrated by a J- or U-shaped relationship between physical activity and EI, with ‘non-regulated’ and ‘regulated’ zones of appetite control seen across the physical activity spectrum (Beaulieu, Hopkins, Blundell, & Finlayson, 2018; Blundell, 2011; Blundell, Gibbons, Caudwell, Finlayson, & Hopkins, 2015; Shook et al., 2015).

This type of study has also been carried out with concurrent

meticulous measurements of quantified and objective physical activity (heart rate flex procedure) and EI (weighed dietary intakes). Conducted over varying periods of time and under free-living or semi free-living conditions, this work has shown that frequent physical activity is weakly but positively related to EI (Hopkins et al., 2019). Complementing these observational studies, certain short-term intervention studies which have incrementally increased the exercise dose have indicated a proportionate increase in EI (Stubbs, Sepp, Hughes, Johnstone, Horgan, et al., 2002; Stubbs, Sepp, Hughes, Johnstone, King, et al., 2002; Whybrow et al., 2008). A further medium-term intervention study has demonstrated that aerobic exercise leads to a reduction in body adipose tissue which can be partially compensated by an increase in EI (Myers et al., 2019). Consequently, it can be concluded that prolonged daily physical activity does lead on average to a mild stimulation of EI. This effect would tend to offset some of the energy expended by the physical activity. This perception of the role of exercise supports the idea of *dynamic* energy balance (rather than *static*) in which there is a two-way interaction between EE and EI (Hopkins & Blundell, 2022; Piaggi et al., 2022).

Two other strategies have also been employed to examine the effect of frequent exercise on food consumption. The first involves individuals being part of controlled intervention of monitored periods of exercise over varying periods of time, whilst measuring changes in daily patterns of EI, hunger and satiety. This procedure – in the form of a clinical trial – requires substantial control over the research environment in order to achieve objective and repeatable outcomes. In a 12-week exercise training study by King et al. (2009), two separate processes were revealed that acted concurrently to influence appetite control: a significant but variable increase in fasting hunger that was offset by a parallel increase in post-prandial satiety (as measured in response to a fixed energy meal). The second strategy involves selecting and comparing individuals on the basis of their degree of physical activity behaviour without any intervention. These strategies are complementary but offer different insights into the relationship of exercise and appetite. For example, in a replication of the classic preload study by Long, Hart, and Morgan (2002), we provided confirmatory evidence for enhanced appetite control in individuals objectively-classified with moderate-to-high physical activity behaviour who showed better compensation following consumption of high-energy compared to low-energy preloads (Beaulieu, Hopkins, Long, Blundell, & Finlayson, 2017). Individuals with greater physical activity behaviour reduced EI to offset the difference in energy consumed from the preloads whereas the individuals with lower physical activity behaviour were insensitive to the nutritional manipulation, indicating a weaker satiety response to food.

To summarise, in addition to the effects of exercise on the appetite-related parameters reported from our systematic review above, it appears that exercise increases the sensitivity of the appetite control system, reducing the susceptibility to overconsumption (Beaulieu, Hopkins, Blundell, & Finlayson, 2016). There is good evidence that this is due to the system operating at a higher level of energy turnover (Hägele et al., 2019; Melby, Paris, Sayer, Bell, & Hill, 2019). The greater the physical activity behaviour (and EE), the greater is the potential for healthy control of appetite. It is worth noting in passing that physical activity (and activity EE) have now been incorporated into a more general theory on the influence of EE on EI (Blundell et al., 2020; Hopkins, Beaulieu, Myers, Gibbons, & Blundell, 2017).

7. Individual variability in the response to prolonged exercise

Under conditions of prolonged physical activity (exercise), people respond very differently to the imposed energy demand and physiological adjustment, and clear individual differences ensue. Similar individual variability is observed when an excess caloric intake is imposed such as that in the Quebec over-feeding studies (Bouchard et al., 1988), or the surplus calorie loading study (Levine, Eberhardt, & Jensen, 1999)

which demonstrated that fat gain after overfeeding was variable and opposed by varying high levels of physical activity energy expenditure (activity thermogenesis). This important study is now often overlooked in discussions of obesity, physical activity and diet. Other studies have reported that after a prolonged exercise training period of 12 weeks or more, large inter-individual differences in body mass and body fat can be measured among participants (Church et al., 2009; Hammond et al., 2019; King et al., 2009; King, Hopkins, Caudwell, Stubbs, & Blundell, 2008; Martin et al., 2019). These differences in body fat are accompanied by differences in perceived hunger and EI (King et al., 2009; Martin et al., 2019), and associated with pre-existing eating behaviour traits (King et al., 2008). Usually in these studies, when the imposed physical activity is monitored and measured, there is a clear average body mass loss; whilst most individuals lose body mass, some actually gain body mass. As noted by statisticians, the average is an abstraction, the reality is variation (Blastland & Dilnot, 2008). This indicates that the cumulative effect of daily EE (or the act of performing exercise itself) is affecting the physiology and metabolism (and psychological state) of people in different ways, as is also the case with prolonged overfeeding. The observed changes in body composition represent neither true nor false individual differences (e.g. Atkinson & Batterham, 2015), they are simply biological facts that identify quantifiable differences between people who show biological heterogeneity. This means that the effect of exercise will vary from person to person; there will be good and poor responders, and there is no single golden rule that can predict a specific outcome.

What is the appropriate interpretation of this complex situation? Our view is that prolonged periods of exercise training (or habitual daily physical activity) in general sensitise the appetite system so that there is better response to imposed energy perturbations. However, the physiological demands of exercise can simultaneously adjust distinct components of the system (fasting hunger, post-prandial satiety, response to energy density of foods, hedonic response) which will not be identical in every person. The patterns of appetite responses leading to adjustments in daily EI, when set against the cumulative energy expended in prolonged exercise, generate differences in energy balance which lead to differences in body composition (especially fat stores) over time.

8. The importance of debate

The role of physical activity for general health and to minimise the damaging effects of obesity is of such importance that it is necessary to counter those claims that physical activity is of little or no value. One headline quote is that 'you cannot outrun a bad diet' (e.g. Malhotra, Noakes, & Phinney, 2015). Such a claim completely distorts the framing of the problem. The issue of obesity is not a question of diet OR inactivity. It is both! Everyone can agree that overconsumption is a major cause of weight gain (and more gain), but this should not entail a disqualification (or denial) of the contribution of physical activity. The excessive zeal of some commentators in denying a role for physical inactivity and sedentariness in obesity is hard to understand; and is misplaced. Such a slogan may cause huge damage to public health by dissuading people from using physical activity as ONE tool to prevent further body mass gain and the accumulation of body fat. We have described how the relation between physical activity, appetite and obesity is complex and the size and form of the outcomes are hard to predict. But, urging people to refrain from exercise, remain physically inactive, or to give up has huge consequences.

A second theme that has been heavily promoted in the last few years is that the effects of physical activity on EE are 'constrained' (e.g. Pontzer, 2015; Pontzer et al., 2016). This argument places physical activity in the context of a metabolic system and claims that as physical activity is increased, it does not generate a proportional increase in EE (due to metabolic savings elsewhere), and therefore this will minimise an effect on negative energy balance. This analysis is based on complex and extensive data sets from different populations in various parts of the

world, including rural and urban groups, and primitive and modern societies; but on the basis of these computations, it is claimed that 'physical activity has little effect on body weight'. The data analyses are complicated and the data are subject to various transformations. However, it is difficult to identify how similarities in the average total EE of different nation states can be used to infer that there is no effect of physical activity on body mass at the individual level of people within those national groups.

More particularly, the Pontzer argument has recently been subjected to a detailed critical analysis, including the statistical treatment of the data (Ward, 2022). Ward, an internet scientific blogger, concludes that although energy compensation exists (as Pontzer claims), a high volume of exercise can still increase total daily EE in most exercisers and will promote body mass loss. This is indeed confirmed in the study of Careau et al. (2021) in which it is estimated that on average 72% of the energy cost of physical activity leads to true EE and therefore contributes to negative energy balance. This is clearly sufficient to bring about body mass loss (in the absence of any compensatory increase in EI). The value for those individuals beyond the 90th centile for BMI was about 50%. It is also worth drawing attention to the work of Westerterp and Plasqui (2009) in which a significant decline in physical activity EE and physical activity level (PAL) over a 10-year period in the same individuals is accompanied by a significant increase in BMI. There was also an inverse relationship between the change in PAL and rate of change of fat mass.

In composing this commentary, we would encourage researchers to adopt a sceptical approach to heavily promoted polemical claims about the futility of physical activity as a factor in body mass control. Our view is that, in reaching for all-embracing explanations of the relationship between physical activity (or activity EE) and obesity, some researchers have placed too much emphasis on the average of large populations (of some nation states) to the exclusion of the huge heterogeneity existing in those populations.

9. Future prospects

There is no doubt that the issue of exercise and body mass loss is an area of contention between advocates and deniers, and this state of affairs is likely to continue. What is surprising is the zeal and conviction of the deniers; the case against is made with forceful certainty as if it is a moral duty to disabuse people of the idea that exercise can be useful as an aid to body mass loss. Even when there is grudging acceptance of the significance of the average, it is claimed that it is of little meaning clinically. This is misplaced since the benefits of weight loss brought about by exercise are accompanied by all the other benefits due to exercise itself.

However, the real problem here is to focus on the average of a distribution to the exclusion of variation. For too long differences between means have been the main criterion when judging the value of a scientific experiment. As noted earlier by statisticians, the average is an abstraction, reality is variation. Exercise is a forceful physiological stimulus with a broad spectrum of effects; the interaction of this with the wide physical, anatomical and metabolic heterogeneity of individuals will result in a range of different individual outcomes. This is to be expected. People respond to exercise (and to various other interventions) in different ways because of their personal bio-psychological profiles. It therefore seems important to try to determine those biomarkers and individual characteristics which differentiate between responders and non-responders to exercise-induced weight loss, and to find strategies in addition to exercise to help non-responders achieve their weight management goals. This seems to us to be a more fruitful avenue than to assert that physical activity is futile thus deterring people from the undertaking and therefore preventing many from achieving the health benefits.

It is worth noting that the widespread physical inactivity and sedentariness in many societies (in addition to lowering EE) allows overconsumption to occur readily and is a probable contributing cause of

weight gain and obesity. Carrying excess fat in the body is usually a deterrent to performing physical activity (some sports such as rugby are an exception to this rule) but having obesity does not deter people living with obesity from overconsuming. Importantly, the relationship between physical activity and adiposity is bi-directional, as noted by Myers et al. (2017) and recently confirmed by a study using the strategy of Mendelian randomisation (Carrasquilla et al., 2022); increasing body fatness induces sedentariness, whilst low physical activity leads to the accumulation of fat. The great hazard to our health is physical inactivity.

Ethical statement

Ethical approval was not required for this commentary.

Declaration of competing interest

The authors report no conflicts of interest.

Data availability

No data was used for the research described in the article.

References

- Atkinson, G., & Batterham, A. M. (2015). True and false interindividual differences in the physiological response to an intervention. *Experimental Physiology*, 100(6), 577–588. <https://doi.org/10.1113/ep085070>
- Beaulieu, K., Blundell, J. E., van Baak, M. A., Battista, F., Busetto, L., Carraça, E. V., et al. (2021). Effect of exercise training interventions on energy intake and appetite control in adults with overweight or obesity: A systematic review and meta-analysis. *Obesity Reviews*, 22(Suppl 4), Article e13251. <https://doi.org/10.1111/obr.13251>. Suppl 4.
- Beaulieu, K., Hopkins, M., Blundell, J. E., & Finlayson, G. (2016). Does habitual physical activity increase the sensitivity of the appetite control system? A systematic review. *Sports Medicine*, 46(12), 1897–1919. <https://doi.org/10.1007/s40279-016-0518-9>
- Beaulieu, K., Hopkins, M., Blundell, J., & Finlayson, G. (2018). Homeostatic and non-homeostatic appetite control along the spectrum of physical activity levels: An updated perspective. *Physiology and Behavior*, 192, 23–29. <https://doi.org/10.1016/j.physbeh.2017.12.032>
- Beaulieu, K., Hopkins, M., Long, C., Blundell, J. E., & Finlayson, G. (2017). High habitual physical activity improves acute energy compensation in nonobese adults. *Medicine & Science in Sports & Exercise*, 49(11), 2268–2275. <https://doi.org/10.1249/mss.0000000000001368>
- Bellicha, A., van Baak, M. A., Battista, F., Beaulieu, K., Blundell, J. E., Busetto, L., et al. (2021). Effect of exercise training on weight loss, body composition changes, and weight maintenance in adults with overweight or obesity: An overview of 12 systematic reviews and 149 studies. *Obesity Reviews*, 22(Suppl 4), Article e13256. <https://doi.org/10.1111/obr.13256>. Suppl 4.
- Blastland, M., & Dilnot, A. W. (2008). *The Tiger that isn't: Seeing Through a World of numbers: Profile*.
- Blundell, J. E. (2011). Physical activity and appetite control: Can we close the energy gap? *Nutrition Bulletin*, 36(3), 356–366. <https://doi.org/10.1111/j.1467-3010.2011.01911.x>
- Blundell, J. E., Gibbons, C., Beaulieu, K., Casanova, N. D. C., Finlayson, G., Stubbs, R. J., et al. (2020). The drive to eat in homo sapiens: Energy expenditure drives energy intake. *Physiology and Behavior*, 219, Article 112846. <https://doi.org/10.1016/j.physbeh.2020.112846>
- Blundell, J. E., Gibbons, C., Caudwell, P., Finlayson, G., & Hopkins, M. (2015). Appetite control and energy balance: Impact of exercise. *Obesity Reviews*, 16, 67–76. <https://doi.org/10.1111/obr.12257>
- Bouchard, C., Tremblay, A., Despres, J. P., Poehlman, E. T., Theriault, G., Nadeau, A., et al. (1988). Sensitivity to overfeeding: The Quebec experiment with identical twins. *Progress in Food & Nutrition Science*, 12(1), 45–72.
- Careau, V., Halsey, L. G., Pontzer, H., Ainslie, P. N., Andersen, L. F., Anderson, L. J., et al. (2021). Energy compensation and adiposity in humans. *Current Biology*, 31(20), 4659–4666.e4652. <https://doi.org/10.1016/j.cub.2021.08.016>
- Carrasquilla, G. D., García-Ureña, M., Fall, T., Sørensen, T. I. A., & Kilpeläinen, T. O. (2022). Mendelian randomization suggests a bidirectional, causal relationship between physical inactivity and adiposity. *Elife*, 11, Article e70386. <https://doi.org/10.7554/eLife.70386>
- Church, T. S., Martin, C. K., Thompson, A. M., Earnest, C. P., Mikus, C. R., & Blair, S. N. (2009). Changes in weight, waist circumference and compensatory responses with different doses of exercise among sedentary, overweight postmenopausal women. *PLoS One*, 4(2), e4515. <https://doi.org/10.1371/journal.pone.0004515>
- Donnelly, J. E., Blair, S. N., Jakicic, J. M., Manore, M. M., Rankin, J. W., & Smith, B. K. (2009). American College of Sports Medicine Position Stand. Appropriate physical activity intervention strategies for weight loss and prevention of weight regain for adults. *Medicine & Science in Sports & Exercise*, 41(2), 459–471. <https://doi.org/10.1249/MSS.0b013e3181949333>
- Edholm, O. G. (1977). Energy balance in man studies carried out by the division of human physiology, national institute for medical research. *Journal of Human Nutrition*, 31(6), 413–431.
- Edholm, O. G., Adam, J. M., Healy, M. J., Wolff, H. S., Goldsmith, R., & Best, T. W. (1970). Food intake and energy expenditure of army recruits. *British Journal of Nutrition*, 24(4), 1091–1107.
- Edholm, O. G., Fletcher, J. G., Widdowson, E. M., & McCance, R. A. (1955). The energy expenditure and food intake of individual men. *British Journal of Nutrition*, 9(3), 286–300.
- Elder, S. J., & Roberts, S. B. (2007). The effects of exercise on food intake and body fatness: A summary of published studies. *Nutrition Reviews*, 65(1), 1–19. <https://doi.org/10.1111/j.1753-4887.2007.tb00263.x>
- Hägele, F. A., Büsing, F., Nas, A., Hasler, M., Müller, M. J., Blundell, J. E., et al. (2019). Appetite control is improved by acute increases in energy turnover at different levels of energy balance. *Journal of Clinical Endocrinology and Metabolism*, 104(10), 4481–4491. <https://doi.org/10.1210/je.2019-01164>
- Hammond, B. P., Stotz, P. J., Brennan, A. M., Lamarche, B., Day, A. G., & Ross, R. (2019). Individual variability in waist circumference and body weight in response to exercise. *Medicine & Science in Sports & Exercise*, 51(2), 315–322. <https://doi.org/10.1249/mss.0000000000001784>
- Hopkins, M., Beaulieu, K., Myers, A., Gibbons, C., & Blundell, J. E. (2017). Mechanisms responsible for homeostatic appetite control: Theoretical advances and practical implications. *Expert Review of Endocrinology and Metabolism*, 12(6), 401–415. <https://doi.org/10.1080/17446651.2017.1395693>
- Hopkins, M., & Blundell, J. E. (2022). Striking a balance: Orexigenic and energy-consuming effects of energy expenditure on body weight. *Obesity*, 30(3), 575–576. <https://doi.org/10.1002/oby.23393>
- Hopkins, M., Duarte, C., Beaulieu, K., Finlayson, G., Gibbons, C., Johnstone, A. M., et al. (2019). Activity energy expenditure is an independent predictor of energy intake in humans. *International Journal of Obesity*. <https://doi.org/10.1038/s41366-018-0308-6>, 2005.
- Jacobs, D. R. (2006). Fast food and sedentary lifestyle: A combination that leads to obesity. *American Journal of Clinical Nutrition*, 83(2), 189–190. <https://doi.org/10.1093/ajcn/83.2.189>
- Jakicic, J. M., Marcus, B. H., Lang, W., & Janney, C. (2008). Effect of exercise on 24-month weight loss maintenance in overweight women. *Archives of Internal Medicine*, 168(14), 1550–1559. <https://doi.org/10.1001/archinte.168.14.1550>
- King, N. A., Caudwell, P. P., Hopkins, M., Stubbs, R. J., Naslund, E., & Blundell, J. E. (2009). Dual-process action of exercise on appetite control: Increase in orexigenic drive but improvement in meal-induced satiety. *American Journal of Clinical Nutrition*, 90(4), 921–927. <https://doi.org/10.3945/ajcn.2009.27706>
- King, N. A., Hopkins, M., Caudwell, P., Stubbs, R. J., & Blundell, J. E. (2008). Individual variability following 12 weeks of supervised exercise: Identification and characterization of compensation for exercise-induced weight loss. *International Journal of Obesity*, 32(1), 177–184. <https://doi.org/10.1038/sj.ijo.0803712>
- Ladabaum, U., Mannalithara, A., Myer, P. A., & Singh, G. (2014). Obesity, abdominal obesity, physical activity, and caloric intake in US adults: 1988 to 2010. *The American Journal of Medicine*, 127(8), 717–727.e712. <https://doi.org/10.1016/j.amjmed.2014.02.026>
- Levine, J. A., Eberhardt, N. L., & Jensen, M. D. (1999). Role of nonexercise activity thermogenesis in resistance to fat gain in humans. *Science*, 283(5399), 212–214. <https://doi.org/10.1126/science.283.5399.212>
- Long, S. J., Hart, K., & Morgan, L. M. (2002). The ability of habitual exercise to influence appetite and food intake in response to high- and low-energy preloads in man. *British Journal of Nutrition*, 87(5), 517–523. <https://doi.org/10.1079/BJNBJN2002560>
- Malhotra, A., Noakes, T., & Phinney, S. (2015). It is time to bust the myth of physical inactivity and obesity: You cannot outrun a bad diet. *British Journal of Sports Medicine*, 49(15), 967–968. <https://doi.org/10.1136/bjsports-2015-094911>
- Martin, C. K., Johnson, W. D., Myers, C. A., Apolzan, J. W., Earnest, C. P., Thomas, D. M., et al. (2019). Effect of different doses of supervised exercise on food intake, metabolism, and non-exercise physical activity: The E-MECHANIC randomized controlled trial. *American Journal of Clinical Nutrition*. <https://doi.org/10.1093/ajcn/nqz054>
- Mayer, J., Roy, P., & Mitra, K. P. (1956). Relation between caloric intake, body weight, and physical work: Studies in an industrial male population in West Bengal. *American Journal of Clinical Nutrition*, 4(2), 169–175. <https://doi.org/10.1093/ajcn/4.2.169>
- Melby, C. L., Paris, H. L., Sayer, R. D., Bell, C., & Hill, J. O. (2019). Increasing energy flux to maintain diet-induced weight loss. *Nutrients*, 11(10). <https://doi.org/10.3390/nu11102533>
- Myers, A., Dalton, M., Gibbons, C., Finlayson, G., & Blundell, J. (2019). Structured, aerobic exercise reduces fat mass and is partially compensated through energy intake but not energy expenditure in women. *Physiology and Behavior*, 199, 56–65. <https://doi.org/10.1016/j.physbeh.2018.11.005>
- Myers, A., Gibbons, C., Finlayson, G., & Blundell, J. E. (2017). Associations among sedentary and active behaviours, body fat and appetite dysregulation: Investigating the myth of physical inactivity and obesity. *British Journal of Sports Medicine*, 51(21), 1540–1544. <https://doi.org/10.1136/bjsports-2015-095640>
- Nhs Digital. (2019). *Statistics on obesity, physical activity and diet*. England, 2019. Retrieved from <https://digital.nhs.uk/data-and-information/publications/statistica/1/statistics-on-obesity-physical-activity-and-diet/statistics-on-obesity-physical-activity-and-diet-england-2019>.
- Office for Health Improvement and Disparities. (2022). *Public health profiles: Physical activity*. Retrieved from <https://fingertips.phe.org.uk/profile/physical-activity/data#page/1>.

- Oppert, J.-M., Bellicha, A., van Baak, M. A., Battista, F., Beaulieu, K., Blundell, J. E., et al. (2021). Exercise training in the management of overweight and obesity in adults: Synthesis of the evidence and recommendations from the European association for the study of obesity physical activity working group. *Obesity Reviews*, 22(S4), Article e13273. <https://doi.org/10.1111/obr.13273>
- Piaggi, P., Basolo, A., Martin, C. K., Redman, L. M., Votruba, S. B., & Krakoff, J. (2022). The counterbalancing effects of energy expenditure on body weight regulation: Orexigenic versus energy-consuming mechanisms. *Obesity*, 30(3), 639–644. <https://doi.org/10.1002/oby.23332>
- Pontzer, H. (2015). Energy expenditure in humans and other primates: A new synthesis. *Annual Review of Anthropology*, 44(1), 169–187. <https://doi.org/10.1146/annurev-anthro-102214-013925>
- Pontzer, H. (2017). *The exercise paradox*. Scientific American. Retrieved from <https://www.scientificamerican.com/article/the-exercise-paradox/>.
- Pontzer, H., Durazo-Arvizu, R., Dugas, L. R., Plange-Rhule, J., Bovet, P., Forrester, T. E., et al. (2016). Constrained total energy expenditure and metabolic adaptation to physical activity in adult humans. *Current Biology*, 26(3), 410–417. <https://doi.org/10.1016/j.cub.2015.12.046>
- Public Health England. (2013). *Obesity and the environment: Increasing physical activity and active travel*. Retrieved from https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/256796/Briefing_Obesity_and_active_travel_final.pdf.
- Public Health England. (2018). *Calorie reduction: The scope and ambition for action*. Retrieved from https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/800675/Calories_Evidence_Document.pdf.
- Saris, W. H., Blair, S. N., van Baak, M. A., Eaton, S. B., Davies, P. S., Di Pietro, L., et al. (2003). How much physical activity is enough to prevent unhealthy weight gain? Outcome of the IASO 1st stock conference and consensus statement. *Obesity Reviews*, 4(2), 101–114. <https://doi.org/10.1046/j.1467-789x.2003.00101.x>
- Shaw, K., Gennat, H., O'Rourke, P., & Del Mar, C. (2006). Exercise for overweight or obesity. *Cochrane Database of Systematic Reviews*, 4, CD003817. <https://doi.org/10.1002/14651858.CD003817.pub3>
- Shook, R. P., Hand, G. A., Drenowatz, C., Hebert, J. R., Paluch, A. E., Blundell, J. E., et al. (2015). Low levels of physical activity are associated with dysregulation of energy intake and fat mass gain over 1 year. *American Journal of Clinical Nutrition*, 102(6), 1332–1338. <https://doi.org/10.3945/ajcn.115.115360>
- Stubbs, R. J., Sepp, A., Hughes, D. A., Johnstone, A. M., Horgan, G. W., King, N., et al. (2002). The effect of graded levels of exercise on energy intake and balance in free-living men, consuming their normal diet. *European Journal of Clinical Nutrition*, 56(2), 129–140. <https://doi.org/10.1038/sj.ejcn.1601295>
- Stubbs, R. J., Sepp, A., Hughes, D. A., Johnstone, A. M., King, N., Horgan, G., et al. (2002). The effect of graded levels of exercise on energy intake and balance in free-living women. *International Journal of Obesity*, 26(6), 866–869. <https://doi.org/10.1038/sj.ijo.0801874>
- Telegraph. (2009). Health warning—exercise makes you fat. Retrieved from <http://www.telegraph.co.uk/science/6083234/Health-warning-exercise-makes-you-fat.html>.
- Thomas, D. M., Bouchard, C., Church, T., Slentz, C., Kraus, W. E., Redman, L. M., et al. (2012). Why do individuals not lose more weight from an exercise intervention at a defined dose? An energy balance analysis. *Obesity Reviews*, 13(10), 835–847. <https://doi.org/10.1111/j.1467-789X.2012.01012.x>
- Time Magazine. (2009). *Why exercise won't make you thin*. Retrieved from <http://content.time.com/time/subscriber/article/0,33009,1914974,00.html>.
- UK Government's Foresight Programme. (2007). *Foresight. Tackling obesity: Future choices - obesity system atlas*. Retrieved from www.gov.uk/government/publications/reducing-obesity-obesity-system-map.
- Ward, S. (2022). *Exercise and weight loss: Responding to herman pontzer*. Retrieved from <https://www.mynutritionscience.com/exerciseweightloss/>.
- Westerterp, K. R., & Plasqui, G. (2009). Physically active lifestyle does not decrease the risk of fattening. *PLoS One*, 4(3), e4745. <https://doi.org/10.1371/journal.pone.0004745>
- Whybrow, S., Hughes, D. A., Ritz, P., Johnstone, A. M., Horgan, G. W., King, N. A., et al. (2008). The effect of an incremental increase in exercise on appetite, eating behaviour and energy balance in lean men and women feeding ad libitum. *British Journal of Nutrition*, 100(5), 1109–1115. <https://doi.org/10.1017/S0007114508968240>