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REVIEW

Control of energy expenditure in humans

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Energy expenditure is determined by body size and body composition and by food intake and physical activity. Body size and body composition are the determinants of resting energy expenditure. Higher weight results in higher energy requirement through a higher resting requirement because of a higher maintenance cost of a larger body. Activity-induced energy expenditure is the most variable component of total energy expenditure. Smaller and leaner subjects generally move more as activity energy expenditure in larger subjects is not higher in proportion to the cost of moving with a higher body weight. Food intake induces changes in energy expenditure as a function of changes in body size and body composition. In addition, energy restriction induces an adaptive reduction of energy expenditure through a lowering of tissue metabolism and a reduction of body movement. An exercise-induced increase in activity expenditure is a function of the training status. In untrained subjects, exercise induces a larger increase in total energy expenditure than can be attributed to the energy cost of a training program. Trained subjects have a higher performance at the same expenditure through a higher exercise economy.

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INTRODUCTION

Energy expenditure in humans is determined by body size and body composition, environment and behavior. A larger body, especially a larger fat-free mass, requires more maintenance and thus induces a higher basal metabolic rate or resting energy expenditure. The main environmental determinant of energy expenditure is ambient temperature, where energy expenditure increases in a cold environment through shivering and in a hot environment through panting. Behavioral determinants of energy expenditure include food intake and physical activity. In normal daily life, environmental factors like ambient temperature are negligible. We generally choose our environment to feel comfortable. We stay in the thermal neutral zone by controlling the temperature of our homes and dress according to climatic conditions when going out. Thus, this review is restricted to determinants including subject characteristics, food intake and physical activity.

Total energy expenditure (TEE) can be split in three components: maintenance or resting energy expenditure (REE); energy expenditure for the processing of ingested food or diet-induced energy expenditure (DEE); and activity-induced energy expenditure (AEE). Here, control of energy expenditure is reviewed by comparing TEE and the three components in relation to differences for the subject characteristics body size and body composition, followed by reviewing effects of changes in food intake and changes in physical activity on energy expenditure.

BODY SIZE, BODY COMPOSITION AND ENERGY EXPENDITURE

From birth, children grow in weight and height, reaching adult values around the age of 18 years. Initially, energy requirement is mainly determined by growth and energy expenditure for body maintenance.[1] Activity energy expenditure as a fraction of TEE increases from 20% at age 1 to ~35% at age 18.[2] The increase is reflected in an increase of the physical activity index (PAI = TEE/REE) from 1.4 to 1.75. Here, the focus is on body size, body composition and energy expenditure in subjects where adult height is reached, that is, age of 18 years and older.

At adult age, the largest component of TEE for a moderately active subject is for body maintenance as measured under resting conditions. DEE represents about 10% of the total amount of energy ingested for an average diet with 10–15 energy% from protein, 30–35 energy% from fat and the remaining energy from carbohydrate.[3] Thus, DEE is 10% of TEE when one eats according to what one needs. AEE is the most variable component of TEE and depends on a subject's lifestyle (Table 1). For a moderately active subject with a PAI of 1.70–1.99, AEE is 30–40% of TEE.

Body size mainly affects the maintenance component of TEE, through the relation between body size and fat-free mass. Larger body size implies a larger fat-free mass (Figure 1). Taller subjects have a larger fat-free mass than subjects with a short stature and fat-free mass is larger in overweight and obese subjects than in lean subjects with the same stature. Thus, REE is generally higher in men than in women of similar weight and height and increases with weight gain at adult age.

The activity component of TEE seems to be similarly affected by body size as REE, judging the similarity of the PAI for subjects categorized according to body mass index (Figure 2). The average PAI is around 1.80 for all body mass index categories except the very highest, as observed before in an analysis of 319 measurements of PAI in adults aged 18–64 years.[4] Thus, TEE increases with body mass as a function of fat-free mass.[5,6] Only when one reaches the morbid obese state, there is no further increase of AEE.

The similarity of the mean value of the PAI in subjects over a wide range of body size does not imply similar body movement as well. Subjects with a higher body mass index, that is, fatter subjects, generally move less because of the higher cost of

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weight-bearing activities. The higher AEE in fatter subjects is not higher in proportion to the higher cost for weight-bearing activities. Obese subjects move slower and have lower endurance.[7,8] Excess body fat prevents optimal physical performance.[9]

In conclusion, energy expenditure is higher in larger subjects due to higher energy expenditure for maintenance. However, smaller and leaner subjects generally move more as activity energy expenditure in larger subjects is not higher in proportion to the cost of moving with a higher body weight.

CHANGES IN FOOD INTAKE AND ENERGY EXPENDITURE

Food intake affects energy expenditure through effects on all three components of TEE. A change in food intake affects energy expenditure primarily through its effect on DEE, where DEE is about 10% of the total amount of energy ingested for an average diet as mentioned above. Thus, increasing intake increases TEE through an increase in DEE and vice versa. In addition, food intake affects REE and AEE as a function of energy balance where effects of overfeeding are different from energy restriction.

Overfeeding induces weight gain where, in normal weight subjects, most of the weight gain is as fat but at least 20% of weight gain is as fat-free mass.[10,11] Overfeeding increases REE as a function of the change in fat-free mass. There does not seem to be an additional effect of overfeeding on physical activity as reviewed before.[12] Doubly labeled water studies showed no change in PAI other than a decrease during massive overfeeding (Figure 3). A recent study suggested a specific effect of overfeeding on energy expenditure in relation to the protein content of the diet.[13] However, the instantaneous 0.54 MJ per day increase in energy expenditure by overfeeding subjects with 130 g protein per day was exactly as expected from the increased DEE of the additional protein ingested. The DEE value of protein is 20–30% of the energy content.[3] Thus, adding 130 g protein, with an energy content of 2.08 MJ, to daily intake increases DEE and thus TEE with 0.42–0.62 MJ per day. Similarly, exchanging fat for protein in an isoenergetic diet increased energy expenditure with an amount equivalent to the difference in processing costs of fat, 0–3% of the energy content and the higher processing costs of protein.[14] Overfeeding does not induce adaptive thermogenesis, a change in energy expenditure not attributable to a change in body size and to the DEE of the additional food to be ingested.

Table 1. Classification of the PAI, total energy expenditure as a multiple of resting energy expenditure, in relation to lifestyle.[47]

Lifestyle	*PAI*
Sedentary or light active	1.40–1.69
Active or moderately active	1.70–1.99
Vigorous or vigorously active	2.00–2.40[a]

Abbreviation: PAI, physical activity index. [a]PAI values >2.4 are difficult to sustain over longer time.

Energy restriction does induce adaptive changes in energy expenditure. The classical Minnesota Experiment, where energy intake of normal weight men was reduced with 8 MJ per day for 24 weeks, resulted in a new energy balance at $<50\%$ of maintenance requirement at the start of the intervention.[15] Most of the starvation-induced reduction in TEE could be explained by decreased maintenance costs of a smaller body, reduction in the processing costs of the decreased amount of food to be ingested and reduction of the costs of moving a smaller body. However, 11% of the reduction in TEE was due to an adaptive change in REE and 35% of the reduction in TEE was due to an adaptive change in AEE. The adaptive change in REE was explained by a lower tissue metabolism and subjects moving less explained adaptive change in AEE. Similar but less pronounced adaptations in energy expenditure have been observed in overweight and obese subjects on an energy-restricted diet. Energy restriction induces a reduction in REE below predicted values, as based on the new body composition reached after underfeeding-induced weight loss.[16–19] The REE reduction in obese subjects losing 10–20% of initial weight, adjusted for changes in body composition, ranges between 3 and 6% of the initial TEE value. Van Gemert *et al.*[20] observed in morbid obese subjects losing on average one-third of initial weight, an average reduction of 7% at 1 year after the start of weight loss and of 4% when weight loss was maintained for more than 3 years. The adaptive AEE reduction induced by restricting energy intake in overweight and obese subjects is larger, and can be explained by a reduction in body movement and an increase in muscle efficiency.[17,21] However, Camps *et al.*[21] observed an energy restriction-induced adaptive reduction of AEE that is not sustained when energy intake meets again TEE.[21] The energy restriction-induced adaptive reduction of REE persists perhaps indefinitely.[17,20]

The difference in effect of overfeeding and energy restriction on REE and AEE probably is a consequence of natural selection. Compensatory mechanisms sparing energy to decrease weight loss and increase weight gain had survival value in an

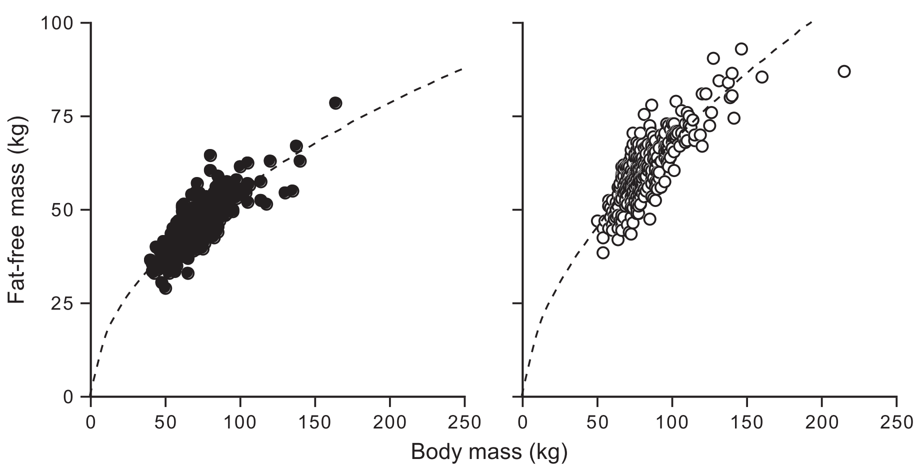

Figure 1. Fat-free mass plotted against body mass for adult subjects; age 18–50 years, with an exponential fitted curve, left figure (closed dots) for women and right figure (open dots) for men (data from Speakman and Westerterp[29]).

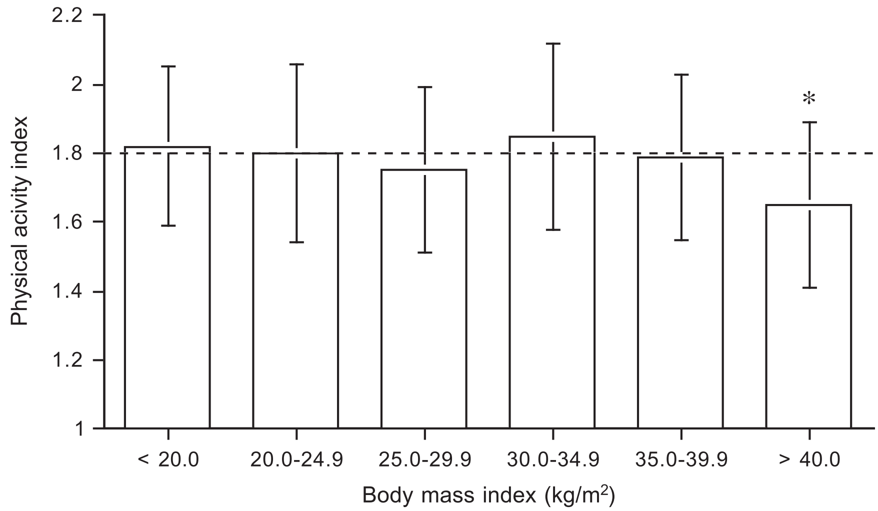

Figure 2. Physical activity index, total energy expenditure as a multiple of resting energy expenditure, and body mass index (data from Westerterp and Speakman[38]). *Significantly different from the other body mass index categories ($P < 0.05$).

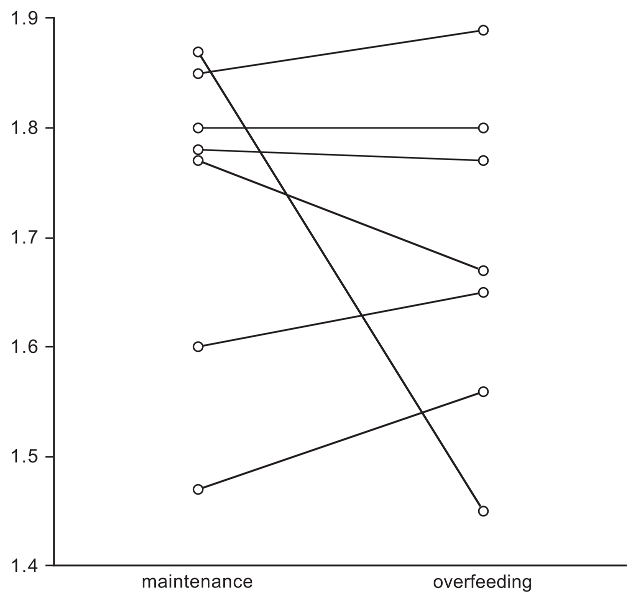

Figure 3. Physical activity index, total energy expenditure as a multiple of resting energy expenditure, before and during overfeeding (data from references[39–45]).

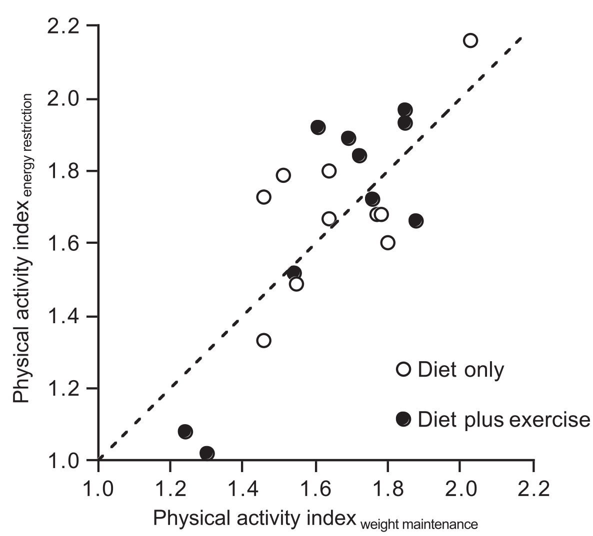

Figure 4. Physical activity index, total energy expenditure as a multiple of resting energy expenditure, during energy-restricted diet with or without exercise as a function of the value at weight maintenance. The dotted line is the line of identity (data from Kempen *et al.*[25]).

environment where food was not always available, as during ancestral life.[22] Humans have developed many adaptations to hunger but not for overconsumption. Never in human history, there has been continual food abundance as during the last 50 years. Thus, we nowadays live in an environment where overeating is common, with the consequent risk for getting overweight and obese.[23]

CHANGES IN PHYSICAL ACTIVITY AND ENERGY EXPENDITURE

Exercise training is an effective strategy to increase TEE, especially by increasing AEE.[24] However, under some conditions, an exercise-induced increase in physical activity is compensated by a decrease in non-training physical activity. One condition is a negative energy balance. Kempen *et al.*[25] observed no effect of exercise training on the PAI when training was combined with an energy-restricted diet (Figure 4). It seems to be difficult to comply with an exercise program without compensating for and exercise-induced increase in energy expenditure by increasing energy intake.[26] If not, at a negative energy balance, exercise-induced energy expenditure is compensated by a reduction in nonexercise activity.[27,28] Another condition where an exercise-induced increase in physical activity is compensated by a decrease in non-training physical activity is in older subjects. Physical activity decreases with increasing age, on average from about age of 50 years onwards.[29] In parallel, exercise training studies show a compensatory decrease in non-training physical activity in older subjects.[30] Then, maintenance of energy balance might explain why exercise training does not increase AEE. Exposing young adults and subjects over 50 years to the same 10-day strenuous hill walking activity induced an increase in food intake in the

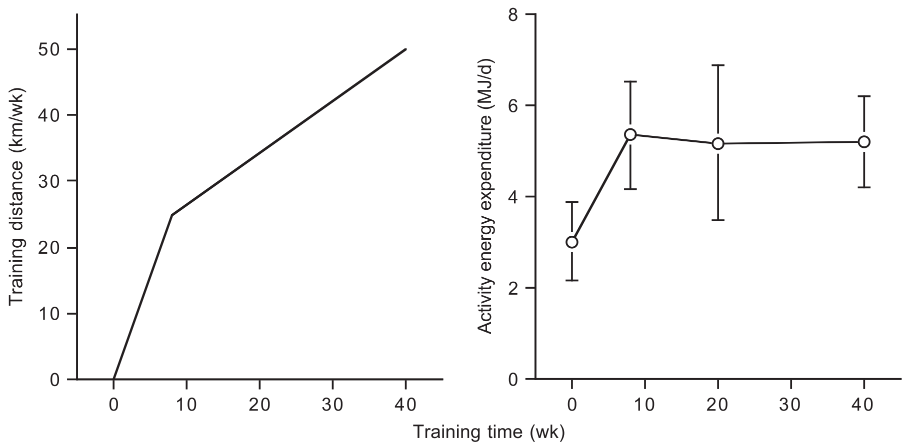

Figure 5. Training distance and activity energy expenditure over a 40-week interval in untrained subjects, training to run a half-marathon competition (data from Westerterp *et al.*[46]).

young subjects, whereas the older subjects ate 4 MJ per day less than the average 21 MJ per day energy expenditure.[31] Similarly, older male cyclists sustained near-maximal rates of energy expenditure during prolonged cycling, but were unable to upregulate energy intake to maintain energy balance. Despite the presence of increased motivation to eat, a more profound counteracting physiological stimulus inhibiting increases in energy intake was present.[32]

Under conditions where exercise training does affect TEE through an increase in AEE, that is, in healthy young adults under *ad libitum* food conditions, the increase in AEE is a function of the training status of the subjects. In untrained subjects, the initial exercise-induced increase in AEE is nearly twice the estimated cost of the training.[33] Exercise training subsequently increases exercise economy. We observed an increase in AEE of about 15 MJ per week in untrained subjects, preparing to run a half-marathon (Figure 5). The increase occurred in the initial phase of the training, where AEE did not show a further increase when the training distance was subsequently doubled from 25 to 50 km per week. The observed increase in AEE of 15 MJ was in line with the costs of running 50 km for the subjects with an average body mass of nearly 70 kg. Exercise training can even decrease walking cost in older adults, delaying the age-related decline in walking economy.[34]

DISCUSSION

The main determinants of energy expenditure are body size and body composition, food intake and physical activity. Food intake and physical activity affect energy expenditure directly and indirectly, the latter through the effect of food intake and physical activity on body size and body composition. Energy expenditure reaches minimal values in subjects with anorexia nervosa and maximal values in morbid obese subjects or elite endurance athletes. In anorectic women, TEE can be below 5 MJ per day.[35] Undereating induces weight loss, resulting in a reduction in body size with a consequent reduction in REE. Chronic energy deficiency reduces AEE through a lower physical capacity with the loss of muscle mass.[15,35] Thus, TEE is less than half the value of 10 MJ per day for a women with average size and PAI. Chronic overeating induces weight gain, resulting in TEE values over 15 MJ per day for women and 20 MJ per day for men with morbid obesity, at least 50% higher than the value at average size and PAI.

The reduction in TEE during energy restriction reduces weight loss. To maximize weight loss for obesity treatment, studies were designed on the effect of intermittent versus continuous energy restriction. However, although intermittent energy restriction consistently reduces body weight and adiposity, it does not seem to be superior to continuous energy restriction for weight loss.[36] Adaptive reduction of TEE is similar at both regimens of energy restriction.

The increase in TEE through physical activity is suggested to be constrained. Pontzer *et al.*[37] concluded, from a comparative analysis of TEE and physical activity data, TEE increases with physical activity al low activity levels but plateaus with higher activity levels. They suggested a model of constrained TEE with metabolic adaptations to physical activity. An explanation is the difference in exercise economy between subjects with a low PAI being untrained and subjects with a high PAI being trained. The training-induced increase in exercise economy limits the effect of an increase in physical activity on TEE and thus explains the curvilinear relation between physical activity and TEE as observed by Pontzer *et al.*[37]

In conclusion, maintenance metabolism is the largest component of TEE, especially at young and old age. Activity energy expenditure is the most variable component of TEE and can be increased when food intake allows. Energy expenditure increases with weight gain at adult age through a consequent increase in maintenance metabolism. Smaller and leaner subjects generally move more as activity energy expenditure in larger subjects is not higher in proportion to the cost of moving with a higher body weight. Energy restriction and overfeeding induce changes in energy expenditure as a function of changes in body size and body composition. In addition, energy restriction induces an adaptive reduction of energy expenditure through a lowering of tissue metabolism and a reduction of body movement. An exercise-induced increase in activity expenditure is a function of the training status.

CONFLICT OF INTEREST

The author declares no conflict of interest.

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