

ORIGINAL COMMUNICATION

Energy metabolism in humans at a lowered ambient temperature

MS Westerterp-Plantenga^{1*}, WD van Marken Lichtenbelt¹, H Strobbe¹ and P Schrauwen¹

¹Department of Human Biology, University of Maastricht, Maastricht, The Netherlands

Objective: Assessment of the effect of a lowered ambient temperature, ie 16°C (61°F), compared to 22°C (72°F), on energy intake (EI), energy expenditure (EE) and respiratory quotient (RQ) in men.

Design: Randomized within-subject design in which subjects stayed in a respiration chamber three times for 60 h each, once at 22°C, and twice at 16°C, wearing standardized clothing, executing a standardized daily activities protocol, and were fed in energy balance (EBI): no significant difference between EE and EI over 24 h). During the last 24 h at 22°C, and once during the last 24 h at 16°C, they were fed *ad libitum*.

Subjects: Nine dietary unrestrained male subjects (ages 24±5 y, body mass index (BMI) 22.7±2.1 kg/m², body weight 76.2±9.4 kg, height 1.83±0.06 m, 18±5% body fat).

Results: At 16°C (EB), EE (total 24 h EE) was increased to 12.9±2.0 MJ/day as compared to 12.2±2.2 MJ/day at 22°C ($P < 0.01$). The increase was due to increases in sleeping metabolic rate (SMR; the lowest EE during three consecutive hours with hardly any movements as indicated by radar): 7.6±0.7 vs 7.2±0.7 MJ/day ($P < 0.05$) and diet-induced thermogenesis (DIT; EE-SMR, when activity induced energy expenditure as indicated by radar = 0): 1.7±0.4 vs 1.0±0.4 MJ/day ($P < 0.01$). Physical activity level (PAL; EE/SMR) was 1.63–1.68. At 16°C compared to at 22°C, rectal, proximal and distal skin temperatures had decreased ($P < 0.01$). RQ was not different between the two ambient temperature situations. During *ad libitum* feeding, subjects overate by 32±12% (at 22°C) and by 34±14% (at 16°C). Under these circumstances, the decrease of rectal temperature at 16°C was attenuated, and inversely related to percentage overeating ($r^2 = 0.7$; $P < 0.01$).

Conclusion: We conclude that at 16°C, compared to 22°C, energy metabolism was increased, due to increases in SMR and DIT. Overeating under *ad libitum* circumstances at 16°C attenuated the decrease in rectal core body temperature.

European Journal of Clinical Nutrition (2002) 56, 288–296. DOI: 10.1038/sj/ejcn/1601308

Keywords: ambient temperature; energy intake; energy expenditure; body temperature; humans

Introduction

Ambient temperature has been shown to affect energy metabolism in field situations. In this controlled study we addressed the questions whether a lowered ambient temperature affects energy expenditure (EE) under energy balance (EB) conditions, and subsequently whether it affects

energy intake (EI) under *ad libitum* feeding conditions. Recently we showed that core temperature and skin temperature were positively related to ambient temperature, even in humans (van Marken Lichtenbelt *et al*, 2001). Within a certain range of ambient temperature, homeotherms, eg humans, have a relatively constant core body temperature (Consolazio *et al*, 1963; Benzinger, 1969; Montgomery, 1976; Johnson, 1979; Webb, 1993; van Marken Lichtenbelt *et al*, 2001), which represents the temperature of deep thermosensitive units and the thermal mass of the body core (Bregelmann & Savage *et al*, 1997). The skin temperature varies relatively more with the temperature of the environment and with metabolic rate as compared to the core temperature. It contributes to the skin blood flow in neutral and warm conditions thus influencing the effective thickness of the body 'shell' according to the core-shell concept (Wyss *et al*, 1974; Johnson, 1979; Webb, 1992). A

*Correspondence: MS Westerterp-Plantenga, Department of Human Biology, University of Maastricht, PO Box 616, 6200 MD Maastricht, The Netherlands.

E-mail: M.Westerterp@HB.Unimaas.nl

Guarantor: MS Westerterp-Plantenga.

Contributors: MSW-P, WDvML and PS designed and supervised the experiments, and analysed the data. HS executed the experiments. MSW-P wrote the manuscript, and DvML and PS gave their comments.

Received 6 April 2001; revised 11 July 2001; accepted 16 July 2001

significant relationship between body temperature and metabolic rate (Kobayashi, 1988; Kraeuchi & Wirz-Justice, 1994; Refinetti, 1997), as well as between ambient temperature and metabolic rate has been shown. In older (Hardy, 1934; Hardy & Du Bois, 1934, 1940; Du Bois, 1936; Hardy & Milhorat, 1939), as well as in more recent studies (Dauncey, 1981; Werner, 1981; Blaza & Garrow, 1983) an inverse relationship between metabolic rate and ambient temperatures between 10 and 30°C has been observed. Until now, changes in energy metabolism have been mainly observed as changes in total or basic metabolic rate. Effects on activity-induced energy expenditure (AEE; Bergh & Ekblom, 1979) and diet induced thermogenesis (DIT) (Rothwell *et al*, 1990) have been dealt with independently. Most of the studies mentioned only executed the measurements for a few hours. The study by Dauncey (1981) assessed total and basal metabolic rate during 24 h, while DIT was measured for a few hours. Mild cold exposure was 22°C, which was compared to 28°C, in women. To expand this further, the present study assessed effects of cold exposure ie, 16°C relative to the usual environmental temperature of 22°C, in men in a well-controlled but relatively normal situation during 60 h. Effects on total EE and its separate components (SMR, DIT, AEE) were addressed simultaneously, and calculated over the last 24 h in EB conditions. Furthermore, possible effects on substrate oxidation and *ad libitum* food intake were assessed.

To study AEE under a lowered ambient temperature condition it was necessary for the daily physical activities to follow a standardized protocol. Studying DIT under a lowered ambient temperature condition also necessitates accounting for possible EI adaptation (Ravussin *et al*, 1986; Pannemans *et al*, 1995; Westerterp-Plantenga *et al*, 1999).

Since from field situations, decreased ambient temperature is generally considered to stimulate appetite (Vander *et al*, 1998), but possible effects from lower ambient temperatures and from increased physical activities have not been distinguished, we also measured the effect on EI under *ad libitum* conditions in this controlled situation. Although LeBlanc (1957) reported no change, Edholm and Goldsmith (1966), in a study of physically active and unacclimatized soldiers deployed to a cold environment, found food consumption increased with exposure to cold climate. Johnson and Kark (1947) showed EI increased with decreasing average local temperature. While assessing the possible change in EI in humans in response to short-term exposure to a lowered ambient temperature, we took the possible changes in EE into account, assessing the effect on EE, while the subjects were fed in EB separately, as mentioned above.

The lowered ambient temperature was 16°C (61°F) and the effects on energy metabolism were compared to those at 22°C (72°F), which was the temperature to which the subjects were acclimatized. At both temperatures daily physical activities and clothing were the same for all subjects and at each occasion. The research question addressed effects of a 60 h exposure to a lowered ambient temperature on EE and its components (SMR, DIT and AEE), as well as on EI. More-

over, we focused on possible relationships between changes in EI, EE and body temperature.

Subjects and methods

Subjects

Nine healthy male volunteers participated in this study. They were recruited from the University staff and students. Physical characteristics (mean±s.d.: age (y) 24±5; body mass index (BMI) (kg/m²), 22.7±2.1; body weight, 76.2±9.4 kg, height, 1.83±0.06 m percentage body fat, 18±5; fat-free mass (kg), 63.3±10.2) showed that all subjects were normal weight. Body composition was determined in the fasted state by hydrodensitometry with simultaneous assessment of the residual lung volume by a helium dilution technique. Percentage body fat was calculated using the equation of Siri (1961). Scores on the Three Factor Eating Questionnaire (Stunkard & Messick, 1985; F1 (cognitive restraint), 5±2; F2 (disinhibition or emotional eating), 4±2; F3 (hunger), 3±2) showed that the subjects were dietary unrestrained, with normal values for disinhibition or emotional eating and hunger, relative to our population (Westerterp-Plantenga *et al*, 1991). Exclusion criteria were medication, intensive sports activities (> 4 times a week), smoking, unhealthy with respect to blood pressure, diabetes, other illnesses, being overweight or obese, dietary restraint. Only one gender was chosen to limit the number of subjects. All subjects signed an informed consent for the study protocol, which was approved by the Medical Ethics Committee of the University of Maastricht.

Procedure

The study took place at the Department of Human Biology, University of Maastricht. Subjects stayed three times for 60 h each (20.00–08.00 h) in the respiration chamber, once at 22°C (72°F), and twice at 16°C (61°F), in random order and counterbalanced, to avoid possible sequence and seasonal influences. Thus a within-subject design was applied. Before and after each stay in the chamber body weight of the subjects was determined. Moreover, the subjects weighed themselves every morning in the chamber, in the fasting state, after voiding. The interval between each stay in the chamber was about 4 weeks for each subject.

Respiration chamber. The respiration chamber consists of two adjoining 14 m³ rooms, each furnished with a bed, chair, television, radio, telephone, intercom, computer, wash bowl and deep freeze toilet. The chamber gives the impression of a normal living room. Communication between the subjects and investigator is possible via an intercom or telephone. Visual contact is also possible through a window in the door and between the two chambers. A third window provides an outside view. Three air locks provide passage for the exchange of food, collection of urine and for sampling of blood. During the experiment, the temperature as well as the

relative humidity (55%rh) was almost constant in the chamber, at 22 or 16°C, during day and night. The measured temperature varied between 21.9 and 22.1°C, and 15.9 and 16.1°C, respectively. The variation in relative humidity was 53–55%rh (Schoffelen *et al*, 1997). Physical activity was monitored by means of a radar system, based on the Doppler principle (Schoffelen *et al*, 1997), validated by Bouten *et al* (1995, 1996).

Outfit. Subjects were required to wear the same outfit all three times times (one T-shirt, one cotton shirt, one jogging-shirt (70% cotton, 30% polyester), one pair of jogging trousers (50% cotton, 50% polyester) and a pair of sports-hoes) during the day (insulation 1.2 clo (ISO 9920, 1995)). At night, subjects wore one T-shirt and boxer-shorts, and they slept under a cotton sheet and a duvet (375 g/m²). The clothing was tested before the protocol began, to assure comfort at 16°C as well as at 22°C.

Body weight measurement and daily activities protocol.

Body weight was determined on a digital scale, accurate to the nearest 0.1 kg, at the start and at the end of each session, in the morning in the fasting state, after voiding. A standard daily activities protocol was applied, which described all activities required by the subjects every hour, and sometimes every 15 min (Appendix 1). Also the meal and snack times were fixed. The aerobic exercise was standardized by consistently using the same music with a fixed rhythm from a radio-cassette, while the subjects performed the same step test (alternating 5 min stepping 5 min sitting), controlled by the experimenter.

Body temperature. Subjects' skin temperatures were registered continuously from 8.00 am to 12.00 pm by means of a thermistor surface contact probe (YSI Series 400 probes; accuracy $\pm 0.01^\circ\text{C}$) fixed to the skin with thin, air-permeable adhesive surgical tape. Proximal skin temperatures were measured at the forehead, the infra-clavicaire zone and thigh; distal skin temperatures were measured at the hand and foot. The core temperatures were measured rectally during the night with a rectal probe about 10 cm internally (YSI Series 400, accuracy $\pm 0.1^\circ\text{C}$); during the day this was measured with a conventional electronic thermometer, 4 cm internally (Philips HP 5315, accuracy 0.1°C). Temperature measurements were thoroughly explained to the subjects, and they were trained in the pre-protocol phase in order to obtain reproducible measurements, before entering the respiration chambers.

The thermometric probes were calibrated to within 0.05°C in a water bath against a reference mercury thermometer (accuracy $\pm 0.02^\circ\text{C}$).

Energy expenditure. Subjects' EE was calculated from oxygen consumption and carbondioxide production (Schoffelen *et al*, 1997). The respiration chamber was ventilated with fresh air at a rate of 70–80 l/min. A dry gas meter (G4

Schlumberger, The Netherlands) measured the ventilation rate. A paramagnetic O₂ analyzer (OA 184A, Servomex) and an infrared CO₂ analyzer (Uras 3G, Hartmann & Braun) were used to analyze the samples of the in- and out-going air. In-going air was analyzed once every 15 min and out-going air every 5 min (Schoffelen *et al*, 1997).

Energy intake and appetite. Subjects' appetite and energy intake were determined as follows. At 22°C and once at 16°C, subjects were fed in EB during the first 24 h, and *ad libitum* during the second 24 h. The other time the subjects stayed at 16°C, they were fed in EB throughout the 60 h. Feeding in EB took place by measuring sleeping metabolic rate (SMR) and multiplying this by a physical activity level (PAL) of 1.65. Thus, energy requirement was calculated for each subject individually. Based upon this, the meals and snacks were prepared (three meals and three snacks per day), using comparable food items each day, which also belonged to the subjects' habitual diets (Appendix 2). All food items were checked for hedonic values beforehand, and only the ones that were liked by all subjects (visual analog scale (VAS) recording at least 60 mm) were included in the menus. All these foods and drinks were of known composition and were weighed before and after each meal or snack occasion to the nearest 0.1 g. The energy content and composition of each diet was calculated using the Dutch food composition table (Voorlichtingsbureau voor de Voeding, 1992).

Macronutrient composition (carbohydrate/protein/fat: 49/15/36 percentage of energy) and energy density (4.5 kJ/g) were kept at comparable values. The food items were the same at both ambient temperatures; only the amounts were adapted to the energy requirements. When the subjects were fed *ad libitum* they could order any food from the list (Appendix 2) at any time by telephone.

Appetite profiles, ie the subjective feelings of motivation to eat, were assessed before and after breakfast, mid-morning, before and after lunch, in the afternoon, before and after dinner, and once in the evening, by ratings on 100 mm anchored VASs, with the following questions: How hungry, full, satiated, thirsty are you? (anchored: not at all/very); how much do you estimate you could eat? (anchored: nothing/very much); how is your desire to eat? how is your appetite? (anchored: very weak/very strong). During the days when the subjects were fed in EB, appetite was described by VAS (Westerterp-Plantenga *et al*, 1999).

Comfort. Comfort ratings representing general physical well-being were monitored nine times in the course of each experimental day using 100 mm VAS. The questions asked how comfortable, satisfied, irritated and fit the subjects felt, how agreeable the ambient temperature was found, and whether the clothing was found to be adapted to the surrounding temperature (anchored: not at all/very).

Data analysis

To check whether the subjects were in EB, the difference between 24 h EE and EI was calculated for each situation (the EB as well as the *ad libitum* situations at both ambient temperatures). Then, the differences between EE and EI were compared with a theoretical difference being 0, indicating no difference between EI and EE, or a neutral EB.

The following comparisons were made for the 24 h periods when the subjects were fed in EB (day 2 at 16°C EB vs day 1 at 22°C) as well when they were fed *ad libitum* (day 2 at 16°C AL vs day 2 at 22°C):

- 24 h energy expenditure (EE in MJ/day) and respiratory quotient (RQ), according to the formula of Weir (1949);
- SMR as the lowest mean EE over three consecutive hours between 24 h and 7:00 h;
- 24 h DIT as the increase in EE above SMR, corrected for AEE, this was achieved by plotting EE against radar output. The intercept of the regression line, at the offset of the radar, thus at zero physical activity, represents the EE in the inactive state: resting EE (RMR), consisting of SMR and DIT. DIT was calculated by subtracting SMR from RMR (Ravussin *et al*, 1986; Pannemans *et al*, 1995; Westerterp-Plantenga *et al*, 1999);
- activity-induced energy expenditure (AEE) by subtracting RMR from total EE (Ravussin *et al*, 1986; Pannemans *et al*, 1995; Westerterp-Plantenga *et al*, 1999), AEE was also expressed as a function of radar output. The individual radar output, corrected for the offset-point was compared between the two environmental temperatures;
- PAL as 24 h EE/SMR;
- RQ as volume CO₂/volume O₂;
- FQ (Food Quotient) as volume CO₂/volume O₂, when the food consumed is oxidized completely; for FQ O₂ consumption (l/day) = 0.966 × protein intake (g) + 2.019 × fat intake (g) + 0.829 × CHO intake (g). CO₂ production (l/day) = 0.774 × protein intake (g) + 1.427 × fat intake (g) + 0.829 × CHO intake (g) (Jequier & Schutz, 1983). FQ is calculated from metabolizable energy;
- the 16 h averages of the ratings on the components of the appetite profile and of the comfort ratings;
- body temperatures (ie rectal, proximal (skin) and distal (skin) temperatures).

Furthermore, for the days in the *ad libitum* feeding situations (day 2 at 16°C AL vs day 2 at 22°C) the following were compared:

- total EI;
- macronutrient composition of EI;
- energy density (ED) of 24 h food intake; ED was calculated as total EI divided by total weight of consumption (including water).

Comparisons were made using ANOVA repeated measures, with a Scheffe *F* test, *post hoc*. A multiple regression analysis was executed on the possible contributions of changes in body temperature and in EE to possible changes in EI.

Statistical analyses were performed using the statistical software program Statview SE + Graphics Abacus concepts Inc. Berkeley, CA, USA. Outcomes were regarded as statistically different if $P < 0.05$.

Results

As indicated in the data analysis section, the comparisons made for the 24 h periods when the subjects were fed in EB concerned day 2 at 16°C EB vs day 1 at 22°C, and when they were fed *ad libitum* day 2 at 16°C AL vs day 2 at 22°C.

Body weight

Fasting state body weights during the EB situations remained constant over each experimental 60 h (both times -0.1 ± 0.1 kg). During *ad libitum* feeding, body weight increased significantly at 22°C ($+0.7 \pm 0.3$ kg) and non-significantly at 16°C ($+0.6 \pm 0.6$ kg). The difference between the increases in body weight at the two ambient temperatures while feeding *ad libitum* was not statistically significant.

Body temperature

In EB, at 16°C compared to at 22°C rectal, proximal and distal skin temperatures decreased. The decrease in rectal temperature at 16°C was not significantly present while the subjects were feeding *ad libitum*, but the decrease in skin temperatures remained (Table 1).

Energy balance

During the 24 h while the subjects were fed in EB, at both ambient temperatures, EI and EE were neither statistically different from each other nor statistically different from zero, indicating that the subjects were indeed in EB.

On the *ad libitum* feeding days at both ambient temperatures, the subjects were in a positive EB. The differences between EI and EE were statistically significantly different from 0, but these differences did not differ between the ambient temperatures. At 16°C EI was $134 \pm 14\%$ of EE; at 22°C EI was $132 \pm 12\%$ of EE. Thus the subjects overate by 32–34%. At 16°C percentage overeating was inversely correlated to the decrease in rectal temperature ($r^2 = 0.7$; $P < 0.01$; Figure 1).

Energy expenditure

In EB, 24 h EE at 16°C was increased by on average $5.7 \pm 2\%$. The increase in EE consisted of the sum of significant increases in SMR, DIT (Figure 2, Table 1; and a non-significant decrease in AEE) at 16°C compared to at 22°C. PAL (EE/SMR) was 1.63–1.68. The radar output did not differ significantly between the occasions with the different ambient temperatures. In the *ad libitum* feeding situations EE was also higher at 16°C than at 22°C (Table 1).

Table 1 Body core and skin temperature ($^{\circ}\text{C}$), energy balance, energy expenditure, (24 h EE; MJ/day) sleeping metabolic rate (SMR; MJ/day), diet-induced thermogenesis (DIT; MJ/day), activity-induced thermogenesis (AEE; MJ/day), respiratory quotient (RQ), and energy intake (24 h EI; MJ/day), during a 60 h stay in the respiration-chamber at 16°C or 22°C , while feeding in energy balance or *ad libitum*. The values at 16°C EB are from the second day of the 60 h stay at 16°C EB; the values at 16°C AL are from the second day of the 60 h stay with day 1 at 16°C EB and day 2 at 16°C AL. The values at 22°C EB and at 22°C AL are from the first day of the 60 h stay with day 1 at 22°C EB and day 2 at 22°C AL. The *P*-values of comparisons are given for the *ad libitum* vs the energy balance situation within an ambient temperature, and for 16 vs 22°C within a feeding regime; $n=9$ normal-weight men

	16°C EB	22°C EB	16°C AL	22°C AL	<i>P</i> -value AL vs EB	<i>P</i> -value 16 vs 22°C
Core temperature ($^{\circ}\text{C}$)	36.4 ± 0.3^a	37.0 ± 0.3^a	36.7 ± 0.3	37.1 ± 0.3	NS	$< 0.01^a$
Proximal skin temperature ($^{\circ}\text{C}$)	32.0 ± 0.8^a	33.5 ± 0.9^a	32.1 ± 0.9^b	33.7 ± 1.0^b	NS	$< 0.01^{a,b}$
Distal skin temperature ($^{\circ}\text{C}$)	27.5 ± 1.7^a	33.0 ± 0.8^a	28.9 ± 1.9^b	33.3 ± 0.9^b	NS	$< 0.01^{a,b}$
Energy balance (MJ/day)	-0.2 ± 0.9^a	-0.3 ± 0.8^b	4.5 ± 2.2^a	4.1 ± 1.9^b	$< 0.01^{a,b}$	NS
24 h EE (MJ/day)	12.9 ± 2.0^a	$12.2 \pm 2.2^{a,c}$	13.4 ± 2.0^b	$12.9 \pm 1.9^{b,c}$	$< 0.05^c$	$< 0.01^c < 0.05^b$
SMR (MJ/day)	7.6 ± 0.7^a	7.2 ± 0.7^a	7.8 ± 0.9	7.3 ± 0.9	NS	$< 0.05^a$
DIT (MJ/day)	1.7 ± 0.4^a	1.0 ± 0.4^a	1.9 ± 0.9	1.5 ± 0.7	NS	$< 0.01^a$
AEE (MJ/day)	3.6 ± 1.2	4.0 ± 1.5	3.7 ± 1.4	4.1 ± 1.5	NS	NS
RQ	0.88	0.86^a	0.89	0.90^a	$< 0.001^a$	NS
24 h EI (MJ/day)	12.7 ± 2.0^a	11.9 ± 2.2^b	17.9 ± 3.5^a	17.0 ± 2.4^b	$< 0.01^{a,b}$	NS

^{a,b,c}Indicate the comparisons with significant differences and their *P*-values.

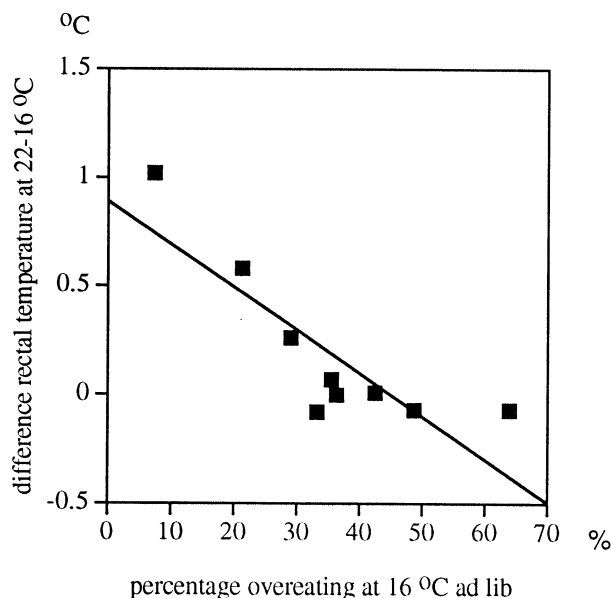


Figure 1 Difference in rectal temperature between an ambient temperature of 22°C and an ambient temperature of 16°C , as a function of percentage overeating; $n=9$ normal weight men; $y = -0.20x + 0.89$; $r^2 = 0.7$; $P < 0.01$.

Substrate oxidation

Differences between *ad libitum* and EB RQ were significant only at 22°C . RQ was significantly higher during *ad libitum* than during EB at 22°C ($P < 0.001$); there were no other significant differences in substrate oxidation data (Table 1).

Energy intake

As mentioned already, on the *ad libitum* feeding days, EI was $132 \pm 12\%$ (at 22°C) and $134 \pm 14\%$ (at 16°C) of EE (Table 1).

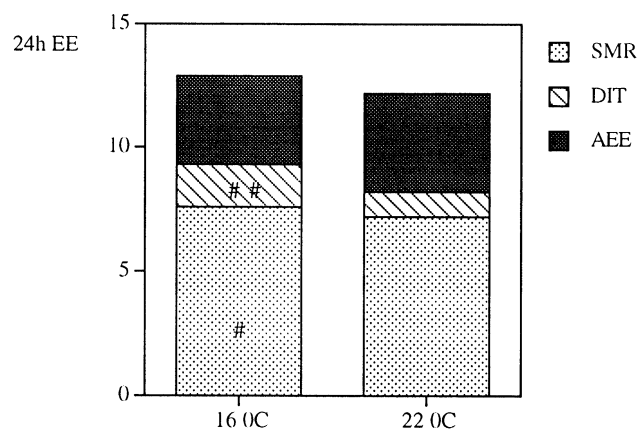


Figure 2 The components sleeping metabolic rate, diet-induced thermogenesis, activity induced energy expenditure of 24 h EE at 16 vs 22°C , during feeding in energy balance; $n=9$ normal-weight men; $\#P < 0.05$, $\#\#P < 0.01$, compared to at 22°C .

Increased EI was correlated with increased EE ($r=0.8$; $P < 0.01$) at 16°C , but not significantly at 22°C ($r=0.6$; $P=0.09$; Figure 3a and 3b). At both ambient temperatures while feeding *ad libitum*, EI was increased through an increase in all meal sizes and snack consumption. Total EI increased at both ambient temperatures by increasing the energy and weight of food in the same proportion as it was presented when feeding in EB. Food choice had not changed, nor had energy density (ED) of total consumption (food and drinks; 4.4 kJ/g) and macronutrient composition (51/14/35 percentage energy from carbohydrate, protein and fat). Meal frequency had remained constant, ie three meals and three snacks per day. The appetite profiles did not show any statistically significant differences between the two days with different temperatures while the subjects were fed in

EB. When they were fed *ad libitum* at both ambient temperatures, appetite, hunger, estimated amount to eat, desire to eat and thirst were significantly decreased ($P < 0.01$), while satiety and fullness were significantly increased ($P < 0.01$; Figure 4), compared to feeding in EB.

Comfort

Comfort ratings (AUC) were all positive, and irritation was low, with no statistically significant differences between the two different ambient temperature situations while the subjects were being fed in EB or *ad libitum*. However, subjective feelings of ambient temperature indicated feelings of a warmer environment at 16°C (AL) than at 16°C (EB).

Discussion

Short-term (60 h) exposure to 16°C (61°F) of normal weight men who were acclimatized to an ambient temperature of

22°C (72°F), caused a significant increase in EE, particularly in SMR and in DIT, and a decreased rectal and skin temperature. This was the case when the subjects were fed in EB, while clothing and daily activities were standardized. Despite rectal and skin temperatures being decreased at 16°C, comfort ratings showed that the men felt comfortable each time; the ratings were not significantly different between both ambient temperatures.

The increase in DIT was partly due to the increase in EI, which was necessary to maintain EB at 16°C.

The increased EE with lowered ambient temperature is consistent with the findings reported by Hardy and Du Bois (1943, 1940), Dauncey (1981), Werner (1981), and by Blaza & Garrow (1983) with different magnitudes of changes in ambient temperature between 30 and 10°C. The increase in SMR is similar to the findings reported by Hardy and Du Bois in women (1940) and the observation by Dauncey (1981), who in fact measured BMR and not SMR. The increase in 24 h DIT not only concerned the absolute value, but also the relative value, ie the percentage of total EI. At both ambient temperatures the macronutrient composition of the food was the same, and FQ was the same, so this could not have affected the DIT (Westerterp-Plantenga *et al*, 1999). Since the difference in DIT cannot completely be explained by the difference in EI, we suggest that the remainder of the increased DIT might have been its facultative component, contributing to preventing a greater decrease in core body temperature. In the study by Dauncey (1981), BMR was also measured during 2–5 h after lunch, thus in fact DIT was also measured, and no differences between the two circumstances with different ambient temperatures were found. The different result might be caused by the difference in the procedure. During the day DIT does not fall back completely to zero, so any relatively short-term measurement does not include the DIT completely (Jequier & Schutz, 1983; Westerterp *et al*, 1998; Westerterp-Plantenga *et al*, 1999).

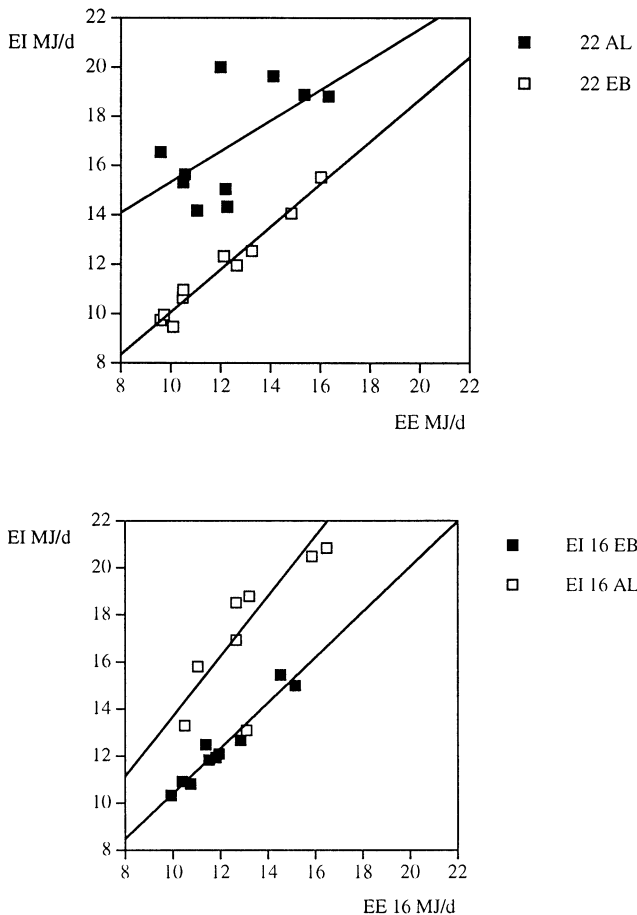


Figure 3 (a) Energy intake as a function of energy expenditure at 22°C, in energy balance (EB; $r=0.9$; $P=0.0001$) and *ad libitum* (AL; $r=0.6$; $P=0.09$). (b) Energy intake as a function of energy expenditure at 16°C, in energy balance (EB; $y=x+0.8$; $r=0.9$; $P=0.0001$), and *ad libitum* (AL; $y=1.3x+0.9$; $r=0.8$; $P < 0.01$).

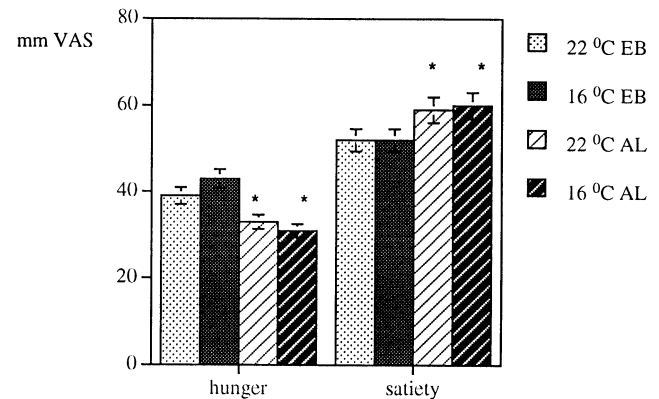


Figure 4 Appetite profile: hunger and satiety at 22 and 16°C during energy balance and *ad libitum* feeding; $n=9$ normal weight men; $*P < 0.01$.

Twenty-four hour AEE decreased non-significantly at 16°C compared to at 22°C, within the identical and standardized activities protocol under both circumstances. Moreover, the PAL was not different between the two ambient temperatures.

Twenty-four-hour RQ was significantly higher at 22°C (*ad libitum*) than at 22°C (EB), indicating a higher carbohydrate oxidation, which is obviously due to overeating. There was no temperature or EE dependency of substrate oxidation, contrary to the finding we observed in women staying at 27°C, when RQ appeared to increase (Westerterp-Plantenga et al, 2001).

Thus, the increased EE at the lower ambient temperature, while executing the same daily activities protocol and wearing the same clothing, indicates that energy requirements are higher at this temperature. An elevated EI was shown spontaneously in this study during the *ad libitum* feeding days; in fact the subjects overate on both of the *ad libitum* feeding days by 32±12% and 34±14%, relative to the different energy requirements on those days.

Overeating during the *ad libitum* feeding days might have been due to the higher normal daily food intake, because of the higher PAL in daily life. At the moderate PAL of 1.63–1.68 in the respiration chamber, overeating resulted in a significantly higher fullness and satiety, and a lowered appetite, hunger, desire to eat, and estimation of how much one could eat. This change in appetite profile also showed that, with the *ad libitum* feeding, the 24 h appetite profile was the result of the EI and not the cause of it. Overeating at 22°C resulted in a significant increase in RQ and in body weight. Overeating at 16°C caused a similar change in the appetite profile as overeating at 22°C, but no significant change in RQ or increase in body weight. The surplus of energy input with *ad libitum* feeding at 16°C attenuated the decrease of core temperature that appeared in the EB situation at 16°C. This is underscored by the outcome of the regression analysis, showing less decrease in rectal temperature at 16°C when overeating was stronger (Figure 1). One might argue that the alternative explanation, that decreases in rectal temperature result in overeating, could be considered, but since the mean data does not show a difference between *ad libitum* overeating between the 16 and 22°C conditions, this explanation seems less likely. In the *ad libitum* feeding situations at both ambient temperatures, overeating occurred to relatively the same extent. Thus a direct relationship between EI and changes in body core temperature was shown, without the necessity that both are related to EE.

We conclude that a lowered ambient temperature with standardized clothing and physical activity in young normal weight men resulted in a decreased core and skin temperature in EB, an increased EE (SMR and DIT), and an increased EI while feeding *ad libitum*. The positive EB while feeding *ad libitum* attenuated the decrease in core body temperature.

Therefore, overeating at a lowered ambient temperature may not only compensate for increased EE, but also attenuate a decrease in core body temperature, in normal weight

men. Thus, in practice, one may preserve core temperature in cold circumstances not only by increased insulation or physical activity, but also by overeating.

Acknowledgements

We wish to thank Paul Schoffelen for his assistance with the respiration chamber measurements, Lock Wouters for helping with the body temperature registrations, and Dr Kathleen Melanson for editing the English text.

References

- Benzinger TM (1969): Heat regulation: homeostasis of control temperature in man. *Physiol. Rev.* **49**, 671–759.
- Bergh U & Ekblom B (1979): Physical performance and peak aerobic power at different body temperatures. *J. Appl. Physiol.* **46**, 885–889.
- Blaza S & Garrow JS (1983): Thermogenic response to temperature, exercise and food stimuli in lean and obese women, studied by 24 h direct calorimetry. *Br. J. Nutr.* **49**, 171–180.
- Bouten CVC, Pannemans DLE, Westerterp KR & Verduin M (1995): Physical activity assessment during standardized activity in a respiration chamber: movement registration versus energy expenditure. *Int. J. Obes. Relat. Metab. Disord.* **19**, 29–35.
- Bouten CVC, van Marken Lichtenbelt WD & Westerterp KR (1996): Body mass index and daily physical activity in anorexia nervosa. *Med. Sci. Sports Exerc.* **28**, 967–973.
- Bregelmann GL & Savage MV (1997): Temperature regulation in the neutral zone. *Ann. N.Y. Acad. Sci.* **813**, 39–50.
- Consolazio CF, Matoush L, Le Roy O & Nelson RA (1963): Environmental temperature and energy expenditures. *J. Appl. Physiol.* **18**, 65–68.
- Dauncey MJ (1981): Influence of mild cold on 24 h energy expenditure, resting metabolism and diet-induced thermogenesis. *Br. J. Nutr.* **45**, 257–267.
- Du Bois EF (1936): *Basal Metabolism in Health and Disease*, 3rd edn, Philadelphia, PA: Lea and Febiger.
- Edholm OG & Goldsmith R (1966): Food intakes and weight changes in climatic extremes. *Proc. Nutr. Soc.* **25**, 113–119.
- Hardy JD (1934): Radiation of heat from the human body. An instrument for measuring the radiation and the surface temperature of the skin. *J. Clin. Invest.* **13**, 593–599.
- Hardy JD & Du Bois EF (1934): Basal metabolism, radiation, convection and vaporization at temperatures of 22–35°C. *J. Nutr.* **8**, 695–703.
- Hardy JD & Du Bois EF (1940): Differences between men and women in their response to heat and cold. *Proc. Natl. Acad. Sci. USA* **26**, 389–398.
- Hardy JD & Milhorat AT (1939): Basal heat loss and production in women at temperatures from 23–36°C. *Proc. Soc. Exper. Biol. Med.* **41**, 94.
- ISO 9920 (1995): *Ergonomics of the thermal environment—Estimation of the thermal insulation and evaporative resistance of a clothing ensemble*. Geneva: IOS.
- Jequier E & Schutz Y (1983): Long term measurements of energy expenditure in humans using a respiration chamber. *Am. J. Clin. Nutr.* **38**, 989–998.
- Johnson JM (1979): Reflex control of skin blood flow by skin temperature: role of core temperature. *J. Appl. Physiol: Respirat. Environ. Exerc. Physiol.* **47**, 1188–1193.
- Johnson RE & Kark RM (1947): Environment and food intake in man. *Science* **105**, 378–379.
- Kobayashi S (1988): Temperature-sensitive neurons in the hypothalamus; a new hypothesis that they act as thermostats, not as transducers. *Prog. Neurobiol.* **32**, 103–135.
- Krauchi K & Wirz-Justice A (1994): Circadian rhythm of heat production, heart rate, and skin and core temperature under unmasking conditions in men. *Am. J. Physiol.* **267**, R819–R829.

- LeBlanc JA (1957): Effect of environmental temperature on energy expenditure and calorie requirements. *J. Appl. Physiol.* **10**, 281–283.
- Montgomery LD (1976): Effect of ambient temperature on the thermal profile of the human forearm, hand, and fingers. *Ann. Biomed. Engng.* **4**, 209–219.
- Pannemans DLE, Bouten CVC & Westerterp KR (1995): 24 h energy expenditure during a standardized activity protocol in young and elderly men. *Eur. J. Clin. Nutr.* **49**, 49–56.
- Ravussin ES, Lillioja TE, Anderson L, Christin C & Bogardus C (1986): Determinants of 24-energy expenditure in man. *J. Clin. Invest.* **78**, 1568–1578.
- Refinetti R (1997): Homeostasis and circadian rhythmicity in the control of body temperature. *Ann. N.Y. Acad. Sci.* **813**, 63–70.
- Rothwell NJ, Stock MJ & Stribling D (1990): Diet-induced thermogenesis. In *Thermoregulation, Physiology and Biochemistry, Chap International Encyclopedia of Pharmacology and Therapeutics*, eds. E Schoenbaum and P Lomax. Sect 131. New York: Pergamon Press.
- Schoffelen PFMA, Westerterp KR, Saris WHM & ten Hoor F (1997): A dual respiration chamber system with automated calibration. *J. Appl. Physiol.* **83**, 2064–2072.
- Siri WE (1961): Body composition from fluid density: analysis of methods. In *Techniques for Measuring Body Composition*, ed. J Brozek & A Herschel, pp 233–244. Washington, DC: National Academy of Sciences, National Research Council.
- Stunkard AJ & Messick S (1985): The Three Factor Eating Questionnaire to measure dietary restraint, distribution and hunger. *Psych. Res.* **29**, 495–502.
- Vander A, Sherman J & Luciano D (1998): Regulation of organic metabolism, growth, and energy balance. In *Human Physiology. The Mechanisms of Body Function*, 7th edn, pp 625–633. New York: WCB/McGraw-Hill.
- van Marken Lichtenbelt WD, Westerterp-Plantenga MS & Van Hooftonck P (2001): Effects of ambient temperature on body temperature and energy expenditure in humans. *Physiol. Behav.* **73**, 235–242.
- Voorlichtingsbureau voor de Voeding (1992): *De handleiding van de Voedingswijzer*. Den Haag.
- Webb P (1992): Temperatures of skin subcutaneous tissue, muscle and core in resting men in cold, comfortable and hot conditions. *Eur. J. Appl. Physiol.* **64**, 471–476.
- Webb P (1993): Daily activity and body temperature. *Eur. J. Appl. Physiol.* **66**, 174–177.
- Weir JBDV (1949): New methods for calculating metabolic rate with special reference to protein metabolism. *J. Physiol.* **109**, 1–9.
- Werner J (1981): Control aspects of human temperature regulation. *Automatica* **17**, 351–362.
- Westerterp KR, Meijer GAL, Saris WHM, Soeters PB, Winants Y & ten Hoor F (1991): Physical activity and sleeping metabolic rate. *Med. Sci. Sports Exerc.* **23**, 166–170.
- Westerterp KR, Wilson SAJ & Rolland V (1998): Diet induced thermogenesis measured over 24 h in a respiration chamber: effect of diet composition. *Int. J. Obes. Relat. Metab. Disord.* **22**, 1–6.
- Westerterp-Plantenga MS, van den Heuvel E, Wouters L & ten Hoor, F (1991): Restrained eating, obesity and cumulative food intake curves during four-course meals. *Appetite* **16**, 149–158.
- Westerterp-Plantenga MS, Rolland V, Wilson SAJ & Westerterp KR (1999): Satiety related to 24 h diet-induced thermogenesis during high protein/carbohydrate vs high fat diets measured in a respiration chamber. *Eur. J. Clin. Nutr.* **53**, 495–502.
- Westerterp-Plantenga MS, van Marken Lichtenbelt WD, Top S & Cilissen C. Energy metabolism in women during short exposure to the thermoneutral zone. *Physiol. Behav.* (in press).
- Wyss CR, Brengelmann GL & Johnson JM (1974): Control of skin blood flow, sweating and heart rate: role of skin vs core temperature. *J. Appl. Physiol.* **36**, 726–733.

Appendix 1 Activity protocol

Evening day 0	
21:00	Arrival in respiration chamber. Body weight measurement.
	Explanations
22:00	Coffee or tea is served
22:00–24:00	Unpacking; reading and watching TV, while sitting
24:00	Time to go to bed
Day 1 and day 2	
8:00	Wake up. Body weight measurement
8:00–8:30	Washing and getting dressed
8:30–9:00	Breakfast
9:00–9:30	Calm activity
9:30–9:45	Dishwashing
9:45–10:00	Making up the bed
10:00–10:30	Stepping in standardized rhythm, while music is playing
10:30–11:00	Refreshing; eating a snack
11:00–12:00	Calm activity
12:00–12:15	Playing with a ball
12:15–13:00	Calm activity
13:00–14:00	Lunch, while sitting
14:00–14:15	Dishwashing
14:15–16:00	Calm activity
16:00–16:30	Stepping in standardized rhythm, while music is playing
16:30–17:15	Refreshing; preparing and eating a snack
17:15–19:00	Calm activity
19:00–20:00	Dinner, while sitting. Last 10 min are spent on dishwashing
20:00–21:30	Calm activity
21:30–24:00	Eating a snack; calm activity
24:00	Time to go to bed
Day 3	
8:00–8:30	See day 1 and 2
8:30–9:00	Preparing for leaving the chamber

Appendix 2

<i>Foods consumed by the subjects</i>	<i>Energy density (kJ/g)</i>	
Breakfast	Wholewheat bread	10.48
	Apricot jam and blueberry jam	10.23
	Sweet spicy biscuit	20.53
Morning snacks	Coffee, tea or water	0
	Chocowafer cookies or	20.23
	wheat cookies or	17.27
	cake	17.57
Lunch	Unsweetened orange juice	1.57
	Lasagne bolognaise or	5.40
	macaroni with cheese and ham or	5.40
	nasi goreng	5.40
	Water	0
Afternoon snacks	Vanilla ice-cream	5.07
	Milk chocolate	22.45
	Chocowafer cookies or	20.23
	cake	17.57
	Fruit (apple, banana, kiwi, mandarin orange)	2.11; 3.75; 1.68; 1.98
Dinner	Water	0
	Toast or sandwich	15.25
	with Gouda cheese 48 + ham, salad, tomato	16.43; 5.73; 0.29; 0.48
	Full fat fruit yogurt or	3.98
	vanilla dessert	3.92
Evening snacks	Paprika crisps and salt crisps	22.62
	water	0