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# Metabolic effects of altering the 24 h energy intake in man, using direct and indirect calorimetry

BY M. J. DAUNCEY*

*MRC Dunn Calorimetry Group, ARC Institute of Animal Physiology,*
*Babraham, Cambridge CB2 4AT*

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1. The metabolic effects of increasing or decreasing the usual energy intake for only 1 d were assessed in eight adult volunteers. Each subject lived for 28 h in a whole-body calorimeter at 26° on three separate occasions of high, medium or low energy intake. Intakes (mean ± SEM) of 13830 ± 475 (high), 8400 ± 510 (medium) and 3700 ± 359 (low) kJ/24 h were eaten in three meals of identical nutrient composition.

2. Energy expenditure was measured continuously by two methods: direct calorimetry, as total heat loss partitioned into its evaporative and sensible components; and indirect calorimetry, as heat production calculated from oxygen consumption and carbon dioxide production. For the twenty-four sessions there was a mean difference of only 1·2 ± 0·14 (SEM) % between the two estimates of 24 h energy expenditure, with heat loss being less than heat production. Since experimental error was involved in both estimates it would be wrong to ascribe greater accuracy to either one of the measures of energy expenditure.

3. Despite the wide variation in the metabolic responses of the subjects to over-eating and under-eating, in comparison with the medium intake the 24 h heat production increased significantly by 10 % on the high intake and decreased by 6 % on the low intake. Mean (± SEM) values for 24 h heat production were 8770 ± 288, 7896 ± 297 and 7495 ± 253 kJ on the high, medium and low intakes respectively. The effects of over-eating were greatest at night and the resting metabolic rate remained elevated by 12 % 14 h after the last meal. By contrast, during under-eating the metabolic rate at night decreased by only 1 %.

4. Evaporative heat loss accounted for an average of 25 % of the total heat loss at each level of intake. Changes in evaporative heat loss were +14 % on the high intake and −10 % on the low intake. Sensible heat loss altered by +9 % and −5 % on the high and low intakes respectively.

5. It is concluded that (*a*) the effects on 24 h energy expenditure of over-feeding for only 1 d do not differ markedly from those estimated by some other workers after several weeks of increasing the energy intake; (*b*) the resting metabolic rate, measured at least 14 h after the last meal, can be affected by the previous day's energy intake; (*c*) the zone of ambient temperature within which metabolism is minimal is probably altered by the level of energy intake.

There is considerable disagreement about the metabolic effects of over-eating in man. The controversy is concerned particularly with the effect on the resting metabolic rate (RMR) at least 12 h after the last meal: some workers (Miller *et al.* 1967; Strong *et al.* 1967) reported no change, while others (Durnin & Norgan, 1969; Apfelbaum *et al.* 1971) reported an increase after several weeks of over-feeding. There is also much interest in the extent to which some people may adapt to over-feeding by increasing their energy expenditure so that there is little or no increase in weight or less weight gain than expected. Owing to inadequate methodology, many studies on the effects of an altered energy intake have relied on calculating the 24 h energy expenditure by extrapolation from measurements made over short periods of time.

In animals other than man the rate of 24 h heat production is found to be dependent on the level of energy intake (Graham *et al.* 1959; Close *et al.* 1971). Furthermore the RMR of young pigs given a high energy intake for one week remains elevated 14–20 h after the last meal (Dauncey & Ingram, 1979). Since this increase in RMR was dependent on nutrient composition it becomes difficult to interpret work in which the relative composition of nutrients has been altered at the same time as the energy intake.

After several days or weeks of under-eating the RMR at least 12 h after the last meal

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* Present address: ARC Institute of Animal Physiology, Babraham, Cambridge CB2 4AT.

Table 1. *Physical characteristics of subjects*

| Subject | Age (years) | Height (m) | Body-wt (kg) | Body fat (% body-wt*) |
|---|---|---|---|---|
| Men | | | | |
| 001 | 39 | 1·714 | 67·9 | 16·3 |
| 003 | 48 | 1·723 | 55·9 | 13·5 |
| 009 | 27 | 1·721 | 57·9 | 9·8 |
| 010 | 38 | 1·724 | 70·1 | 16·7 |
| Women | | | | |
| 104 | 36 | 1·682 | 66·9 | 24·1 |
| 105 | 30 | 1·668 | 53·3 | 21·0 |
| 107 | 39 | 1·648 | 56·8 | 21·1 |
| 109 | 25 | 1·618 | 48·4 | 15·7 |
| Mean ± SEM | 35 ± 2·7 | 1·69 ± 0·01 | 60 ± 2·8 | 17 ± 1·6 |

* From sum of four skinfold thicknesses (Durnin & Womersley, 1974).

decreases. In the short-term this is due mainly to a decrease in the metabolic activity of the tissues (Grande *et al.* 1958), while in the long-term the loss of metabolically active tissue also becomes important in the reduced RMR (Keys *et al.* 1950). However, the effects on metabolic rate during only 24 h of under-feeding or over-feeding are unknown. The present study was therefore carried out to determine the metabolic effects of increasing or decreasing the usual daily energy intake of adult men and women, while maintaining constant the percentage of energy supplied by protein, fat and carbohydrate in the diet. Heat production, respiratory quotient (RQ) and evaporative and sensible heat losses were measured throughout a period of 24 h while the subject lived in a whole-body calorimeter on a high, medium or low energy intake. Part of this work has been the subject of preliminary communications (Dauncey, 1979*a*, *b*).

## METHODS

### *Subjects*

Eight volunteers, four men and four women, took part in the study. Six of the subjects had taken part in other experiments with the calorimeter and the other two were familiarized with the experimental procedures before starting the study. The subjects were chosen to cover a wide range of age and body-weight, but none was excessively overweight or underweight. Physical characteristics of the subjects are given in Table 1.

### *Experimental*

Each subject occupied the calorimeter at 26° on three separate occasions of high, medium or low energy intake. The order was not systematic and not known in advance by the subject. A period of 1 month was allowed between each session, because of monthly variations in heat production which probably occur in women (Aschoff & Heise, 1972). An ambient temperature of 26° was chosen after preliminary studies had shown it to be the most comfortable temperature throughout a 24 h period for a wide variety of subjects. Standard clothing of thin cotton shirt and trousers was worn in the calorimeter.

The subject lived in the calorimeter from 09.30 hours on day 1 until 14.00 hours on day 2. The postural activity was standardized but the subject was otherwise free to read, write, telephone, listen to the radio or watch television. Meals were provided at 09.00, 13.30 and 18.00 hours on day 1 and 09.30 hours on day 2. There were two 30 min cycling periods, at the low work load of 0·5 N at 50 rev./min, at 14.00–14.30 hours and 18.30–19.00 hours on day 1. The cycling was intended both to prevent the 24 h energy expenditure from being markedly lower than normal and to provide information on the metabolic effect of exercise after a meal. Two 30 min periods of standing were from 22.00 hours on day 1 before going to bed, and from 09.30 hours on day 2 after getting out of bed.

A standard procedure was also carried out for the measurement of the RMR 14 h after the last meal. An observer switched on the lights at 08.25 hours on day 2 and buzzed on an intercom if the subject appeared to be asleep. The subject could be seen through the windows of the calorimeter and outer room. The subject had been instructed previously to remain lying quietly awake until the end of the observation period at 09.30 hours. Checks to ensure that the subject was awake were made frequently by an observer who buzzed on the intercom if the subject's eyes were closed. The measurement of energy expenditure between 08.30 and 09.30 hours will be referred to as the standardized metabolic rate (SMR). Examples of the ways in which the calorimeter was used for the different activities have been illustrated (Dauncey, 1979*c*).

### *Energy intake*

*Week preceding entry into the calorimeter.* To minimize the metabolic effects of food eaten during the week preceding entry into the calorimeter the subject was asked to eat approximately the same food for the week before and exactly the same on the day before each session. During the 8 d before each session the subject weighed everything eaten and drunk so that firstly the first 7 d energy intake could be used for calculating the medium intake in the calorimeter, and secondly the food intake before entering the calorimeter would be known. It was impractical and not the aim of the experiment for the intake to be standardized before each session. The dietary intakes were analysed using the Department of Health and Social Security Food Tables which are largely based on McCance and Widdowson's (1967) food tables. These food tables allow the calculation of metabolizable energy intake.

*In the calorimeter.* All meals were based on a unit system, with one unit equivalent to 20 g rye crispbread, 10 g margarine, 35 g corned beef, 14 g digestive biscuits and 13·5 g milk chocolate; 50 g tomato were also eaten with each meal. The diet was easy to reproduce and had a relatively high proportion of fat to ease the consumption of the high intake. The contributions to total metabolizable energy made by protein, fat and carbohydrate were 16, 50 and 34% respectively.

The aim for the high and low intakes was for the subject to double or halve the medium intake. In practice it was found during the first meal of the high intake that some of the subjects could not double their normal intake and the intakes were reduced accordingly. Three typical 24 h sessions of low, medium and high energy intake were, respectively, 4400 kJ eaten as three meals of one unit/meal, 8800 kJ eaten as three meals of two units/meal, and 13200 kJ eaten as three meals of three units/meal.

### *Energy expenditure*

Energy expenditure was measured by both indirect and direct calorimetry. The methods for estimating heat production and evaporative and sensible heat losses have been published (Dauncey & Murgatroyd, 1978; Dauncey *et al.* 1978). A paramagnetic oxygen analyser and infra-red carbon dioxide analyser were used to measure the gas concentrations of air entering and leaving the calorimeter. The gas analysers were calibrated before each 28 h session and the ventilation rate before and after each series of experiments. Heat production was calculated after making a correction for the difference in volume between the ingoing and outgoing air which occurs when the RQ is less than unity. Evaporative heat loss was determined from the ventilation rate and the ingoing and outgoing wet-and-dry-bulb temperatures. Sensible heat loss was estimated from the temperature difference across a water-cooled heat exchanger. A full calibration of evaporative and sensible heat losses was made

Table 2. *Energy intakes (/24 h) for the three 8 d periods of weighed intake before each session in the calorimeter*

(Mean values with their standard errors and ranges for each 8 d period)

| | Metabolizable energy intake* (kJ/24 h) | | | |
|---|---|---|---|---|
| | | | Range | |
| Subject | Mean | SEM | Maximum | Minimum |
| 001 | 8530 | 602 | 11230 | 6720 |
| | 9640 | 405 | 10760 | 7850 |
| | 10230 | 752 | 13530 | 7200 |
| 003 | 8850 | 311 | 10240 | 7560 |
| | 6800 | 438 | 8090 | 4400 |
| | 7450 | 265 | 9110 | 6510 |
| 009 | 12680 | 711 | 14980 | 9240 |
| | 11260 | 723 | 13340 | 7880 |
| | 12270 | 672 | 14820 | 9830 |
| 010 | 5590 | 902 | 10870 | 2020 |
| | 5990 | 811 | 11420 | 3740 |
| | 7380 | 827 | 10990 | 3940 |
| 104 | 11060 | 784 | 15110 | 7970 |
| | 9810 | 661 | 12790 | 7510 |
| | 9930 | 564 | 12080 | 7300 |
| 105 | 9420 | 497 | 11023 | 6650 |
| | 10040 | 830 | 13080 | 7500 |
| | 9460 | 508 | 12160 | 7520 |
| 107 | 10520 | 468 | 12220 | 8570 |
| | 10120 | 296 | 11250 | 8730 |
| | 11000 | 646 | 13280 | 8240 |
| 109 | 7520 | 937 | 12120 | 3380 |
| | 7420 | 635 | 10880 | 5030 |
| | 7280 | 461 | 9030 | 5060 |

* Calculated from Department of Health and Social Security food tables (based on McCance & Widdowson, 1967).

before and after each series of experiments and a calibration using a standard power input was made before and after each individual experiment. All measurements were monitored continuously and recorded on paper tape at 5 min intervals for computer analysis.

## *Analysis of results*

To determine the effects of 1 d of over-feeding on energy expenditure, differences between the medium *v.* high sessions were assessed using the paired *t* test. Similarly the effects of under-feeding were examined by comparing the medium *v.* low sessions using the paired *t* test. For this study the *t* test was considered to be the most appropriate form of statistical analysis. The relation between energy intake and energy expenditure in the calorimeter was examined by fitting linear and quadratic regression coefficients.

Table 3. *Energy intakes of subjects in calorimeter, from* 13.30 *hours on day* 1 *to* 13.30 *hours on day* 2

| Session in calorimeter† . . . | Metabolizable energy intake* (total kJ) | | | Order of treatments: Energy intake | | |
|---|---|---|---|---|---|---|
| Subject | High (H)† | Medium (M)† | Low (L)† | 1st | 2nd | 3rd |
| 001 | 12973 | 8768 | 2988 | L | M | H |
| 003 | 14736 | 8895 | 4444 | H | M | L |
| 009 | 13026 | 8843 | 4534 | H | L | M |
| 010 | 13250 | 5890 | 2223 | L | M | H |
| 104 | 16846 | 10411 | 4359 | M | H | L |
| 105 | 13229 | 8849 | 4382 | L | H | M |
| 107 | 13404 | 8906 | 4376 | M | L | H |
| 109 | 13169 | 6613 | 2318 | H | M | L |
| Mean ±SEM | 13829±475 | 8397±510 | 3703±359 | | | |

* Percentages of energy supplied by protein, fat and carbohydrate were the same for each subject and each level of intake.

† For details, see p. 258.

## RESULTS

### *Energy intake*

*Before entering the calorimeter.* Not only was there a wide variation in the usual energy intake from one subject to the next but also in the intake of any one subject. Thus, during the 8 d of weighing the food intake, a subject often ate twice as much on one day as on another. This point is illustrated in Table 2 which gives the mean ±SEM and range of 24 h energy intakes for each series of weighed intakes. Comparisons of the mean 24 h intakes for 1, 3, 5 and 8 d before each session were made. There was no significant difference ($P > 0\cdot05$) between the intakes before the high *v*. medium or medium *v*. low sessions in the calorimeter.

*In the calorimeter.* The energy intakes of the subjects while in the calorimeter are given in Table 3. Since subject 001 found it impossible to attempt consumption of the high intake meal on day 2, he ate the energy equivalent of the medium intake as a liquid meal (Complan: Glaxo-Farley Food Ltd, Plymouth, Devon; and Lucozade: Beecham Products, Brentford, Middlesex). Subject 009 was unable to increase his usual intake in the calorimeter; he was an athlete and often ran 30–65 km/week. His medium session was therefore designated high and the remaining two sessions as medium and low. It should be noted that although the greatest energy intake of each subject while in the calorimeter was designated high, it did not necessarily differ markedly from the intake which might be eaten on one of the days when outside the calorimeter. This was because of the wide range of 24 h energy intake within each subject, as shown in Table 2.

### *Energy expenditure in the calorimeter*

If the net change in heat storage in a subject's body over a given period is zero, there should be no difference between the direct and indirect measures of energy expenditure made over that period. In the present study of twenty-four experiments, the mean (±SEM) percentage difference between 24 h heat production and total heat loss from 13.30 hours on day 1, was 1·2±0·14%. The small difference between heat production and total heat loss could have been due to inaccuracies in the measurement of $O_2$, $CO_2$, evaporative heat loss, sensible heat loss and the ventilation rate; heat storage by the body; or differences in the response time for $O_2$, $CO_2$ and evaporative heat loss as compared with that for sensible heat loss. Since experimental error was involved in the estimates of both heat production and heat loss it would be wrong to ascribe greater accuracy to either one of the measures of energy expenditure.

Table 4. *Energy expenditures of subjects in calorimeter, from* 13.30 *hours on day* 1 *to* 13.30 *hours on day* 2

| | Heat production (total kJ) | | |
|---|---|---|---|
| Session in calorimeter‡... | High | Medium | Low |
| Subject | | | |
| 001 | 9121 | 8516 | 8280 |
| 003 | 9310 | 8315 | 7498 |
| 009 | 9685 | 8641 | 8371 |
| 010 | 9023 | 8076 | 7828 |
| 104 | 9501 | 8730 | 7589 |
| 105 | 7767 | 7237 | 6791 |
| 107 | 8139 | 8112 | 7361 |
| 109 | 7590 | 6261 | 6240 |
| Mean ± SEM | 8767* ± 288 | 7986 ± 297 | 7495† ± 253 |

* Significantly greater than medium: $P < 0·001$ (paired $t$ test).
† Significantly less than medium: $P < 0·01$ (paired $t$ test).
‡ For details, see p. 258.

For periods of less than 24 h, agreement between heat production and total heat loss would not be expected, because of the circadian variation in body temperature and heat storage by the body. Since heat production gives the better indication of true energy expenditure during these short periods, the values for heat production rather than total heat loss will be presented.

24 *h Heat production.* Table 4 gives the values of 24 h heat production in the calorimeter. The mean (±SEM) energy expenditure (%) on the high intake was significantly greater by 10±2·1 than that on the medium intake ($P < 0·001$). That on the low intake was significantly less by 6±1·6 than that on the medium intake ($P < 0·01$). Despite the wide range of energy intakes for any one session, the range of energy expenditures was quite narrow. This reflected the influence of physical activity in determining energy expenditure and the importance of maintaining the activity pattern constant in any studies designed to determine the effect of other factors on energy expenditure.

*Metabolic rate during different times of the day and night.* Mean (±SEM) values of heat production during three 4 h periods of the day and two 4 h periods of the night are given in Table 5. The effect of over-feeding on metabolic rate was more pronounced during the night than the day. In comparison with the medium intake, heat production on the high intake increased by 14% during the night but by only 7% during the day. The difference throughout the night, from 22.30 to 09.30 hours, was significant ($P < 0·001$), as were the differences during the day-time; for example, from 11.30–22.30 hours on day 1 ($P < 0·005$). During the two 4 h periods of the day when the meal was followed by 30 min of cycling the increase in heat production on the high intake was no greater than when the meal was followed by sitting.

In contrast with over-feeding, the effects of under-feeding were more pronounced during the day, when heat production decreased by 9% ($P < 0·05$ at 11.30–22.30 hours on day 1) in comparison with the medium intake. At night there was no significant difference between the medium and low intakes. The small difference of 3% between midnight and 04.00 hours decreased with time, so that between 04.00 and 08.00 hours the heat production on the low intake was almost identical with that on the medium intake.

All the individuals did not respond in exactly the same way to an altered energy intake. Two sets of results are shown in Figs. 1 and 2 which give the metabolic rates at 30 min intervals for each of the three sessions. There is a time lag in the response of the system but this would be the same for each session. The most noticeable differences between individuals

Table 5. *Heat production of subjects during periods of day and night (total kJ) and standardized metabolic rate (SMR) (kJ/min)*

(Mean values with their standard errors for eight subjects)

| | | Session in calorimeter* | | | Paired *t* test: *P* | |
|---|---|---|---|---|---|---|
| | Time (h) | High | Medium | Low | High *v.* Medium | Medium *v.* Low |
| Day 1 | 13.30–17.30 | 1836±65 | 1728±66 | 1548±54 | <0·025 | <0·005 |
| Day 1 | 18.00–22.00 | 1868±71 | 1700±71 | 1557±49 | <0·01 | <0·02 |
| Day 2 | 09.30–13·30 | 1551±52 | 1457±47 | 1355±45 | <0·02 | <0·005 |
| Night | 00.00–04.00 | 1108±36 | 963±33 | 930±33 | <0·001 | NS |
| Night | 04.00–08.00 | 1070±44 | 946±38 | 950±35 | <0·005 | NS |
| SMR | 08.30–09.30 | 4·558±0·144 | 4·098±0·149 | 4·154±0·149 | <0·005 | NS |

NS, not significant.
* For details, see p. 258.

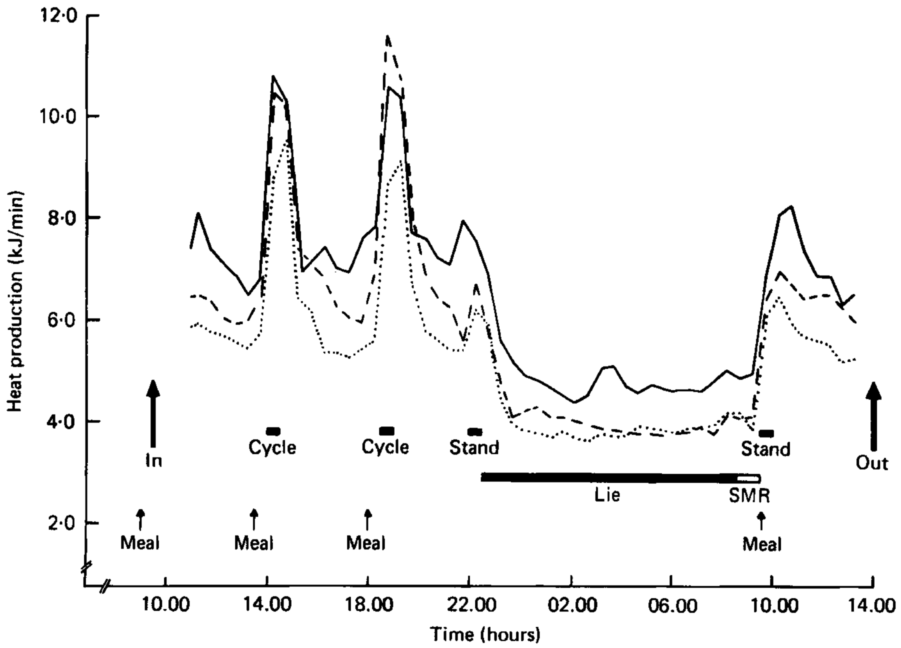

Fig. 1. Metabolic rate of subject 003 during three sessions of 28 h in the whole-body calorimeter at 26°. Energy intakes were high (——), medium (– – –) or low (....) and of identical percentage contributions from protein, fat and carbohydrate. Unless otherwise stated the subject was sitting and able to read, write, listen to the radio or watch television. Cycling was at the low work load of 0·5 N at 50 rev./min. The subject slept for most of the period of lying but was always awake for the measurement of standardized metabolic rate (SMR). Mean values of heat production (kJ/min) for each 30 min period are plotted.

occurred during the day: in some instances there were equally large differences in metabolic rate between the three sessions, in others the difference between high and medium intakes was greatest, while in others there was little difference between the high and medium intakes but the heat production on the low intake was considerably reduced.

*SMR.* Over-feeding by an average of 68% for 24 h resulted in a mean (±SEM) increase in

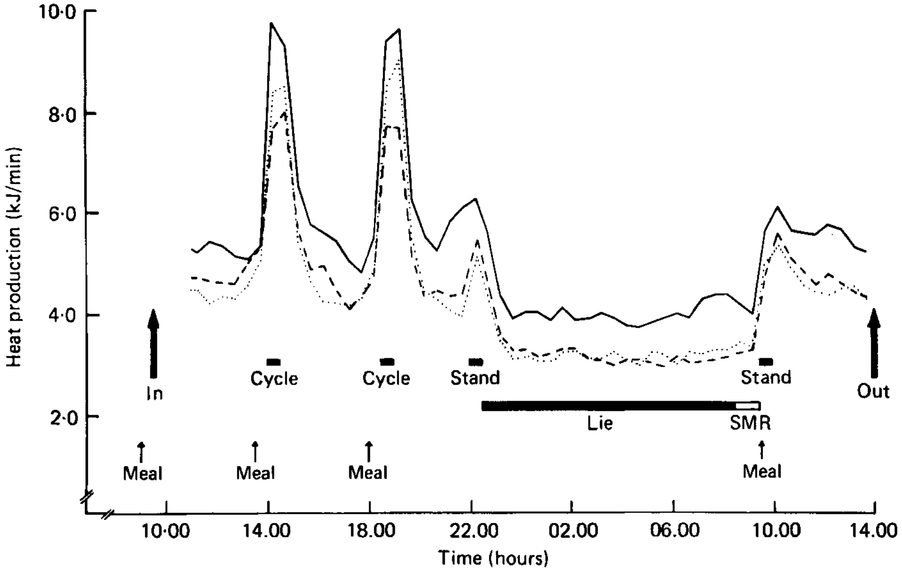

Fig. 2. Metabolic rate of subject 109 during three sessions of 28 h in the whole-body calorimeter at 26°. Energy intakes were high (——), medium (– – –) or low (....) and of identical percentage contributions from protein, fat and carbohydrate. Unless otherwise stated the subject was sitting and able to read, write, listen to the radio or watch television. Cycling was at the low work load of 0·5 N at 50 rev./min. The subject slept for most of the period of lying but was always awake for the measurement of standardized metabolic rate (SMR). Mean values of heat production (kJ/min) for each 30 min period are plotted.

SMR of $12 \pm 3\%$ ($P < 0·005$). This measurement was taken between 14 and 15 h after the last meal, with the subject in an undisturbed, comfortable environment. There was no difference between the SMR on the medium intake and that on the low intake.

The average increase in SMR during over-feeding was approximately the same in the women as in the men. Three of the men increased their heat production by 15, 20 and 11%. Only subject 010 showed no change in SMR. This was an individual who had maintained his body-weight constant for 6 months on an intake of only approximately 6000 kJ. The four women increased their SMR by 11, 8, 4 and 25% when on the high intake.

*Calculation of energy expenditure during the night from SMR.* The RMR at least 12 h after eating is sometimes used for calculating the metabolic rate during the night by workers who have no facilities for making the overnight measurement. When the heat production between 00.00 and 08.00 hours on the high intake was calculated from the SMR there was found to be good agreement between the actual and calculated values. However, using this method of calculation the night-time heat production was over-estimated on average by 3 and 6% for the medium and low intakes respectively.

### *Relation between 24 h energy intake and energy expenditure*

The relation between energy intake and energy expenditure in the calorimeter was examined by calculating linear and quadratic regression coefficients for each subject over the three levels of intake. Since there was no significant quadratic coefficient for the 24 h from 13.30 hours on day 1, the relation could be summarized by the linear coefficient. This coefficient gave the increase in heat production (kJ) per unit increase in energy intake (kJ). The calculation therefore took into account the fact that both the total energy intake and the relative amount by which the intake was altered varied between individuals. The mean

Table 6. ***Partition of** 24 **h heat loss of subjects in calorimeter into its evaporative and sensible components, from** 13.30 **hours on day** 1 **to** 13.30 **hours on day** 2*

| Session in calorimeter... | High | Medium | Low |
|---|---|---|---|
| | Evaporative heat loss (total kJ) | | |
| Subject | | | |
| 001 | 1868 | 1979 | 2002 |
| 003 | 2671 | 1967 | 1636 |
| 009 | 2944 | 2379 | 2188 |
| 010 | 2048 | 1621 | 1630 |
| 104 | 2165 | 2100 | 1856 |
| 105 | 2057 | 1566 | 1494 |
| 107 | 2222 | 2461 | 2002 |
| 109 | 1798 | 1572 | 1344 |
| Mean ± SEM | 2222 ± 139 | 1956 ± 124 | 1769* ± 102 |
| | Sensible heat loss (total kJ) | | |
| 001 | 7248 | 6422 | 6109 |
| 003 | 6493 | 6226 | 5849 |
| 009 | 6565 | 6100 | 6112 |
| 010 | 6774 | 6344 | 6152 |
| 104 | 7241 | 6462 | 5708 |
| 105 | 5596 | 5589 | 5141 |
| 107 | 5882 | 5663 | 5232 |
| 109 | 5668 | 4530 | 4805 |
| Mean ± SEM | 6433‡ ± 233 | 5917 ± 230 | 5639† ± 182 |

Significantly less than medium: *$P < 0·02$, † $P < 0·05$ (paired *t* test).
‡ Significantly greater than medium: $P < 0·01$ (paired *t* test).

(± SEM) linear regression coefficient was 0·125 ± 0·034 and varied between 0·082 and 0·176. This indicated that on average 12·5% of the increase in energy intake was accounted for by an increase in heat production, with a range of 8–18%. The mean (± SEM) correlation coefficient between energy intake and energy expenditure was 0·96 ± 0·02.

### *RQ*

The mean (± SEM) values of RQ for the high, medium and low intakes were 0·831 ± 0·093, 0·809 ± 0·071 and 0·787 ± 0·004 respectively. In comparison with the medium intake the RQ was 3% greater ($P < 0·025$) on the high intake and 3% less ($P < 0·02$) on the low intake. This finding was in agreement with the studies of Dewar & Newton (1948) on mice. These workers determined respiratory exchanges over 24 h periods and found a linear relation between non-protein RQ and the quantity of food eaten.

### 24 *h Partition of heat loss*

Evaporative heat loss accounted for between 24 and 26% of the 24 h total heat loss. This was the situation on each level of intake when the comparison was made for the whole group or for men and women separately. Individual values for evaporative heat loss and sensible heat loss are given in Table 6. Although there was a 14% increase in evaporative heat loss from the medium to the high intake, with a mean of 20% for men and 7% for women, the difference was not statistically significant. This was probably because one man and one woman each showed a decrease in evaporative heat loss on the high intake. On average there was a decrease of 10% in evaporative heat loss ($P < 0·02$) between the medium and low intakes. The lower evaporative heat loss was found in all subjects except the one man

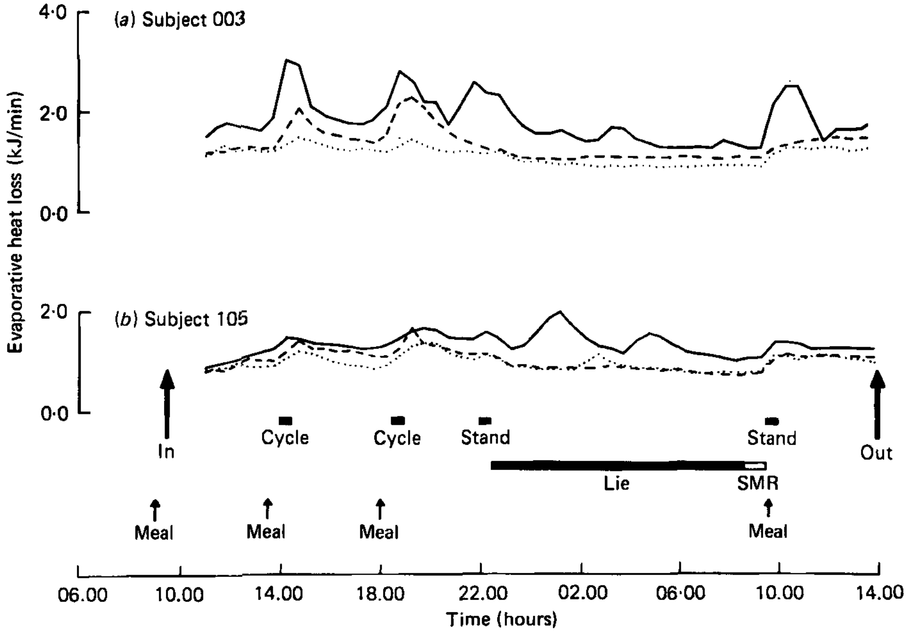

Fig. 3. Evaporative heat losses of subjects 003 (*a*) and 105 (*b*) during three sessions of 28 h in the whole-body calorimeter at 26°. Energy intakes were high (——), medium (– – – –) or low (....) and of identical percentage contributions from protein, fat and carbohydrate. Unless otherwise stated the subject was sitting and able to read, write, listen to the radio or watch television. Cycling was at the low work load of 0·5 N at 50 rev./min. The subject slept for most of the period of lying but was always awake for the measurement of standardized metabolic rate (SMR). Mean values of heat production (kJ/min) for each 30 min period are shown.

who had shown no increase in evaporative heat loss on the high intake. The individual variation in the response of evaporative heat loss throughout the period in the calorimeter to changes in energy intake is indicated in Fig. 3.

In comparison with the medium intake, sensible heat loss was 9% greater on the high intake and 5% smaller on the low intake. Both these differences were significant ($P < 0·01$, $P < 0·05$ respectively).

### *Subjective comments on ambient temperature*

At the end of each session the subject was asked to comment on the temperature inside the calorimeter. In general the comments showed that the subjects felt comfortable during the 24 h on the medium intake. They tended to be warmer on the high intake when they were sometimes conscious of sweating, especially during and after exercise. On the low intake they tended to feel cool although they were not conscious of shivering.

## DISCUSSION

Under the conditions of these experiments the 24 h energy expenditure of human adults was elevated by approximately 10% when the energy intake was increased by an average of 5400 kJ. The increase in metabolic rate was greatest at night and the RMR remained elevated for at least 14 h after the last meal. The increase in metabolic rate was no greater during exercise after a meal than at any other time. The ways in which these findings are consistent with those of some workers but in direct disagreement with the conclusions of others are discussed later.

The present results agree with those found with other animals after several days or weeks on a given energy intake. The 24 h energy expenditure is dependent on the level of energy intake in both sheep and pigs (Graham *et al.* 1959; Close *et al.* 1971), while the RMR of pigs 14–20 h after feeding remains increased on a high energy intake (Dauncey & Ingram, 1979). In none of these studies was all or even most of the increase in intake accounted for by an increase in energy expenditure.

Sims (1976) concluded from 10 years of over-feeding studies in man that 'we have no good measure of the total increase in thermogenesis accompanying weight gain and over-feeding with carbohydrate, but it appears unlikely that this could account for more than 10–12%'. However, an increased form of heat production, sometimes termed luxuskonsumption, has been postulated by some workers to operate as a homoeostatic mechanism for energy balance in some individuals during over-feeding such that the weight gain is zero or at least much less than would be expected. The suggestion has been made that there might be either a period of more than a few days (Miller & Mumford, 1973) or a critical size of overload of approximately 84000 kJ (Garrow, 1978*a*) before this mechanism operates. Apfelbaum *et al.* (1971) over-fed subjects a daily excess of 6300 kJ for 15 d and this work has been quoted as providing evidence for the postulated luxuskonsumption (Miller, 1975; Garrow, 1978*b*). The work of Durnin & Norgan (1969), who over-fed six subjects a total excess of 293000 kJ during 6 weeks, should also provide evidence of luxuskonsumption. However, although both these groups (Durnin & Norgan, 1969; Apfelbaum *et al.* 1971) found an increase in energy expenditure, it was not great enough to be the postulated luxuskonsumption since it did not account for all or even most of the extra energy intake. Moreover the increase in energy expenditure was of the same order as that found in the present study. Therefore neither the duration of over-feeding nor the total excess energy intake appear to have a substantial effect on the increased heat production in normal subjects. The continuous measurement of the 24 h energy expenditure of subjects who have over-fed for several weeks is needed to check this point, and a fuller discussion of the factors which may be involved in the response to over-feeding is given by Dauncey (1979*d*).

During over-feeding in the present study there was on average a significant increase in the RMR at least 14 h after the last meal, whereas Gulick (1922), Munro (1950), Miller *et al.* (1967), Strong *et al.* (1967) and Glick *et al.* (1977) all concluded that the basal metabolic rate (BMR) was unaltered during over-feeding. However, of these studies the first two (Gulick, 1922; Munro, 1950) were each on only one subject and in the former the BMR was measured only during over-feeding and then compared with normal values in standard tables. Glick *et al.* (1977) based their conclusions on mean values from four overweight and four normal weight individuals, but inspection of their results indicates that the normal subjects showed an increase in 'BMR' while those who were over-weight showed a decline. This agreed with the findings of Passmore *et al.* (1955*a*, *b*) and Passmore *et al.* (1963) where three men of normal weight increased their BMR while two obese women showed no change. Miller *et al.* (1967) also found a wide variation in the response of six individuals to over-feeding with a range of −8·3 – +7·7% change in BMR. Although Strong *et al.* (1967) reported no change in BMR the range was between −3 and +6% and the metabolic rates were higher by an average of 8·5% during the night. It therefore appears that the term basal metabolic rate is inappropriate for describing the RMR at least 12 h after the last meal, since the influence of diet is not necessarily excluded from the measurement. The term SMR should therefore be used instead of BMR, a suggestion in agreement with Krogh & Lindhard (1920) who referred to their measurement of metabolism at rest in the postabsorptive state as standard metabolism.

Benedict *et al.* (1919) and Grande *et al.* (1958) found a reduced BMR after under-feeding subjects of normal weight for several days, weeks or months. Since the present study showed no effect of under-feeding for 1 d on SMR, the effects of a reduced energy intake on the postabsorptive metabolic rate must take several days to become established.

Sims (1976) has listed a number of processes which may account for diet-induced thermogenesis. Part of the elevated SMR during over-feeding may have been due to the continued processing of the extra food while part may have been due to an increase in protein turnover (Garlick *et al.* 1978), glucose recycling or sodium pumping. The mechanisms by which metabolic rate is altered with a change in energy intake may be connected with alterations in thyroid hormone and catecholamine metabolism. Although an increase in energy intake does not change the concentrations of circulating thyroid hormones in the pig (D. L. Ingram and S. E. Evans, personal communication), the rate of utilization of thyroxine increases on a high energy intake (Ingram & Kaciuba-Uscilko, 1977). Also, the $\beta$-blocker propranolol reduces the overnight metabolic rate of pigs on a high energy intake (Dauncey & Ingram, 1979) and a similar capacity for propranolol to reduce the RMR on a weight-maintenance diet has since been found in obese humans (Jung *et al.* 1979).

Work on energy metabolism in other animals has shown an interaction between nutrition and environment with, in general, the level of energy intake as the main determinant of energy expenditure within the zone of thermal neutrality, whereas below the critical temperature the environmental temperature plays an increasing role as the temperature falls. Close & Mount (1978) suggested that the effective critical temperature could be calculated from the temperature at which a marked increase in evaporation occurs. The values of critical temperature they obtained from this method agreed well with those calculated from the extra thermoregulatory heat produced in the cold. The present study showed that the critical temperature in man, as indicated by a marked increase in evaporative heat loss, is probably dependent not only on the time of day but also on the energy intake. The comment of the subjects that they were warmest on the high energy intake was reflected in the increased evaporative heat loss of six of the subjects during over-feeding. This in turn indicated a decrease in the zone of minimal metabolism.

Although the group as a whole showed significant changes in 24 h metabolism with a change in energy intake, at one extreme there was one subject who showed no increase in metabolic rate during over-eating, while in another subject under-eating had no marked effect. This variation may have been a consequence of the subjects not being on a controlled energy intake and level of activity for several weeks before the study. Alternatively the speculation is that those who showed little tendency to increase their metabolism when over-eating are the type who are prone to obesity, whereas the reverse is true of those who showed no decrease in metabolic rate on the low intake. The causes of the variation should be the subject of further investigation.

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