Effects of overfeeding by gastric intubation on body composition of adult female rats and on heat production during feeding and fasting

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1. The effects of overfeeding by gastric intubation on the body composition and energy metabolism of adult female rats were studied in three experiments.

2. In Expt 1 there were significant ($P < 0.001$) linear increases in carcass dry matter, fat and energy during a 10 d period as metabolizable energy (ME) intake was increased from 160 to 300 kJ/d.

3. In Expt 2 rats were fed to maintain weight (130 kJ/d) or given approximately 270 kJ/d for 120 d. Measurements of fed and fasting heat production (FHP) were made at intervals. FHP (kJ/d per kg metabolic weight ($W^{0.75}$)) decreased by 15% over the 120 d period on both treatments. The mean carcass weight of the overfed rats increased from 216 to 465 g, over 90% of the increase being due to fat.

4. In Expt 3 rats were fed to maintain weight (137 kJ/d) or given approximately 300 kJ/d for 6, 12, 18, 24 or 30 d. There were significant linear increases ($P < 0.001$) with time in carcass weight, dry matter, fat and energy. FHP, measured before slaughter, increased from 118 to 160 kJ/d but remained constant at 334 kJ/d per kg $W^{0.75}$.

5. In all three experiments there were significant ($P < 0.01$) increases in carcass crude protein (nitrogen $\times 6.25$) in response to overfeeding.

6. The efficiency of utilization of energy for production (Expt 1) or for maintenance and production (Expts 2 and 3) averaged 0.92, 0.86, 0.88 respectively.

7. It is concluded that FHP per kg $W^{0.75}$ may be regarded as constant over a wide range of body compositions in adult rats made obese by gastric intubation, and that energy utilization conforms to classical concepts.

Whereas the energy intake of adult domesticated animals is usually restricted by man in the interests of economic production, the energy consumption of adult man is affected by environmental and social factors. In affluent societies energy consumption frequently exceeds expenditure with the result that body-weight and body fat increase (Garrow, 1978). The relationships between food intake, metabolic rate and energy retention in the human are still not clearly established and conflicting reports on the effects of overfeeding on the energy balance and weight gain of normal adult humans have been published (Passmore *et al.* 1955; Miller & Mumford, 1967; Apfelbaum *et al.* 1971; Sims *et al.* 1973; Norgan & Durnin, 1980).

The laboratory rat provides a useful model for studies on overfed adults, since it is possible to induce it to consume excess energy by feeding high-fat diets (Mickelsen *et al.* 1955), by offering a varied diet (Scalafani & Springer, 1976) or by gastric intubation (Cohn & Joseph, 1959). Experimental animals may be kept in controlled environmental conditions for long periods and body composition accurately determined, thus eliminating many of the assumptions which have to be made with *homo sapiens*.

Experiments with overfed adult rats were begun in our laboratory in 1974 and preliminary

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Table 1. *Composition and analysis (g/kg dry matter) of the experimental diets*

Diet...	1	2
Expt...	1 and 2	3
Starch	500	310
Sucrose	250	250
Casein	100	120
Fatted skim-milk (400 g fat/kg)	—	150
Maize oil	100	120
Minerals*	40	40
Vitamins†	10	10
Crude protein (nitrogen × 6·25)	97	138
Crude fat	98	186
Ash	46	50
Gross energy (MJ/kg)	18·7	20·6

* The mineral mixture supplied (g/kg diet): calcium orthophosphate 17·4, potassium chloride 10·8, disodium hydrogen sulphate 4·6, magnesium sulphate 8 mg, sodium fluoride 0·4 mg.

† The vitamin mixture supplied (mg/kg diet): ascorbic acid 200, choline chloride 750, myo-inositol 50, nicotinic acid 20, riboflavin 5, pyridoxine hydrochloride 5, thiamin hydrochloride 5, calcium pantothenate 15, folic acid 0·5, biotin 100 μg, cyanocobalamin 10 μg.

results have been published (McCracken, 1975, 1976; McCracken & Gray, 1976; McCracken & McNiven, 1982). Gastric intubation was chosen as the feeding technique since this method ensures controlled consumption of a balanced diet. The aims of the experiments to be described were (1) to establish the efficiency of utilization of energy for fattening in the overfed adult rat (2) to simulate obesity and examine the changes in body composition (3) to study the relationship between body mass and fasting heat production (FHP). Expt 1 was a short-term experiment to measure the efficiency of energy utilization. In retrospect it was considered that the high efficiency obtained may have been partly due to the environmental temperature being below thermoneutrality (Sørenson, 1962) and subsequent experiments were conducted at 30°. Expt 2 was designed to provide information on long-term changes in body composition and FHP. Expt 3 was intended to overcome some of the problems of interpretation in Expt 2 due to possible carry-over effects of intermittent fasting, and to examine the time-course relationship of protein deposition during overfeeding.

EXPERIMENTAL

Certain aspects of methodology were common to the three experiments. Adult, female Norway Hooded rats which had been bred in the laboratory were used. In Expts 1 and 2 they were approximately 5 months old and in Expt 3 they were 10 months old at the start of the experiment. This difference in age was not considered to be of importance. The diets used in the three experiments contained similar ingredients, but in Expt 3 the fat content was increased to conform with previous experiments by McNiven (1980) (Table 1). They were mixed to a slurry with warm water immediately before feeding and administered by gastric intubation. Representative samples were taken at each feeding time for dry matter (DM) determinations (100° in a forced-draught oven for 24 h). The DM content of the slurry was approximately 0·75 g/ml in Expts 1 and 2 and 0·85 g/ml in Expt 3.

Rats slaughtered for carcass analysis were immediately eviscerated and undigested food residues removed from the gastrointestinal tract. The carcasses were prepared for analysis

by autoclaving for 20 min and then homogenizing with approximately 200 ml water in a Kenwood mixer. The homogenate was freeze-dried and milled. The dried samples were analysed for crude protein (nitrogen × 6·25; CP) by the macro-Kjeldahl method, for ash by ignition in a muffle furnace at 450° for 8 h, and for diethyl ether extract by the Soxhlet method (light petroleum 40–60° b.p.). Carcass energy was calculated from protein and fat using the factors 23·8 and 39·3 MJ/kg respectively (Brouwer, 1965). The energy contents of the diets were determined in an adiabatic bomb calorimeter.

Expt 1

Eighteen rats (mean weight 227 g) were fed on diet 1 (Table 1) *ad lib.* in powder form for 7 d, and subsequently as a slurry, three times daily, by gastric intubation. During the first 3 d the volume administered was increased (12, 15, 18 ml/d on consecutive days) to facilitate adaptation to the procedure. The rats were then randomly allocated to one of six groups. One group (T1) was slaughtered for initial carcass composition. Groups T2–T6 respectively were given 4, 5, 6, 7 or 8 ml/feed, three times daily, for 10 d. They were kept singly in wire cages. Room temperature was 24 ± 1°. Faeces were collected over the 10 d period for the estimation of digestible energy (DE) intake. Metabolizable energy (ME) was calculated as 0·96 DE. At the end of the feeding period all rats were slaughtered, certain organs were removed and weighed and the carcasses analysed. Statistical analysis of the results was based on analysis of variance.

Expt 2

Eighteen rats (mean weight 220 g) were allocated to one of six groups. They were placed in wire cages, three rats per cage, and given diet 1 (Table 1) by gastric intubation. For the first 5 d all rats were fed twice daily at 09.00 and 17.00 hours and given 5 ml diet/feed, i.e. an intake designed to maintain zero energy balance. Room temperature was 30 ± 1°. On the 5th day, fed heat production was measured for 24 h in a closed-circuit respiration chamber (Waring & Brown, 1965; Gray & McCracken, 1976). The rats were fasted overnight and FHP measured during the period 24–48 h after the last feed. Two groups (T5 and T6) were slaughtered for initial carcass composition. One group (T1) was returned to the initial feeding regimen and fed to maintain body-weight. In order to do this, intake was reduced to 9 ml/d and eventually to 8 ml/d. The other groups (T2–T4) were increased to 10 ml/feed over 5 d. They were maintained on the respective treatments for 120 d. At approximately 20 d intervals heat production was measured for 24 h during feeding and then during fasting as described above. At the end of the experiment the rats were slaughtered and the carcasses analysed.

Expt 3

Forty-two rats (mean weight 260 g) were grouped into six weight blocks and allocated to one of seven treatment groups (T1–T7) which were randomized within weight blocks.

The T1 rats were slaughtered for initial carcass composition. The T7 rats were fed to maintain zero energy balance (8 ml/d). Rats in groups T2–T6 respectively were fed 20 ml/d in two feeds for 6, 12, 18, 24 or 30 d. After the appropriate feeding period, the FHP of each rat was measured for 24 h in a closed-circuit respiration chamber (Waring & Brown, 1965; McNiven, 1980) before slaughter. Room and chamber temperatures were 30 ± 1°. Since only two chambers were available the rats were started on the experiment over a 3 d period. On day 1 of the experimental period, each rat received 4 ml/feed at 09.00 and 20.00 hours. T1 rats were placed in the respiration chamber at 09.00 hours on the following day and slaughtered 24 h later. T2–T6 rats received 6, 7, 8, 9, 10 ml per feed on days 2–6 respectively to allow the stomach to become accustomed to the large volume of feed. On day 6, T2 rats received 4 ml at the 20.00 hours feed and were placed in the respiration chamber at 09.00 hours on day 7. The same procedure was followed with T3–T6 rats. The rats were kept

Table 2. *Expt 1. Final live weight, weights of liver and epididymal fat and total body water (g) of rats killed for initial carcass composition (T1) or tube-fed 12, 15, 18, 21 or 24 ml/d (T2–T6 respectively) of a synthetic diet† as a slurry for a 10 d period*

(Mean values for three rats, 10 df)

Treatment	Final live wt	Liver wt	Epididymal fat	Total body water
T1	227	6·4	18·4	122
T2	232	6·6	17·8	124
T3	245	6·8	22·7	124
T4	254	7·4	21·6	131
T5	272	7·9	26·1	134
T6	287	8·4	29·8	132
Statistical significance	***	***	**	NS
SEM	4·5	0·21	1·70	3·7

NS, not significant; ** $P < 0·01$, *** $P < 0·001$.
† Diet 1; for details, see Table 1.

in pairs during the feeding period to facilitate excreta collection but FHP measurements were made on individual animals. The diet used in this experiment (diet 2, Table 1) was found to produce a slurry, of a suitable consistency for tube-feeding, with a DM content of 0·85 g/ml. The ME content of the diet was determined on nine pairs of rats during a 7 d collection period. The faeces and urine were collected together in 50 ml oxalic acid (25 g/l). The excreta were removed daily and held at −20° until the end of the collection period, when the mixture was weighed, homogenized and analysed for energy.

Three animals died prematurely as a result of food entering the lungs during feeding. Analysis of variance and linear regression were conducted using an iterative procedure to adjust for missing plots.

RESULTS

Expt 1

There were highly significant linear responses ($P < 0·001$) in live weight and liver weight (Table 2) and in gain of carcass DM, fat and energy (Table 3) to the increasing levels of energy intake.The weight of epididymal fat increased by 66% from T2 to T6 ($P < 0·01$) and there was a small but significant increase ($P < 0·01$) in carcass CP. Body water was not significantly different between treatments and this was reflected in the significant ($P < 0·01$) difference in the energy content of the carcass gain which ranged from 15·5 MJ/kg on the low-intake diets (T2) to 30·8 MJ/kg for the T6 rats.

The linear regression of energy retention (ER) *v.* ME was highly significant and yielded the equation (Fig. 1):

$$\text{ER(kJ/d)} = 0·915(\pm 0·042)\text{ME} - 130·8 \quad (r\,0·99).$$

Expt 2

There was no significant change in carcass weight as a result of prolonged feeding at low intake (T2) (Table 4). There was a significant reduction in carcass CP ($P < 0·01$) and an increase in mean carcass fat, though this failed to attain statistical significance. Carcass CP increased ($P < 0·05$) by 14% on the high-intake diet (T3) and there were highly significant

Table 3. *Expt 1. Increases in carcass content of dry matter (DM), crude protein (nitrogen × 6·25; CP), fat and energy of rats tube-fed 12, 15, 18, 21 or 24 ml/d (T2–T6 respectively) of a synthetic diet† for a 10 d period*

(Mean values for three rats, 8 df)

Treatment	DM gain (g)	CP gain (g)	Fat gain (g)	Energy gain (kJ)	Energy content of carcass gain (kJ/g)
T2	4·0	1·1	2·3	116	15·5
T3	13·9	1·1	11·6	480	26·5
T4	19·7	1·1	17·9	721	27·9
T5	34·4	2·5	31·4	1282	28·8
T6	47·4	2·3	43·8	1761	30·8
Statistical significance	***	**	***	***	**
SEM	1·30	0·20	1·05	41·1	2·04

** $P < 0·01$, *** $P < 0·001$.
† Diet 1; for details, see Table 1.

Table 4. *Expt 2. Carcass composition of starting controls after 48 h fast (T1), rats given diet 1† to maintain body-weight for 120 d with intermittent 48 h fasting periods (T2) and those given diet 1† (20 ml/d) to increase body-weight for 120 d with intermittent 48 h fasting periods (T3)*

(Mean values for six, three and nine rats T1–T3 respectively, 15 df)

Treatment	Carcass wt (g)	Carcass CP (g)	Carcass fat (g)	Carcass DM (g)	Carcass energy (MJ)
T1	216	41·9	32·9	84·9	2·3
T2	211	33·8	49·4	90·7	2·7
T3	465	48·2	264·2	321·8	11·5
Statistical significance	***	***	***	***	***
SE of a difference T1 *v.* T2	8·7	2·13	10·87	10·78	0·41

CP, crude protein (nitrogen × 6·25); DM, dry matter.
*** $P < 0·001$.
† For details, see Table 1.

($P < 0·001$) increases in carcass DM, fat and energy. The FHP (kJ/kg metabolic weight ($W^{0·75}$)) of all four groups declined by approximately 15% over the 120 d period but there was no significant difference between the low- and high-intake groups (Fig. 2). The mean ME intake, energy retention, FHP and calculated efficiency of energy utilization for maintenance and production (k) of the three T3 groups on seven occasions during the experiment are shown in Table 5. FHP increased from 100 to 161 kJ/rat per d and a corresponding decline in energy retention during overfeeding from 124 to 67 kJ/rat per d yielded a mean value for k of 0·87.

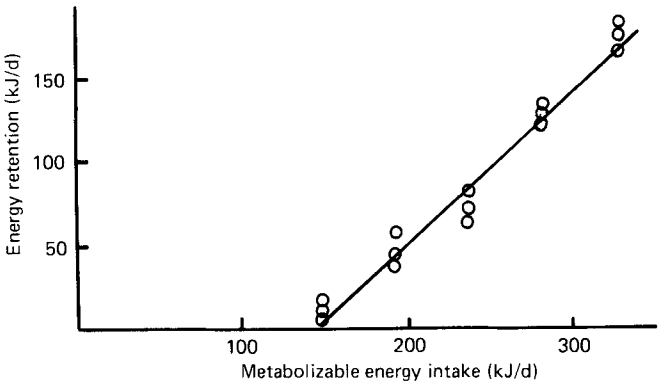

Fig. 1. Expt 1. Energy retention (kJ/d; ER) *v.* metabolizable energy intake (MJ; ME) of adult rats given diet 1 (Table 1) by gastric intubation for 10 d (Expt 1).

$$ER(kJ/d) = 0{\cdot}915(\pm 0{\cdot}042)\ ME - 130{\cdot}8 \quad (r\,0{\cdot}99).$$

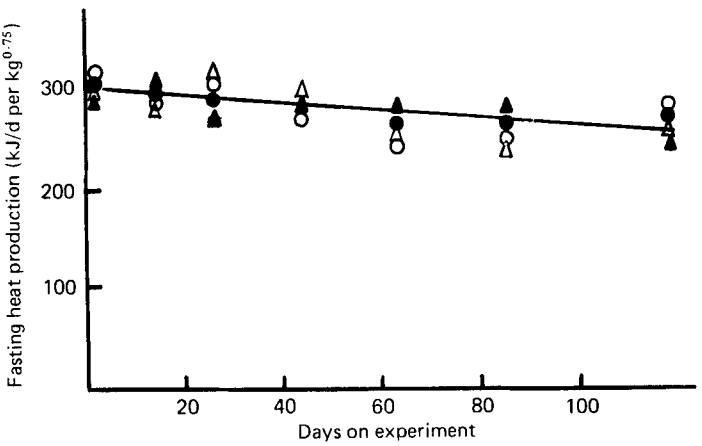

Fig. 2. Expt 2. Fasting heat production (kJ/d per kg body-weight ($W^{0{\cdot}75}$); FHP) of adult rats given diet 1 (see Table 1) to maintain constant body-weight (▲) or to increase body-weight (○, ●, △) for 120 d with intermittent 48 h fasting periods (Expt 2).

$$FHP(kJ/d \text{ per kg body-weight}^{0{\cdot}75}) = 305 - 0{\cdot}40(\pm 0{\cdot}087)\,D \quad (r\,0{\cdot}67),$$

where D is days overfeeding.

Table 5. *Expt 2. Energy utilization (kJ/rat per d) of force-fed rats as determined by indirect calorimetry on seven occasions during a 120 d experiment*

(Mean values with their standard errors for three groups with three rats/group)

Day of experiment	ME intake	ER		FHP		Net energy		*k*	
		Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
0	157·4	38·4	2·13	100·3	1·62	138·7	1·73	0·88	0·010
9	269·9	123·6	2·01	104·3	0·31	227·9	2·12	0·84	0·012
24	284·0	125·8	3·32	118·1	2·58	243·9	1·99	0·86	0·006
42	266·2	106·0	2·45	122·6	1·22	228·6	1·87	0·86	0·010
62	268·0	111·5	2·72	118·5	1·36	230·0	1·58	0·86	0·006
84	267·0	101·2	4·15	130·0	2·83	231·2	5·61	0·87	0·019
117	270·3	67·4	3·21	161·3	0·59	228·7	1·31	0·85	0·007

ME, metabolizable energy; ER, energy retention; FHP, fasting heat production; *k*, calculated efficiency for maintenance and production.

Table 6. *Expt 3. Carcass composition (g) and energy retention (MJ; ER) of rats force-fed for 0, 6, 12, 18, 24 or 30 d (T1–T6 respectively) 20 ml diet 2/d (Table 1) or given 8 ml/d for 54 d (T7)*

(Mean values for five or six rats, 28 or 22 df)

Treatment	No. of rats	Carcass analyses					Energy content of gain (MJ/kg)	ER† (MJ)
		Wt (g)	DM (g)	CP (g)	Fat (g)	Energy (MJ)		
T1	6	244	107·0	44·6	53·7	3·20	—	—
T2	6	263	116·0	45·6	60·2	3·49	18·4	0·31
T3	6	285	140·4	45·6	85·8	4·50	29·4	1·32
T4	5	311	162·0	48·5	106·7	5·41	31·0	2·26
T5	5	338	194·0	48·1	136·2	6·57	33·9	3·35
T6	5	365	218·1	48·5	162·0	7·54	35·3	4·25
T7	6	257	117·5	44·9	63·2	3·59	30·7	0·37
Statistical significance		***	***	**	***	***	**	***
SEM (*n* 5)		3·3	4·1	0·86	4·60	0·173	3·19	0·179

DM, dry matter; CP, crude protein (nitrogen × 6·25).
** $P < 0·01$, *** $P < 0·001$.
† See below for ME intakes.

Expt 3

The ME:gross energy (GE) value for diet 2 was 0·925 ± 0·004 and the ME content of the diet was 19·1 MJ/kg DM. The mean ME intakes for T2–T6 rats respectively were 1·26, 3·24, 5·29, 7·28, 9·18 MJ.

There were highly significant ($P < 0·001$) linear increases in carcass weight, DM, fat and energy with increasing period of time on the high-energy intake (Table 6). Carcass CP increased ($P < 0·01$) by 10% between T1 and T6 rats, the linear component being highly significant. Approximately 10% of the CP increase was in the liver. The mean carcass weight of the rats which were fed to maintain constant body-weight (T7 rats) increased slightly over the 42 d feeding period and this was associated with increases in carcass DM, fat and energy but not carcass CP or body water. The energy content of the gain was lowest in T2 rats, corresponding to the period when the daily energy intake was being increased, and highest in the T6 rats ($P < 0·01$) where 90% of the carcass gain was fat.

The FHP (Table 7) increased from 118 kJ/d in group T1 to 160 kJ/d in group T6 ($P < 0·001$). A regression equation of the form, $FHP = aW^b$ yielded the equation:

$$FHP = 317(\pm 23·9)\text{kJ/d per kg } W^{0·72} \quad (r\ 0·871).$$

However, when the value 0·75 was inserted for b, the mean value for a was 334 kJ/d and there were no significant treatment effects.

Using the mean value for FHP and the energy retention values in Table 6, the calculated values of k for T2–T6 rats respectively were 0·86, 0·86, 0·87, 0·90, 0·91 (SEM 0·013).

DISCUSSION

Despite the fact that the animals used in all three experiments had attained stable adult weight before the period of force-feeding, rapid and prolonged weight gains occurred as a result of the high-energy intakes achieved by tube-feeding. In Expt 1 the rats given 24 ml/d (approximately 18 g DM/d) gained 6 g/d containing 4·7 g DM of which over 90% was fat. Although there were differences in environmental temperature, age, feeding levels employed

Table 7. *Expt 3. Fasting heat production (FHP) of adult rats force-fed for 0, 6, 12, 18, 24 or 30 d (treatments T1–T6 respectively) 20 ml diet 2/d (Table 1)*

(Mean values for five or six rats, 21 df)

Treatment...	T1	T2	T3	T4	T5	T6	Statistical significance	SEM (n 5)
FHP (kJ/d)	118	125	132	139	147	160	***	3·5
FHP (kJ/d per kg body-wt$^{0·75}$)	336	337	333	330	329	338	NS	8·9

NS, not significant; *** $P < 0·001$.

and length of experimental period in the three experiments, the trends in body gain and composition were consistent. The energy content of the gain was considerably higher than that found by McNiven (1980) in rats voluntarily consuming a small excess of energy above maintenance and gaining weight much more slowly than in the present experiments. It is not possible to evaluate whether this difference is due to the level of food intake, the method of feeding or the strain of rat. The major implication for studies on adult humans is that energy gain or loss may be poorly correlated with changes in body-weight. This conclusion is supported by the studies of Passmore *et al.* (1963), Cohn & Joseph (1968) and Drenick *et al.* (1968).

Of particular interest are the changes in carcass composition of the rats in Expt 2 which were fed to maintain body-weight but intermittently fasted for the determination of FHP. Although carcass weight was slightly reduced at the end of the experiment there was a 50% increase in carcass fat and complementary decreases in carcass CP and water. The loss of protein, corresponding to approximately 1 g/fasting period, suggests that the rats were unable to make good the deficit between fasting periods. Whilst the situation is not precisely the same as that caused by crash dieting programmes it indicates that the end-product of such a programme could easily be an increase rather than a decrease in body fat even if subsequent food intake were controlled.

During overfeeding there were small but consistent increases in carcass CP. In Expt 1 these were significantly related to energy intake and in Expt 3 there was a linear increase during the 30 d period. Approximately 10% of the increase was in the liver. Estimates of the N content of adipose tissue (K. J. McCracken, unpublished results) suggest that 20–40% of the increased CP could be associated with the adipose tissue. This indicates that at least half the increase may be associated with the muscle. Further work is required to elucidate the sites and nature of the N retained during overfeeding.

The efficiency of utilization of energy for production (Expt 1) or for maintenance and production (Expts 2 and 3) was consistently high and indicated that a considerable amount of the fat retention may have arisen from the direct incorporation of absorbed fatty acids rather than from *de novo* synthesis. The values are similar to those calculated from the results of short-term calorimetric studies on adult humans (Dauncey, 1980; Zed & James, 1982), though the dietary fat contents were lower than those normally consumed by humans. The highest efficiency was recorded in Expt 1 and this is consistent with the view that part of the heat increment arising from the extra energy ingested would be used to offset the extra-thermoregulatory heat production below the zone of thermoneutrality (Sørenson, 1962).

The levels of energy intake achieved in these experiments (in some instances up to 2·5 times the maintenance energy requirement) are the highest known to the authors in overfeeding studies on adult rats. Despite this, and the length of the experimental period

Table 8. *Expt 3. Percentage increases over the initial values in metabolic body-weight ($W^{0.75}$) lean body mass (total weight − fat) and fasting heat production (FHP) of rats overfed for 6, 12, 18, 24 or 30 d (T2–T6 respectively)*

Treatment	$W^{0.75}$ (kg)	Lean body mass	FHP
T2	4·6	5·9	4·7
T3	12·4	4·7	11·8
T4	21·1	7·9	17·5
T5	28·8	6·6	24·3
T6	36·4	6·7	35·9

in Expt 2, there was no reduction in efficiency of energy utilization. This is compatible with the classical view of energy metabolism and contrary to the theories of 'luxuskonsumption' or 'diet-induced thermogenesis'. Although one must be cautious in extrapolating from rats to humans it is the opinion of the authors that the rat model described in this paper in terms of stage of maturity, pattern of feeding, environmental temperature and accuracy of measurement of food intake, is more appropriate to the human than studies on young growing rats kept at relatively low environmental temperatures.

The measurements of energy expenditure by indirect calorimetry in Expts 2 and 3 are in good agreement with the carcass values. The mean ME intake of the overfed rats during the 120 d period in Expt 2 was 27·0 MJ/rat. The mean daily FHP was 122 kJ corresponding to 14·65 MJ over the complete period. Applying the mean k value (Table 5) the expected ER is 8·9 MJ, whereas at slaughter the value was 9·3 MJ. The total ME intake of the maintenance group was 12·9 MJ/rat of which only 0·4 MJ was retained. Correcting for the fasting periods the calculated maintenance requirement was 105·3 kJ/d compared with the mean value of 91 kJ/d for FHP measured in the respiration chamber.

In Expt 3 the mean ME intake of the maintenance group was 137 kJ/d. Correcting for ER the maintenance requirement was 129 kJ/d or 354 kJ/kg $W^{0.75}$ compared with the mean value for FHP of 334 kJ/kg $W^{0.75}$, determined in the respiration chamber. This represents an efficiency of utilization for maintenance of 0·94, and indicates good agreement between energy expenditure measured by indirect calorimetry and by the slaughter technique.

One of the main objectives of the study was to establish whether the relationship between FHP and $W^{0.75}$ would alter as a consequence of overfeeding and the resultant changes in body composition. Interpretation of the results of Expt 2 was complicated by the lack of replication and by the losses of body protein which occurred as a consequence of the successive fasts. Expt 3 was designed to overcome this difficulty but was consequently subject to the problems of animal variation. However, the results of these two experiments confirm that, over a wide range of body-weight and body composition, FHP of the adult rat may be regarded as proportional to the $W^{0.75}$ irrespective of the previous plane of nutrition. This statement is in agreement with the results of McCracken & Gray (1976) and Deb *et al.* (1976) with rats and Blaxter (1976) with sheep.

In contrast, there was no apparent relationship between the increased FHP and lean body mass (Table 8). This is in conflict with the results of Chesters (1975) and Pullar & Webster (1977). The difference may be due to the age of the rats or to the use of normal rather than genetically-obese animals. In either instance it would be a mistake to attempt to imply any deep physiological significance to the results since the whole body metabolism is the integration of a wide variety of metabolic rates in different tissues. However, the present results are compatible with the view that white adipose tissue is highly active and contributes

significantly to the maintenance requirement. The conclusion also has practical significance to overfeeding experiments with adult humans in that it provides a basis for calculating the maintenance requirement under standard conditions.

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