Sex, body composition and regulation of food intake during growth in the Zucker rat

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1. Food intake and rates of protein, lipid and energy deposition during growth were measured for lean and congenitally obese (fatty) Zucker rats offered from 34 d of age to slaughter at 66 d of age, one of six semi-synthetic diets containing casein (C) in the following amounts (g C/kg): 40C, 100C, 150C, 300C, 500C and 700C.

2. In Expt 1, groups of four male rats were offered each diet to appetite. The digestibility of dietary protein and metabolizability of dietary energy were determined. Total carcasses were analysed for protein, energy and lipid at 34 and 66 d of age. The results showed that, given diets containing 300C or above, both fatty and lean males regulate food intake so as to sustain a maximal rate of protein deposition. This maximal rate was greater in males than in females, and the sex difference was more marked in lean rats. Diets containing less than 300C did not permit maximal protein deposition and, in this instance, both sexes and phenotypes showed a similar reduction in food intake and protein deposition. The rate of deposition of body lipid did not appear to be controlled in either phenotype.

3. In Expt 2, fatty and lean rats were pair-fed diets 100C and 500C. Carcass composition at 66 d of age confirmed that obesity in the fatty rat was not due to hyperphagia but to an abnormal pattern of energy utilization between fat deposition (too much), and protein deposition and heat production (too little).

4. In Expt 3, fatty and lean, male and female rats were given diets 100C and 500C to slaughter at 66 d of age. The carcasses were analysed into different parts by weight, and according to protein and lipid contents of viscera, pelt and subcutaneous fat, and empty carcass. Fatty rats stored approximately 0·53 of their protein in the empty carcass, lean rats approximately 0·65.

5. The results confirm that food intake in the Zucker rat is intimately related to the capacity of the animals for protein deposition, but this capacity differs between sexes and between phenotypes, and the distribution of body protein in the fatty rat eating *ad lib.* is not that of a normal rat.

Pullar & Webster (1974) suggested that young lean and congenitally obese 'fatty' rats (Zucker & Zucker, 1971) might regulate food intake so as to sustain the same, normal rate of skeletal and muscle growth, even though the rate of fat deposition was grossly accelerated in the obese indiviuals. Radcliffe & Webster (1976) compared rates of food intake and protein and lipid deposition in fatty and lean female Zucker rats offered diets ranging in casein (C) content from 40 to 700 g/kg and showed that rates of protein deposition were identical for both phenotypes, reaching a maximum at dietary C concentrations of 300 g/kg or above. Rates of lipid deposition were markedly affected both by phenotype and diet. We concluded that during growth, food intake in the Zucker rat was intimately linked to the capacity of the animals for protein deposition whether the diet permitted maximal deposition or not, and that the rate of retenticn of energy and its deposition in lipid were of no importance in the control of food intake.

Although these observations do reveal glimpses of a fundamental principle of appetite control in the growing rat, there are several questions to be answered before that principle can be seen with any clarity. It is known that in normal strains of rats, males eat more, grow faster and deposit protein faster than females (see Schemmel, Mickelson & Motawi, 1972). Interactions between sex differences and fatty *v*. lean (phenotype) differences on food intake

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and growth in the Zucker rat have not been studied previously. There is evidence however that in the ob/ob mouse, lean males eat more and grow faster than lean females but that obese individuals of both sexes eat and grow at the same rate (Alonso & Maren, 1955). Secondly, regulation of food intake to sustain 'a normal rate of skeletal and muscle growth' (Pullar & Webster, 1974) or to sustain a normal rate of protein deposition (Radcliffe & Webster, 1976) are not necessarily the same thing if the distribution of body protein differs between fatty and lean individuals. The experiments described here were designed to examine how sex, phenotype, body composition and dietary protein content interact to influence food intake and growth in the Zucker rat.

EXPERIMENTAL

Animals and diets

Forty-four fatty and thirty-six lean male Zucker rats and eight female rats of each phenotype were used. Rats were taken at 24 d of age from a breeding colony at The Rowett Research Institute begun by hysterectomy and maintained under conditions of minimal disease. Families of rats in the breeding colony were give a commercial pelleted diet (Oxoid; H. C. Styles (Bewdley) Ltd, Bewdley, Worcs.). Weaned rats were then kept in minimal disease conditions in a room at an air temperature of 20° with a 12 h (09.00–22.00 hours) light–dark cycle. They were fed on Oxoid until 34 d of age when four male rats of each phenotype were killed (the 'initial slaughter' groups). The remainder were given one of six semi-synthetic diets containing C in one of the following proportions (g C/kg): 40C, 100C, 150C, 300C, 500C and 700C. Details of these diets have been given previously (Radcliffe & Webster, 1976, Table 1).

In Expt 1 four male rats of each phenotype were given *ad lib.* access to one of the six experimental diets until slaughter at 66 d of age. In Expt 2 two groups of four male fatty rats ('pair-fed' fatty rats) were given from 34 to 66 d of age the same amount of food as that consumed on the corresponding day by lean rats from Expt 1 given diets 100C or 500C. In Expt. 3 groups of four rats of each phenotype and each sex were given *ad lib.* access to diets 100C or 500C from 34 d to slaughter at 66 d of age.

Any uneaten or spilled food was weighed daily so as to give a daily record of food intake. Fresh tap-water was available at all times.

Balance trials

Details of the procedures used have been given by Radcliffe & Webster (1976). In Expts 1 and 2, two balance trials were done for each animal. No balance trials were done in Expt 3, because by that time there was sufficient evidence from which to estimate with high precision the metabolizable energy (ME, kJ/g dry matter (DM)) contents of the highly-digestible semi-synthetic diets.

Methods of analysis

Rats were killed by carbon dioxide inhalation. Samples of food, urine and faeces were treated the same way as before (Radcliffe & Webster, 1976), as were carcasses from the 'initial slaughter' groups and those killed at 66 d of age in Expts 1 and 2. Immediately after slaughter of rats from Expt 3, the contents of their guts were removed by flushing out with water. The guts were then blotted dry and weighed. The remainder of the viscera were then removed, weighed and added to the guts. The pelt and adherent fat were then stripped off the eviscerated carcass and both were weighed. The four sets of viscera, carcass and pelt for rats in each group were pooled into a single sample for analysis. Samples were cut up into small

Table 1. *Body-weight and body composition of fatty and lean male Zucker rats fed on stock diet† and killed at 34 d of age*

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

Phenotype	Body-wt (g)	Body composition		
		Protein (g)	Lipid (g)	Energy (MJ)
Fatty	106 ±3·3	16·0±0·76	22·0±1·0	1·18±0·05
Lean	89·5±1·4	15·6±0·88	4·55±0·2	0·53±0·01
Statistical significance of difference‡	**	NS	**	**

NS, not significant.
* *P* < 0·05, ** *P* < 0·01.
† Oxoid, H. C. Styles (Bewdley) Ltd, Bewdley, Worcs.
‡ The Student's *t* test was used to test for statistical differences.

sections, autoclaved, minced and freeze-dried as described previously (Radcliffe & Webster, 1976).

All analyses were done in triplicate. Gross energy was determined by adiabatic bomb calorimetry, nitrogen content by the macro-Kjeldahl method of Davidson, Mathieson & Boyne (1970) and lipid content of carcasses by the method of Atkinson, Fowler, Garton & Lough (1971).

Except where indicated to the contrary, all results were subjected to analysis of variance.

RESULTS

Table 1 shows that fatty and lean male Zucker rats differed markedly in body-weight and body composition by 34 d of age. Fatty rats contained four times as much lipid as lean rats but body protein was the same for the two phenotypes. Body-weight and body protein were both approximately 10 % higher in these males than in age-matched female rats but body lipid contents were approximately the same (Radcliffe & Webster, 1976).

The apparent digestibility of the energy content of most diets was approximately 0·95 (Table 2). The apparent digestibility of N was more than 0·93 except for groups given diets 40C and 100C. The apparent metabolizability of all but the extreme diets (40C and 700C) was more than 0·9. Fatty and lean rats digested energy and N, and metabolized food energy with equal efficiency. Moreover, the metabolizability of diets 100C and 500C for fatty rats was the same whether they ate *ad lib.* or were restricted to the food intake of the lean rats on the same diet.

Table 3 presents ME intakes from 34 to 66 d of age and body composition at 66 d of age for the male rats given the six experimental diets in Expt. 1. Fig. 1 illustrates the interactions between phenotype, sex and diet that determined ME intake and gains of weight, protein and fat in the Zucker rat, by comparing gains in body constituents estimated by the comparative slaughter technique for male rats with those obtained for females by Radcliffe & Webster (1976).

Considering first the results for male rats (Table 3): in both phenotypes, maximum rates of protein retention were not achieved with diets containing less than 300 g C/kg (300C). At 300C or above protein deposition was maximal for both fatty and lean rats, although in these male animals there was a significant difference in rate of protein deposition between the two phenotypes. Diets containing the least protein (40C and 100C) produced the same, low, rates of protein deposition in both phenotypes.

Table 2. *Expts 1 and 2. Mean values for apparent digestibility of energy and nitrogen, and metabolizability of diets containing casein (C) jn the following amounts (g C/kg): 40C, 100C, 150C, 300C, 500C and 700C for fatty and lean male Zucker rats*

	Diet†	Phenotype	Digestibility N	Digestibility Energy	Meta-bolizability
Expt 1	40C	Fatty	0·87	0·94	0·88
	40C	Lean	0·77	0·91	0·83
	100C	Fatty	0·92	0·92	0·91
	100C	Lean	0·90	0·92	0·91
	150C	Fatty	0·95	0·96	0·93
	150C	Lean	0·93	0·93	0·90
	300C	Fatty	0·97	0·95	0·91
	300C	Lean	0·97	0·96	0·90
	500C	Fatty	0·94	0·96	0·91
	500C	Lean	0·96	0·96	0·92
	700C	Fatty	0·97	0·96	0·87
	700C	Lean	0·98	0·96	0·88
Expt 2	100C	Fatty (pair-fed)‡	0·91	0·92	0·91
	500C	Fatty (pair-fed)‡	0·97	0·97	0·91

† For details, see Radcliffe & Webster (1976).
‡ Pair-fed to lean rats in Expt. 1.

Table 3. *Expt 1. Metabolizable energy (ME) intake from 34 to 66 d of age and body composition at 66 d of age in fatty and lean male Zucker rats given ad lib access to diets containing casein (C) in the following amounts (g C/kg): 40C, 100C, 150C, 300C, 500C and 700C*

Diet†	Phenotype	ME intake (MJ)	Body composition at 66 d of age Wt (g)	Protein (g)	Lipid (g)	Energy (MJ)
40C	Fatty	5·00	81·7	11·3	24·4	1·02
	Lean	4·52	75·7	12·0	8·74	0·563
100C	Fatty	12·4	307	32·8	153	6·60
	Lean	9·35	154	31·0	34·5	2·00
150C	Fatty	14·2	407	38·3	211	8·86
	Lean	10·1	283	49·8	49·8	3·02
300C	Fatty	16·3	463	47·3	224	9·77
	Lean	10·6	317	56·2	66·2	3·83
500C	Fatty	13·1	370	47·1	163	7·16
	Lean	10·3	300	58·7	47·4	3·21
700C	Fatty	12·7	314	48·1	116	5·50
	Lean	10·8	265	56·8	31·9	2·50
SE of difference		0·30	11·7	3·22	12·6	0·21
Statistical significance of:						
Phenotype	**	**	**	**	**	**
Diet	**	**	**	**	**	**

† For details, see Radcliffe & Webster (1976).
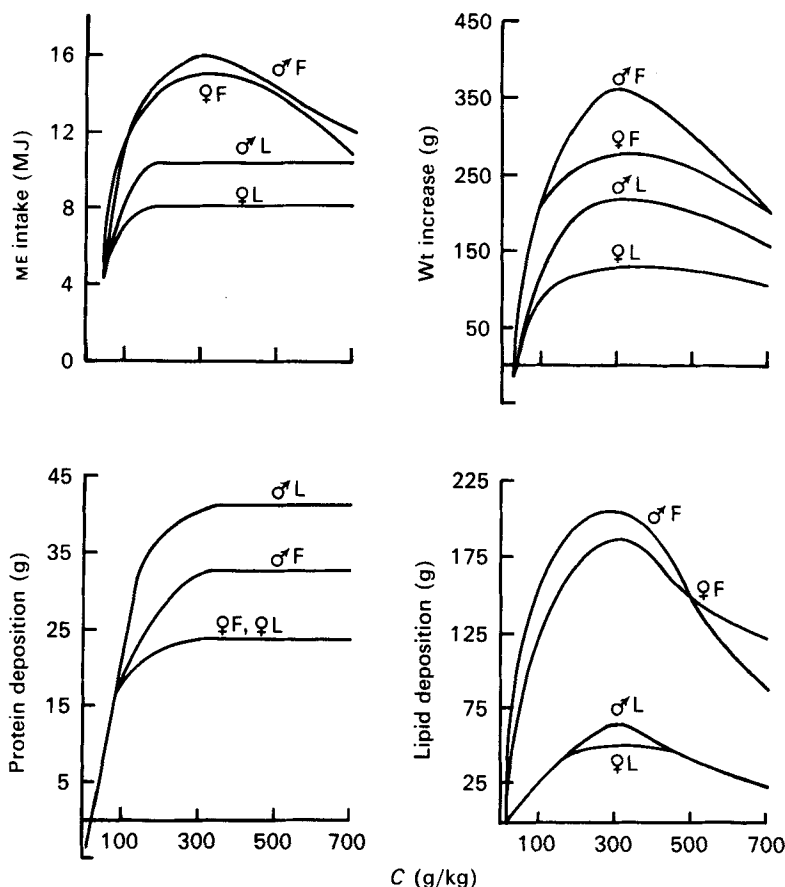** $P < 0.01$.

Fig. 1. Metabolizable energy (ME) intake (MJ) and gains (g) in body-weight, protein and lipid between 34 and 66 d of age in fatty and lean, male and female Zucker rats (F♂, F♀, L♂ and L♀ respectively). The rats were offered to appetitie diets containing casein (*C*) in the following amounts (g *C*/kg): 40*C*, 100*C*, 150*C*, 300*C*, 500*C* and 700*C*. Details of the diets and the results for the female rats were reported by Radcliffe & Webster (1976). The male animals are those from Expt 1 of this study (for details, see p. 484).

ME intake was constant for lean males receiving diets with 150–700 g *C*/kg. Rates of retention of energy and lipid were maximal on diet 300*C* and decreased slightly as dietary *C* content increased to 700 g/kg. For the fatty rats ME intake was greatest on diet 300*C*. Intake, weight gain, lipid and energy retention all decreased sharply as dietary *C* content was increased above this level.

Fig. 1 shows that the pattern of ME intake was similar in male and female fatty rats although slightly higher in the males. Lean males had significantly higher ME intakes than lean females except for diet 40*C*, which promoted no growth. Protein deposition was similar for both sexes and phenotypes for diets 40*C* and 100*C*, but the plateaux for maximal protein deposition differed between sexes and phenotypes. For females it was the same for both phenotypes. Lean males had the greatest rate of protein deposition and fatty males were intermediate. Patterns of lipid deposition were similar although not identical for the two sexes within each phenotype reaching a peak at 300*C* and decreasing at high concentrations of dietary protein. The results of Expt 1 with male rats thus confirm the conclusion of Radcliffe & Webster (1976) that appetite control in the growing rat is intimately linked to the capacity of the

Table 4. *Expts* 1 *and* 2. *Gains in body constituents between* 34 *and* 66 *d of age in lean male rats and fatty males pair-fed to the* ad lib. *intake of the lean males diets containing casein* (C) *in the following amounts* (g C/kg): 100C *and* 500C

(Mean values with their standard errors for four rats per group. The Student's *t* test was used to assess the significance of differences)

		Gains in body constituents				Heat pro-duction‡ (MJ)
Diet†	Phenotype	Wt (g)	Protein (g)	Lipid (g)	Energy (MJ)	
100C	Lean	64·5 ± 2·8	15·4 ± 1·1	30·0 ± 2·3	1·47 ± 0·1	7·88
	Fatty	142 ± 1·3	13·2 ± 0·30	92·7 ± 7·4	3·74 ± 0·33	5·54
Statistical significance of difference		**	NS	**	**	
500C	Lean	210 ± 1·9	43·1 ± 2·7	42·8 ± 2·6	2·68 ± 0·04	7·62
	Fatty	152 ± 8·9	20·1 ± 0·50	100 ± 3·7	4·33 ± 0·02	6·17
Statistical significance of difference		**	**	**	**	

NS, not significant.
** $P < 0.01$.
† For details, see Radcliffe & Webster (1976).
‡ Metabolizable energy intake minus energy retention between 34 and 66 d of age.

animals for protein deposition. However, while this capacity is the same in females of both phenotypes, males have a greater capacity for protein deposition than females, and the extent of this effect of sex on growth differs between the phenotypes.

Table 4 compares gains in protein, lipid and energy in fatty and lean male rats pair-fed diets 100C and 500C, and shows clearly that the greater rate of lipid deposition in the fatty was not due to hyperphagia *per se*, but to an abnormal partition of ME between fat (too much), protein and heat (both too little).

Table 5 compares values for ME intake for fat and lean rats of both sexes given diets 100C and 500C in Expt 3, and also gives mean weights of different body components at 66 d of age. Values for ME intake are similar to those from Expt 1 for males and to those from Radcliffe & Webster (1976) for females. There were statistically significant differences in the weights of nearly all the measured body components attributable individually to diet, sex and phenotype. Fatty rats were significantly heavier in terms of body-weight, pelt and adherent fat, liver, gut, kidneys and abdominal fat. There was however no significant effect of phenotype on empty carcass weight. All measured traits were significantly heavier for diet 500C than for 100C. The difference between males and females was much more marked on diet 500C, which permitted maximum protein retention, than on diet 100C, which restricted protein retention. The significance or otherwise of interactions between diet, sex and phenotype in determining the weights of these body components are listed in Table 5.

The distribution of body protein and lipid between the viscera, pelt and adherent sub-cutaneous fat, and empty carcass is shown in Table 6, which gives single values for the chemical composition of the pooled samples of these tissues from the four rats in each group. In all instances fatty rats deposited more protein (in absolute terms) in the pelt and less in the empty carcass than lean rats. In relative terms all fatty rats deposited between 0·53 and 0·55 of their protein in the empty carcass, lean rats between 0·62 and 0·69. The proportion of protein in the carcass was approximately the same for both sexes, although the difference between fatty and lean rats in absolute amount of protein in the carcass was greater for males than for females. In three of the four groups, fatty rats had more protein in the

Table 5. *Expt 3. Metabolizable energy* (ME) *intake from 34 to 66 d of age and weights of pelt, carcass and viscera at 66 d of age for male and female fatty and lean Zucker rats offered to appetite diets containing casein* (C) *in the following amounts* (g C/kg): 100C *and* 500C

				Wt (g)						
Diet†	Pheno- type	Sex	ME intake	Body	Pelt and sub- cutaneous fat	Empty carcass	Liver	Gut	Kidneys	Visible abdomi- nal fat
100C	Fatty	♂	11·8	344	150	127	13·2	7·96	2·45	37·9
	Lean	♂	8·4	163	24·3	109	10·6	6·57	1·97	5·04
	Fatty	♀	11·4	302	112	123	15·4	8·40	2·42	32·6
	Lean	♀	7·0	180	33·8	117	12·3	8·19	1·86	2·34
500C	Fatty	♂	13·6	434	181	172	25·0	10·8	5·46	38·4
	Lean	♂	10·8	308	71·4	211	20·0	9·61	3·18	15·5
	Fatty	♀	12·9	340	140	123	17·0	10·7	4·01	33·2
	Lean	♀	8·7	205	46	125	12·9	9·6	2·49	9·4
SE of difference			0·92	7·7	4·6	5·7	0·66	0·2	0·3	2·00
Statistical significance of:										
Phenotype			**	**	**	NS	**	**	**	**
Diet			**	**	**	**	**	**	**	**
Sex			**	**	**	**	**	**	**	**
Phenotype × sex			NS	**	**	*	NS	**	NS	NS
Phenotype × diet			NS	*	NS	**	**	NS	**	**
Sex × diet			NS	**	**	**	**	**	**	NS
Phenotype × sex × diet			NS	**	**	**	NS	**	NS	NS

NS, not significant.
* *P* < 0·05, ** *P* < 0·01.
† For details, see Radcliffe & Webster (1976).

viscera. The lipid contents of all tissues were considerably greater in fatty rats than in lean rats, the biggest difference being in the amount of subcutaneous fat adherent to the pelt. Table 6 therefore provokes the conclusion that although the regulation of appetite in lean and fatty rats may be linked intimately to the capacity of the animals for protein deposition (Radcliffe & Webster, 1976), food intake in the fatty is not regulated so as to achieve a normal rate of growth in muscle as suggested by Pullar & Webster (1974). In terms of skeletal muscle (and probably bone) development fatty rats are still stunted even at *ad lib.* intake.

DISCUSSION

Many of the conclusions that can be drawn from this study with male and female, fatty and lean Zucker rats simply confirm those which we presented on the basis of previous work which involved females only (Radcliffe & Webster, 1976). In neither sex is obesity in the fatty due to hyperphagia *per se* but to a lower rate of heat production leading to an increased efficiency of retention of ME, principally as fat. The lower heat production of fatty rats pair-fed to lean animals (Table 4) can be attributed, in part, to the fact that the amounts of ME required for the deposition of 1 kJ as protein and as lipid in the Zucker rat are 2·25 and 1·36 kJ respectively, i.e. lipid deposition is energetically more efficient than protein deposition. However, even after this has been taken into account, residual or 'maintenance' heat production is still much higher in lean than in fatty rats (Pullar & Webster, 1977). The extent to which this can be attributed to differences between the phenotypes in total protein

Table 6. *Expt 3. The protein and lipid contents of the viscera, pelt and subcutaneous (sc) fat, and empty carcasses of fatty and lean, male and female Zucker rats offered to appetite diets containing casein (C) in the following amounts (g C/kg): 100C and 500C, from 34 d of age to slaughter at 66 d of age*

(Pooled samples from groups of four rats)

			Chemical composition (g)							
			Viscera		Pelt and sc fat		Empty carcass		Total	
Diet *	Pheno-type	Sex	Pro-tein	Lipid	Pro-tein	Lipid	Pro-tein	Lipid	Pro-tein	Lipid
100C	Fatty	♂	4·3	30·2	11·9	97·0	19·8	30·5	36·0	158
	Lean	♂	2·6	4·1	6·4	9·9	20·0	12·0	29·0	26
	Fatty	♀	4·8	27·4	9·6	93·0	17·3	19·6	31·7	140
	Lean	♀	3·2	2·7	7·0	12·4	18·6	9·9	28·8	25
500C	Fatty	♂	5·8	25·3	16·5	113·0	24·6	29·7	46·9	168
	Lean	♂	6·8	10·3	15·7	21·8	37·5	16·9	60·0	49
	Fatty	♀	6·2	28·6	12·6	102·0	21·2	24·0	40·0	155
	Lean	♀	4·4	6·5	9·7	18·2	23·7	10·3	37·8	35

* For details, see Radcliffe & Webster (1976).

synthesis is currently under investigation using a technique similar to that of Garlick, Millward & James (1973).

In general, the effect of dietary protein content on appetite and growth in males resembles its effect in females. Male animals of both phenotypes given diet 40C ate similar, small amounts, lost body protein and gained little or no lipid. Fatty and lean rats of both sexes sustained the same positive rates of protein deposition on diet 100C. At higher dietary protein contents, rates of protein deposition were greater for males than for females, the difference being more pronounced in the lean animals, as each sex and phenotype reached its own potential for protein deposition. In this respect the Zucker rats behaved in a similar way to ob/ob mice (Alonso & Maren, 1955). Thus while the potential for protein deposition was not the same for each sex and phenotype, it is still reasonable to conclude that, given diets containing from 300 to 700 g C/kg, both fatty and lean rats regulate their food intake so as to sustain the maximum rate of protein deposition of which they are capable.

As dietary C content increased from 300 to 700 g/kg, lean rats maintained a constant ME intake, retained a decreasing proportion of dietary protein, retained less energy as fat and therefore lost an increasing proportion of dietary energy as heat. Fatty rats reduced ME intake and lipid deposition as the dietary C concentration was increased from 300 to 700 g/kg. Heat production (calculated as ME intake minus energy retention) remained rather constant. It appeared that as dietary protein content was increased, the fatty rats were able to get their dietary requirements for growth at a lower intake of food energy. However, total protein intake was still approximately twice as great on 700C as on 300C.

Johnson, Zucker, Cruce & Hirsch (1971) showed that fatty rats given a conventional diet have both more fat cells and bigger fat cells than their lean siblings. We do not know, at present, whether the decrease in body lipid content that occurred in our fatty rats as casein concentration was increased from 300C to 700C was due to a decrease in fat cell numbers or cell size or both. Young children that become obese resemble the Zucker fatty rat in that they have more fat cells than their lean counterparts (Knittle, 1965). Further examination of the response of Zucker fatty rat to diets of varying protein content may cast some light on childhood obesity.

The existence of this plateau for the maximal rate of protein deposition for each sex and

phenotype, in circumstances where ME intake, protein intake, lipid and energy deposition and heat production all differ, does indicate very strongly that protein deposition is the most finely regulated of these variables during growth in the rat, and that the main mechanism for this regulation is by controlling the intake of nutrients. Protein intake per se does not appear to be particularly important so long as protein content is sufficient to support maximum protein deposition and the rate of deposition of energy as fat during growth appears to have no appreciable effect on appetite.

The fact remains however that fatty and lean rats do differ in the composition of their fat-free body mass, so they are not regulating intake so as to grow exactly the same sort of lean animal. The difference in the distribution of body protein between fatty and lean Zucker rats is rather similar to that which exists between fat and lean mice of the ob/ob strain. Obese mice have 40 % less protein in their hind-limbs than lean mice (Bergen, Kaplan, Merkel & Leveille, 1975) but contain about the same amount of protein over all (Alonso & Maren, 1955). Irradiated mice treated with homologous bone marrow cells have relatively more protein in the pelt and less in the carcass than irradiated mice treated with isologous bone marrow cells (Kretchmar, McArthur & Congdon, 1965) but food intake and total body protein content are similar in the two groups (McArthur, Kretchmar & Congdon, 1963). Rats with lesions in the ventromedial hypothalamus (VMH) usually thought to induce primary hyperphagia, also appear to regulate food intake so as to achieve the same rate of protein deposition as sham-operated controls (Holm, Hustvedt & Løvo, 1975), although these authors do not state how the protein is distributed through the body.

Taken together, these observations provoke a conclusion which differs somewhat from the earlier suggestion of Pullar & Webster (1974). Lipid deposition is, as we surmised earlier, of little or no importance in regulating food intake during growth. However, given diets adequate in protein content, fatty and lean rats do not regulate food intake to sustain similar rates of growth of lean, active body mass. Appetite regulation in Zucker rats, and probably in VMH-lesioned rats and ob/ob mice as well, appears to be related intimately to protein deposition (the difference between protein synthesis and catabolism), but not in any obvious way to the sites, and thus the nature of the proteins being deposited.

In this, as in the previous experiment (Radcliffe & Webster, 1976) rats given diets low in protein (40C, 100C and 150C) grew more slowly, deposited protein more slowly and ate less than rats getting diets containing 300 g C/kg or more. Moreover, the limits to protein deposition and food intake appeared to be the same for both sexes, i.e. growth was being limited by some property of the diet rather than the different genetic potentials of the different sexes and phenotypes. The results presented here do no more than confirm our earlier conclusion that in these circumstances fatty and lean rats restrict their intake of food energy to that required to support the limited amount of protein deposition possible at these low protein intakes. In other words, a low-protein diet is one which contains energy in relative excess and rats elect to restrict their intake of these diets, rather than eat more so as to get more protein for growth, either because they are unable to dispose of an excess of energy as heat or fat (Meyer, 1958) or because increased food intake would not, in fact, increase protein deposition. These possibilities are being explored.

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