ELSEVIER

Thermochimica Acta 349 (2000) 43–51

thermochimica acta

www.elsevier.com/locate/tca

Energy metabolism and lipogenesis in humans

A. Chwalibog*, G. Thorbek

The Royal Veterinary and Agricultural University, Copenhagen, Bülowsvej 13, 1870 Frederiksberg C, Denmark

Received 14 July 1999; received in revised form 30 September 1999; accepted 30 September 1999

Abstract

Data from an experiment with adult humans in which the energy metabolism was measured by indirect calorimetry were used in a biological model of nutrient oxidation, lipogenesis and retention at the whole body level. Six male and four female adult volunteers (53–90 kg body weight) were asked to estimate the amount of a fixed diet, which would cover their normal degree of satiation, corresponding to their requirement of metabolizable energy (ME) for maintenance. The ME intake in relation to metabolic body weight ($kg^{0.75}$) showed a great variation with 466 kJ in Group A (n=2), 406 kJ in Group B (n=5) and 379 kJ in Group C (n=3). The heat production was lower than the ME intake in Group A and B, causing a positive energy retention about 1800 (Group A) and 525 kJ/d (Group B). In Group C heat production exceeded ME intake causing a negative retention of 1200 kJ and mobilization of body fat. Oxidation of protein contributed with 14% to the total heat production for all groups. Oxidation of carbohydrate contributed in Group A, B and C with 55, 45 and 41% while oxidation of fat contributed with reverse values of 31, 40 and 46%, respectively. Lipogenesis occurred in all participants with 900 kJ/day in Group B and 600 kJ/day in Group A and C, corresponding to 50 and 34 g carbohydrate entering the fat metabolism via de novo lipogenesis. The present results indicate that the rate of lipogenesis in adult humans depends on carbohydrate and energy supply from a diet.

Keywords: Humans; Energy balance; Heat production; Lipogenesis; Substrate oxidation

1. Introduction

A theory with respect to the calculation of substrate oxidation in the body from indirect calorimetry was introduced by Lusk in 1928 [1]. This theory was later used by Brouwer, who developed the equations for calculating the net oxidation of protein (OXP), carbohydrate (OXCHO) and fat (OXF) in animals based on the non-protein respiratory quotient (RQnp) from measurements of gas exchange and nitrogen excretion in urine [2]. Based on the stoichiometry of the oxidative reactions, alternative equations have been proposed for calculating substrate oxidation in man [3–6]. However, in accordance with the theory of Lusk, the calculations of substrate oxidation are only valid when the RQnp is below 1 and the interpretation of results achieved when RQnp>1 is doubtful [7]. Since values of RQnp>1 may occur when fat is synthesized from carbohydrate, due to decarboxylation processes [8,9], a method of calculating nutrient oxidation when RQnp is below or above 1 by combining data from gas exchange measurements with nitrogen and energy balances has been proposed [10].

* Corresponding author. Tel.: +45-35-28-30-44; fax: +45-35-28-30-20.
E-mail address: AC@KVL.DK (A. Chwalibog)

0040-6031/00/$ – see front matter
PII: S0040-6031(99)00495-5

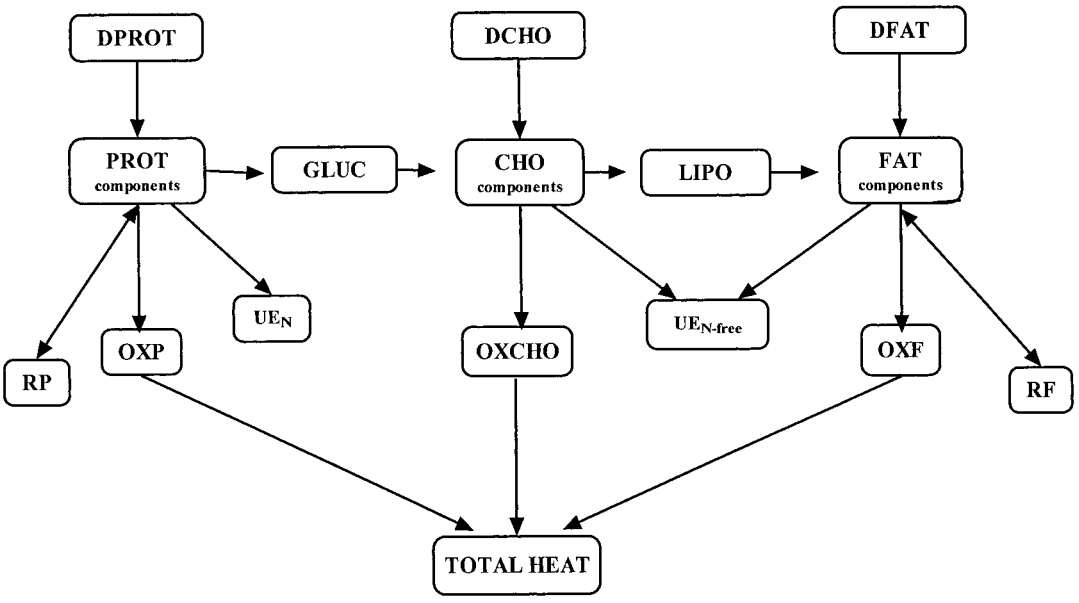

Fig. 1. Model of nutrient oxidation and retention. Protein digested (DPROT), retained (RP), oxidized (OXP), urinary energy from nitrogenous fraction (UE_N) and from nitrogen free fraction ($UE_{N\text{-free}}$), and contribution of energy from protein to carbohydrate (GLUC). Carbohydrate digested (DCHO), oxidized (OXCHO), and lipogenesis (LIPO). Fat digested (DFAT), retained (RF) and oxidized (OXF).

Recently gas exchange and balance measurements have been used in order to quantify the oxidation of nutrients in the intact body of man [11], in piglets and growing pigs [12], in growing calves [13,14] and in female mink [15,16]. Nutrient oxidation has also been investigated in rats during food-deprivation periods [17], and in comparative studies between pigs, mink, and rats [18].

The combination of indirect calorimetry with nitrogen and energy balances enables not only the estimation of nutrient oxidation together with protein and fat retention or mobilization in the body, but also the calculation of energy transfer between protein, carbohydrate and fat in order to quantify the major catabolic and anabolic processes, in accordance with the model shown in Fig. 1.

According to the model digested protein (DP), being equal to the PROT-group is utilized for protein retention in the body (RP). Deaminated amino acids are oxidized (OXP) with a concomitant loss of energy with nitrogenous substances excreted in urine (UE_N) and contribution of energy to carbohydrate metabolism (GLUC). The UE_N together with urinary energy originating from carbohydrate and fat metabolism ($UE_{N\text{-free}}$) provides the total energy loss in urine. Digested carbohydrate (DCHO) together with GLUC constitute the carbohydrate components (CHOc) which are oxidized (OXCHO) and used for de novo lipogenesis (LIPO). Digested fat (DFAT) and lipids from LIPO constitute the fat components (FATc), which are oxidized (OXF) and retained in the body (RF). If the FATc are reduced by undernutrition body fat is mobilized and oxidized to cover the energy requirement. The energy from OXP, OXCHO and OXF make up the total heat production (HE).

Currently, the model has been validated for growing pigs, rats and mink [18], demonstrating partition of nutrients between oxidation and retention and a substantial contribution of carbohydrate to lipogenesis depending on dietary composition and level of energy supply. In the present paper a similar approach has been used to quantify nutrient metabolism in adult man. Moreover, emphasis has been put on the quantification of lipogenesis in order to answer the question as to how much fat can be synthesized from carbohydrate and whether lipogenesis in humans is related to dietary composition and energy supply in relation to maintenance requirement.

2. Experimental

2.1. Subjects and diets

The data were taken from a previous experiment with adult humans in which the energy metabolism was measured by indirect calorimetry including a 24 h measurements of the gas exchange [19]. The study was carried out at the Research Institute of Human Nutrition, The Royal Veterinary and Agricultural University, Copenhagen and approved by the Municipal Ethical Committee of Frederiksberg and Copenhagen.

The experiment included six male and four female non-obese, non-smoking, healthy volunteers from 22 to 47 years of age in the body weight (BW) range from 53 to 90 kg. All subjects consumed the same amount of a basal diet, identically composed for each meal of breakfast, lunch and dinner. The total basal diet contained 56 g digestible protein (DP), 206 g digestible carbohydrate (DCHO) and 62 g digestible fat (DFAT), calculated by the DANKOST dietary assessment software (National Food Agency, Søborg, Denmark). This basal diet was individually supplemented with sandwiches, rolls and biscuits in accordance with the subjects normal degree of satiation, established by a preliminary interview. Milk, tea, coffee and beer were offered according to the wishes of the subjects. The total amount of digested nutrients and energy from the basal diet and the supplemented cost in the individual subjects is shown in Table 1.

2.2. Experimental procedure

The gas exchange of the subjects was measured twice separated by 4 weeks and the females were measured at the same time in their menstrual cycle. The subjects were not in ward, but all consumed their fixed dinner the evening before the start of the experiment next morning when the respiration chamber was entered at 08.25 after voiding. Breakfast was served at 08.30, lunch at 12.30, dinner at 18.00 and the next morning breakfast at 08.30. Tea or coffee was served between meals. The chamber was left at 10.00 after voiding. The gas exchange was measured between 10.00–10.00 with the subjects bicycling for 15 min at 10.30 and 15.00 and being in bed from 23.00 to 08.00. The amount of urine excreted during stay in the chamber was weighed and analysed for nitrogen content.

The measurements of gas exchange were carried out by means of a respiration unit working according to the open-air-circuit principle. The unit consists of two independent working chambers with a floor area of 6.5 m^2 and a hight of 2.25 m equipped with a comfortable bed and facilities for a pleasant 24 h stay. The volume of the gas passing through the chamber was measured by the differential pressure technique and its concentration by infrared absorption (CO_2) and by paramagnetism (O_2). The unit was frequently calibrated by means of CO_2-test gas showing differences between in- and outlet of CO_2 below 1%.

Table 1
Sex, age and body weight (BW) of subjects and daily intake of digested protein (DP), carbohydrate (DCHO), fat (DFAT) and energy (DE) in individual diets

Subject No.	Sex	Age (year)	BW (kg)	DP (g)	DP (kJ)	DCHO (g)	DEHO (kJ)	DFAT (g)	DFAT (kJ)	DE (kJ)
1	M	22	90.0	81.1	1935	332	5844	85.5	3399	11178
7	M	27	76.4	88.6	2114	308	5415	94.4	3753	11282
5	M	23	75.8	79.9	1906	296	5204	85.4	3396	10506
11	M	30	74.8	78.3	1868	293	5158	81.0	3221	10247
9	M	47	73.8	88.0	2100	299	5255	91.8	3650	11005
3	M	25	67.2	88.6	2114	308	5415	94.4	3753	11282
2	F	25	72.6	81.7	1949	298	5246	87.2	3467	10662
6	F	23	62.5	66.3	1582	269	4729	70.1	2787	9098
10	F	45	60.4	69.1	1649	264	4639	71.9	2859	9147
4	F	34	53.3	70.6	1685	282	4961	75.6	3006	9652

2.3. Calculations

The energy content of digested protein, carbohydrate and fat was calculated from the individually registered amount of digested nutrients (Table 1) as:

$$\mathrm{DP\,(kJ)} = \mathrm{DP\,(g)} \times 23.86$$

$$\mathrm{DCHO\,(kJ)} = \mathrm{DCHO\,(g)} \times 17.58$$

$$\mathrm{DFAT\,(kJ)} = \mathrm{DFAT\,(g)} \times 39.76$$

$$\mathrm{DE\,(kJ)} = \mathrm{DP\,(kJ)} + \mathrm{DCHO\,(kJ)} + \mathrm{DFAT\,(kJ)}$$

The amount of metabolizable energy (ME), heat production (HE), retained energy in the body (RE), and the non-protein respiratory quotient (RQnp) were calculated from the 24 h measurements of O_2-consumption, CO_2-production and nitrogen excreted in urine (UN) with constants and factors by [2], while heat from oxidation of protein (OXP), carbohydrate (OXCHO) and fat (OXF) was calculated as described in [10] as:

$$\mathrm{ME\,(kJ)} = \mathrm{DE\,(kJ)} - \mathrm{UE\,(kJ)}$$

where

$$\mathrm{UE\,(kJ)} = \mathrm{UN\,(g)} \times 41.0$$

$$\mathrm{HE\,(kJ)} = 16.18 \times \mathrm{O_2,1} + 5.02 \times \mathrm{CO_2,1} - 5.99 \times \mathrm{UN\,(g)}$$

$$\mathrm{RE\,(kJ)} = \mathrm{ME\,(kJ)} - \mathrm{HE\,(kJ)}$$

$$\mathrm{OXP\,(kJ)} = \mathrm{UN\,(g)} \times 6.25 \times 18.42$$

$$\mathrm{OXCHO\,(kJ)} = (-2.968 \times \mathrm{O_2,1} + 4.147 \times \mathrm{CO_2,1} - 2.446 \times \mathrm{UN\,(g)}) \times 17.58$$

$$\mathrm{OXF\,(kJ)} = (1.719 \times \mathrm{O_2,1} - 1.719 \times \mathrm{CO_2,1} - 1.963 \times \mathrm{UN\,(g)}) \times 39.76$$

Retained protein (RP), energy in urine from the nitrogenous fraction (UE_N), the residual energy from deaminated amino acids (GLUC), lipogenesis from carbohydrate (LIPO) and energy in urine from non-nitrogenous fraction ($UE_{N\text{-free}}$) were calculated according to the model (Fig. 1) as:

$$\mathrm{RP\,(kJ)} = \left(\frac{\mathrm{DP\,(g)}}{6.25} - \mathrm{UN\,(g)}\right) \times 6.25 \times 23.86$$

$$\mathrm{UEN\,(kJ)} = \mathrm{UN\,(g)} \times 0.90 \times 24.9$$

$$\mathrm{GLUC,(kJ)} = \mathrm{DP,(kJ)} - \mathrm{RP,(kJ)} - \mathrm{UEN,(kJ)} - \mathrm{OXP,(kJ)}$$

$$\mathrm{LIPO,(kJ)} = \mathrm{DCHO,(kJ)} + \mathrm{GLUC,(kJ)} - \mathrm{OXCHO,(kJ)} - \mathrm{UEN-free,(kJ)}$$

where

$$\mathrm{UEN-free\,(kJ)} = \mathrm{UE\,(kJ)} - \mathrm{UEN\,(kJ)}$$

Fat retention (RF) was calculated either from the energy balance:

$$\mathrm{RF\,(kJ)} = \mathrm{ME\,(kJ)} - \mathrm{HE\,(kJ)} - \mathrm{RP\,(kJ)}$$

or with the model:

$$\mathrm{RF\,(kJ)} = \mathrm{DFAT\,(kJ)} + \mathrm{LIPO\,(kJ)} - \mathrm{OXF\,(kJ)}$$

A multifactor analysis of variance with age and gender as covariates was performed to test differences between the two experiments, and the equality of means was tested by Student's *t*-test [20].

3. Results

3.1. Energy metabolism and oxidation of nutrients

There were no significant differences ($P>0.05$) between the first and second measurements of the individual 24 h gas exchange, and as the individual diets were identical in both experiments, all result presented are mean values from the two experiments.

It was sought by preliminary interviews to estimate the subjects' requirements of food for covering their energy requirements for maintenance. However, measurements of the subjects' intake of metabolizable energy (ME) in relation to their metabolic body weight ($kg^{0.75}$) showed a great variation (Fig. 2).

The graph indicates that three groups appeared, five subjects Nos. 2–6–7–9–10 being close to each other (Group B), while Nos. 3–4 (Group A) and Nos. 1–5–11 (Group C) were respectively above or below the curve for Group B. The energy metabolism was measured individually and the mean values from the three groups are shown in Table 2.

The daily ME intake was 466, 406 and 376 kJ/$kg^{0.75}$ for Groups A, B and C, respectively. The heat production (HE) was below the ME intake in Groups A and B, causing a positive energy retention of about 1800 and

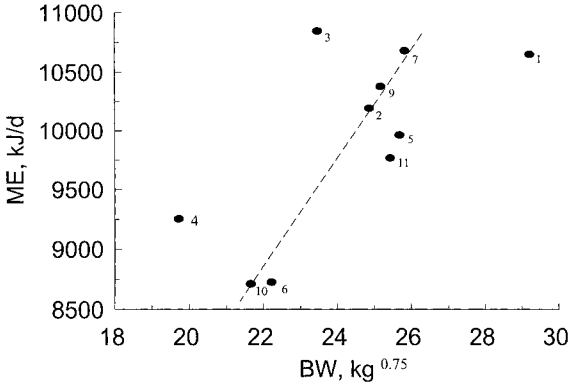

Fig. 2. Intake of metabolizable energy (ME) in relation to metabolic body weight ($kg^{0.75}$) of the subjects.

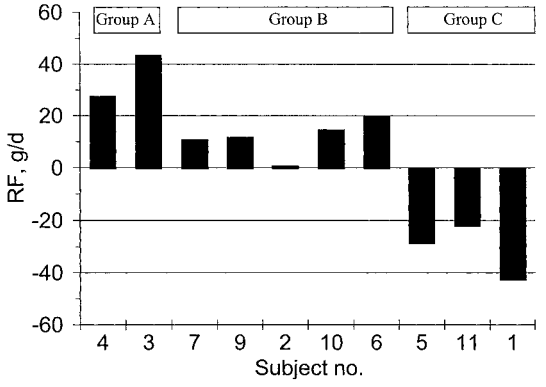

Fig. 3. Retained fat (RF) in individual subjects.

525 kJ/day respectively, while HE exceeded ME in Group C causing energy mobilization from the body of 1200 kJ/day.

The protein retention (RP) was slightly positive in all groups with a mean value of about 4 g/day. The fat retention (RF) was positive in Groups A and B with 36 and 12 g/day, while it was negative in Group C with 31 g/day, indicating body fat mobilization (Fig. 3).

The oxidation of protein (OXP) was fairly constant for all groups with values between 13–15% of HE (Table 3). The oxidation of carbohydrate (OXCHO) decreased from Groups A to C and B with values of 55, 45 and 41%, while the oxidation of fat (OXF) increased with reverse values of 31, 40 and 46%.

3.2. Protein metabolism

The individual intake of digested protein (DP) varied from 66 to 88 g/day (Table 1) and the nitrogen excretion in urine followed the intake except from No. 3. This subject had a very low amount of urine in both experiments, probably caused by not following the instruction to empty the bladder before leaving the chamber, and the data were omitted from the calculation of protein metabolism (Table 4).

The main part of the digested protein (DP) was about 75% oxidized for Groups B and C, while only 3.5% was retained. Energy in urine from nitrogenous fraction was 14.5% of DP, leaving 7.5% for entering the carbohydrate and fat metabolism.

3.3. Carbohydrate and fat metabolism

The main intake of digested carbohydrate (DCHO) was 5187 (SEM 111) kJ/day for all the groups, with a slight addition of 137 kJ or 2.6% from protein metabolism (Table 5).

Table 2
Energy metabolism, metabolizable energy (ME), heat production (HE), retained protein (RP) and retained fat (RF)

	Group A	Group B		Group C	
	Mean	Mean	SEM	Mean	SEM
n	2	5		3	
BW (kg)	60.3	69.1	3.2	80.2	4.9
ME (kJ/day)	10051	9741	425	10132	268
ME ($kJ/kg^{0.75}$)	466	406	4.0	379	7.3
HE (kJ/day)	8250	9214	549	11321	433
HE ($kJ/kg^{0.75}$)	384	383	10.6	423	6.2
RP (kJ/day)	387	70	80	42	54
RF (kJ/day)	1414	457	125	−1231	243

Table 3
Oxidation of protein (OXP), carbohydrate (OXCHO) and fat (OXF) in relation to heat production (HE) and non-protein respiratory quotient (RQnp)

	Group A Mean	Group B		Group C	
		Mean	SEM	Mean	SEM
n	2	5		3	
HE (kJ/day)	8250	9214	549	11321	433
OXP/HE (%)	14.2	15.0	0.77	12.7	0.37
OXCHO/HE (%)	54.5	44.7	2.52	40.9	3.47
OXF/HE (kJ)	31.4	40.2	2.20	46.4	3.42
RQnp	0.890	0.858	0.017	0.842	0.011

Table 4
Protein metabolism. Digested protein (DP), retained protein (RP), oxidized protein (OXP), energy in urine from nitrogenous fraction (UE_N) and the residual energy from deaminated amino acids (GLUC)

	Group A Mean	Group B		Group C	
		Mean	SEM	Mean	SEM
n	1[a]	5		3	
DP (kJ/day)	1900	1879	112	1903	19.4
RP/DP (%)	14.2	4.4	4.26	2.2	2.86
OXP/DP (%)	62.0	73.8	3.29	75.5	2.23
UE_N/DP (%)	12.1	14.4	0.63	14.7	0.44
GLUC/DP (%)	6.2	7.4	0.35	7.5	0.23

[a] Subject no 3 omitted caused by technical reasons.

The main part of carbohydrate components (CHOc) was79% oxidized for Group B and 84% for Groups A and C. Energy in urine from non-nitrogenous materials ($UE_{N\text{-free}}$) was fairly constant for all subjects at about 4%, so that 17% or about 900 kJ/day was left for lipogenesis (LIPO) in Group B and 12% or 640 kJ/day in Groups A and B.

The main intake of digested fat (DF) was 3329 (SEM 112) kJ/day for all the groups and the supplement from LIPO constituted 22% of the CHOc in Group B and 12% in Groups A and C (Table 6).

The main part of the fat components (FATc) was 65 and 88% oxidized, corresponding to about 2600 and 3700 kJ/day in Groups A and B, respectively, and

Table 5
Carbohydrate metabolism. Digested carbohydrate (DCHO), contribution of energy from deaminated amino acids (GLUC), carbohydrate components (CHOc), oxidized carbohydrate (OXCHO), energy in urine from non-nitrogenous fraction ($UE_{N\text{-free}}$) and lipogenesis (LIPO)

	Group A Mean	Group B		Group C	
		Mean	SEM	Mean	SEM
n	2	5		3	
DCHO (kJ/day)	5188	5057	156	5402	221
GLUC (kJ/day)	117	140	13.7	144	5.5
CHOc (kJ/day)	5305	5197	167	5546	223
OXCHO/CHOc (%)	84.7	78.6	2.54	83.6	8.10
$UE_{N\text{-free}}$/CHOc (%)	3.6	4.3	0.32	4.2	0.15
LIPO/CHOc (%)	11.8	17.1	2.35	12.2	8.63

Table 6
Fat metabolism. Digested fat (DFAT), lipogenesis (LIPO), fat components (FATc), oxidized fat (OXF) and retained fat (RF)

	Group A	Group B		Group C	
	Mean	Mean	SEM	Mean	SEM
n	2	5		3	
DFAT (kJ/day)	3380	3303	202	3339	59
LIPO (kJ/day)	624	902	149	651	425
FATc (kJ/day)	4004	4205	336	3990	367
OXF/FATc (%)	65.2	88.3	3.76	132.2	8.43
RF/FATc (%)	34.8	11.7	3.76	−32.2	8.43

leaving about 1400 and 500 kJ/day for fat retention. The fat oxidation in Group C was about 5200 kJ/day, exceeding the FATc by 32% causing a body fat mobilization of about 1200 kJ/day corresponding to 30 g/day fat.

4. Discussion

In this investigation data from indirect calorimetry combined with intake of nutrients were used in a biological model (Fig. 1). The model describes the overall pathways of protein, carbohydrate and fat as they are partitioned between catabolic and anabolic processes in terms of energy flow, but does not describe the intermediary processes. The calculations were carried out with constants generally accepted in studies of energy metabolism in animals [2] and with equations proposed in [10]. However, the calculation of heat production and nutrient oxidation with fixed constants based on a standard composition of dietary protein, carbohydrate and fat is subject to some errors. Each amino acid, fatty acid and a component of carbohydrate fraction has different enthalpies and different RQ values and the average constants do not represent the true values for a particular composition of nutrients [6]. Thus, the presented method of calculation should be considered as an approximation of the 'real metabolism' and as such provides only overall values of substrate disappearance [21]. This is assumed to be equal to net nutrient oxidation plus the net values of nutrient retention.

It was sought by preliminary interviews with the participants to estimate their energy requirements for maintenance. However, the measurements showed a great variation in their estimation with five subjects (Group B) being close to each other with a metabolizable energy intake of 406 kJ/kg$^{0.75}$, while two (Group A) were above with 466 kJ/kg$^{0.75}$ and three (Group C) were below Group B with 379 kJ/kg$^{0.75}$, causing, as discussed later, a great variation in their fat retention. It is remarkable that Group B was close to values generally accepted as maintenance requirement for farm animals [22].

Protein oxidation (Table 2) contributed from 12 to 17% to the total heat production being in the range measured for growing pigs [12,18], calves [14] and growing rats [17], but much lower than in adult mink where protein oxidation was the main energy source with about 35% of the total heat production [16]. Oxidation of carbohydrate followed the amount of ingested carbohydrate with the highest contribution of 55% of heat production in Group A, decreasing to 45 and 41% in Groups B and C, respectively. The contribution was much lower than in growing pigs [18] caused by a lower intake of carbohydrate in humans in relation to pigs. The contribution of heat from fat oxidation was reverse to OXCHO increasing from 31 to 46% of HE, and being much higher than in normally fed pigs, where no OXF occurred, as heat from OXP and OXCHO was sufficient to cover energy requirements [12].

The individually measured protein retention varied as expected in adults with a mean value around 0.5 g/day. The majority of digested protein was oxidized (62–76%) and about 14% excreted with urine, leaving 7% of protein energy to enter the carbohydrate metabolism mainly by gluconeogenesis. The validity of this figure is questionable for different reasons. Although there is a relationship between nitrogen excreted in urine and OXP, the relationship is not direct as a part of the deaminated protein is not directly

oxidized but enters fat synthesis or ketogenesis via acetyl-CoA. Therefore, OXP is likely to be overestimated and the residual energy (GLUC) from catabolized protein being transferred to carbohydrate metabolism will be underestimated. However, in this investigation the contribution of GLUC to the carbohydrate components was below 3% in all subjects, and may be considered to be of negligible importance for further quantification. The main part of the CHOc was oxidized but it is remarkable that all subjects transferred a part to the fat components in the process of de novo lipogenesis. The FATc, being composed from digested fat and fat from lipogenesis, was mainly oxidized and the residue retained in the body in Groups A and B, while in Group C fat oxidation exceeded the FATc, hence body fat was mobilized and oxidized (Fig. 3). Thus, in no case did the contribution of energy from OXP and OXCHO cover the energy requirements, thereby causing fat oxidation.

Hypothetically, it can be expected that when the energy supply from protein and carbohydrate can cover energy requirements, there is no net fat oxidation and all dietary fat and fat from lipogenesis is finally retained in the body. This is the situation in fast growing animals fed with a high carbohydrate load and a relatively low supply of fat. For example, in growing pigs fed with 65% of digestible energy from digestible carbohydrate and 10% from digestible fat, and with a total metabolizable energy supply of about 1.3 MJ/kg$^{0.75}$ [12], the oxidation of carbohydrate and protein could cover energy requirements for maintenance and growth and no net oxidation of fat occurred. In this investigation the contribution of digestible carbohydrate and fat was 50% and 32% of digestible energy, respectively, and metabolizable energy supply was about 0.4 MJ/kg$^{0.75}$, giving an entirely different substrate input for the oxidative processes. However, even the substrate contribution to catabolism was different. In adult man fed diets with relatively lower carbohydrate level and a higher level of fat than in growing pigs, the contribution of carbohydrate to lipogenesis was in Groups A and B between 29–55 g/day (except subject 7 with 80 g/day), constituting from 15 to 21% of FATc. It is also interesting to note that in the negative fat balance in Group C not all carbohydrates were oxidized but 10–16 g/day (except 85 g/day in No. 11) were still used for lipogenesis.

Although the present figures are attributed to a great individual variation they may indicate an obligatory requirement of carbohydrate for cell replacement in adult man. It may be speculated that de novo lipogenesis from carbohydrate is a necessary process even in adult humans, being a source of long chain fatty acids necessary for synthesis of structural fat which are incorporated in the lipids of cell membranes and liposomes. Also de novo lipogenesis may be essential by providing special fatty acids for cellular regulation [23].

The present results are in disagreement with previous conclusions from measurements of gas exchange in man [3,24,25], indicating that man has a negligible ability to synthesize fat from carbohydrate. Theoretically a RQnp above 1.0 indicates that synthesis of fatty acids from carbohydrate exceeds fat oxidation [5,6], and the calculated values of OXF become negative. It is assumed [25], based on stoichiometric calculations [3], that the negative values of OXF are numerically equal to the amount of fat synthesized de novo. Consequently, the lipogenesis is underestimated as it is only determined when RQnp>1.0, while the conversion of carbohydrate to fat at RQnp<1.0 is not detected. In this way de novo lipogenesis represents the amount of fat which is retained in the body, but not the total amount of fat which was synthesized from carbohydrate and then oxidized and/or retained in the body. In the present investigation the RQnp varied between 0.819 and 0.891and in order to estimate the total net lipogenesis it was calculated as a difference between energy in CHOc minus OXCHO and urinary energy from non-nitrogenous fraction ($UE_{N\text{-}free}$). The same method was used for calculation of lipogenesis in growing pigs [18] showing a substantial lipogenesis even when intake of carbohydrate was below energy requirements for growth. This approach seems to be justified more than the method used in the studies on man usually showing very small lipogenesis [3,24,25], as it is only determined as an abundance of lipogenesis over fat oxidation, but not the total amount of fat from de novo lipogenesis. Based on our experiments with growing pigs [19] and this investigation with adult man it may be concluded that in both investigated species carbohydrate are utilized for lipogenesis, although the extend of LIPO depends on the amount of ingested carbohydrate and fat (diet composition) and the phy-

siological stage (maintenance, growth etc). The large differences among species are really dietary differences. In humans when energy supply from oxidized nutrients covers requirements, a surplus of carbohydrate would not be oxidized but used for fat deposition in the body.

References

[1] G. Lusk, The Elements of the Science of Nutrition, 4th Edition, Saunders, Philadelphia, 1928.
[2] E. Brouwer, in K.L. Blaxter (Ed.), 3rd Symposium on Energy Metabolism in Farm Animals, EAAP-Publication 11, Academic Press, New York, 1965, p. 41.
[3] K.J. Acheson, T. Schutz, E. Bessard, E. Ravussini, E. Jéquier, Am. J. Physiol. 246 (1984) E62.
[4] L. Garby, A. Astrup, Acta Physiologica Scandinavica 129 (1987) 443.
[5] E. Ferrannini, Metabolism 37 (1988) 287.
[6] G. Livesey, M. Elia, Am. J. Clin. Nutr. 47 (1988) 608.
[7] M. Elia, G. Livesey, Am. J. Clin. Nutr. 47 (1988) 591.
[8] K. Christensen, A. Chwalibog, S. Henckel, G. Thorbek, Comparative Biochemistry and Physiology 91A (1988) 463.
[9] K. Jakobsen, G. Thorbek, Br. J. Nutr. 69 (1993) 333.
[10] A. Chwalibog, K. Jakobsen, S. Henckel, G. Thorbek, J. Anim. Physiol. Anim. Nutr. 68 (1992) 123.
[11] G. Thorbek, A. Chwalibog, K. Jakobsen, S. Henckel, Ann. Nutr. Metabol. 38 (1994) 8.
[12] A. Chwalibog, G. Thorbek, Archives Anim. Nutr. 48 (1995) 53.
[13] A. Chwalibog, K. Jensen, G. Thorbek, Archives Anim. Nutr. 49 (1996) 255.
[14] A. Chwalibog, A.-H. Tauson, G. Thorbek, Zeitschrift für Ernährungswissenshaft 36 (1997) 313.
[15] A.-H. Tauson, R. Fink, A. Chwalibog, Zeitschrift für Ernährungswissenshaft 36 (1997) 317.
[16] A.-H. Tauson, H. Sørensen Juul, S. Wamberg, A. Chwalibog, J. Nutr. 128 (1998) 2615S.
[17] A. Chwalibog, K. Jakobsen, A.-H. Tauson, G. Thorbek, Comparative Biochemistry and Physiology Part A 121 (1998) 423.
[18] A. Chwalibog, A.-H. Tauson, R. Fink, G. Thorbek, Thermochim. Acta 309 (1998) 49.
[19] A. Astrup, G. Thorbek, J. Lind, B. Isaksson, Am. J. Clin. Nutr. 52 (1990) 777.
[20] SAS, 1990. SAS/STAT User's Guide, Version 6, Statistical Analysis System Institute, Cary, NC, 1990.
[21] J.M. Kinney, in: J.M. Kinney, H.N. Tucker (Eds.), Energy Metabolism: Tissue Determinants and Cellular Corollaries, Raven Press, New York, 1992, p. 113.
[22] A. Chwalibog, Acta Agricultuae Scandinavica 41 (1991) 147–160.
[23] M.K. Hellerstein, J.-M. Schwarz, R.A. Neese, Annul. Rev. Nutr. 16 (1996) 523.
[24] K.J. Acheson, T. Schutz, E. Bessard, J.P. Flatt, E. Jéquier, Am. J. Clin. Nutr. 45 (1987) 78.
[25] E. Jéquier, in: J.M. Kinney, H.N. Tucker (Eds.), Energy Metabolism: Tissue Determinants and Cellular Corollaries, Raven Press, New York, 1992, p. 123.