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Energy expenditure and oxidation of carbohydrate and fat in humans during day and night

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Abstract

Energy expenditure (EE) and substrate oxidation were measured in six male and four female adult humans during day (10.00–23.00) and night (23.00–07.00). All subjects received diets of the same composition, but four subjects (Group I) had a higher intake of metabolizable energy (ME) than EE, while ME was near EE in three subjects (Group II) and below EE in three subjects (Group III). The EE varied from 388 kJ/h in Group I to 540 kJ/h in Group III during day and from 248 to 351 kJ/h during night. However, the reduction from day to night was identical for all subjects with a night value of 64% of the day value. Oxidation of carbohydrate (OXCHO) was fairly constant with 223 kJ/h during day and being reduced to 100 kJ/h during night in all subjects. Oxidation of fat (OXF) varied from 121 kJ/h in Group I to 223 kJ/h in Group III during day and from 98 to 190 kJ/h by night. The decreased EE from day to night was of the same magnitude independent of the ME intake, while the contribution from OXCHO and OXF to EE depended of ME intake. When ME intake was above EE (Group I), relatively more carbohydrate (56%) than fat (31%) was oxidized during day, leaving a surplus of dietary fat for fat retention. Nevertheless, during night the contributions from OXCHO and OXF were similar (40%). When energy supply was below EE (Group III), the contributions from OXCHO and OXF to EE were similar (45%) during day. However, during night the contribution from OXCHO was reduced (29%) while OXF increased (54%). This investigation indicates that during day the major oxidative fuel is carbohydrate, while fat oxidation reflects the difference between OXCHO and EE; however, during night changes in the energy status are accommodated by increasing OXF.

Keywords: Energy expenditure; Carbohydrate oxidation; Fat oxidation; Fat retention

1. Introduction

Measurements by means of indirect calorimetry have provided important insights regarding the extent to which the whole body energy metabolism in humans and animals responds to nutrient supply, environment, exercise and disease. In humans, emphasis has been given to establish standards for basal energy expenditure (EE) and energy costs of physical activity and diet-induced thermogenesis. In recent years also increasing attention has been given to evaluate partition of nutrient metabolism between oxidation and retention in the body under different nutritional conditions (for details, see [1–6]). The results are mostly based on 24 h measurements and demonstrate average daily values. However, to our knowledge, there are no quantitative results concerning potential differences in substrate oxidation and

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their contribution to total EE during daytime and nighttime.

Data from a previous experiment with humans in which energy metabolism and lipogenesis were studied [7] have been used in the present investigation to quantify carbohydrate and fat oxidation during day and night and to evaluate whether the fall in EE during night is consistent with diurnal changes in contribution from carbohydrate and fat oxidation to total EE.

2. Experimental

2.1. Subjects and diets

The experiment included six male and four female non-obese, healthy volunteers 22–47 years of age and with a body weight ranging from 53 to 90 kg. The experiment had been carried out at the Research Department of Human Nutrition, the Royal Veterinary and Agricultural University, and approved by the Municipal Ethical Committee of Frederiksberg and Copenhagen [8].

All subjects consumed an identical basal diet of 7.40 MJ, individually supplied with extra sandwiches and rolls according to the subjects' normal degree of satiation. The diet was supposed to cover 24 h energy requirement with an energy balance around zero. However, the individual 24 h measurements of metabolizable energy (ME) in relation to EE showed that only few subjects were able to consume in accordance with their requirement. The ME intake (Fig. 1) in subject 3–4–6–10 (Group I) was above EE, in subject 7–9–2 (Group II) near EE and in subject 11–5–1 below EE (Group III).

The mean intake of digested protein, carbohydrate and fat for the three groups and ME intake, EE and retained fat are shown in Table 1. The energetic composition of the diets was fairly constant for all subjects with 18% of energy contributed from protein, 50% from carbohydrate and 32% from fat.

2.2. Experimental

The subjects consumed a fixed dinner the evening before the experiment started. 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 breakfast next morning at 08.30. Physical activity was performed for 15 min at 10.30 and at 15.00 on a stationary bicycle with a work corresponding to 66.2 kJ/15 min [9]. The subjects were in bed from 23.00 to 08.00 and left the chamber at 10.15 after voiding. The 24 h measurements of oxygen consumption and carbon dioxide production were carried out from 10.00 to 10.00 by means of an open-air-circuit respiration unit (indirect calorimetry) [8], but for this investigation 24 h measurements were separated into two periods 10.00–23.00 (daytime) and 23.00–07.00 (nighttime). The experiment was repeated after 4 weeks, and with no significant differences ($P > 0.05$) between the data, the results presented are mean values from the two experiments.

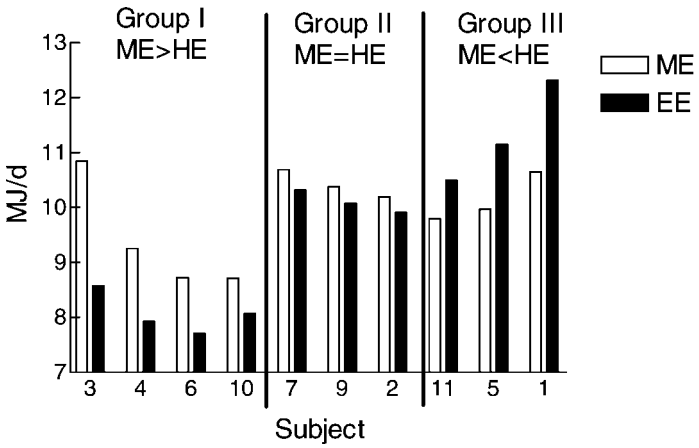

Fig. 1. Intake of ME and EE during 24 h measurements. Group I: ME > EE, Group II: ME = EE, Group III: ME < EE.

Table 1
Body weight (BW), digested protein (DP), carbohydrate (DCHO), and fat (DF) intake of ME, EE and retained fat (RF) during 24 h measurements

Group No.	Subject No.	BW (kg)	DP (g/day)	DCHO (g/day)	DF (g/day)	ME (kJ/day)	EE (kJ/day)	RF	
								(kJ/day)	(g/day)
I	3–4–6–10	61	73.7	281	78.0	9385	8071	1047	26
II	7–9–2	74	86.1	302	91.1	10423	10103	301	7
III	11–5–1	80	79.8	307	84.0	10132	11322	−1232	−31

2.3. Calculations

EE was calculated from O_2 consumption, CO_2 production and nitrogen excretion in urine (UN) in accordance with [10] as

$$\text{EE (kJ)} = 16.18 \times O_2\ (l) + 5.02 \times CO_2(l) - 5.99 \times \text{UN (g)}$$

Oxidation of carbohydrate (OXCHO) and fat (OXF) was calculated in accordance with [11] as

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

$$\text{OXF (kJ)} = ((1.719 \times O_2\ (l) - 1.719 \times CO_2(l) - 1.963 \times \text{UN (g)}) \times 39.76$$

As there was no separate collection of urine during day and night, it was assumed that urinary nitrogen excretion was similar during day and night. The results were evaluated by Student's *t*-test [12].

Table 2
EE (kJ/h) during day (10.00–23.00) and night (23.00–07.00)

Group No.	Day		Night		Night/day (%)	
	Mean	S.E.M.[a]	Mean	S.E.M.	Mean	S.E.M.
I	388	9.7	248	6.2	64.0	0.94
II	486	6.1	310	6.7	64.0	1.97
III	540	20.2	351	20.3	65.0	1.35

[a] Standard error of mean.

3. Results

3.1. Energy expenditure

The EE (Table 2) depended on body weight and food consumption, and varied between the groups from 388 to 540 kJ/h during day and from 248 to 351 kJ/h during night, with all differences being significant ($P < 0.05$). However, in spite of the variation, the reduction in EE from day to night was identical for all groups, the mean night value being 64.3% (S.E.M. = 0.72) of the day value.

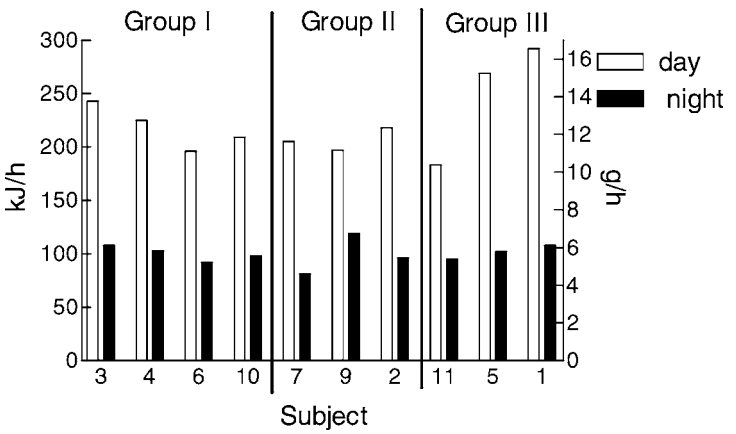

Fig. 2. OXCHO during day (10.00–23.00) and night (23.00–7.00).

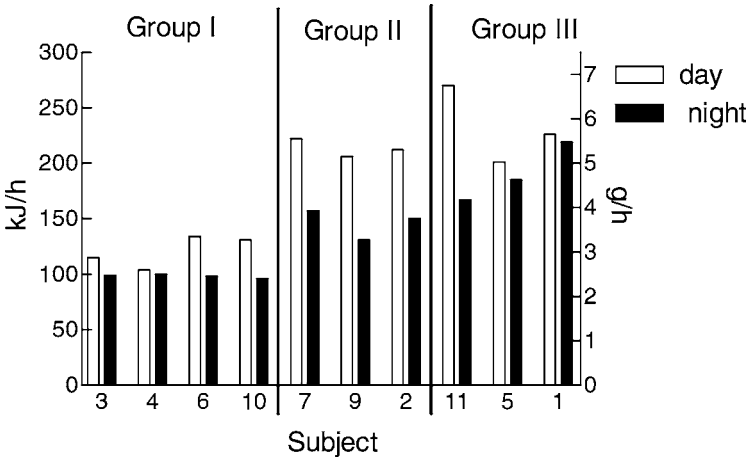

Fig. 3. OXF during day (10.00–23.00) and night (23.00–7.00).

Table 3
OXCHO and OXF during day (10.00–23.00) and night (23.00–07.00)

Group No.	OXCHO (kJ/h)				OXF (kJ/h)			
	Day		Night		Day		Night	
	Mean	S.E.M.[a]	Mean	S.E.M.	Mean	S.E.M.	Mean	S.E.M.
I	218	10.2	100	3.4	121	7.0	98	0.9
II	206	6.1	99	11.1	213	4.7	146	7.8
III	248	33.2	102	3.8	223	20.2	190	15.7

[a] Standard error of mean.

3.2. Oxidation of carbohydrate and fat

The individual values of OXCHO and OXF during day and night are demonstrated in Figs. 2 and 3, while the mean values of the groups are shown in Table 3.

The OXCHO was fairly constant for all subjects with a variation between groups from 206 to 248 kJ/h by day and from 99 to 102 kJ/h by night, corresponding to an oxidation of 12–14 and 5.7 g carbohydrate/h by day and night, respectively. Thereby the mean night value was reduced to 45% of the day value.

The OXF varied between 121–223 kJ/h by day and 98–190 kJ/h by night, corresponding to an oxidation of 3.0–5.7 and 2.5–4.8 g fat/h. The reduction between day and night values was not significant ($P > 0.05$).

Table 4
Contribution of OXCHO and OXF to total EE during day (10.00–23.00) and night (23.00–07.00)

Group No.	Day				Night			
	OXCHO/EE (%)		OXF/EE (%)		OXCHO/EE (%)		OXF/EE (%)	
	Mean	S.E.M.[a]	Mean	S.E.M.	Mean	S.E.M.	Mean	S.E.M.
I	56.2	1.84	31.2	2.09	40.4	0.43	39.7	0.91
II	42.5	1.23	43.9	0.41	31.7	1.41	47.2	3.31
III	45.7	4.83	43.3	4.88	29.0	0.62	54.0	1.23

[a] Standard error of mean.

3.3. Contribution of oxidized carbohydrate and fat to total EE

In Group I, in which the ME intake was above EE, OXCHO contributed with 56% and OXF with 31% to EE during daytime, while both nutrients contributed with 40% during nighttime (Table 4). In Group III, in which the ME intake was below EE, the contribution from OXCHO and OXF was similar, about 44% during daytime, while during nighttime the contribution from OXCHO was reduced to 29% and OXF increased to 54%.

4. Discussion

The present results are based on measurements of O_2 consumption and CO_2 production by indirect calorimetry and on analysis of urinary nitrogen excretion. Calculations of EE and substrate oxidation are sensitive to errors in the measurements of gas exchange within the calorimeter [4] and can be biased by the potential pitfalls in the interpretation of data from gas exchange measurements [5,13–16]. However, the overall error of gas exchange measurements in our experiment was less than ±1% [8], and furthermore, there were no differences between the measurements which were performed twice with 4 weeks intervals. This provides a good evidence of a high accuracy of the experiment. The calculations of EE, OXCHO and OXF include values of UN from 24 h collection of urine which were equally divided between daytime and nighttime. This may cause an error in estimation of OXCHO and OXF, but has a negligible effect on EE values [5]. Although the average daily protein oxidation (OXP) calculated from UN was relatively small, 14.2% (S.E.M. = 0.51) of EE, with a coefficient of variation of 11%, any potential changes in OXP between day and night [17] could affect absolute values of OXCHO and OXF, but the proportions between OXCHO and OXF would not be changed.

All subjects consumed diets of similar composition which were supposed to cover their energy requirement with an energy balance near zero. However, the amount of diet consumed and consequently ME intake was either above (Group I), near (Group II) or below (Group III) EE and thereby being above, near or below individual energy requirements. These differences were mirrored in daily fat retention, being positive when ME was “overconsumed” or negative, indicating body fat mobilization, when ME was “underconsumed”, showing that even small changes in proportion of ME:EE influence fat retention.

The EE measured during daytime included EE from activity and from dietary-induced thermogenesis (DIT), consequently being higher than EE during “asleep”. In this experiment, a separation between different components of EE was not evaluated and it can only be speculated that the differences between day and night were primarily due to activity and DIT as there is only a small diurnal variation in the basic metabolic rate [18]. However, it is interesting to note that the reduction of EE during night was exactly the same (64% of day value) in all subjects independent of their sex, body weight and energy intake during daytime.

The reduction of EE during night was consistent with carbohydrate oxidation which was reduced from 12 to 14 g carbohydrate/h during day and to 5.7 g carbohydrate/h during night. This substantial difference between day and night and the similar amount of OXCHO during night may be explained by a strict control of carbohydrate balance [18] in order to maintain glucose homeostasis. During daytime when carbohydrates are consumed, body glycogen reserves are saturated and the major part of dietary carbohydrate is oxidized. During night, the supply of carbohydrate from the digestive tract is limited to a small amount of low digestible non-starch polysaccharides due to a rapid transit time of starch and a high rate of glucose absorption occurring after a meal [19] and in consequence, the major source of OXCHO is body glycogen which is used to a strict limit, preventing its total depletion. Since the same amount of carbohydrate was oxidized, the rest of energy was supplied from OXF, simply reflecting the difference between OXCHO and EE [1,4].

In conclusion, this investigation indicates that during day the major oxidative fuel is carbohydrate, while fat oxidation reflects the difference between OXCHO and EE. During night, when the contribution from glycogen stores becomes limited, changes in the energy status are accommodated by increasing OXF.

References

[1] J.P. Flatt, E. Ravussin, K.J. Acheson, E. Jéquier, J. Clin. Invest. 76 (1985) 1019.
[2] J.O. Hill, J.C. Peters, G.W. Reed, D.G. Schlundt, T. Sharp, H.L. Greene, Am. J. Clin. Nutr. 54 (1991) 10.
[3] K.R. Westerterp, Am. J. Clin. Nutr. 57 (1993) 759S.
[4] S.A. Jebb, A.M. Prentice, G.R. Goldeberg, P.R. Murgatroyd, A.E. Black, W.A. Coward, Am. J. Clin. Nutr. 64 (1996) 259.
[5] A. Chwalibog, G. Thorbek, Arch. Anim. Nutr. 53 (2000) 253.
[6] B.J. Sonko, A.M. Prentice, W.A. Coward, P.R. Murgatroyd, G.R. Goldberg, Eur. J. Clin. Nutr. 55 (2001) 10.
[7] A. Chwalibog, G. Thorbek, Thermochim. Acta 349 (2000) 43.
[8] A. Astrup, G. Thorbek, J. Lind, B. Isaksson, Am. J. Clin. Nutr. 52 (1990) 777.
[9] G. Thorbek, A. Chwalibog, K. Jakobsen, S. Henckel, Ann. Nutr. Metabol. 38 (1994) 8.
[10] E. Brouwer, in: K.L. Blaxter (Ed.), Proceedings of the Third Symposium on Energy Metabolism in Farm Animals, EAAP-Publication 11, Academic Press, New York, 1965, p. 441.
[11] A. Chwalibog, K. Jakobsen, S. Henckel, G. Thorbek, J. Anim. Physiol. Anim. Nutr. 68 (1992) 123.
[12] SAS, SAS/STAT User's Guide, Version 6, Statistical Analysis System Institute, Inc, Cary, NC, 1990.
[13] M. Elia, G. Livesey, Am. J. Clin. Nutr. 47 (1988) 591.
[14] G. Livesey, M. Elia, Am. J. Clin. Nutr. 47 (1988) 608.
[15] E. Ferrannini, Metabolism 37 (1988) 287.
[16] J.M. Kinney, Overview: indirect calorimetry—theory and practice. in: J.M. Kinney, H.N. Tucker (Eds.), Energy Metabolism: Tissue Determinants and Cellular Corollaries, Raven Press, New York, 1992, p. 113.
[17] P.J. Garlick, G.A. Clugston, R.W. Swick, J.C. Waterlow, Am. J. Clin. Nutr. 33 (1980) 1983.
[18] E. Jéquier, Overview: indirect calorimetry—theory and practice. in: J.M. Kinney, H.N. Tucker (Eds.), Energy Metabolism: Tissue Determinants and Cellular Corollaries, Raven Press, New York, 1992, p. 123.
[19] A.J. Griffiths, S.M. Humphreys, Mo.L. Clarck, B.A. Fielding, K.N. Frayn, Am. J. Clin. Nutr. 59 (1994) 53.