Massive overfeeding and energy balance in men: the *Guru Walla* model[1–3]

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ABSTRACT To determine the magnitude of the thermogenic response to a massive long-term overfeeding, an energy-balance study was carried out in nine lean, young Cameroonian men participating in a traditional fattening session: the *Guru Walla*. Food intake, body weight, body composition, activity, and metabolic rates were recorded during a 10-d baseline period and over the 61–65 d of fattening. Total energy expenditure (TEE) was measured by using doubly labeled water during the baseline period and the final 10 d of *Guru Walla*. Cumulative overfeeding consisted of 955 ± 252 MJ ($\bar{x}$ ± SD) mainly as carbohydrate. Body-weight increase was 17 ± 4 kg, 64–75% as fat. Metabolic rates increased but TEE did not. However, when accounting for the reduction in physical activity, substantial thermogenesis was observed but its amplitude was not greater than that observed under less extreme carbohydrate-overfeeding conditions. If luxuskonsumption does exist, it is not related to the magnitude of the cumulative overfeeding. *Am J Clin Nutr* 1992;56:483–90.

KEY WORDS Luxuskonsumption, body weight, body composition, physical activity, diet-induced thermogenesis, doubly labeled water, Cameroon

Introduction

The existence of adaptive mechanisms in humans that regulate body weight despite varying food intakes is a long-standing subject of debate. A reduction in energy expenditure has been reported during restrictive regimens and underfeeding (1, 2). However, the adaptation to raised energy intakes is still controversial though well established in animal studies (3).

Neumann (4) first addressed this issue 89 y ago (4), using himself as a subject in a 3-y dietary study. He demonstrated that he was able to maintain his weight within narrow limits despite considerable variation in energy consumption and put forward the "luxuskonsumption" concept, whereby excess energy was dissipated during overeating. Many authors followed his work; some (2, 5–10) were in agreement with the theory of luxuskonsumption, also called "wastage energy expenditure" (5) or "facultative thermogenesis" (11), whereas others (12–21) failed to confirm Neumann's findings in comparable overfeeding studies and cast doubts on the reality of the phenomenon. They argued that if complete energy balances were obtained, no unexpected energy gap would be found.

Garrow (22) proposed, in a well-known review, that a threshold in cumulative overfeeding could trigger luxuskonsumption. This is suggested in the results of the Vermont Prison Studies by Sims et al (9, 23), which include massive long-term overfeeding. It was observed in a group of lean volunteers who gained, in addition, 20% of their original weight, that 50% more energy than their previous maintenance intake was required to maintain their new body weight. Unfortunately, the design of the study did not allow complete energy-balance measurements, and the question of the magnitude of thermogenesis during a long-term and massive overfeeding still remains unanswered.

We addressed the issue on the basis of an energy-balance study performed from July to October 1988 in free-living volunteers who were participating in a traditional fattening session (*Guru Walla*) in the Massas, an ethnic group from northern Cameroon. This social institution, aimed at prestige acquisition (24), includes a massive overfeeding representing twice or threefold the habitual daily intake. The measurement of energy intake is here set against changes in body weight, body composition, activity, metabolic rates, and total daily energy expenditure (TEE).

Subjects and methods

Nine lean young adult men volunteered for study throughout the *Guru Walla* session, having been fully informed of our goals and procedures. Their physical characteristics are shown in **Table 1.** The research protocol was approved by the Committee on Human Investigation of the Xavier Bichat Medical School. A thorough clinical examination was made before the fattening session. In addition, a wide-spectrum antiparasite [Zentel (albendazole); Smith-Kline and French, Paris] effective on all intestinal worms endemic in the region was given to all nine subjects.

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TABLE 1
Age and physical characteristics of subjects*

Age (y)	28.6 ± 4.9 (23–35)
Height (cm)	183.7 ± 4.8 (177–194)
Weight (kg)	68.5 ± 6.5 (60.9–79.6)
BMI†	20.3 ± 1.6 (18.2–23.1)
Body fat (%)‡	11.5 ± 3.1 (7.5–15.3)

* $\bar{x}$ ± SD (range); $n = 9$.
† BMI, body mass index (kg/m^2).
‡ From skinfold thickness.

The fattening sessions are traditionally performed during the rainy season and last ≈2 m. Following the *Guru Walla* tradition, all participants began the session within an interval of 5 d; each one was isolated in a different house with his own female attendant devoted exclusively to the preparation of *Guru Walla* meals. Meals were given continuously, day and night, at ≈3-h intervals (except when subjects had to fast for the needs of the experimental protocol).

During the observation periods, food intake and spontaneous activity were recorded continuously. Baseline data before the fattening session were obtained for each subject over 7–10 d. Data were recorded for 3 d every 10 d during the session. In addition, measurements were done for another 10 d at the end of the session.

Food intake

Food was weighed by specially trained assistants working 24-h shifts during the measurement periods. A light-weight beam scale (type 565; Terraillon, Annemasse, France), weighing to 10 kg with a precision of 5 g, was used. Meal preparation and meal composition were recorded. Foods were weighed every time a meal was prepared and ingested. Snacks eaten, such as fruits or groundnuts, were also weighed before ingestion following standard procedure (25). Vomiting, if any, was also recorded.

Activity

Spontaneous physical activity was assessed by using two independent methods. First, a time-allocation survey was done by local assistants who recorded activities, postures, and pace minute by minute. This was done for the waking day in the control period and for 24 h during the overfeeding period. Reference was made to tables of energy expenditure [expressed in multiple of basal metabolic rate (BMR)], including data from the literature (26) and data from Cameroonian populations (P Pasquet, 1986, unpublished observations). Second, activity was monitored using a wrist watch–type movement-recording electronic device (accelerometer) designed by INSERM U305 (Technologie Biomédicale, Toulouse, France), very similar in its features and performance to that described by Avons (27). The device was attached with a light plastic bracelet to the wrist of the nondominant arm. Activity scores were read at 5-d intervals with an external digital reading device (Inserm U305).

Body weight and body composition

Body weight was measured every day during the baseline period and every 10 d during the fattening session, by using a portable field survey beam scale (CMS Weighing Equipment, Ltd, London), weighing ≤ 120 kg with a precision of 50 g. When weighed, the subject was in shorts, had fasted overnight, and had emptied his bladder.

Body composition was assessed by using three different methods concurrently: *1*) by anthropometry, according to the Durnin and Womersley four-sites method (28) with a Holtain/Tanner Whitehouse skinfold caliper (Holtain Ltd, Crosswell, UK), frequently recalibrated; *2*) by body-impedance analysis (29) with a BIA 101 (RJL Systems, Detroit), according to Segal et al (30) in the standard conditions described above for body weighing; and *3*) by isotopic dilution (deuterium) with measurements of total body water (31) and estimates of fat-free mass (FFM), assuming 73.2% water in FFM (32). Oral doses of 0.05 g ^2H_2O/kg were given at the end of the control period and at the end of the final 10 d of the overfeeding period for eight of the nine fasting subjects in the study. Urine samples were collected after a 4-h fasting equilibration period (a predose urine sample was also collected to assess the isotope baseline value). Isotope abundance in urine was measured by mass spectrometry.

Metabolic rates

Resting metabolic rates (RMRs) were measured on waking every 2 d during the baseline period and every 10 d during the overfeeding period, the subjects having refrained from eating for the 11–12 h preceding the measurement. Postprandial RMRs were measured twice at the end of the baseline period and every 10 d during the overfeeding session. All RMR measurements were in duplicate, separated by a 10-min rest. For postprandial metabolic rates (ppMRs), sampling took place twice at each measurement session, 60 min and 100 min after the preceding meal.

The energy expenditure of moderate exercise was assessed at the end of both control and overfeeding periods under standardized conditions (≥ 4 h after the last meal) at 50 W on a Monarch bicycle ergometer (Monark-Crescents, Valberg, Sweden).

Measurements were performed by indirect calorimetry with the Douglas bag technique (33). Exhaled gases were collected for ~10–12 min, by using a mouthpiece connected to a 150-L polyvinyl bag (Ealing Harvard, France). Gas volume was measured with an Ealing/Harvard dry gas meter. The concentrations of oxygen and carbon dioxide were measured by using portable paramagnetic oxygen analyzers (model 570 A and 580 A; Servomex, Saint Denis, France) and an infrared portable carbon dioxide analyzer (model PSA 404, scale range 0–6%; Servomex). Recalibration with fresh dried air and with two standard gases [99.995% N and 5.5% CO_2 in N (Alphagaz, Paris)] was done every two measurements for oxygen analyzers and every day for the carbon dioxide analyzer. Gas volumes were corrected to be expressed in standard temperature, pressure, and dry conditions. Gas exchange rates were converted into energy units by using equation 30 of Elia and Livesey (34).

Total daily energy expenditure (TEE)

TEE was assessed by the doubly labeled water method (DLW). The DLW method, first applied to small mammals (35), was

recently validated in humans (36, 37) and used under tropical conditions (38). It allows TEE to be estimated from total carbon dioxide production during 10–15-d periods in adults. The method is based on the isotopic equilibrium between the oxygen expired as carbon dioxide and the oxygen in body water. The DLW method consists—after loading subjects with water enriched with stable isotopes—of the measurement in the subject's urine of the difference between the elimination rates of ^{18}O (which relates to water and carbon dioxide outputs) and of ^{2}H (which relates to water output alone).

Eight fasting subjects, of the nine in the study, each received two oral doses of DLW, a mixture of $^{2}H_2O$ with 0.05 g ^{2}H/kg body wt, and $H_2{}^{18}O$ with 0.15 g ^{18}O/kg body wt. One dose was given at the beginning of the control period and the other at the beginning of the final 10 d of *Guru Walla*. One urine sample was collected after a 4-h fasting equilibration period and then every day for 10 d in both measurement periods. A predose urine sample was also collected to assess the isotope baseline value. Samples were then frozen at −18 °C.

Isotope abundance in urine was measured by using a gas-isotope-ratio mass spectrometer (Sira II; VG Isotech, Manchester, UK) after reduction of water vapor over hot uranium for deuterium measurement and after equilibration of urine with purified carbon dioxide for ^{18}O measurement. The ^{2}H and ^{18}O elimination rates were calculated by using the multiple point method (37). ^{18}O and ^{2}H dilution spaces and total body water (TBW) were calculated at time zero by using the slope-intercept multipoint procedure (39).

Mean daily carbon dioxide production rate (L/d) was calculated by using a modification of Lifson and McClintock's equation (35, 40).

$$rCO_2 = \frac{1}{2f_3} \times \frac{Vo}{18.02}\left[1.01\ ko - 1.04\ kd\left(\frac{f_2x + (1-x)}{f_1x + (1-x)}\right)\right] \times 22.4$$

where ko and kd are ^{18}O and ^{2}H disappearance-rate constants; f_3 is 1.039, the breath carbon dioxide isotope-fractionation factor; f_2 and f_1 are 0.990 and 0.945, respectively, ^{18}O and ^{2}H fractionation factors in water-vapor losses (41); x is the proportion of water loss that undergoes fractionation (control period, 0.15; overfeeding, 0.10); Vo = TBW (mL) determined from the dilution space of $H_2{}^{18}O$ (mid $H_2{}^{18}O$ + $^{2}H_2O$ dilution space was also used in the computation of rCO_2, and the results are not significantly different).

Daily oxygen consumption was then calculated by using the rCO_2 and an estimate of the respiratory quotient (RQ), ie, the food quotient (FQ) obtained from the macronutrient composition of the diet in both periods of observation (42), adjusted for the calculated fat synthesis during the overfeeding-measurement period. TEE was then calculated according to equation 38 of Ben Porat et al (43).

Biological samples

Total, 24-h urine samples were collected during the final 10 d of *Guru Walla*, for 4 d continuously on 0.5 mol H_2SO_4/L, and their total nitrogen content was measured according to Kjehldahl's method. The energy equivalent of nitrogen was considered to be 33 kJ/g. The possible presence of urinary glucose was checked by using Clinistix tests (Ames, Puteaux, France).

Stools were collected continuously during the same 4 d as above, in topped vessels and weighed within 12 h; aliquot samples were then dried and burned in a bomb calorimeter to assess their energy content.

Samples of red sorghum (*Sorghum caudatum*) and cow milk, which together constitute > 95% of the energy intake of the *Guru Walla*, were collected for chemical analysis. Gross energy content was determined by burning aliquot samples in a bomb calorimeter.

Results

Energy and nutrient intakes

Results in Table 2 include *1*) daily gross energy intake corrected for energy lost through vomiting; when vomiting occurred the whole meal's gross energy content was factored into calculation of losses; *2*) available energy calculated after exclusion of measured fecal and urinary losses; and *3*) the macronutrient composition of this high-carbohydrate, high-fiber regimen, which was fairly constant during the two observation periods ($\chi^2 = 2.17$ with 2 df) despite a slight increase of the fat fraction due to increased milk consumption following the *Guru Walla* tradition.

Mean gross energy content in feces for the collection period was 5024 ± 1035 MJ/d (ie, 15.4 ± 3.3% of gross energy intakes), including the energy of fiber (47 ± 4.2% of dry matter). The percentage of water in feces was 78 ± 1.9%. Urinary nitrogen content was 5.4 ± 2.1 g/d. No glucose was found in the urine samples. Digestibility and urine energy content were assumed to be constant throughout the study and the control period. Total cumulative overfeeding during the session was 955 ± 252 MJ (228 ± 60 Mcal) ($\bar{x}$ ± SD), ranging from 518 to 1377 MJ, and the mean increase in daily energy intake was 124.9 ± 46.6% (range 56–212%) of baseline intakes. Cumulative overfeeding computed from food-composition tables (44) alone resulted in a mean estimate 14.7% higher (1095 ± 303 MJ).

Changes in body weight and composition

Table 3 presents the increases in body weight and the concomitant changes in body composition after *Guru Walla*. The

TABLE 2
Energy and macronutrient intakes during the control and *Guru Walla* periods*

	Control	*Guru Walla*
Gross energy (MJ/d)†	16.8 ± 2.7	36.6 ± 5.1
	(13.1–20.8)	(29.5–46.1)
Available energy (MJ/d)‡	12.9 ± 2.1	28.2 ± 3.6
	(10.6–16.2)	(23.6–33.9)
Carbohydrate (%)	74.9 ± 3.7	70.1 ± 2.8
Percentage of gross energy	(68.2–80.1)	(65.4–74.2)
Fat (%)	10.6 ± 2.0	15.2 ± 2.0
Percentage of gross energy	(8.7–13.8)	(12.2–19.2)
Protein (%)	14.5 ± 2.2	14.7 ± 1.3
Percentage of gross energy	(11.2–19.1)	(13.4–17.5)

* $\bar{x}$ ± SD, (range); n = 9 for 61–65 d of fattening, $\bar{x}$ = 62.2 d.
† Corrected for energy in vomit.
‡ Corrected for losses in feces and urine and for monosaccharides (assuming 15.6 kJ usable energy/g glucose).

TABLE 3
Increases in body weight and changes in body composition after the *Guru Walla* fattening session

	$\bar{x} \pm$ SD (range)*
	kg
Body weight	+17.0 ± 4.0 (+11.7 to +23.2)
Fat mass	
From skinfold thickness	+10.8 ± 2.4 (+6.6 to +13.3)
By bioelectrical-impedance analysis	+11.6 ± 2.3 (+9.1 to +15.6)
From total body water measurement by deuterium dilution†	+11.7 ± 1.6 (+9.4 to +14.2)
Lean body mass	
From skinfold thickness	+6.2 ± 2.3 (+1.9 to +10.3)
By bioelectrical-impedance analysis	+5.4 ± 2.7 (+1.9 to +8.9)
From total body water measurement by deuterium dilution†	+4.5 ± 3.8 (−1.6 to +9.4)

* $n = 9$ except where noted otherwise.
† $n = 8$.

mean increase in body weight was 17 ± 4 kg, or 24.9 ± 5.5% (range 17–33%). The amplitude of mean body-composition changes was globally comparable whatever the method used. Increases in fat mass explain 64 ± 9.3% to 75 ± 20% of total body-mass changes. In the meantime FFM increased from 7.3 ± 6% to 10 ± 3.4%.

Changes in spontaneous activity

We observed a clear decrease in spontaneous activity, as calculated by the time-allocation method, in all nine subjects during *Guru Walla*. Mean physical activity level (PAL) was 1.849 ± 0.135 times BMR (range 1.660–2.101) during the baseline control period and 1.423 ± 0.090 times BMR (range 1.336–1.490) during the fattening session. The most dramatic reduction in activity was observed at the beginning of *Guru Walla*, whereas PAL tended to increase, on average, throughout the session. The minimum resting component of energy expenditure (REE) was estimated to be BMR plus 10% of TEE, allowing for thermogenesis on the basis of the overall individual PALs over 24 h [for example, if PAL = 1.8 × BMR, then estimated REE = (1 + 0.18) × BMR]. On this basis the mean decrease in physical activity (PAL − REE) over the fattening session was 59 ± 10% (range 41–71%).

Overall activity as measured with activity meters also showed a clear reduction during overfeeding. However, measurements were available for only 20 continuous d, on average, during the *Guru Walla* period. Mean decrease was 40 ± 20.6% (4145 ± 1371 and 2440 ± 816 arm-movement counts/24 h in control and *Guru Walla* periods, respectively), which is less than was estimated by the time-allocation method. Moreover, higher between-subject variability was observed (range 5–64%).

Changes in metabolic rates

Mean RMRs, ppMR, and activity metabolic rates (AMRs) in control and overfeeding periods are presented in **Table 4.** Baseline RMRs fit into theoretical BMR values according to Schofield's standards (45) ($r = 0.67$; $P < 0.05$).

During *Guru Walla*, RMR increased dramatically in all subjects and the mean rise was 43.5 ± 10.1% (range 32–64%). Expressed per kilogram of lean tissue, RMRs rose by 35.5 ± 10.5% (range 21–57%). Most of the time, measured overall RQs were above unity in all subjects during the fattening session. Mean values varied slightly from 1.07 ± 0.07 after 10 d of overfeeding to 1.04 ± 0.06 during the last 10 d.

Means of consecutive measurements of ppMR were not statistically different (paired t test = 0.6; $P > 0.05$) and therefore results on ppMRs correspond to metabolic rates between 60 and 100 min after the last meal. Like RMRs, ppMRs increased dramatically and significantly in all subjects except one during overfeeding, and the mean rise was 26.4 ± 12.3% (range 7–48.5%). Mean overall RQs varied from 1.09 ± 0.03 after 1 wk of fattening to 1.07 ± 0.05 at the end of the session.

Data on 50-W cycling metabolic rate during the *Guru Walla* period were obtained on only four subjects. However, the results showed a significant 18 ± 5.0% increase in AMR at the end of *Guru Walla* and overall RQs averaged 0.89 ± 0.03.

Energy balance

Table 5 presents individual mean daily energy intake, TEE, body-weight changes, and the PALs during the control period and the last 10 d of overfeeding of the eight subjects that received DLW.

The subjects doubled their energy intakes when overfed, but we also observed

1) no increased mean daily TEE during the last 10 d of *Guru Walla* (in two subjects TEE was increased whereas it was lowered in three and remained almost the same in three,

2) a reduction of the PAL in all subjects, and

3) an increase in body weight of ≈1 kg in 10 d.

Discussion

The fattening sessions resulted in a mean extra energy intake of 955 MJ and an increase of 17 kg in body weight. Whereas metabolic rate was increased in resting, postabsorptive, or exercising states, TEE, as measured during the final 10 d of *Guru Walla* by the DLW method, did not change with respect to pre-session baseline values.

Over the whole overfeeding session, we noted a 43.5% mean increase of RMR, which is much higher than previously reported in the literature. Indeed, numerous studies (2, 18–20, 46–53)

TABLE 4
Resting metabolic rates (RMRs), postprandial metabolic rates (ppMRs) and activity metabolic rates (AMRs) after the *Guru Walla* fattening session*

	Control	*Guru Walla*
	kJ/min	
RMR	5.08 ± 0.30 [5]	7.26 ± 0.72 [12]†
ppMR	6.37 ± 0.60 [2]	8.01 ± 0.54 [6]†
AMR‡	19.54 ± 0.76 [2]	23.26 ± 1.14 [2]§

* $\bar{x} \pm$ SD; $n = 9$ except where noted otherwise. Numbers of measurements per subject in brackets.
‡ $n = 4$.
†§ Significantly different from control period: †$P < 0.001$; §$P < 0.01$ (paired t test).

TABLE 5
Individual daily energy intake (EI), total energy expenditure (TEE), body-weight changes, and physical-activity level (PAL) for subjects during the control period and the final 10 d of the *Guru Walla* fattening session

	EI		TEE		Weight changes		PAL*	
Subject	Control	*Guru Walla*	Control	*Guru Walla*	Control	*Guru Walla*	Control	*Guru Walla*
	MJ/d				*g/d*			
1	10.6	27.6	14.2	9.2	−190	+240	1.877	1.363
2	16.2	21.9	13.5	12.3	+70	+50	1.720	1.368
3	13.9	28.9	17.3	15.7	−150	+110	1.906	1.418
4	15.1	20.4	15.8	16.1	−170	+40	1.970	1.360
5	11.8	27.6	12.2	15.8	−190	+160	1.742	1.478
6	10.6	27.7	14.5	15.1	−50	+200	1.814	1.541
7	13.2	24.7	12.6	13.1	−90	+10	2.101	1.449
8	10.6	21.8	12.5	15.5	0	+60	1.852	1.589
$\bar{x} \pm$ SD	12.7 ± 2.2	25.1 ± 3.1†	14.1 ± 1.7	14.1 ± 2.5	−96 ± 90‡	+110 ± 82§	1.873 ± 0.122	1.445 ± 0.085†

* Multiple of basal metabolic rate (BMR).
† Significantly different from control period, $P < 0.001$ (paired t test).
‡ Significantly different from 0, $P < 0.05$ (paired t test).
§ Significantly different from 0, $P < 0.01$ (paired t test).

have shown clear increases in oxygen consumption at rest in overfed subjects, ranging from 5% to 27%. Moreover, the response was rapid and its magnitude was out of proportion with the concomitant increase in metabolically active tissue (FFM increased by 7–10% depending on the method of assessment). This corroborates the results of many other investigators (2, 18, 19, 46, 48, 49, 51, 53) but not all (20, 52).

Given the negative balance during the control period before the beginning of the *Guru Walla* (caused by intense work during this period of the agricultural cycle), the increase in RMR could be partly explained by the return to normal from an adapted rate (54). This is doubtful, however, because no per se decrease in basal energy expenditure was found in African populations experiencing seasonal cycling of energy intake and energy balance (55).

However, the marked rise above unity of overall RQ values during the overfeeding suggests that some de novo lipogenesis from carbohydrates, as observed elsewhere (56), was still proceeding in our subjects who fasted 11–12 h, ie, at least part of the increased heat production reflects tissue-storage–induced obligatory thermogenesis.

Because the energy and the nutrient contents of the meals before measurement were globally comparable in both experimental periods, it can be concluded from our results (mean increase of 26.4%) that overfeeding induced a clear increase in heat production at rest, postprandially. This result agrees with most of the findings of the literature (20, 48, 50, 51, 57).

We reported a significant, 18% increased metabolic rate when cycling at 50 W at the end of the overfeeding session. This result agrees with results from some previous reports (2, 7, 58). However, our data hardly substantiate the existence of a per se overfeeding-induced effect on AMR, ie, decreased mechanical work efficiency. Indeed, considering the experimental conditions, 4–5 h after the preceding meal a residual postabsorptive ingestive thermic effect has to be taken into account. Moreover, the increase in RMR as measured after an 11–12-h fast itself relates to ≥ 65% of the increase in AMR. Last, we cannot exclude a partial effect of moving heavier legs when cycling at the end of fattening.

Mean TEE, as estimated by the DLW method, remained apparently fairly constant at 14.1 MJ/d during the baseline period and during the final 10 d of fattening. However, the mean PAL of the subjects was substantially lowered by ≈0.4 times BMR during the latter period. This is equivalent to 3.6 MJ/d, ie, some 30% of the energy in excess on average.

Do our results allow the magnitude of the overfeeding-induced thermogenesis to be determined and do they substantiate the existence of a facultative component of the diet-induced thermogenesis during massive overfeeding? The increase of energy expenditure depends on two sets of factors: on the obligatory energy costs induced by the effects of changes in body weight and composition (FFM) on activity and RMRs, respectively, and on the diet-induced thermogenesis (DIT), which includes the obligatory cost of storing the excess nutrients and the hypothetical faculative regulatory thermogenesis.

If the data stemming from the time-allocation survey (PALs) are used together with the measured RMR to estimate TEE during the control period (59), comparison with DLW measures during the same period gives similar mean figures: 13.6 ± 1.8 vs 14.1 ± 2.1 MJ/d. Only a nonsignificant 3.6% higher mean estimate is noted when using DLW.

On these bases, a mean predicted TEE for the overfeeding observation period can be calculated by using the PALs observed at the end of fattening. Hence, the minimal factorial predicted TEE (ie, excluding any adaptive process) could be estimated on the basis of control RMR adjusting proportionally both rest fraction of PAL (< 1.15 × BMR, allowing for BMR plus thermogenesis) and activity fraction of PAL (> 1.15 × BMR) for the effects of increased FFM and total body mass, respectively. Any difference between TEE measured from DLW and predicted TEE should be interpreted as DIT.

During the final 10 d of *Guru Walla,* mean daily TEE, as measured by DLW, was 14.1 MJ. Predicted TEE was 12 ± 1.25 MJ/d. The mean difference of 2.1 MJ/d accounted for 16.6% of

the 12.3-MJ/d mean excess energy ingested at the end of fattening. When excluding one subject (1)—given the surprisingly low TEE estimates during the overfeeding observation period (9.2 MJ/d) compared with 24-h RMRs as measured by indirect calorimetry (9.8 MJ/d) in a somewhat active subject—the DIT amounted to 23.4% of mean excess energy intake.

Few studies have given estimates of TEE during overfeeding and assessed the thermogenic response to overfeeding. However, analysis of the available literature (20, 21, 46, 47, 51, 53, 60, 61) gives the average figure of 14.5% of excess energy intake for the latter.

It appears that DIT depends on the type of overfeeding. The highest values are reported in studies where carbohydrate is the main nutrient (53, 61). Recently, Bandini et al (53) overfed 14 adolescents for 2 wk with a high-carbohydrate diet. DLW was used to measure TEE, and the estimated thermic effect of overfeeding was found to be 18.2% of the energy in excess. Earlier, Schutz et al (61) had fed, for 7 d, three lean men with increasing amounts of very-high-carbohydrate supplements and gave the figure of 27%, the largest value of DIT reported in man. Our findings (16.6% or even the less conservative 23.4%) are therefore within the range of the reported values.

Mean TEE (14.1 MJ/d), measured by DLW, did not change significantly between the baseline reference period and the end of the overfeeding experimental period. Given the high RQs observed during this later period, we assume the average body weight increases of 1.1 ± 0.82 kg in 10 d to be only the reflection of fat synthesis. This accounted for 4.3 ± 3.3 MJ/d. Therefore ≈6.7 ± 3.6 MJ/d remained unaccounted for, ie, on average, 26.3% of the energy intake (25% when excluding subject 1). One can argue that a 10-d period of observation is not sufficient for realistic assessments of changes in body weight and composition. Because the mean daily PAL during the last 10 d of *Guru Walla* is not different from the average activity level during the whole fattening session, and considering the higher values of RMR and body weight at the end of *Guru Walla*, we assume that mean daily overfeeding TEE does not exceed that observed during the final 10 d. As estimated by deuterium dilution on the eight subjects, daily amounts of fat and fat-free tissue synthesized were 185 ± 28 and 77 ± 55 g/d, respectively. This accounts for 7.8 ± 1.1 MJ/d. Thus, given a total energy intake of 27.5 ± 2.8 MJ/d during *Guru Walla*, some 5.8 ± 4.5 MJ/d, or ≥ 20.7%, of the total energy intake (18.7% when excluding subject 1) is not accounted for when setting up the energy balance and considering the entire fattening session.

How can this discrepancy be explained? Had the energy intake been overestimated, and/or the energy deposition, or the energy expended been underestimated during the overfeeding session?

First, could intake measurements be at fault, ie, overestimated during overfeeding, underestimated during the baseline period, or both? Food intakes were carefully checked during measurements of overfeeding. Because observation was discontinuous, our volunteers may have eaten more during the five, 3-d measurement periods over the first 50 d than between measurement periods. However, continuous monitoring performed during the last 10 d of the overfeeding session yielded an even bigger gap between observed and expected energy cost of weight gain (on average, 1.1 ± 0.82 kg weight gain for 118 MJ extra energy).

Energy losses incurred through vomiting included the whole amount of energy from the previous meal. The bias, if any, results in underestimated energy intake. Furthermore, no noticeable complaints of diarrhea, which would overestimate available energy, were made within and between follow-up sessions.

Total unmeasured energy losses in tropical conditions do not exceed 200 kJ/d, of which energy from nitrogen losses through sweat can be estimated to a maximum total 126 kJ/d (mainly urea, 3.5 g/d) (62). We assumed this to hold for both control and *Guru Walla* periods. An increased loss of nitrogen through skin substantial enough to explain a significant fraction of energy loss during overfeeding is quite unlikely and there was no indication of it.

It may be legitimate to question the metabolizable energy intake during baseline period because we made the assumption that the percentage of energy lost in feces was similar in the two periods. In fact the possible underestimation of baseline intakes would result in an overestimation of the amount of overfeeding of limited extent. Moreover, no changes in energy bioavailability were reported in previous experiments with overfeeding diets (13, 19, 46, 63), and the observed fecal energy losses (15.4 ± 3.3% of gross intake, on average) are compatible with losses in high-fiber diets (64).

There is no reason to suspect an analytical error in the estimation of fat and lean body mass because we used classical and extensively used methods and calculations. However, we cannot exclude an underestimation in the energy density of the deposited tissues during fattening. For example, as already emphasized (37, 65), the hydration of FFM could be more variable than the 73.2% we used. Indeed, we observed a substantial increase in body-water flux in our subjects; observation from food alone (excluding drinking water) gives the figure 6.6 ± 0.8 L/d ingested water, whereas we observed 2.4 ± 0.4 L/d during the reference period. This corroborates the estimated total water flux calculated from the isotopic approach:

$$rH_2O = TBW \times Kd = 8.6 \pm 1.1 \text{ L/d and } 5.2 \pm 0.8 \text{ L/d}$$

during the overfeeding and the reference observation period, respectively. Therefore, in such a particular physiological situation, it can be speculated that the actual FFM hydration coefficient is higher than assumed. This would result in a fat-deposition rate higher than estimated. This kind of underestimation could explain, at least partially, the observed discrepancy in the energy balance.

An underestimation of TEE is possible because the DLW method involves some assumptions that could be invalid in the particular conditions of our study. One problem in relation to the DLW model—and not accounted for in our analysis—concerns the effect of potential labeled-hydrogen sequestration into newly deposited tissue on estimated rates of carbon dioxide production. If only fat is synthesized de novo during the last 10 d of *Guru Walla*, and assuming 0.5333 g water equivalents incorporated in 1 g fat (66), a 6.1% underestimation of TEE is possible.

Another assumption is that the natural isotopic abundance (background value) remains constant during the observation period. Because the overfeeding DLW-measurement session took place at the end of September as the rainy season was coming to an end, possible season-induced isotopic background changes may have occurred and the drinkable water may have become more and more isotopically heavy during the study period. The observation of isotopic baseline changes in body water was not

possible in our enriched subjects. Nevertheless, Coward (39) reported only a possible 1.6% underestimation of carbon dioxide production rates in Gambian infants during the entire period between the rainy and dry seasons, in which the most rapid isotopic background changes are observed.

On this basis, the conjunction of both possible background changes and deuterium sequestration gives the mean figure of 15.2 MJ/d for TEE, and the amplitude of the reevaluated thermogenesis is 27.2% of the energy in excess. However, even taking into account these very plausible estimates, there is still a discrepancy between the energy expenditure, body-weight changes, and energy intake, and the source of error in the data remains unidentified.

Despite this, consistent thermogenesis is observed in this study, especially when using the previously corrected values of TEE (DIT = 15.2 − 12.0 = 3.2 MJ/d). Given the high measured RQs, a significant component of this thermogenesis could be plausibly attributed to an extra-obligatory heat production due to costly glycogen production and degradation from carbohydrates before their storage as fat, as hypothesized recently (56, 67). On the basis of the measured postabsorptive nonprotein RQ (1.08 on average), the total cost of de novo lipogenesis during the final 10 d can be estimated as 1.3 MJ/d from the tables of Elia and Livesey (33) and assuming a cost of 0.33 kJ/kJ deposited fat (56).

Therefore, considering a DIT of 3.2 MJ/d, the existence of a facultative component of thermogenesis, suggesting some energy-wasting adaptive process during overfeeding (luxuskonsumption), can be legitimately considered.

In summary, long-term massive high-carbohydrate overfeeding does induce an increase in metabolic rates, notably resting values, and thermogenesis. However, the latter is not greater than that measured under less extreme conditions of carbohydrate overfeeding. If luxuskonsumption does exist its magnitude is not related to the amount of cumulative overfeeding. ■

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