Variations and determinants of energy expenditure as measured by whole-body indirect calorimetry during puberty and adolescence[1–3]

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ABSTRACT

Background: Adolescence is characterized by rapid anatomic, physiologic, and behavioral alterations expected to induce changes in metabolic rate.

Objective: The aim of the present study was to investigate variations in daily energy expenditure (DEE) and its main components during adolescence and to quantify their significant determinants.

Design: Eighty-three children and adolescents (44 boys and 39 girls aged 10–16 y) participated in this cross-sectional study. Tanner stages ranged from 1 to 5. Body composition was assessed by both the skinfold-thickness method and bioimpedance analysis. Energy expenditure (EE) was determined continuously over 24 h by using 2 whole-body calorimeters. The subjects followed a standardized activity program that included four 15-min periods of exercise on a cycle ergometer.

Results: Body composition, DEE, sleeping EE (SEE), resting EE, and EE during meals, miscellaneous activities, and physical exercise varied significantly with sex and stage of puberty. The DEE of boys and girls averaged 8.22 and 7.60 MJ in prepubertal children, 11.35 and 9.10 MJ in pubertal children, and 11.73 and 9.68 MJ in postpubertal adolescents, respectively. The significant determinants of DEE and SEE, respectively, were fat-free mass (r^2 = 0.842 and 0.826), sex (r^2 = 0.017 and 0.022), and season (r^2 = 0.021 and 0.011). Stage of puberty and fat mass were not significant factors. DEE and SEE adjusted for fat-free mass were on average 5% higher in boys than in girls and 6% higher in spring than in autumn.

Conclusions: The DEE of adolescents measured under standardized conditions varied with sex, body composition, and season, but not with stage of puberty. These variables could be predicted accurately from fat-free mass, sex, and season. *Am J Clin Nutr* 1999;69:1209–16.

KEY WORDS Adolescents, children, body composition, energy metabolism, calorimetry, puberty, season, sex, fat mass, fat-free mass, energy expenditure

INTRODUCTION

Adolescence is characterized by faster growth than during any other period except the first year of life. This period of development involves anatomic, physiologic, and behavioral changes that usually begin between the ages of 9 and 13 y in girls and 10 and 14 y in boys. The sexual dimorphism in anthropometric indexes emerges during the 5 y of adolescence (10–15 y of age in girls and 12–17 y of age in boys). Boys gain more lean tissue, especially skeletal muscle, than girls, whereas girls gain more adipose tissue than boys (1). These alterations are expected to induce changes in metabolic rate and energy requirements of adolescents because energy expenditure (EE) is closely related to fat-free mass (FFM) (2, 3). Therefore, there is a need for more information about variations in EE during this important period of life to estimate their energy requirements accurately.

The aim of the present cross-sectional study was, therefore, to investigate the variations in daily EE (DEE) and its main components [sleeping EE (SEE), basal metabolic rate (BMR), resting EE (REE), and EE during meals and physical activity] during puberty and adolescence, and to quantify the effects of sex, stage of puberty, body composition, physical fitness, and season. EE was measured by whole-body indirect calorimetry according to a standardized activity program.

SUBJECTS AND METHODS

Subjects

Sixty-two adolescents, 4 groups of 15–16 boys or girls aged 12–13 or 14–16 y, participated in this study. The volunteers were recruited from 2 high schools in the suburbs of Clermont-Ferrand, France. The study was carried out during spring and autumn with 7 or 8 subjects per group during each period. Before the study began, the purpose and objectives were carefully explained to each subject and his or her parents. Written informed consent was obtained from all adolescents and their parents. The experimental protocol was approved by the National Ethical Committee on Human Research for Medical Sciences.

All subjects had a thorough physical examination and a medical history was taken. Only children aged 12–16 y who were appar-

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ently healthy, were not suffering from any diagnosed disease, and were taking no medication known to influence energy metabolism were included. Their usual activity (number of hours per week of physical training at school or in clubs and usual types of leisure) was assessed by interview in the presence of their parents. Weight was measured to the nearest 0.1 kg with a portable digital metric scale, which was calibrated by using standard weights. Obesity was defined by a body mass index (BMI; kg/m^2) above the 90th percentile for chronologic age (4). Pubertal development (Tanner stage) of the adolescents was assessed from secondary sexual characteristics, ie, breast development and pubic hair in girls, and genital development, ie, testes and penis, and pubic hair in boys (5).

Peak oxygen uptake (peak $\dot{V}O_2$) was measured in all subjects by using a cycle ergometer. The subjects performed several successive 3.5-min steps against increasing braking forces until exhaustion. The first step corresponded to 17.5 W. The exercise intensity was then increased by 17.5-W steps. The pedaling frequency was 70 rpm. Heart rate was recorded continuously (Cardiovit CS-6/12; Scheller AG, Baar, Switzerland). Oxygen consumption and carbon dioxide production were measured continuously by open-circuit respirometry and averaged every 30 s by using an automated on-line system (CPX ID; Medical Graphics, St Paul). The criteria for reaching peak $\dot{V}O_2$ were a respiratory quotient >1.1 and a maximal heart rate close to the theoretical maximum [220 − age (y)].

Determination of body composition

Body composition was assessed by using both the skinfold-thickness method (SFT) and bioimpedance analysis (BIA). Bicipital, tricipital, subscapular, and suprailiac skinfold thicknesses were measured in each subject by the same investigator using a Harpenden skinfold caliper (Holtain Ltd, Bryberian, United Kingdom). Percentage fat mass (FM) was estimated from regression equations that took into account age and sex (6). FFM was calculated as the difference between measured body weight and estimated body FM. FFM was also determined by using an impedance analyzer (model BIA 101; RJL Systems, Detroit), with 4 cutaneous probes and current at 50 kHz, and the prediction equation of Guo et al (7). This equation takes into account sex and anthropometric measurements: lateral calf, midaxillary, and subscapular skinfold thicknesses, and arm muscle circumference. FM was calculated by subtracting FFM from body weight. Upper arm muscle area was estimated from upper arm circumference and triceps skinfold thickness by using equations validated with magnetic resonance imaging in 9.5-y-old children (8).

Measurement of EE

EE was determined with whole-body indirect calorimetry by using 2 comfortably equipped open-circuit calorimetric chambers (9). Air flow, oxygen and carbon dioxide concentration of air entering and leaving the chambers, as well as ambient temperature, relative humidity, and atmospheric pressure were recorded every minute (10). The accuracy for gas exchange measurements was determined gravimetrically by continuous injection of carbon dioxide and nitrogen into the chamber. The recovery was 99.5 ± 0.6% for periods of 6–8 h and 97.2 ± 1.6% for periods of 15 min, simulating variations in physical activity (11). EE was calculated from oxygen consumption, carbon dioxide production, and 24-h urinary nitrogen excretion by using Brouwer's equation (12) over 5-min periods during exercise and 15-min periods for the rest of the day. EE was then pooled into 6 main periods: *1*) actual sleep (from 2300 to 0700), *2*) BMR (from 0700 to 0800), *3*) meals (lunch and dinner, 2 h including two 30–45-min periods of eating plus two 15–30-min postprandial periods of resting), *4*) rest (10 h, composed of seated activities such as schoolwork, video games, parlor games, and watching television), *5*) cycling exercises plus recovery periods (30 min × 4), and *6*) miscellaneous activities (1 h), including breakfast, washing, and dressing.

Timing of measurements and program of activities

Subjects spent 36 h in 2 whole-body calorimetric chambers, from 1900 to 0700 2 d later, which included 1 evening and 1 night for adaptation to the environment and adjustment of gas concentrations followed by 24 h of measurements. Before entering the chambers, the subjects were fitted with probes for continuous recording of heart rate by telemetry (Life Scope 6; Nikon Kohden, Tokyo).

During the 24-h measurement period subjects followed a defined activity program. They awoke at 0700, BMR was measured from 0700 to 0800, and they got up at 0800. They underwent four 15-min periods of exercise (at 0930, 1100, 1500, and 1730) at 4 intensities (40%, 50%, 30%, and 60% of peak $\dot{V}O_2$, respectively) on a cycle ergometer (Ergomega; Sorem, Toulon, France) at a pedaling rate of 70 rpm. Between the exercise sessions, subjects recorded only seated activities (schoolwork, reading, parlor games, video games, and watching television). Volunteers were offered breakfast at 0800, lunch at 1300, a snack at 1600, and dinner at 1930. They went to bed at 2200. Supervision was continuous while subjects were in the calorimetric chambers.

Statistical analysis

Values are expressed as least-squares means ± SDs. Data were analyzed by using SAS software (13). Two- or three-way analyses of variance were performed by using the general linear model (GLM) procedure. Adjusted means (least-squares means) were compared by *t* test. Stepwise multiple regression on the whole set of data was used to determine the significant predictors of EE. Single and multiple linear regression analyses were performed by using the GLM procedure. Differences were considered significant at $P < 0.05$. Agreement between the BIA and SFT methods was assessed by using the test of Bland and Altman (14).

RESULTS

Subjects

The distribution of the 62 adolescents between the 5 pubertal (Tanner) stages was not balanced. There were only 3 prepubertal girls. Therefore, to study the effects of stage of puberty on anthropometry, physical capacities, and energy expenditure, the results obtained previously (9) with 21 prepubertal children (12 boys and 9 girls) in the same conditions and with the same equipment were added to the results of the present study.

The distribution of the 83 subjects according to chronologic age and stage of puberty is presented in **Figure 1**. They were distributed among 6 groups of boys or girls of similar ages: 10.5 ± 0.5, 12.6 ± 0.4, and 15.0 ± 0.8 y. None of them were obese despite great variations in each anthropometric variable in each group. However, there were no significant differences in height, weight, or BMI between boys and girls at 10.5 and 12.6 y of age. Similarly, in the 15.0-y-old groups, height, body weight, and BMI were slightly but not significantly higher in males than in females.

The subjects were also distributed among 6 groups according to sex and stage of puberty: prepubertal (Tanner stage 1), pubertal (Tanner stages 2, 3, and 4), and postpubertal (Tanner stage 5)

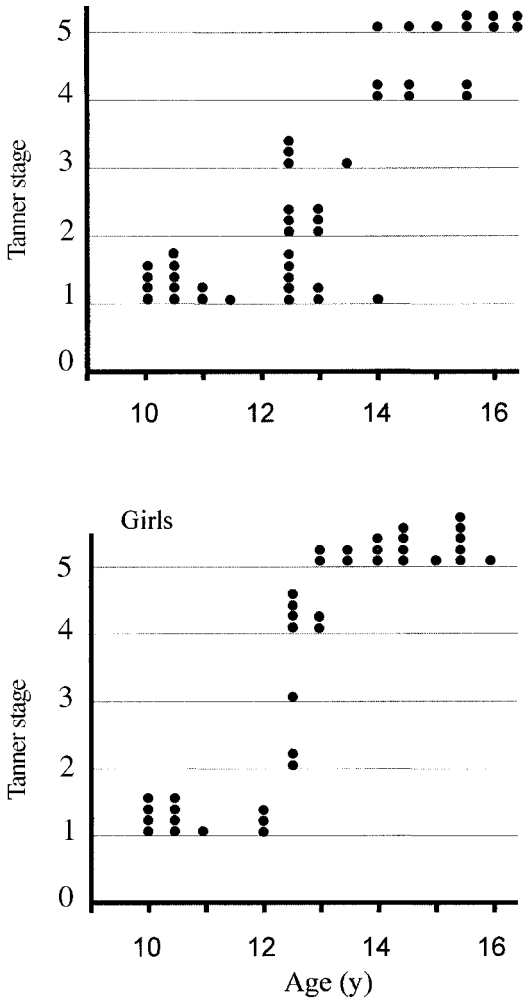

FIGURE 1. Distribution of boys and girls among 0.5-y classes according to Tanner stage of puberty.

(**Table 1**). At the same stage of puberty, boys were significantly older than girls: 0.7 and 1.3 y for prepubertal and pubertal children, respectively. Although the postpubertal girls were slightly younger than postpubertal boys, 8 of them had had their periods for >1 y, and 5 others for >2 y, which indicated that they had reached puberty much earlier than the boys. Height and body weight varied significantly with sex and stage of puberty. At the same stage of puberty, boys were on average 6 cm taller and 5.9 kg heavier than girls. BMI varied significantly with sex and stage of puberty, the difference between boys and girls being the greatest in pubertal adolescents.

Body composition

There were no significant differences between the results obtained by the 2 methods (SFT and BIA) and the mean values were the same for 3 of the 4 age groups of subjects. However, the FFM of 12–13-y-old boys predicted by the BIA method was 1.1 kg (3.1%) lower than FFM predicted by the SFT method ($P < 0.002$). There was satisfactory agreement between the BIA and SFT methods for the estimation of FFM because the 95% CI of the bias (mean difference) was from −0.51 to 0.04 kg (1.4% of FFM) and the limits of agreement (mean difference in FFM ± 2 SD) were −2.41 and 1.94 kg (–6.2% and 5.0% of FFM) (**Figure 2**). Therefore, the results obtained by the BIA method were used to adjust peak $\dot{V}O_2$ and EE for FFM as in the previous study with prepubertal children (9).

Body composition varied significantly with sex and chronologic age. However, differences in FFM and FM between boys and girls were not significant at 10.5 and 12.6 y of age. On the contrary, in the 15.0-y-old adolescents, FFM was 7.2 kg higher ($P < 0.001$) but FM was 3.0 kg lower ($P < 0.004$) in boys than in girls. In other respects, FFM was on average 9.3 kg higher in the 12.6-y-old than in the 10.5-y-old group and 11.7 kg higher in the 15.0-y-old than in the 12.6-y-old group of male adolescents. In females, the differences were 10.6 and 5.9 kg, respectively. The corresponding figures for FM were 2.9 kg ($P < 0.01$) and –1.2 kg (NS) in boys, and 2.4 and 2.2 kg in girls ($P < 0.05$). Consequently, the percentage FM was significantly lower at 15.0 y than at 12.6 y of age in boys ($P < 0.001$), but not significantly different in girls. Upper arm muscle + bone area was 26.6% greater in boys than in girls at 15 y of age ($P < 0.001$) and the difference between 12.6 and 15.0 y of age was greater in boys than in girls.

Body composition also varied significantly with sex and stage of puberty (Table 1). FFM was 15.0 kg higher in pubertal than in prepubertal boys ($P < 0.001$) and 4.2 kg higher in postpubertal than in pubertal boys ($P < 0.06$). The differences were 9.1 ($P < 0.001$) and 5.6 kg ($P < 0.01$), respectively, in girls. FM did not vary significantly with stage of puberty in boys, but was significantly greater in postpubertal than in pubertal and prepubertal girls ($P < 0.03$). Consequently, the percentage FM was significantly lower in postpubertal than in pubertal and prepubertal boys ($P < 0.08$ and $P < 0.001$, respectively), but did not vary significantly with stage of puberty in girls.

Physical capacities

Adolescents performed 3–11 h of physical training per week (6.7 h on average). There were no significant differences between groups, but there were great variations in each group. Peak $\dot{V}O_2$ also varied significantly with sex and stage of puberty ($P < 0.001$, Table 1). Differences between boys and girls were greater at the same stage of puberty than at the same chronologic age, especially in pubertal adolescents, probably because of greater differences in body weight and FFM. Peak $\dot{V}O_2$ was 0.66 L/min higher in pubertal than in prepubertal boys ($P < 0.001$) and 0.36 L/min higher in postpubertal than in pubertal boys ($P < 0.01$). The corresponding figures were 0.25 and 0.25 L/min in girls ($P = 0.06$). Peak $\dot{V}O_2$ adjusted for FFM was also significantly higher in boys than in girls; the differences were 0.22 L/min ($P < 0.02$) and 0.40 L/min ($P < 0.001$) in pubertal and postpubertal adolescents, respectively. Peak $\dot{V}O_2$ adjusted for FFM was 0.17 L/min higher in postpubertal than in pubertal boys ($P < 0.05$), and tended to be lower in pubertal and postpubertal than in prepubertal girls ($P = 0.07$).

Daily energy expenditure

The mean DEEs of prepubertal, pubertal, and postpubertal boys and girls measured in the same environmental conditions and with the same activity program are presented in **Table 2**. DEE varied significantly with sex, stage of puberty, and season; it was 25% and 21% higher in boys than in girls at the pubertal and postpubertal stages, respectively ($P < 0.001$). However, the difference was not significant in prepubertal children. DEE was also significantly higher in pubertal than in prepubertal children:

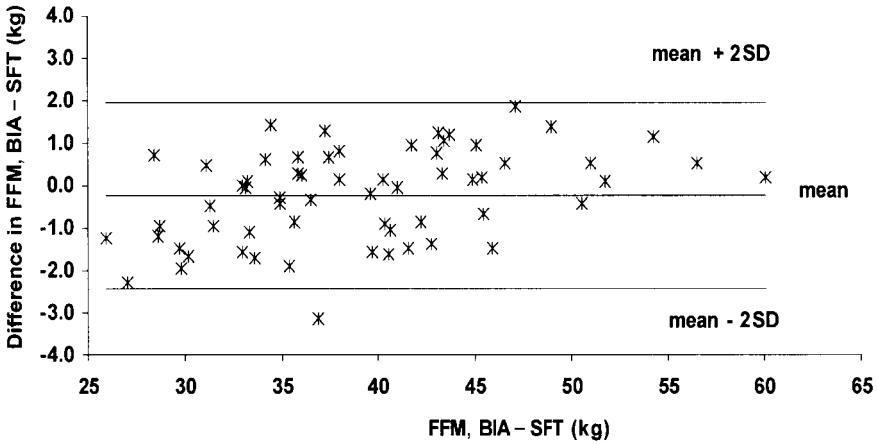

FIGURE 2. Differences in fat-free mass (FFM) content of adolescents estimated by the bioimpedance analysis (BIA) and the skinfold thickness (SFT) methods.

38% higher in boys ($P < 0.001$) and 20% higher in girls ($P < 0.01$). The differences were not significant between pubertal and postpubertal adolescents. In other respects, DEE tended to be higher in spring than in autumn ($P < 0.10$). However, because of the great differences in body size and composition between groups, DEE was adjusted for FFM. Adjusted DEE was significantly higher in boys than in girls ($P < 0.02$), the difference being greater in postpubertal than in pubertal and prepubertal subjects. Furthermore, adjusted DEE tended to be lower in postpubertal than in pubertal girls ($P = 0.06$).

SEE, BMR, REE, and EE during meals and miscellaneous activities

SEE varied significantly with sex, stage of puberty, and season (Table 2). It was on average 10%, 27%, and 18% higher in boys than in girls at the prepubertal, pubertal, and postpubertal stages, respectively ($P = 0.08$, $P < 0.001$, and $P < 0.001$). In other respects, SEE was 35% ($P < 0.001$) and 17% ($P < 0.02$) higher in pubertal than in prepubertal boys and girls, respectively. However, the differences were not significant between pubertal and postpubertal adolescents. In addition, SEE was significantly higher in spring than in autumn. Finally, SEE adjusted for FFM was significantly higher in boys than in girls (5% higher on average, $P < 0.02$), and in spring than in autumn ($P < 0.03$), but it did not vary significantly with stage of puberty.

BMR varied significantly with sex ($P < 0.001$), but not significantly with stage of puberty ($P < 0.07$). However, the ratio of SEE to BMR was significantly different between prepubertal, pubertal, and postpubertal adolescents (0.886 ± 0.054, 0.923 ± 0.077, and 0.945 ± 0.048, respectively). The lower values may result from the restlessness of prepubertal children and some pubertal adolescents during BMR measurement in the calorimeters, as suggested by the fluctuating heart rates. This result stresses the better reliability of SEE measurements in children and young adolescents.

REE and EE during meals and during miscellaneous activities were on average 60%, 71%, and 75% higher than SEE. They varied significantly with sex and stage of puberty but not with season. REE and EE during meals or miscellaneous activities were

TABLE 1
Physical characteristics of subjects depending on stage of puberty and sex[1]

	Prepubertal		Pubertal		Postpubertal		*P*		
	Boys ($n = 20$)	Girls ($n = 12$)	Boys ($n = 15$)	Girls ($n = 9$)	Boys ($n = 9$)	Girls ($n = 18$)	Stage	Sex	Stage × sex
Age (y)	11.5 ± 0.3[2]	10.8 ± 0.3	13.8 ± 0.3	12.5 ± 0.4	15.0 ± 0.4	14.6 ± 0.3	0.001	0.002	0.41
Body weight (kg)	36.0 ± 1.6	32.1 ± 2.1	52.5 ± 1.9	42.8 ± 2.4	55.2 ± 1.7	51.1 ± 1.7	0.001	0.001	0.29
Height (cm)	145.1 ± 1.7	138.9 ± 2.2	160.1 ± 2.0	153.4 ± 2.5	169.9 ± 2.5	164.9 ± 1.8	0.001	0.001	0.90
BMI (kg/m^2)	16.9 ± 0.5	16.6 ± 0.6	20.2 ± 0.5	18.2 ± 0.7	19.1 ± 0.7	18.8 ± 0.5	0.001	0.06	0.27
Relative BMI[3]	0.95	0.95	1.06	0.98	0.97	0.94			
FFM (kg)	27.9 ± 1.2^a	24.8 ± 1.5^a	42.9 ± 1.4^{c,d}	33.8 ± 1.7^b	47.1 ± 1.7^d	9.5 ± 1.2^c	0.001	0.001	0.10
Fat mass									
(kg)	8.1 ± 0.7^a	7.3 ± 0.8^a	9.6 ± 0.8^a	9.0 ± 1.0^a	8.1 ± 1.0^a	11.6 ± 0.7^b	0.02	0.29	0.02
(%)	21.7 ± 1.0^c	22.7 ± 1.3^c	18.0 ± 1.2^b	20.7 ± 1.5^{b,c}	14.6 ± 1.5^a	22.7 ± 1.1^c	0.012	0.001	0.02
Upper arm FFM area (cm^2)	26.5 ± 2.1^a	22.6 ± 3.4^a	33.5 ± 1.5^{b,c}	25.9 ± 2.0^a	37.7 ± 2.0^c	29.0 ± 1.4^a	0.002	0.001	0.60
Peak $\dot{V}O_2$ (L/min)	1.64 ± 0.07^a	1.42 ± 0.09^a	2.30 ± 0.08^c	1.67 ± 0.10	2.66 ± 0.10^d	1.92 ± 0.08^b	0.001	0.001	0.006
Adjusted peak $\dot{V}O_2$ (L/min)	1.98 ± 0.05^{b,c}	1.91 ± 0.07^b	1.96 ± 0.06^b	1.74 ± 0.6	2.13 ± 0.08^c	1.73 ± 0.05^a	0.24	0.001	0.02

[1] Prepubertal, Tanner stage 1; pubertal, Tanner stages 2, 3, and 4; postpubertal, Tanner stage 5; FFM, fat-free mass; $\dot{V}O_2$, oxygen consumption. Values in the same row with different superscript letters are significantly different, $P < 0.05$.

[2] Least-squares mean ± SD.

[3] Actual BMI divided by the value of the 50th percentile of BMIs recorded in France for 18 000 teenagers in 1997 (J Tichet, S Vol, unpublished observations).

TABLE 2
Energy expenditure (EE) of children and adolescents as measured by whole-body indirect calorimetry and variation with stage of puberty, sex, and season[1]

	Prepubertal		Pubertal		Postpubertal		*P*		
EE variables	Boys	Girls	Boys	Girls	Boys	Girls	Stage	Sex	Stage × sex
Measured EE									
Daily EE (MJ)	8.22 ± 0.27[a,2]	7.60 ± 0.35[a]	11.35 ± 0.31[c]	9.10 ± 0.40[b]	11.73 ± 0.39[c]	9.68 ± 0.28[b]	0.0001	0.0001	0.024
Sleeping EE (kJ/min)[3]	3.76 ± 0.12[a]	3.42 ± 0.16[a]	5.08 ± 0.14[c]	3.99 ± 0.18[b]	5.18 ± 0.18[c]	4.39 ± 0.13[b]	0.0001	0.0001	0.045
BMR (kJ/min)	4.61 ± 0.25	4.18 ± 0.42	5.71 ± 0.19	4.35 ± 0.24	5.35 ± 0.24	4.69 ± 0.17	0.068	0.0003	0.149
Resting EE (kJ/min)	5.75 ± 0.22[a]	5.40 ± 0.28[a]	8.18 ± 0.25[c]	6.57 ± 0.32[b]	8.41 ± 0.32[c]	6.92 ± 0.23[b]	0.0001	0.0001	0.031
EE meals (kJ/min)	6.48 ± 0.21[a]	6.17 ± 0.28[a]	8.41 ± 0.24[c]	7.13 ± 0.32[b]	8.66 ± 0.31[c]	7.14 ± 0.22[b]	0.0001	0.0001	0.047
EE miscellaneous (kJ/min)	6.51 ± 0.23[a]	6.45 ± 0.30[a]	8.49 ± 0.27[c]	7.21 ± 0.35[a,b]	8.85 ± 0.34[c]	7.56[b] ± 0.24	0.0001	0.0004	0.044
EE of exercises (kJ/min)	12.57 ± 0.45[b]	10.85 ± 0.58[a]	17.62 ± 0.51[c,d]	13.72 ± 0.69[c]	18.83 ± 0.66[c]	14.97 ± 0.47[c]	0.0001	0.0001	0.072
DEE − EE of exercises (MJ)	6.71 ± 0.22[a]	6.30 ± 0.29[a]	9.24 ± 0.25[c]	7.45 ± 0.33[b]	9.47 ± 0.33[c]	7.88 ± 0.23[b]	0.0001	0.0001	0.024
EE adjusted for FFM									
Daily EE (MJ)	9.55 ± 0.19	9.47 ± 0.25	10.02 ± 0.21	9.47 ± 0.24	9.64 ± 0.29	8.89 ± 0.18	0.086	0.016	0.211
Sleeping EE (kJ/min)	4.35 ± 0.09	4.25 ± 0.12	4.49 ± 0.10	4.16 ± 0.11	4.25 ± 0.14	4.04 ± 0.08	0.240	0.018	0.487
BMR (kJ/min)	5.16 ± 0.24	4.85 ± 0.39	5.44 ± 0.17	4.71 ± 0.22	4.80 ± 0.23	4.65 ± 0.14	0.212	0.055	0.263
Resting EE (kJ/min)	6.71 ± 0.18	6.75 ± 0.24	7.22 ± 0.20	6.83 ± 0.23	6.90 ± 0.28	6.36 ± 0.17	0.121	0.106	0.271
EE meals (kJ/min)	7.35 ± 0.19	7.39 ± 0.26	7.54 ± 0.21	7.37 ± 0.24	7.28 ± 0.29	6.63 ± 0.18	0.089	0.172	0.201
EE miscellaneous (kJ/min)	7.53 ± 0.20	7.89 ± 0.27	7.47 ± 0.22	7.49 ± 0.25	7.24 ± 0.30	6.96 ± 0.18	0.143	0.869	0.285
EE of exercises (kJ/min)	14.80 ± 0.32	13.97 ± 0.43	15.39 ± 0.35	14.34 ± 0.40	15.33 ± 0.48	13.66 ± 0.29	0.397	0.0003	0.414
DEE − EE of exercises (MJ)	7.77 ± 0.17	7.79 ± 0.23	8.18 ± 0.19	7.75 ± 0.21	7.80 ± 0.26	7.26 ± 0.16	0.082	0.058	0.226

[1] Prepubertal, Tanner stage 1; pubertal, Tanner stages 2, 3, and 4; postpubertal, Tanner stage 5; DEE, daily EE; BMR, basal metabolic rate. Values in the same row with different superscript letters are significantly different, $P < 0.05$.
[2] Least-squares mean ± SD.
[3,4] Significant effect of season: [3] $P = 0.018$, [4] $P = 0.032$.

on average 20% higher in boys than in girls at the pubertal and postpubertal stages ($P < 0.001$), but the difference was not significant in prepubertal children. In other respects, REE was 42% and 22% higher in pubertal than in prepubertal boys and girls, respectively ($P < 0.001$). The differences between pubertal and postpubertal adolescents were not significant. The results were similar for EE during meals and miscellaneous activities but the differences between boys and girls were 30% and 14% at the pubertal and prepubertal stages, respectively ($P < 0.001$ and $P < 0.05$). Finally, REE and EE during meals and miscellaneous activities, when adjusted for FFM, did not vary significantly with sex, stage of puberty, or season.

Energy expenditure during physical exercise

The mean external mechanical power (EMP) of the 4 exercises performed on a cycle ergometer by boys and girls, respectively, were 53 ± 14 and 40 ± 10 W in prepubertal children, 81 ± 7 and 53 ± 19 W in pubertal adolescents, and 91 ± 10 and 59 ± 16 W in postpubertal adolescents. Heart rate increased continuously during the cycling periods in sedentary subjects but reached plateaus after 5–8 min in trained subjects. Mean EE during the four 30-min sessions (each including 15 min of cycling and 15 min of recovery) varied significantly with sex, stage of puberty, and season (Table 2). EE was 16%, 28%, and 26% higher in boys than in girls at the prepubertal, pubertal, and postpubertal stages, respectively ($P < 0.02$, $P < 0.001$, and $P < 0.001$). In other respects, EE during physical exercise was significantly higher at the pubertal than at the prepubertal stage, by 40% in boys ($P < 0.001$) and by 26% in girls ($P < 0.002$). The differences were not significant between pubertal and postpubertal adolescents. When adjusted for FFM, mean EE during physical exercise did not vary significantly with stage of puberty or season, but it was significantly higher in boys than in girls ($P < 0.001$; Table 2).

Heart rate during cycling at steady state (6th to 15th min) was similar in boys and girls, and slightly but not significantly higher in prepubertal children than in pubertal and postpubertal adolescents. Heart rate averaged 150 ± 16, 162 ± 15, 136 ± 10, and 175 ± 17 beats/min for each of the 4 sessions. EE adjusted for FFM and EMP did not vary significantly with stage of puberty but was significantly higher in boys than in girls (398 compared with 371 W on average). Net work efficiency of cycling was calculated as the ratio between EMP and the increase in EE during cycling (EE during cycling at steady state − SEE); it did not vary significantly with sex or stage of puberty and averaged 0.221 ± 0.018.

Significant determinants of DEE and SEE

Stepwise regression analyses were performed to determine the significant determinants of DEE and SEE in the 83 prepubertal, pubertal, and postpubertal children by using the following variables: sex, stage of puberty, FFM, FM, peak $\dot{V}O_2$, and season (spring compared with autumn). DEE was best explained by FFM ($r^2 = 0.842$, $P < 0.001$), season ($r^2 = 0.021$, $P < 0.001$), and sex ($r^2 = 0.017$, $P < 0.04$). Peak $\dot{V}O_2$, stage of puberty, and FM were not significant predictors of DEE. The latter could be predicted by using the following equation ($r^2 = 0.880$, residual SD = 677):

$$\text{DEE} = 4462 + 187.7\ \text{FFM} - 547\ \text{season} - 508\ \text{sex} \quad (1)$$

where DEE is in kJ/d, season is 1 for spring and 2 for autumn, and sex is 1 for males and 2 for females.

However, DEE also depends on physical activity. Therefore, EE corresponding to the 4 cycling exercises (15 min cycling and 15 min recovery for each) was subtracted from DEE. The significant determinants of "DEE − EE of exercises" were also FFM ($r^2 = 0.815$, $P < 0.001$), season ($r^2 = 0.023$, $P < 0.001$), and sex ($r^2 = 0.014$, $P < 0.01$). Peak $\dot{V}O_2$, stage of puberty, and FM were not significant determinants of DEE – EE of exercises. The latter

could be predicted by using the following equation (r^2 = 0.853, residual SD = 602):

$$\text{DEE} - \text{EE of exercises} = 3772 + 148.6\ \text{FFM} - 466\ \text{season} - 372\ \text{sex} \quad (2)$$

The significant determinants of SEE were FFM (r^2 = 0.826, $P < 0.001$), season (r^2 = 0.011, $P < 0.004$), sex (r^2 = 0.022, $P < 0.05$), and peak $\dot{V}O_2$ (r^2 = 0.007, $P < 0.05$). Stage of puberty and FM were not significant determinants of SEE. The corresponding predicting equation was as follows (r^2 = 0.865, residual SD = 155):

$$\text{SEE} = 877 + 31.8\ \text{FFM} - 108\ \text{season} - 81\ \text{sex} + 176.6\ \text{peak}\ \dot{V}O_2 \quad (3)$$

DEE and SEE adjusted for FFM were on average 5% lower in girls than in boys and 6% lower in autumn than in spring.

DISCUSSION

This cross-sectional study enabled direct comparison of DEE and its main components in children and adolescents at 3 stages of puberty in the same environment and with the same activity program simulating a school day. The average height, body weight, and BMI of adolescents who participated in this study, as well as the SD, were close to those recently recorded in France for 18 000 teenagers, as reflected by the relative BMI (J Tichet, S Vol, unpublished observations, 1997; Table 1). Our subjects could be considered representative of the French adolescent population.

Physical characteristics and body composition of children and adolescents could have been compared at the same chronologic ages and at the same stages of puberty, but the postpubertal boys had reached puberty closer to the time of measurement than did postpubertal girls. This could explain the relatively small differences in age, height, body weight, and FFM between postpubertal and pubertal boys. Nevertheless, FFM was 19.2 kg higher in postpubertal than in prepubertal boys, whereas FM was the same. In girls the differences were 14.7 kg for FFM and 4.6 kg for FM, which resulted in great differences in body composition between postpubertal boys and girls.

After one evening and one night of adaptation to the calorimetric chambers, the subjects felt comfortable and relaxed for the next 24 h of measurement. Daily, sleeping, resting and exercise EEs were measured accurately. The reliability of BMR in prepubertal and pubertal children is disputable because of the restlessness of some of them during this measurement period. Therefore, the discussion will deal mainly with DEE and SEE.

DEE, SEE, REE, and EE during meals, miscellaneous activities, and exercise varied significantly with sex and stage of puberty. Furthermore, the interaction between sex and stage of puberty was significant. EEs were significantly higher in boys than in girls at the pubertal and postpubertal stages. However, the differences were not significant at the prepubertal stage. For adolescents, the differences in EE of adolescents were greater between the prepubertal and the pubertal stages than between the pubertal and the postpubertal stages. This may have partly resulted from the differences in body composition of subjects between the 3 pubertal stages because body weight and FFM were not significantly different between pubertal and postpubertal boys. Therefore, EEs were adjusted for FFM. Adjusted DEEs and SEEs were significantly higher in boys than in girls at the pubertal and postpubertal stages, whereas adjusted DEE and SEE were similar in prepubertal boys and girls. Adjusted DEE and its various components did not vary significantly with stage of puberty.

The main determinant of DEE, DEE − EE of exercise, and SEE was FFM, which explained 84%, 81%, and 82% of the variance, respectively. Sex was the second most significant determinant and explained only 1.7%, 1.4%, and 2.2% of the variance, respectively. These results obtained during sleep and over 24-h periods confirmed those obtained for BMR and REE in obese and nonobese children and adolescents (3, 15–17); EEs adjusted for FFM were higher in boys than in girls. On the contrary, stage of puberty was not a significant factor of DEE, DEE − EE of exercises, and SEE; EEs adjusted for FFM did not vary significantly with stage of puberty. This result disagrees with those obtained for BMR in adolescents (3, 16). It might result from the small differences in body weight and FFM between pubertal and postpubertal boys. In fact, 3 of the 15 pubertal boys had physical characteristics close to those of the postpubertal boys. FM was not a significant determinant of EE. FM was found to be a significant factor of EE only in studies including obese and nonobese children or adolescents and explained <4% (15) or 1% (16) of the variance in REE, probably because of the lower metabolic rate of adipose tissue than of the organs (18). Finally, season was the third significant determinant of DEE, DEE − EE of exercises, and SEE. It explained 2.1%, 2.3%, and 1.1% of the variance. SEE adjusted for FFM and sex was significantly higher in spring than in autumn. However, adjusted DEE did not vary significantly with season. To our knowledge, such a difference has not yet been shown in children or adolescents.

Sex differences in adjusted DEE and SEE were partly explained by differences in hormonal status, FFM composition, and tissue metabolic activity. The role of androgens in energy metabolism has been shown in farm animals by comparing the EEs of entire and castrated animals. In addition, administration of testosterone to castrated lambs with similar food intake significantly increased EE (19). In humans, a close correlation was shown in maturing boys, but not in girls, between urinary 17-ketosteroid excretion resulting from testosterone catabolism and basal oxygen consumption adjusted for differences in body composition (20). Furthermore, the BMR of imminently pubertal boys was higher than that of prepubertal boys (21).

Skeletal muscles were estimated to account for ≈20% of whole-body oxygen uptake (22). Furthermore, 40–50% of the variability in BMR adjusted for differences in FFM, FM, age, and sex was ascribed to the variability in skeletal muscle metabolic rate (23). Females had slightly higher proportions of type I fiber, smaller fiber areas, and lower glycolytic potential than males, which may partly explain some of the sex differences in EE (24). In addition, Na^+-K^+ ATPase activity has been shown to be lower in women than in men (25) and it was related to a lower resting metabolic rate, independent of differences in FFM. Other factors such as basal hepatic gluconeogenesis, sympathetic nervous activity, and decreased body core temperature might explain the lower metabolic rate in females (26).

In other respects, protein turnover has been shown to contribute ≈20% of the resting metabolic rate in young adults (27) and 24% in children and adolescents (28). Plasma growth hormone, insulin-like growth factor I, and insulin concentrations increase during puberty and serum concentrations of insulin-like growth factor I peak between 13 and 15 y and 14 and 17 y of age in girls and boys, respectively (29–31). These hormones promote protein accretion during puberty (32, 33). Furthermore, noctur-

nal growth hormone release is greater in pubertal than in prepubertal children and is correlated with plasma testosterone concentration in boys and energy expenditure in adolescents (34). However, the contribution of muscle mass to FFM increases and that of organ mass decreases during puberty (18, 22). Because the metabolic rate of organs is ≈20 times that of resting skeletal tissue (18), the alterations in FFM composition during puberty should reduce SEE and DEE adjusted for differences in FFM and may compensate for the increase in EE resulting from alterations of hormonal status and metabolic rate of tissues during puberty.

In conclusion, stage of puberty was not a significant determinant of DEE and SEE in adolescents. Differences in EE between prepubertal, pubertal, and postpubertal adolescents were mainly due to differences in body composition because EE adjusted for FFM did not vary significantly with stage of puberty. Increases in metabolic rate due to changes in hormonal status could be compensated for by decreases in EE resulting from alterations in body composition. However, DEE and SEE measured under standardized conditions and adjusted for FFM were significantly higher in boys than in girls. The DEE of children and adolescents, as measured under standardized conditions, could be predicted from FFM, sex, and season with a residual SD of 0.67 MJ, ie 7.1%.

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