Metabolic response to small and large ^{13}C-labelled pasta meals following rest or exercise in man

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The metabolic response to a 150 or 400 g ^{13}C-labelled pasta meal was studied for 8 h following rest or exercise at low or moderate workload (*n* 6). Following rest, the 400 g meal totally suppressed fat oxidation (*v.* 14·1 g following the 150 g meal) and a small amount of glucose was converted into fat (4·6 g), but fat oxidation remained high in subjects who had exercised following both the small (21·8 and 34·1 g) and large meal (14·1 and 32·3 g). Exogenous glucose oxidation was significantly higher in subjects who had remained at rest both following the small (67·6 g *v.* 60·4 and 51·3 g in subjects who exercised at low and moderate workloads) and large meal (152·2 *v.* 123·0 and 127·2 g). Endogenous glucose oxidation was similar in the three groups following the 150 g meal (42·3–58·0 g), but was significantly lower following the 400 g meal in subjects who had exercised at low workload (24·2 *v.* 72·2 g following rest; *P* < 0·05), and was totally suppressed in those who had exercised at moderate workload. As a consequence, a larger positive glycogen balance was observed in subjects who exercised before the large meal (182·8–205·1 g *v.* 92·4 g following rest; *P* < 0·05). Total fat oxidation calculated from 08.00 hours to 20.00 hours was similar in subjects who exercised at low and moderate workloads. These results indicate that: (1) *de novo* lipogenesis, which plays only a minor role for the disposal of an acute dietary carbohydrate load, is totally suppressed following exercise, even when a very large carbohydrate load is ingested; (2) the reduction in glycogen turnover as well as a preferential conversion of glucose into glycogen are responsible for the increase in glycogen stores following exercise; (3) for a similar energy expenditure, exercise at low workload for a longer period does not favour fat oxidation when the post-exercise period is taken into account.

Stable isotope: *De novo* lipogenesis: Glycogen stores

Changes in body fat and mass might be more closely related to changes in fat intake than to changes in energy intake (Jéquier, 1992; Flatt, 1995; Proserpi *et al.* 1997), since whole-body *de novo* lipogenesis is small in man (Acheson *et al.* 1982, 1984, 1985, 1987; Hellerstein *et al.* 1996; Hellerstein, 1999), except with prolonged hyperenergetic diets high in carbohydrates (Acheson *et al.* 1988; De Garine & Koppert, 1991; Horton *et al.* 1995; Calles-Escandón *et al.* 1996; Hellerstein *et al.* 1996; Aarsland *et al.* 1997). Also, for a given increase in energy expenditure, it has been suggested that exercise at low workload with a higher contribution of fat oxidation to the energy yield could favour reduction in body fat (Thompson *et al.* 1998). However, when computing the net effect of exercise on fat balance, it should be taken into account that fat oxidation increases following exercise, particularly following exercise at a higher intensity (Broeder *et al.* 1991), even when carbohydrates are ingested in the recovery period (Bielinski *et al.* 1985; Broeder *et al.* 1991).

There are, however, no data on the combined effects of exercise of various intensities and durations on the metabolic fate of dietary carbohydrates, and on energy

Table 1. Characteristics of the healthy sedentary male subjects and fasting plasma glucose concentration

(Mean values with their standard errors for six subjects per group)

| | Rest | | Exercise | | | |
| | | | Low workload | | Moderate workload | |
	Mean	SE	Mean	SE	Mean	SE
Age (years)	26·3	1·4	23·7	0·8	27·2	1·1
Height (m)	1·81	0·03	1·76	0·03	1·80	0·02
Weight (kg)	75·2	2·6	72·3	3·1	75·4	4·5
BMI (kg/m^2)	22·9	0·6	23·5	1·3	23·2	1·1
V_{O_2}max (ml/kg per min)	46·9	1·5	50·9	2·1	50·2	2·0
Plasma glucose (mmol/l)	4·3	0·2	4·3	0·4	4·1	0·2

and substrate balance. In the present experiment energy expenditure, substrate oxidation, whole-body *de novo* lipogenesis, oxidation *v.* storage of exogenous glucose and glycogen turnover were followed for 8 h following small (150 g) and large meals (400 g) of ^{13}C-labelled pasta, after rest or exercise of different intensities and duration, but with the same energy expenditure.

Methods

Subjects

The experiment was conducted in three groups of six healthy sedentary male subjects matched for BMI and maximum O_2 consumption/min (V_{O_2}max; Table 1). The subjects gave their informed written consent to participate in the study, which was approved by the Institutional Board on the use of human subjects in research. All subjects had a normal fasting plasma glucose concentration (Table 1). None of the subjects was a smoker, a heavy drinker, under medication, or had gained or lost weight (more than 2 kg) over the previous year.

Experimental protocol

The subjects were studied following ingestion of 150 and 400 g pasta (dry weight) in random order, and 2 weeks apart in order to allow for the tracer to disappear from the body. For 2 d before each experiment, the subjects were asked to rest, and were provided with pre-packaged meals (125 kJ/kg per d; containing (% total energy content) 20 protein, 45 carbohydrate, 35 fat).

The subjects reported to the laboratory at 07.30 hours following an overnight fast and a standardized breakfast (approximately 25 kJ/kg; containing (% total energy content) 13 protein, 45 carbohydrate, 42 fat) taken between 06.30 and 07.00 hours. Subjects in the first group rested for the entire morning. Subjects in the second group exercised from 08.00 to 11.00 hours on a cycle ergometer (Ergomeca, La Bayette, France) at 37·1 (SE 1·7) % V_{O_2}max (72·9 (SE 1·9) W). Finally, subjects in the third group rested from 08.00 to 09.30 hours and then exercised for 90 min (from 09.30 to 11.00 hours) at a workload (57·3 (SE 1·6) % V_{O_2}max; 153·7 (SE 5·4) W) chosen so that the total energy

expenditure over the 3 h period was similar in the second and third groups.

Between 11.00 and 12.00 hours the subjects ingested 150 or 400 g pasta (Crealis, Brive, France), containing 111 and 297 g starch, boiled for 7 min in water (100 g pasta/l, with 7 g table salt/l) and served with steamed onions and tomatoes with salt and pepper (60 ml/100 g dry pasta). The small and large experimental meals provided 2500 and 6700 kJ respectively (% total energy content; 83 carbohydrate, 16 protein, 1 fat). Approximately 0·55 % of the semolina in the pasta was derived from durum wheat grown in an atmosphere containing 0·1 % CO_2 artificially enriched in ^{13}C ($^{13}CO_2$:CO_2 approximately 11 %; Eurisotop, France; actual ^{13}C:C of the grains 11·1%). The average final ^{13}C:^{12}C in the cooked pasta was +23·6 (SE 0·2) ‰ δ ^{13}C PDB$_1$ (National Office of Standards; *n* 36). Examination of the glucose derived from the pasta, using NMR spectroscopy of ^{13}C, confirmed that the glucose in the meals was uniformly labelled with ^{13}C.

Measurements and calculations

O_2 consumption (V_{O_2}) and CO_2 production (V_{CO_2}) (Tissot Spirometer; Warren-Collins Inc., Braintree, MA, USA; O_2 and CO_2 analysers MGA-1100, Marquette Electronics Inc., Milwaukee, WI, USA) were measured at regular intervals (10 min collection periods every 30 min in the morning, and the first 3 h in the afternoon; every 1 h thereafter). Protein oxidation and the associated amount of energy provided were calculated from urea excretion in urine (Synchron Clinical System, CX7, Beckman, Anaheim, CA, USA) over the 3 h preceding the meals (at rest or exercise), and over the 8 h following the meals, and V_{O_2} and V_{CO_2} were corrected for protein oxidation (Livesey & Elia, 1988). The tables developed by Elia & Livesey (1988) were used for the calculation of glucose and fat oxidation when the non-protein RQ was less than 1·0, or for the calculation of glucose oxidation, the amount of glucose converted into fat, and the amount of fat synthesized, when the non-protein RQ was larger than 1·0.

The amount of glucose provided from the ^{13}C-labelled starch ingested that was oxidized was calculated from ^{13}C:^{12}C in expired CO_2 (Fig. 1). For this purpose, 80 ml samples of expired gas were collected in Vacutainers (Becton Dickinson, Franklin Lakes, NJ, USA). After removal of N_2 and water vapour in liquid N_2 ($-196°C$) and an isopropyl dry ice slush trap ($-80°C$), the ^{13}C:^{12}C was determined using mass spectrometry (Prism; Micromass, Manchester, UK) and expressed with reference to the International Standard PDB$_1$ (^{13}C:^{12}C 1·12372 %): ‰ δ ^{13}C PDB$_1$ = $[(R_{spl}/R_{std}) - 1] \times 1000$, where R_{spl} and R_{std} are the ^{13}C:^{12}C in the sample and standard respectively. The amount of labelled glucose (x) oxidized was then calculated as follows (Péronnet *et al.* 1990):

$$x = V_{CO_2}[(R_{exp} - R_{ref})/(R_{exo} - R_{ref})]/(k_1 \times k_2),$$

where R_{exp} is the observed isotopic composition of expired CO_2, R_{ref} is the isotopic composition of expired CO_2 in the morning at rest, R_{exo} is the isotopic composition of the carbohydrates ingested, k_1 is the volume of CO_2 provided

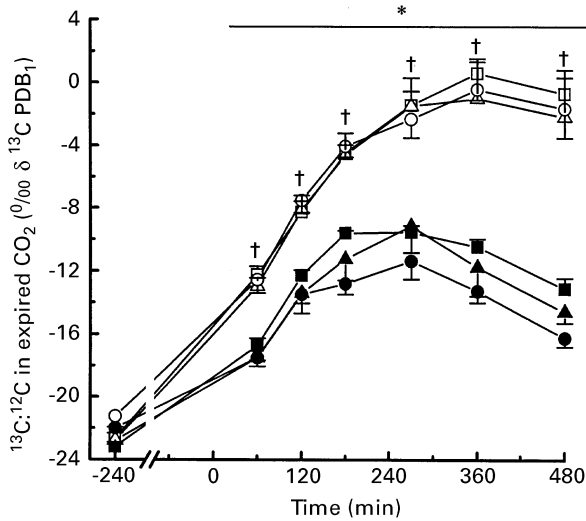**Fig. 1.** Isotopic composition of expired CO_2 following the small (150 g pasta; ■, ▲, ●) and large (400 g pasta; □, △, ○) meals (ingested between -60 and 0 min) in healthy sedentary male subjects who rested (■, □) and exercised at low (▲, △) or moderate (●, ○) workload in the morning. Values are means with their standard errors represented by vertical bars for six subjects. For details of subjects and procedures, see p. 672. Mean values were significantly different from those pre-ingestion: *$P < 0.05$. Mean values were significantly different from those for subjects receiving the small meal: †$P < 0.05$.

by the oxidation of glucose (0·746 l/g), and k_2 is the fractional recovery at the mouth of the CO_2 produced in tissues. When uniformly-labelled glucose is the tracer, the value of k_2 has been estimated at 54 % by Schneiter *et al.* (1995). The amount of exogenous glucose oxidized was also corrected for the oxidation of exogenous ^{13}C-labelled proteins, assuming that 31 % of the protein ingested was oxidized (Boirie *et al.* 1996); 6·3 and 16·7 g for the small and large meals respectively, which is equivalent to the oxidation of 7·1 and 18·7 g glucose in terms of CO_2 production (protein oxidation yields 0·836 l CO_2/g *v.* 0·746 l CO_2/g for glucose oxidation; Livesey & Elia, 1988). The value of R_{exo} was measured from a 5 g sample of the cooked pasta ingested in each experiment. After being dried at 40°C, a 0·8 g aliquot was ground and combusted with CuO (1·5 g; 180 min at 500°C). Following cryodistillation as described earlier the ^{13}C:^{12}C in the CO_2 produced was analysed by mass spectrometry.

The amount of endogenous glucose oxidized was calculated as the difference between total glucose oxidation and exogenous glucose oxidation. The amount of exogenous glucose that was converted into glycogen was estimated as the difference between the total amount of glucose provided by the meal and the amount of exogenous glucose oxidized, taking into account the amount of glucose converted into fat, if any, and assuming that all the glucose released from the starch had been absorbed. Experimental data concerning the rate of absorption of a large carbohydrate load are lacking. However, Acheson *et al.* (1982) deemed reasonable the assumption that glucose from a 479 g carbohydrate meal was entirely absorbed over 5 h. Finally, based on the

amounts of glycogen stores utilized (endogenous glucose oxidation) and on the amount of glucose deposited as glycogen, the net balance of glycogen stores was computed.

Blood samples

Blood samples were withdrawn at regular intervals (-60, 0, 60, 120, 180, 360 and 480 min) from an indwelling catheter (Baxter Health Care Corp., Valencia, CA, USA) placed in an antecubital vein, immediately before the meal was ingested, for the measurement of concentrations of plasma glucose (Sigma Diagnostics; Sigma, Mississauga, Ontario, Canada) and insulin (KTSP-11001; Immunocorp Sciences, Montreal, Quebec, Canada).

Statistics

Data are presented values with their standard errors. The main effects of workload (rest, or low and moderate), glucose load (150 and 400 g meals) and time, as well as workload–glucose load–time interactions were tested by ANOVA with repeated measures on glucose load and time (Statistica package; StatSoft, Tulsa, OK, USA). The Newman–Keuls *post hoc* test was used to identify the location of significant differences ($P < 0.05$) when ANOVA yielded a significant F ratio.

Results

Observation in the morning

Energy expenditure was higher in subjects submitted to exercise, but was not significantly different for subjects working at low and moderate workloads (Table 2). Protein oxidation ranged between 8·4 and 16·4 g, providing approximately 5 % of the energy yield. Glucose and fat oxidation were both significantly higher in subjects who exercised than in subjects who remained at rest ($P < 0.05$

Table 2. Energy expenditure (EE) and substrate utilization over the 3 h period preceding a small (150 g pasta) or large (400 g pasta) meal in healthy sedentary male subjects‡

(Mean values with their standard errors for six subjects per treatment group)

| | | Rest | | Exercise | | | |
| | | | | Low workload | | Moderate workload | |
	Meal	Mean	SE	Mean	SE	Mean	SE
EE (kJ)	Small	1464·1	15·5	5008·5*	526·3	5244·5*	371·7
	Large	1444·8	42·8	4977·8*	647·2	5207·2*	451·9
Proteins (g)	Small	11·9	1·4	8·4	1·3	15·7†	0·6
	Large	11·1	1·6	13·1	1·5	16·4*	0·6
Glucose (g)	Small	41·2	7·2	158·3*	9·0	192·5*†	22·6
	Large	39·1	2·3	143·3*	12·4	176·7*†	26·3
Fat (g)	Small	13·7	2·4	55·5*	13·3	43·8*	3·2
	Large	14·4	0·6	58·4*	13·4	49·2*	3·2

Mean values were significantly different from those for subjects at rest: *$P < 0.05$.
Mean values were significantly different from those for the low-workload group: †$P < 0.05$.
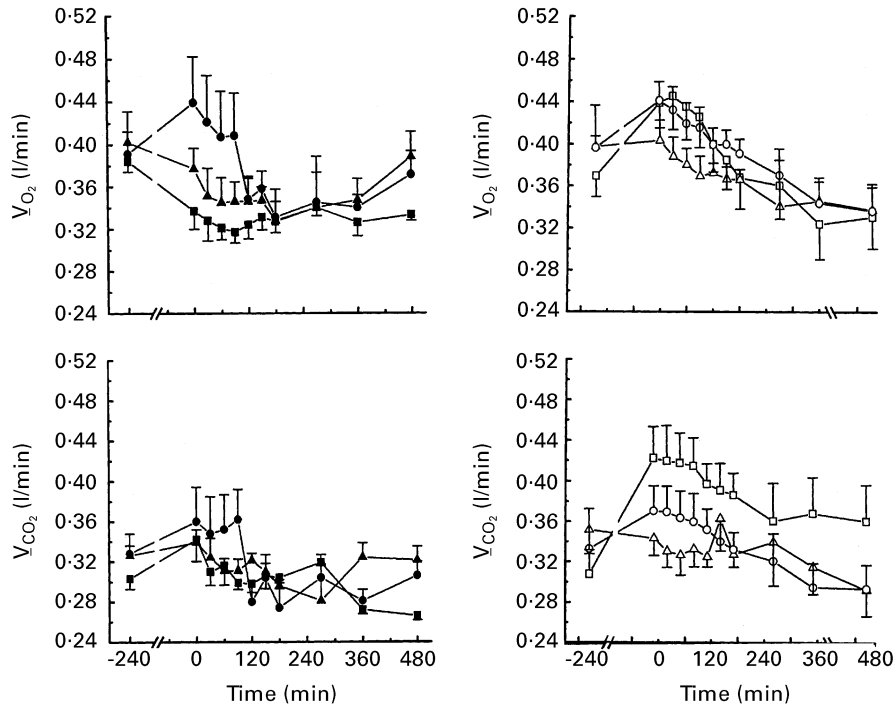‡ For details of subjects and procedures, see p. 672.

Fig. 2. Respiratory exchanges at the beginning of the experiment (08.00 hours; −240 min), and following the small (150 g pasta; ■, ▲, ●) and large (400 g pasta; □, △, ○) meals (ingested between −60 and 0 min) in healthy sedentary male subjects who rested (■, □) and exercised at low (▲, △) or moderate (●, ○) workload in the morning. Values are means with their standard errors represented by vertical bars for six subjects. For details of subjects and procedures, see p. 672.

in both cases), and glucose oxidation was significantly higher in subjects who exercised at moderate workload than in subjects who exercised at low workload ($P < 0.05$).

Energy expenditure and substrate oxidation following the meal

Respiratory exchanges following the small and large pasta meals are shown in Fig. 2. Energy expenditure over the 8 h following the meal was significantly higher (approximately 14–18 %; $P < 0.05$) in subjects who remained at rest than in subjects who exercised in the morning, following the large meal but not the small meal (Table 3). Protein oxidation was similar in the three groups and was not modified by the amount of pasta ingested. Total glucose oxidation was significantly higher following the large than the small meal in subjects who remained at rest ($P < 0.05$), and was similar in the three groups following the small meal. In contrast, following the large meal total glucose oxidation was significantly lower in subjects who exercised in the morning ($P < 0.05$). *De novo* lipogenesis was observed only following the large meal in subjects who remained at rest in the morning, with 13·3 (SE 11·3) g glucose converted into 4·6 (SE 4·0) g fat. In contrast, fat oxidation significantly contributed to the energy yield in the other experimental situations ($P < 0.05$), and was significantly higher in subjects who exercised at moderate workload in the morning ($P < 0.05$).

Exogenous and endogenous glucose oxidation and glycogen balance

The amount of exogenous glucose oxidized was slightly but significantly lower ($P < 0.05$), while the amount of exogenous glucose that was deposited in the form of glycogen was significantly higher ($P < 0.05$) in subjects who exercised *v.* those who remained at rest in the morning, following both the small and the large meals (Table 3). Endogenous glucose oxidation was similar in the three groups following the small meal. In contrast, following the large meal, when compared with subjects who remained at rest in the morning, endogenous glucose oxidation was significantly lower in subjects who exercised at low workload ($P < 0.05$), and was totally suppressed in subjects who exercised at moderate workload. As a consequence, the net positive glycogen balance was markedly and significantly higher in subjects who exercised in the morning ($P < 0.05$).

Overall carbohydrate and fat balances

When the small meal was ingested, the net negative balance of glycogen stores over the period 08.00–20.00 hours (minus the 1 h meal period) was higher in subjects who exercised than in those subjects who remained at rest (Table 4). The balance was positive when the large meal was ingested, and was smaller in subjects who exercised compared with those that remained at rest in the morning. In subjects who exercised in the morning, the negative fat

Table 3. Energy expenditure, substrate oxidation and glycogen balance following a small meal (150 g pasta) or a large meal (400 g pasta) in healthy sedentary male subjects§

(Mean values with their standard errors for six subjects per treatment group)

| | | Rest | | Exercise | | | |
| | | | | Low workload | | Moderate workload | |
	Meal	Mean	SE	Mean	SE	Mean	SE
Energy expenditure (kJ)	Small	3406·6	130·2	3384·8	154·1	3641·8	178·5
	Large	4591·0*	289·0	3728·3†	122·2	4006·4†	139·9
Proteins (g)	Small	37·0	3·6	34·6	2·3	36·2	4·3
	Large	38·2	4·6	36·6	4·4	33·2	4·1
Total glucose (g)	Small	125·6	8·9	108·7	11·7	93·6	5·6
	Large	224·3*	18·4	145·6†	6·2	124·9†	18·7
Fat (g)	Small	14·1	2·5	21·8	4·7	34·1†	3·1
	Large	−4·6*	4·0	14·1†	2·1	32·3†	3·7
Exogenous glucose (g)	Small	67·6	3·9	60·4†	8·1	51·3†	3·9
	Large	152·2*	7·4	123·0*†	6·7	127·2*†	10·2
Endogenous glucose (g)	Small	58·0	6·3	45·2	13·1	42·3	5·7
	Large	72·2	15·7	24·2†	8·6	−2·3*†‡	9·7
Glycogen synthesized (g glucose)	Small	55·4	3·9	62·7†	8·1	71·7†	3·9
	Large	164·6*	14·2	207·0*†	6·7	202·8*†	10·2
Glycogen balance (g glucose)	Small	−2·6	8·9	17·4	11·1	29·4	5·6
	Large	92·4*	28·7	182·8*†	5·9	205·1*†	18·7

Mean values were significantly different from those of subjects receiving the small meal: *$P < 0.05$.
Mean values were significantly different from those of subject at rest: †$P < 0.05$.
Mean values were significantly different from those of the low-workload group: ‡$P < 0.05$.
§ For details of subjects and procedures, see p. 672.

balance was significantly higher than that in subjects who remained at rest ($P < 0.05$), and was similar in subjects who exercised at low and moderate workloads, and following the small and large meals. In contrast, in subjects who remained at rest in the morning, the negative fat balance was significantly lower following the large meal than the small meal ($P < 0.05$).

Plasma glucose and insulin concentrations

Plasma glucose and insulin concentrations were both significantly increased above pre-meal values following ingestion of 150 or 400 g pasta ($P < 0.05$), and remained elevated for 3 h after ingestion (Fig. 3). Peak plasma glucose concentrations which were observed at the end of the 1 h meal period were similar following the small (7·0 (SE 0·2) mmol/l) and large meals (7·1 (SE 1·2) mmol/l) in subjects who had remained at rest in the morning. In contrast, the values observed in subjects who had exercised were significantly higher following the large meal (8·9–9·6 mmol/l) than following the small meal (6·8–7·9 mmol/l; $P < 0.05$). The response of plasma insulin concentration to the small meal was similar in the three groups. In response to the large meal, plasma insulin concentration reached higher values in subjects who exercised at low workload $v.$ those who remained at rest or exercised at moderate workload in the morning.

Discussion

The purpose of the present experiment was to describe the metabolic fate of small and large dietary carbohydrate loads, and the associated changes in energy expenditure, substrate utilization, glycogen turnover and fat stores, in subjects who had previously rested or exercised at either low or moderate workload. Glucose provided by a starch

Table 4. Glycogen and fat balance over the 12 h observation period after ingestion of a small meal (150 g pasta) or a large meal (400 g pasta) in healthy sedentary male subjects‡

(Mean values with their standard errors for six subjects per treatment group)

| | | Rest | | Exercise | | | |
| | | | | Low workload | | Moderate workload | |
	Meal	Mean	SE	Mean	SE	Mean	SE
Glycogen balance (g)	Small	−51·7	8·2	−152·8†	20·7	−175·2†	25·6
	Large	61·7*	12·0	19·9*†	18·8	23·5*†	21·4
Fat balance (g)	Small	−29·2	4·0	−74·7†	8·6	−78·0†	4·6
	Large	−19·1*	1·7	−76·7†	9·0	−79·5†	5·6

Mean values were significantly different from those of subjects receiving the small meal: *$P < 0.05$.
Mean values were significantly different from those for subjects at rest: †$P < 0.05$.
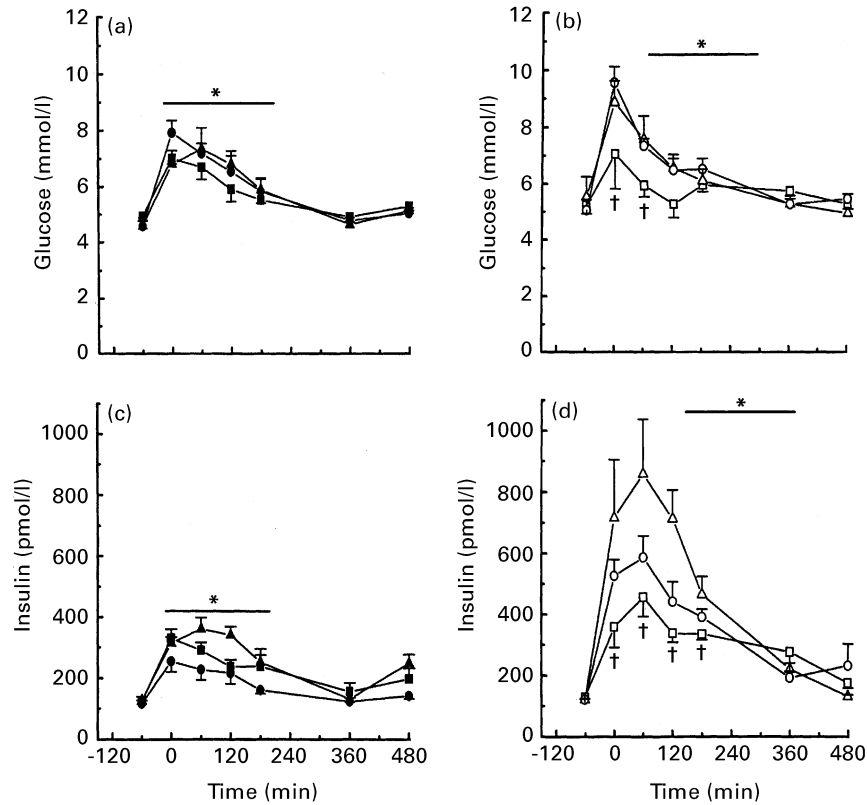‡ For details of subjects and procedures, see p. 672.

Fig. 3. Plasma glucose (a,b) and insulin (c,d) concentrations in response to the small (150 g pasta; ■, ▲, ●) and large (400 g pasta; □, △, ○) meals (ingested between −60 and 0 min) in healthy sedentary male subjects who rested (■, □) and exercised at low (▲, △) or moderate (●, ○) workload in the morning. Values are means with their standard errors represented by vertical bars for six subjects. For details of subjects and procedures, see p. 672. Mean values were significantly different from those pre-ingestion: *$P < 0.05$. Mean values were significantly different from those after exercise: †$P < 0.05$.

meal could be oxidized or stored in the form of glycogen and/or fat. The respective contributions of these various metabolic routes, which are critical for the final fat and body mass balance, could be modified following exercise, particularly following exercise at a higher workload which favours glycogen utilization.

Whole-body de novo *lipogenesis*

Whole-body de novo lipogenesis is a metabolic pathway of minor importance for the disposal of an acute excess of dietary carbohydrates in man (Acheson *et al.* 1982, 1984, 1985, 1988; Hellerstein *et al.* 1996; Hellerstein, 1999). Results from the present experiment are in line with these previous findings. The small meal provided only approximately 2300 kJ *v.* an energy expenditure ranging from 3385 to 3642 kJ over the 8 h observation period, and no net *de novo* lipogenesis was observed in any of the three groups. The 400 g meal provided approximately 6700 kJ in the form of glucose, which was well in excess of the energy expenditure for the following 8 h period (3728–4591 kJ). However, a net synthesis of fat was observed in only subjects who remained at rest, and an average of only 13·3 g glucose (approximately 4 % of the 330 g load) was converted into 4·6 g fat. When subjects exercised before

the meal, either at low or moderate workload, the small amount of glucose that was converted into fat in subjects who remained at rest in the morning was diverted away from *de novo* lipogenesis. These results lend further experimental support to the hypothesis that the development of obesity could be more closely related to fat ingestion than to carbohydrate ingestion in excess of energy needs (Jéquier, 1992; Flatt, 1995; Proserpi *et al.* 1997). However, ingestion of excess dietary carbohydrates for several days (Acheson *et al.* 1988; Horton *et al.* 1995; Calles-Escandón *et al.* 1996, Hellerstein *et al.* 1996; Aarsland *et al.* 1997;) or months (De Garine & Koppert, 1991) has been shown to increase *de novo* lipogenesis, and to result in fat deposition. This phenomenon could be higher in obese *v.* non-obese subjects (Horton *et al.* 1995), and in female subjects during the follicular phase (Faix *et al.* 1993). It could also differ from one subject to the other; in the present study, although the average amount of fat synthesized was only 4·6 g, large inter-individual differences were present, with three of the subjects converting up to 35–45 g glucose into 12–16 g fat.

Exogenous glucose oxidation

Results from the present experiment indicate that the

oxidation of exogenous glucose provided by the starch increased with the amount ingested, and for a given amount ingested was lower following exercise (at both low and moderate workload) than rest.

Several studies on the oxidation of exogenous glucose at rest have been performed using ^{13}C-labelling (Mosora *et al.* 1976, 1981; Ebiner *et al.* 1979; Ravussin *et al.* 1980; Krzentowski *et al.* 1982, 1983; Jandrain *et al.* 1984; Acheson *et al.* 1985; Normand *et al.* 1992; Schneiter *et al.* 1995; Burelle *et al.* 1999), but only two studies have looked at the effect of a previous exercise period (Krzentowski *et al.* 1982; Schneiter *et al.* 1995). In most of these studies the amount of exogenous glucose ingested was only 100 g (Mosora *et al.* 1976, 1981; Ebiner *et al.* 1979; Ravussin *et al.* 1980; Krzentowski *et al.* 1982, 1983; Jandrain *et al.* 1984; Burelle *et al.* 1999) or lower (Mosora *et al.* 1981; Normand *et al.* 1992), and the amount of exogenous glucose oxidized was, accordingly, low (11–37 g over a 3–8 h period). In the present study, following the small meal, the amount of exogenous glucose oxidized (52·2 g) was slightly higher. This probably stems from the fact that the amount of glucose ingested was slightly higher (123 g), and that the observation period was longer than in most of these studies. In addition, in all these studies but one (Burelle *et al.* 1999) it was assumed that the recovery of ^{13}CO$_2$ at the mouth was complete and, as a consequence, the oxidation of exogenous glucose could have been underestimated.

Acheson *et al.* (1985) and Schneiter *et al.* (1995) are the only authors who have studied the metabolic fate of a higher amount of carbohydrates using ^{13}C-labelling. In the study by Acheson *et al.* (1985), approximately 500 g maltodextrins naturally enriched in ^{13}C was provided in three meals over 5 h. The amount of exogenous glucose oxidized over the 14 h observation period was 155 g for the subjects maintained on a mixed diet (31 % of the load). Results from the present study are in good accordance with these previous findings, with 123–152 g exogenous glucose oxidized (approximately 41 % of the load). In the study by Schneiter *et al.* (1995), the subjects were fed a mixed meal (60 kJ/kg with 168 g carbohydrates) following 45 min exercise at 5 km/h and 10 % slope on a treadmill. Over the following 4 h observation period 74 g exogenous glucose was oxidized (44 % of the load). However, no control situation (carbohydrate ingestion following rest) was included. In addition, it cannot be ascertained whether the [^{13}C] glucose used as tracer accurately followed the metabolic fate of the carbohydrate mixture provided by the meal. Indeed, one technical limitation of performing this type of study is that large doses of carbohydrates can be ingested only in a single meal, in the form of starch. However, labelled starch is not readily available, except for starch derived from plants with the C$_4$ photosynthetic cycle, with a comparatively low ^{13}C-enrichment (Lefèbvre, 1985). The pasta used in the present study was labelled by using grains grown in an atmosphere enriched in ^{13}C. This technique allows uniform labelling of all the organic constituents of the plant, including starch, at a very high level, and it can be assumed that the metabolic fates of the tracer and tracee were similar.

In the present experiment, the amount of exogenous

glucose oxidized following the large meal (123–152 g, providing 52–54 % of the energy yield) was much higher than in the study by Schneiter *et al.* (1995), with ingestion of 168 g carbohydrates (74 g glucose oxidized), probably because the amount of starch ingested was also much larger (297 g) and the observation period was longer (8 h *v.* 4 h). In addition, the amount of exogenous glucose oxidized was lower in subjects who had exercised *v.* those who had remained at rest. This might be related to the lower glycogen stores following exercise, favouring conversion of glucose into glycogen, thus sparing exogenous glucose from oxidation.

Glycogen synthesis and breakdown

Large amounts of glycogen could be deposited and oxidized at the same time following carbohydrate ingestion. In the study by Acheson *et al.* (1985) over the 14 h observation period following ingestion of approximately 500 g ^{13}C-labelled carbohydrates, 260 g carbohydrates was oxidized, and 242 g was converted into glycogen (502 − 260 = 242 g), while at the same time 81 g glycogen was oxidized (endogenous glucose oxidation). In the more recent study by Schneiter *et al.* (1995) 168 g ^{13}C-labelled carbohydrates was ingested 30 min after exercise. Over the following 8 h, 74 g exogenous carbohydrates was oxidized, and 91 g glycogen was synthesized, while 52 g was oxidized.

Results from the present experiment further indicate that the level of glycogen stores at the time of the meal modifies the respective contributions of glycogen synthesis *v.* glycogen breakdown (endogenous glucose oxidation) in the balance of glycogen stores. Indeed, following the large meal, in subjects who exercised in the morning, glycogen synthesis was higher, while endogenous glucose oxidation was lower or suppressed, compared with results in subjects who remained at rest. The reduction in glycogen turnover when carbohydrates were ingested following exercise resulted in a larger positive glycogen balance, which was about twofold higher in subjects who had exercised than in subjects who had remained at rest.

Carbohydrate ingestion immediately following exercise favours glycogen storage (Ivy, 1992). However, few data show a stimulation of glycogen synthase in this situation (Ivy & Kuo, 1998). Results from the present experiment suggest that glycogen accretion when carbohydrates are ingested following exercise might rather depend on the inhibition of glycogen phosphorylase and a reduction in endogenous glucose oxidation. This, in turn, could be due to the observed increase in fat oxidation, through the glucose–fatty acid cycle (Randle, 1998).

Thermogenic effect of the pasta meals

One way to dispose of an excess energy intake in the form of dietary carbohydrates is an increase in energy expenditure due to both the obligatory metabolic cost associated with the digestion, absorption and storage of carbohydrates, and a facultative increase in energy expenditure under the control of the sympathetic system (Jéquier, 1992). In the present experiment the energy expenditure observed over

the 8 h following the small meal was similar in the three groups. In contrast, following the large meal, the energy expenditure was significantly lower in subjects who exercised at low or moderate workload (3728–4006 kJ) *v.* those who remained at rest in the morning (4591 kJ; $P < 0.05$). This difference cannot be accounted for by differences in the obligatory cost associated with glycogen synthesis (this was actually higher in subjects who exercised in the morning: 203–207 *v.* 165 g glucose converted into glycogen), or *de novo* lipogenesis, since the energy cost of converting 13·3 g glucose into fat is only about 42 kJ (Jéquier, 1992). It is, therefore, tempting to hypothesize that ingestion of the meal was accompanied by a lower facultative increase in energy expenditure in subjects who exercised *v.* those who remained at rest in the morning. This could be due to the fact that in subjects who had exercised glycogen stores were reduced, allowing for disposal of a larger portion of the glucose present in the meal and, thus, reducing the need for disposal through facultative thermogenesis.

Fat oxidation and overall fat balance

It has been suggested that for the prevention and/or treatment of obesity low-intensity long-duration exercise should be favoured in order to increase fat oxidation (Thompson *et al.* 1998). However, the net effect of exercise on body fat balance depends not only on the amount of fat oxidized during the period of exercise, but also on the amount oxidized in the recovery period. In the present experiment, fat oxidation was favoured in the recovery period following exercise, when compared with the results in subjects who remained at rest in the morning, as has been shown by several authors (Krzentowski *et al.* 1982; Bielinski *et al.* 1985; Broeder *et al.* 1991; Schneiter *et al.* 1995; Phelain *et al.* 1997), following the small as well as the large meal, in spite of the large availability of glucose. The contribution of fat oxidation to the energy yield following exercise also increased with increasing workload, as reported by Broeder *et al.* (1991). Thus, the compensatory increase in fat oxidation following prolonged exercise is not blunted by ingestion of carbohydrates, even in large amounts, particularly when the exercise intensity is comparatively high.

When the overall fat balance was calculated from 08.00 to 20.00 hours, fat oxidation was similar in the two groups who exercised following both the small and the large meals (Table 4). Accordingly, exercise at low workload was not more efficient than exercise at moderate workload in reducing body fat.

Plasma glucose and insulin concentrations

The regulation of fat *v.* glucose oxidation is at least in part under the control of insulin, which reduces fat mobilization and oxidation, and which has also been shown to stimulate hepatic *de novo* lipogenesis modestly in obese and diabetic patients (Hellerstein, 1999). In the present experiment, in subjects who remained at rest suppression of fat oxidation and the conversion of glucose into fat which was observed following the large meal were, indeed, associated with a higher plasma insulin concentration than was observed following the small meal.

As for the effect of exercise, data from Mikines *et al.* (1988*a,b*) showed an increased insulin sensitivity in man 2 h after a single bout of aerobic exercise, using euglycaemic hyperinsulinaemic clamp techniques. However, data from Krzentowski *et al.* (1982) indicated that when a 100 g oral glucose load was administered immediately after exercise, the response of plasma insulin concentration was similar to that observed following rest, while the increase in plasma glucose concentration was much larger. Results from the present experiment following the small meal (123 g glucose in the form of starch, with a lower glycaemic index than that of glucose; Truswell, 1992) are in line with these observations by Krzentowski *et al.* (1982); although the differences did not reach statistical significance, the plasma glucose concentration was consistently higher in subjects who had exercised than in those who had remained at rest. No data appear to be available in the literature on a much larger amount of carbohydrates being ingested immediately following exercise. Results from the present study show that in this situation the responses of both plasma glucose and plasma insulin concentrations were higher than those following a period of rest. However, this did not further promote *de novo* lipogenesis, and did not inhibit fat oxidation, which remained similar to that observed following the small meal.

Protein balance

Protein oxidation was similar in the three groups following the small and large pasta meals (33·2–38·2 g), and was lower than the amount of proteins ingested in the large pasta meal (54 g). This observation is in line with results from several studies showing that ingestion of a single meal rich in proteins stimulates net protein synthesis (Boirie *et al.* 1996; Wagenmakers, 1998). The present data do not allow speculation about the respective contributions of changes in protein breakdown *v.* synthesis in the observed increase in net protein synthesis following the large meal. These contributions might be different following exercise *v.* rest, since whole body protein turnover might be modified following endurance exercise (Tipton & Wolfe, 1998).

In conclusion, these results indicate that: (1) *de novo* lipogenesis, which plays only a minor role in the disposal of an acute dietary carbohydrate load, was totally suppressed following exercise, even when a very large carbohydrate load was ingested; (2) the reduction in glycogen turnover, as well as a preferential conversion of glucose into glycogen, were responsible for the increase in glycogen stores following exercise; (3) for a similar energy expenditure, exercise at low workload for a longer period did not favour fat oxidation when the post-exercise period was taken into account.

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