Substrate Oxidation During Exercise in the Rat Cannot Fully Account for Training-Induced Changes in Macronutrients Selection

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This study investigated spontaneous dietary adaptation to regular exercise in relation to substrate oxidation measured during exercise. Male Wistar rats were offered permanent access to the three sources of macronutrients supplemented with minerals and vitamins. The rats remained sedentary or were trained daily during 3 weeks at moderate intensity (20 m · min^{-1}, 2 hours). Body weight, total caloric intake, and macronutrients selection were recorded throughout the experiment. Energy expenditure and substrate oxidation were measured before, during, and after an exercise identical for trained and untrained rats (10 m · min^{-1}, 1 hour). Training reduced body weight gain (2.27 *v* 5.57 g · day^{-1}), increased protein intake (52.6% *v* 39.2%), and decreased carbohydrate intake (21.3% *v* 39.5%). Basal and running energy expenditure, as well as glucose and lipid oxidation, remained essentially comparable in trained and untrained rats. The relative contribution of glucose oxidation (Gox) to total energy expenditure decreased during exercise (52.2%, average of all rats) relative to before exercise (60.8%). Gox during exercise was positively correlated with resting Gox before exercise, showing that preexercise substrate oxidation was a strong determinant of running substrate oxidation. However, the slope was smaller for the trained than for the untrained rats, showing that exercise increases Gox less in trained rats than in untrained ones. We conclude from this study that, since food selection but not substrate oxidation changed following training, food intake adapted to substrate requirements induced by regular training and not the contrary. However, large differences remained between the mixture ingested, in which lipids accounted for only 26% of the energy, and the mixture oxidized during exercise, in which lipids accounted for 50.7% of the substrate oxidized. Such a difference may be related to metabolic requirements during the rest of the day and/or to the distribution of macronutrients intake relative to exercise. This question deserves further investigation with recording of macronutrients selection, energy expenditure, and substrate oxidation over 24 hours.

THE EFFECTS OF EXERCISE on diet selection in the rat, as well as in humans, are influenced by numerous variables, such as age, gender, species, and type intensity and duration of exercise, etc.[1,2] The exact mechanisms underlying this variability are not well understood. One major hypothesis is that food intake is modified to compensate for the fuel mix oxidized during exercise.[3,4] Indeed, in addition to increasing energy expenditure, exercise modifies the utilization of the various energy sources of the body and therefore induces new nutrient requirements. Accordingly, long-lasting, low-intensity exercise that increases energy expenditure and lipid oxidation usually increases consumption of diets high in fat. In contrast, exercise of higher intensity and lower duration that depletes glycogen stores tends to increase carbohydrate intake.[5-7] On the other hand, despite the fact that the energy derived from protein catabolism during exercise is never more than 5% to 15% of total energy requirements,[8-10] an increased protein intake with regular exercise is a most reproducible observation.[2,5] Increased protein requirement for protein repair and muscle growth is a possible explanation for this regular increase in protein intake.[11,12]

To our knowledge, there is no study in which energy expenditure and substrate oxidation during exercise have been measured simultaneously along with macronutrient diet selection. The goal of the present work was to study if macronutrient selection resulting from exercise training is related to substrate oxidation during exercise.

METHODS

Animals

Twenty-four male Wistar Rats (IFFA Credo, France; 180 g at the beginning of the experiment) were used. They were housed in a quiet temperature-controlled room (23 ± 1°C) with a 12-hour/12-hour reversed light-dark cycle (10 PM to 10 AM light). Food and water were always available ad libitum in the housing cages. Food was offered in three separate food cups containing either protein, carbohydrate (CHO), or fat, with each macronutrient being supplemented with minerals and vitamins. The position of the food cups was randomly assigned to avoid diet selection due to position preferences. Energy intake and body weight were measured daily at 10 AM. To avoid alteration of taste due to oxidation, the fat diet was completely renewed twice a week (Monday through Thursday). The rats were adapted for 2 weeks on the macronutrient selection paradigm before the start of the experiment. Energy intake and macronutrients selection during the last 4 days were recorded and used as the reference baseline for spontaneous intake.

Preparation of the Macronutrients

The carbohydrate diet (3.44 kcal/g) included 85% pregelatinized corn starch, 8% commercial grade sucrose, 2% cellulose powder, 4% salt mixture (UAR 205b, Ville Moisson/Orge, France), and 1% vitamin mixture (UAR 200). The protein diet (3.43 kcal/g) included 93% casein, 2% cellulose powder, 4% salt mixture, and 1% vitamin mixture. The fat diet (7.88 kcal/g) included 91% lard, 2% sunflower oil, 4% salt mixture, and 1% vitamin mixture.

Adaptation to Running Conditions

Great care was taken to avoid measurements of respiratory exchanges in rats stressed by the exercise procedure. This was done by housing the rats in the metabolic treadmill for 1 to 2 hours before the run. At this time, the electrical grid at the rear of the treadmill was switched on (100V DC, 50 mA) so that the rats were able to discover that the grid was electrified while exploring the treadmill and were not further

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Submitted June 10, 1997; accepted January 21, 1998.

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0026-0495/98/4707-0002$03.00/0

stressed by the necessity to run in order to escape the electrical shock. Under this schedule, all of the rats ran spontaneously when the treadmill was put into motion. It was thus possible to switch off the current during exercise to avoid electrical shocks due to accidental contact of the tail or of the limbs of the rats with the grid. This further reduced the stress and favored voluntary running. Running was also favored by the fact that the speed (10 m · min^{-1}) was low enough to allow even the untrained rats to pace without excessive effort with the speed of the treadmill. During the exercise, the current was switched on manually when a rat rested more than 5 seconds on the electrical grid.

Maximal oxygen consumption ($\dot{V}O_2$max) tests were performed on some rats to estimate the intensity of the exercise (Fig 1). During these tests, we would consider that an animal could not continue the exercise if it did not leave the grid after 5 seconds of electrical stimulation or returned to the grid more than three times within 1 minute.

Visual inspection of the running rats, together with the fact that the rats produced few feces and urine and did not try to run backward, facing the electrical grid during the run, suggested that this procedure minimized stress during exercise.

Experimental Procedure

After completion of the 2-week adaptation to the macronutrients selection paradigm, rats were divided into two groups. The first group (n = 9) was submitted to training on a motor-driven treadmill. Rats of the second group (n = 15) were untrained and remained in their home cage while the trained rats were running. However, on two separate occasions, the untrained rats were exercised (15 minutes, 5 to 10 m/min) in order to be accustomed to the treadmill.

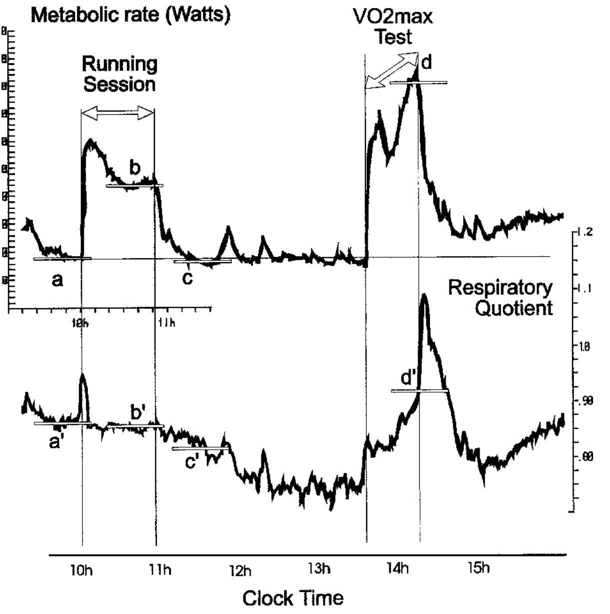

Fig 1. Example of result drawn from the data file of an untrained rat. Upper curve (fat): total metabolic rate; lower curve (thin): respiratory quotient. After time for the rat to adapt to the treadmill and to rest quietly, preexercise resting metabolism and RQ were recorded at level (a) and (a′), respectively. The exercise session was started at 10 AM and lasted 1 hour. The speed of the treadmill was maintained constant at 10 m · min^{-1} throughout. Usually, 30 minutes was required for the rat to pace regularly at lowest energetic cost. Metabolic rate and RQ while running were therefore recorded as the average value during the second 30 minutes of the exercise (b, b′). Postexercise metabolic rate (c) and RQ (c′) were recorded between 30 minutes and 1 hour after exercise. In the present example, the rat was also submitted to a $\dot{V}O_2$max test in the afternoon. The rat was warmed up at 10 m · min^{-1} for 15 minutes, then the speed of the treadmill was increased progressively until the rat was unable to pace with the speed. $\dot{V}O_2$max (d) and RQ (d′) were recorded at the end of the $\dot{V}O_2$max test.

The trained rats were exercised 7 days a week for 3 weeks. They were housed on the treadmill after weighing, between 8 AM and 9 AM, and the exercise was started at the beginning of the night period (10 PM). Food was never available in the treadmill, so that the rats were at least 2 hours postprandial at the onset of exercise. Running speed and duration were progressively increased over the first week to achieve the final speed and duration of 20 m · min^{-1} and 2 hours (slope, 0% throughout).

Measurement of Substrate Oxidation During Treadmill Running

Oxygen consumption and carbon dioxide production were measured during treadmill running by means of a metabolic treadmill built in the laboratory. Care was taken to get a true value of resting energy expenditure before exercise by visual inspection of the behavior of the rat and of the on-line graphic output of the respiratory exchanges. Figure 1 gives an individual example of data collected during an experiment.

During the calorimetric measurements, trained and untrained rats were submitted to the same exercise protocol (1 hour, 10 m · min^{-1}, 0% slope). Respiratory exchanges were recorded at 10-second intervals from 2 hours before to 2 hours after exercise by means of a calorimetric device described in previous publications.[13,14] Glucose and lipid oxidation rates were computed using stoechiometric formulas, assuming that the respiratory quotient (RQ) was indicative of nonprotein respiratory quotient (NPRQ).[14] For the sake of easy comparisons between values, total metabolic rate, as well as intensity of glucose and lipid oxidation, have been expressed in watts.

Statistics

Before statistical comparisons, metabolic values were normalized according to the power two thirds of body weight expressed in kilograms.[15] Within-group comparisons used the *t* test for paired samples (two-tailed). Intergroup comparisons used the *t* test for unpaired samples (two-tailed). Random distribution of trained and untrained rats into subgroups was tested using the nonparametric binomial test based on signs.

RESULTS

Data Analysis According to Training Status of the Rats

Body weight at the time of the running test was greater in trained than in untrained rats (Table 1). This resulted from the fact that, due to technical constraints, the untrained rats were tested in the calorimetric treadmill, while rats of the other group were still under training, and thus were 1 to 2 weeks younger than the trained ones. Body weight gains measured during the 4 days preceding the calorimetric studies were smaller in trained than in untrained rats. During this period, no differences in caloric intake were observed between the two groups, but the trained rats ate significantly more protein than the untrained ones. This increase occurred at the expense of the intake of carbohydrate. Fat intake remained stable. The training-induced increase in protein intake was also apparent when food choice was analyzed within each group in reference to the baseline intake measured at the end of the adaptation period. Indeed, food selection was not modified in untrained rats, but protein intake was significantly increased in the trained group (from 43.4% to 52.6%, $P < .05$, Student's paired t test). On the other hand, the lack of changes in food choice in the untrained rats suggest that the age and weight difference between the trained and untrained rats at the time of the study were too small to induce significant physiological changes.

Preexercise energy expenditure measured while the rats rested quietly on the treadmill before the start of the exercise was similar in trained and in untrained rats. Energy expenditure during running was also similar in trained and in untrained rats. Postexercise energy expenditure was decreased by 10% to 12% in both groups relative to preexercise resting metabolism, but the phenomenon was statistically significant only in the untrained group.

Preexercise glucose oxidation (Gox) was not different between trained and untrained rats and accounted for 60% to 62% of total energy expenditure. During exercise, glucose and lipid oxidation both increased sharply. The increase in lipid oxidation was significantly higher than the increase in Gox in trained (3.29 W/kg$^{(0.66)}$ ± 0.24 *v* 1.64 W/kg$^{(0.66)}$ ± 0.33; $P < .01$), but not in untrained (2.75 W/kg$^{(0.66)}$ ± 0.35 *v* 2.31 W/kg$^{(0.66)}$ ± 0.30; $P = .45$) rats. However, this trend was not sufficient to induce a significant difference in substrate oxidation during exercise between trained and untrained rats (Table 1). However, in both groups, the participation of Gox to total energy expenditure decreased significantly during exercise (Table 1). This relative decrease in Gox persisted after the completion of exercise in untrained rats (49.1% *v* 60.4%; $P < .01$) and the trend also existed in trained rats (50.1% *v* 61.6%; $P = .06$).

Table 1. Differences in Metabolic and Behavioral Parameters Between Untrained and Trained Rats

Variable	Untrained (n = 15)	(SEM)	Trained (n = 8)	(SEM)
Body weight (g)	232.1	(6.3)	275†	(6.4)
Δ Body weight (g)	22.3	(6.3)	9.1†	(1.4)
Energy intake (kJ)	76.7	(4.2)	73.0	(3.1)
Glucose intake (%)	39.5	(4.7)	21.3†	(4.9)
Lipid intake (%)	21.3	(4.8)	26.3	(7.2)
Protein intake (%)	39.2	(2.7)	52.6†	(4.2)
Metabolic rate (W/kg$^{0.66}$)				
Before exercise	5.97	(0.28)	6.14	(0.28)
During exercise	11.02§	(0.20)	11.08§	(0.36)
After exercise	5.25§	(0.11)	5.19$^{\text{NS}}$	(0.31)
Lipid oxidation (W/kg$^{0.66}$)				
Before exercise	2.34	(0.27)	2.29	(0.33)
During exercise	5.11§	(0.47)	5.61§	(0.33)
After exercise	2.65$^{\text{NS}}$	(0.22)	2.59	(0.20)
Gox (W/kg$^{.66}$)				
Before exercise	3.60	(0.25)	3.82	(0.42)
During exercise	5.91§	(0.47)	5.47§	(0.33)
After exercise	2.59§	(0.28)	2.59§	(0.17)
Gox (% of total metabolic rate)				
Before exercise	60.4	(3.6)	61.6	(5.6)
During exercise	53.7§	(4.2)	49.3§	(2.5)
After exercise	49.1‡	(4.7)	50.1$^{\text{NS}}$	(2.1)

Horizontally: *$P < .05$; †$P < .01$ (untrained *v* trained). Two-tailed unpaired *t* test.

Vertically: not significant (NS), ‡$P < .05$; §$P < .01$ *v* same parameter before exercise. Two-tailed paired *t* test.

Table 2. Differences in Metabolic and Behavioral Parameters Between Glucose and Lipid Eaters

Variable	Glucose Eaters (n = 12; T = 2, U = 10)	(SEM)	Lipid Eaters (n = 11; T = 6, U = 5)	(SEM)
Body weight (g)	241.3	(7.5)	253.3	(29.7)
Δ Body weight (g)	19.4	(2.3)	16.1	(02.4)
Energy intake (kJ)	76.2	(4.2)	74.4	(6.3)
Glucose intake (%)	48.4	(2.5)	16.5†	(2.9)
Lipid intake (%)	11.1	(2.2)	36.2†	(5.7)
Protein intake (%)	40.6	(3.3)	47.4	(5.0)
Metabolic rate (W)				
Before exercise	5.75	(0.25)	6.31	(0.50)
During exercise	11.13§	(0.20)	11.30§	(0.98)
After exercise	5.19‡	(0.11)	5.30‡	(0.59)
Lipid oxidation (W)				
Before exercise	2.23	(0.20)	2.48	(0.31)
During exercise	5.36§	(0.45)	5.41§	(0.70)
After exercise	2.62‡	(0.22)	2.59$^{\text{NS}}$	(0.31)
Gox (W)				
Before exercise	3.54	(0.28)	3.82	(0.39)
During exercise	5.75§	(0.42)	5.89§	(0.70)
After exercise	2.57‡	(0.25)	2.71§	(0.33)
Gox (% of total metabolic rate)				
Before exercise	61.1	(3.6)	60.5	(6.3)
During exercise	52.5§	(3.7)	52.6§	(6.2)
After exercise	49.2§	(4.4)	49.6‡	(6.1)

NOTE. Statistics as in Table 1.

Abbreviations: T, trained rats; U, untrained rats.

Data Analysis According to Diet Selection of the Rats

Since only weak differences in energy expenditure during exercise were observed between trained and untrained rats, we reanalyzed the data according to spontaneous diet selection to verify if, in these rats, diet selection, rather than training status, could be a component susceptible to influence substrate oxidation during exercise (Table 2).

Thus, the rats were grouped according to the average CHO intake of all the rats (33% of total energy intake) between those in which CHO intake accounted for more than 33% of the daily caloric intake (glucose eaters, n = 12) and those in which CHO intake accounted for less than 33% (n = 11).

Fewer trained rats than expected from a random distribution were classified as glucose eaters. Glucose intake accounted for 48% of total caloric intake in glucose eaters versus 16.5% of caloric intake in the other rats. Protein intake was comparable in glucose eaters (41%) and in the other rats (47%), so that the caloric intake of the two groups differed only according to glucose and fat intakes. Body weight, body weight gain, and energy intake were not different. Also, no differences were observed between these groups in any of the energetic parameters measured before, during, and after exercise. In particular, despite the large differences in food choice, Gox provided the same 60% to 61% of preexercise resting metabolism in both groups. This proportion decreased to 52% to 53% during exercise and further decreased to 49% to 50% after exercise. Postexercise resting metabolism was significantly decreased in comparison to preexercise resting metabolism in both groups. This decrease was due to decreased oxidation of glucose.

Data Analysis According to Preexercise Resting Glucose Oxidation

This mode of analysis was aimed at studying if the preferential use of a substrate at rest was related to diet selection and/or substrate oxidation during exercise. Thus, the rats were grouped according to the average preexercise resting Gox (60.8% of total energy expenditure) between glucose users (basal Gox, 74%; n = 10) and lipid users (basal Gox, 52.6%; n = 14) (Table 3).

The trained and untrained rats were evenly distributed between glucose and lipid users. Body weight, body weight gain, and energy intake were not different between the two groups. Food selection was also similar, confirming that, in the rats of this experiment, no relationship existed between diet selection measured over 24 hours and substrate oxidation measured at rest before exercise. Preexercise resting metabolism, running metabolism, and postexercise resting metabolism were not different between the two groups. The relationship between Gox at rest and Gox during exercise (Fig 2) showed that the larger the contribution of Gox to resting metabolism before exercise, the larger the contribution of Gox to running metabolism during exercise. However, the slope was smaller for trained than for untrained rats (0.5 *v* 1.41; $P < .01$), confirming that the increase in Gox induced by exercise was smaller in trained rats. Finally, as observed in the other groups, postexercise metabolism was significantly decreased after exercise. In both groups, this phenomenon occurred as a result of a decreased glucose oxidation, while lipid oxidation was not modified.

Table 3. Differences in Metabolic and Behavioral Parameters Between Glucose and Lipid Users

Variable	Glucose Users (n = 10; T = 4, U = 6)	(SEM)	Lipid Users (n = 13; T = 5, U = 8)	(SEM)
Body weight (g)	239.6	(11.7)	263.1	(7.3)
Δ Body weight (g)	18.2	(2.7)	16.9	(3.4)
Energy intake (kJ)	75.7	(3.6)	79.4	(5.9)
Glucose intake (%)	35.5	(5.1)	42.9	(4.2)
Lipid intake (%)	17.4	(4.4)	27.5	(8.0)
Protein intake (%)	47.1	(4.2)	42.9	(4.2)
Metabolic rate (W)				
Before exercise	6.28	(0.28)	5.58	(0.22)
During exercise	10.85§	(0.28)	11.24§	(0.28)
After exercise	5.19§	(0.11)	5.22‡	(0.28)
Lipid oxidation (W)				
Before exercise	1.65	(0.25)	2.65†	(0.17)
During exercise	4.07§	(0.47)	6.22†§	(0.22)
After exercise	2.12^{NS}	(0.20)	2.93*^{NS}	(0.25)
Gox (W/kg$^{0.66}$)				
Before exercise	4.63	(0.22)	2.93	(0.14)
During exercise	6.81§	(0.50)	4.99§	(0.22)
After exercise	3.07§	(0.22)	2.29‡	(0.31)
Gox (% of total metabolic rate)				
Before exercise	74.0	(3.2)	52.6†	(2.1)
During exercise	62.5§	(4.4)	45.4†§	(1.6)
After exercise	59.0§	(3.8)	43.4†‡	(4.7)

NOTE. Statistics as in Table 1.

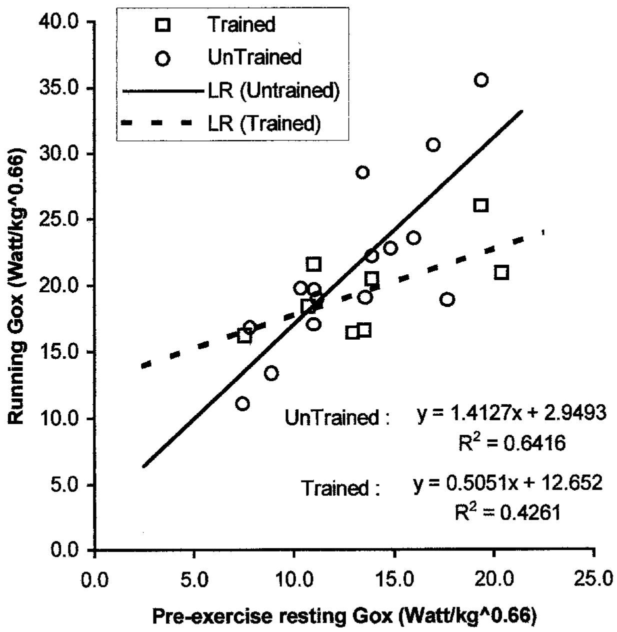

Fig 2. Relationship between Gox before and Gox during exercise in trained and untrained rats. The larger the Gox before exercise, the larger the Gox during exercise. However, the exercise-induced increase in Gox was smaller in trained than in untrained rats ($P < .05$).

DISCUSSION

In this study, regular exercise at moderate intensity in male rats allowed selection of macronutrient intake, reduced body weight gain, and did not affect caloric intake, but modified diet selection: protein intake was enhanced at the expense of CHO intake, while lipid intake was not affected. Further analysis of the data according to diet selection and substrate oxidation of the rats showed that substrate oxidation during exercise could not be predicted from diet selection or training status, but was correlated with resting substrate oxidation before exercise.

One major hypothesis to explain the changes in food selection induced by exercise is that they reflect the substrate requirements of the exercise.[3,4] It was a major goal of this experiment to verify this point. We observed that regular exercise induced the partial replacement of CHO intake by the intake of protein, while lipid intake was not significantly modified. This result is in general agreement with the literature since (1) an increased protein intake is the most reproducible response to exercise,[5,12,16,17] and (2) exercise training of moderate intensity, such as the training procedure used in this experiment, contrary to high-intensity exercise, can preserve or even increase lipid intake.[5,18,19]

However, in this study, comparison of food selection between trained and untrained rats was not in direct agreement with the changes in substrates requirements that could be expected according to the exercise-induced alterations in substrate oxidation. In particular, since the exercise and postexercise periods increased lipid more than glucose utilization, it could be expected to observe a larger fat intake at the expense of glucose in the trained rats. In fact, glucose intake did decrease, but largely at the benefit of protein intake. This occurred despite the fact that during exercise, amino acid oxidation cannot supply more that 10% to 15% of total energy expenditure.[8-10] Moreover, in normal conditions, most of the amino acids are oxidized after conversion to glucose. On general grounds, differences between 24-hour food selection and substrate oxidation during exercise suggest that metabolic adaptations distant from exercise are more likely to influence the feeding strategies than the metabolic changes during exercise. In the present study, it was not possible to measure the pattern of macronutrient intake throughout the day, but previous studies have shown that macronutrient selection indeed varies between night and day and can be modified by changes in nutrient requirements induced by food restriction.[20,21] In addition, in a recent study, it was also demonstrated that diet selection of rats trained at high intensity exhibited large within-day variations and, in particular, was modified by running[22]: CHO intake (ie, energy intake) was increased before exercise, while protein intake (ie, intake of structural elements for protein synthesis and muscle repair)[23,24] was increased after exercise. This pattern of macronutrient intake suggested a fine adjustment to the metabolic needs induced by exercise, and the preexercise increase in CHO intake was interpreted as an anticipatory adjustment to the energy requirements of the high-intensity exercise. In the present experiment, we reproduced experimental conditions similar to the ones of the experiment cited earlier, except that exercise was of moderate intensity. It is thus highly probable that such an adapted pattern of macronutrient selection occurred, so that during the hours preceding exercise, it was adjusted to provide a fuel mixture well adapted to substrate oxidation during exercise. We believe this mechanism is most likely at the base of the discrepancy observed in this study between 24-hour diet selection and substrate oxidation during exercise.

The fact that we observed a strong positive correlation between substrate oxidation during exercise and substrate oxidation at rest immediately before exercise is also an important point of this study. According to this correlation, the more glucose oxidized at rest, the more oxidized during exercise. The possibility of anticipating glucose oxidation, and thus lipid oxidation, during exercise, provides a tool that may be useful for athletes to control their training or anticipate their performance, and could help clinicians use exercise in overweight people to favor lipid, rather than glucose utilization.

Therefore, it is important to further understand how the relationship between preexercise and exercise energy metabolism evolves in relation to dietary manipulations and in relation to intensity and duration of exercise. In addition, we observed that postexercise Gox was usually decreased, while lipid oxidation remained unchanged or even increased compared with resting preexercise values. This phenomenon is also important to take into account if the purpose of the exercise is to favor body weight loss, because it has the potential to induce a negative energy balance. It has already been observed after weight lifting in humans and was considered to be a potential mechanism of excess postexercise oxygen consumption (EPOC).[25] However, in the present study, we did not observe EPOC after exercise, certainly because only exercise intensities above 75% of $\dot{V}O_2$max can induce a significant EPOC.[26,27] In some cases, we even observed a slight decrease in energy expenditure that, we suggest, can be explained by the fact that despite the care taken to reduce the stress, some rats were slightly nervous before the run.

Figure 1 gives a good example of this point. In this rat, postexercise energy expenditure was increased after the $\dot{V}O_2$max test that increased metabolism to greater than 8 W and RQ to greater than 1, but not after the test exercise that was performed at 4.5 W with a RQ of 0.83. This also shows that if EPOC is associated with a lower postexercise RQ,[25] lipid utilization during the postexercise period may also be stimulated after mild-intensity exercise.

In conclusion, this experiment suggests that exercise-induced changes in substrate oxidation that occur outside of the exercise session may be the most important component that drives the dietary changes observed in subjects submitted to regular exercise. This result agrees with other studies that suggested exercise-induced changes in postexercise metabolism may be more important than exercise itself in affecting 24-hour energy expenditure and substrate oxidation.[26,28-30] Understanding the energetic requirements induced by exercise outside of the exercise period would help to improve exercise and nutritional support to better reach one of the two major goals of exercise training: performance and body weight loss.

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