The onset of fatigue during prolonged endurance exercise after high-fat and high-carbohydrate meals

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Whitley, Helena A., S. M. Humphreys, I. T. Campbell, M. A. Keegan, T. D. Jayanetti, D. A. Sperry, D. P. MacLaren, T. Reilly, and K. N. Frayn. Metabolic and performance responses during endurance exercise after high-fat and high-carbohydrate meals. J. Appl. Physiol. 85(2): 418–424, 1998.—We studied the effects of preexercise meal composition on metabolic and performance-related variables during endurance exercise. Eight well-trained cyclists (maximal oxygen uptake 65.0 to 83.5 ml·kg⁻¹·min⁻¹) were studied on three occasions after an overnight fast. They were given isoenergetic meals containing carbohydrate (CHO), protein (P), and fat (F) in the following amounts (g/70 kg body wt): high-carbohydrate meal, 215 CHO, 26 P, 3 F; high-fat meal, 50 CHO, 14 P, 80 F. On the third occasion subjects were studied after an overnight fast. Four hours after consumption of the meal, subjects started exercise for 90 min at 70% of their maximal oxygen uptake, followed by a 10-km time trial. The high-carbohydrate meal compared with the high-fat meal resulted in significant decreases (P < 0.05) in blood glucose, plasma nonesterified fatty acids, plasma glycerol, plasma chylomicron-triacylglycerol, and plasma 3-hydroxybutyrate concentrations during exercise. This was accompanied by an increase in plasma insulin (P < 0.01 vs. no meal), plasma epinephrine, and plasma growth hormone concentrations (each P < 0.05 vs. either of the other conditions) during exercise. Despite these large differences in substrate and hormone concentrations in plasma, substrate oxidation during the 90-min exercise period was similar in the three trials, and there were no differences in performance on the time trial. These results suggest that, although the availability of fatty acids and other substrates in plasma can be markedly altered by dietary means, the pattern of substrate oxidation during endurance exercise is remarkably resistant to alteration.

Isoenergetic meals; fat oxidation; carbohydrate oxidation; performance

The onset of fatigue during prolonged endurance exercise is associated with depletion of the body’s muscle glycogen stores (1, 18). For this reason there has been great interest over the years in nutritional means of increasing the supply of exogenous carbohydrate both before and during exercise (3, 9, 31, 37, 38). In contrast, there has been little research regarding dietary fat manipulation and the availability of fat both before and during exercise.

Several studies have shown that a high-fat diet can significantly enhance exercise performance in rats (24, 32) and dogs (16). In humans, results have been less consistent. Short-term feeding of a high-fat (low-carbohydrate) diet impairs performance, apparently through lowering of muscle glycogen concentrations (19). Longer term adaptation to such a diet improves endurance performance at moderate intensity (21), but responses are variable, and in other studies no consistent effect was found (28).

Dietary and pharmacological methods have also been used to show that increasing the availability and oxidation of fatty acids during endurance exercise reduces the degradation of muscle glycogen (5, 11, 12, 33). This suggests that there is potential for exogenous fat to reduce carbohydrate oxidation and consequently delay fatigue during endurance exercise. However, exercise performance was not measured in these studies, and the meals given were nonisoenergetic, which may affect the relative contribution of substrates to overall energy expenditure. In rats, an increased availability of fatty acids before exercise has been shown to delay the development of exhaustion during prolonged endurance exercise (17).

Substrate supply before exercise may be manipulated by feeding meals containing different proportions of carbohydrate and fat. Ingestion of dietary fat primarily raises the plasma triacylglycerol (TAG) rather than the nonesterified fatty acid (NEFA) concentration. This may be beneficial, however, because chylomicron-TAG is a good substrate for the enzyme lipoprotein lipase (LPL) in skeletal muscle (4), and thus dietary fatty acids derived from chylomicrons could contribute to fatty acid oxidation in muscle (15). Ingestion of carbohydrate loads several hours before exercise will suppress plasma NEFA concentrations and decrease the rate of fat oxidation. This is associated with an elevation in the concentration of plasma insulin before exercise and an increase in the rate of carbohydrate oxidation during exercise (7, 25). Neufer et al. (26) and Sherman et al. (30) reported that a relatively large preexercise carbohydrate meal (200–312 g) eaten 4 h before exercise improves endurance performance in cyclists. Particular combinations of carbohydrate and fat, however, lead to maintained plasma NEFA concentrations probably because adipose tissue LPL will release fatty acids directly in the form of NEFA from chylomicron-TAG (14, 36). Such meals may therefore increase the availability of fatty acids to skeletal muscle while also providing carbohydrate.

The purpose of this study was to investigate the metabolic and performance-related responses during endurance exercise after isoenergetic high-fat and high-carbohydrate preexercise meals and to compare these with a control situation with no preexercise meal.
Because it was believed to be important to compare isoenergetic meals, the amounts of carbohydrate given in the two test meals were necessarily different, and, as will be described, this may be important in interpreting the results.

MATERIALS AND METHODS

Subjects. Eight male endurance-trained cyclists participated in this study. All subjects were competing regularly in both regional and national championship events. Their physical characteristics are shown in Table 1. Subjects were given both verbal and written instructions outlining the experimental procedure, and written informed consent was obtained. The study was approved by the Ethics Committee of Liverpool John Moores University and the South Manchester Medical Research Ethics Committee.

Experimental design. Subjects made an initial visit to the laboratory for familiarization with the testing equipment and to perform a maximal cycle ergometer test to determine maximal oxygen uptake (V˙O2max). Height, body mass, and percent body fat estimated from skinfold thickness (10) were also measured at this visit.

The subjects then attended the laboratory on three occasions in a balanced design. All subjects were studied 1 day/wk during 1 calendar mo. Subjects completed a 2-day dietary and physical activity record before each of the three trials; they were asked to keep their diet and activity the same before each test day. Two days before each test they undertook a low-intensity training ride at a heart rate of 45–50 beats/min below maximum, and they rested during the day before each test. They consumed a low-fat meal (<3.5% energy from fat) the evening before each study; a list of suitable foods was provided to help them achieve this. In this way, variations in diet and exercise before the 3 study days were minimized. A dietary profile of the macronutrients for each subject for the 2 days before each meal was chosen to typify a breakfast cereal as described by Whitley et al. (36).

At 3 h 15 min after consumption of the meal, subjects arrived at the laboratory. A cannula was placed retrogradely in a large vein draining a hand that was warmed throughout the study in a heated box to provide arterialized blood (23). The cannula was kept patent with slow saline infusion (0.9% NaCl). Indirect calorimetry was performed by using an online automated gas analyzer (Exercise Tester, P. K. Morgan, Chatham, Kent, UK).

At 4 h after the meal, subjects started exercise for 90 min on their own bicycle mounted on a Kingcycle trainer (EDS Portaprompt, High Wycombe, UK) at an intensity corresponding to 70% of their V˙O2max. A 3-min recovery period then followed, during which the subject cycled at a reduced exercise intensity. This enabled the experimenter to program the Kingcycle trainer software to perform a simulated 10-km time trial, realistic of a competitive situation. A 2-min warm-up period was included in the Kingcycle trainer software program to enable the subject to reach an optimum work intensity for the simulated 10-km time trial. Time-trial protocols have been shown to result in improved performance evaluation compared with time-to-exhaustion tests in well-trained cyclists (20), and use of the Kingcycle trainer has been shown to give extremely reproducible results for time trials (27). Blood samples (10 ml), indirect calorimetry, heart rate (Polar Sport Tester, Polar Heart Rate Monitors, Polar Electro, Kempele, Finland), and ratings of perceived exertion (RPE) were obtained at rest and at 15, 30, and 60 min during the continuous ride. The same measurements were recorded on completion of the 90 min and in the final few minutes of the 10-km time trial. The test protocol is illustrated in Fig. 1.

Analytic methods. Blood samples were drawn into 10 ml heparinized syringes (Monovette, Sarstedt, Leicester, UK). A portion (20 µl) was used immediately for measurement of blood glucose concentration in duplicate (HemoCue B-glucose photometer, Hemocue, Sheffield, UK). From the remaining blood, plasma was separated rapidly at 4°C and frozen for later determination of plasma NEFA and TAG concentrations by enzymatic methods. In addition, a portion of the plasma was deproteinized with perchloric acid (7% wt/vol) in preparation for plasma glycerol, lactate, and 3-hydroxybutyrate (3-OHB) determination by enzymatic methods. All enzymatic methods were adapted to an IL Monarch centrifugal analyzer.

Table 2. Composition of test meals

<table>
<thead>
<tr>
<th>Variable</th>
<th>High-Fat Meal</th>
<th>High-Carbohydrate Meal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carbohydrate, g</td>
<td>26.0</td>
<td>6.6</td>
</tr>
<tr>
<td>Fat, %Energy</td>
<td>73.9</td>
<td>10.7</td>
</tr>
<tr>
<td>Carbohydrate, %Energy</td>
<td>20.0</td>
<td>86.3</td>
</tr>
<tr>
<td>Energy, kcal</td>
<td>4,002</td>
<td>4,000</td>
</tr>
</tbody>
</table>

Table 1. Physical characteristics of the cyclists

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age, yr</td>
<td>21</td>
<td>19–34</td>
</tr>
<tr>
<td>Height, m</td>
<td>1.80</td>
<td>1.75–1.84</td>
</tr>
<tr>
<td>Body mass, kg</td>
<td>69.5</td>
<td>63.0–80.0</td>
</tr>
<tr>
<td>Body mass index, kg/m²</td>
<td>22.1</td>
<td>19.4–24.4</td>
</tr>
<tr>
<td>%Body fat</td>
<td>9.07</td>
<td>7.0–12.0</td>
</tr>
<tr>
<td>V˙O2max, ml·kg⁻¹·min⁻¹</td>
<td>74.6</td>
<td>65.0–83.5</td>
</tr>
<tr>
<td>Power output at 70% V˙O2max, W</td>
<td>245</td>
<td>200–275</td>
</tr>
<tr>
<td>Plasma cholesterol, mmol/l</td>
<td>4.27</td>
<td>3.28–5.91</td>
</tr>
<tr>
<td>HDL cholesterol, mmol/l</td>
<td>1.04</td>
<td>0.73–1.56</td>
</tr>
</tbody>
</table>

Values are for 8 subjects. V˙O2max, maximal oxygen uptake; HDL, high-density lipoprotein.
differences in substrate oxidation and energy expenditure during each trial. Because nitrogen excretion was not measured in this study, values were taken from similar studies in resting subjects by Flatt et al. (13). The value used was 0.11 mg nitrogen·kg body weight·h⁻¹, equivalent to 3 g protein oxidation/h for a 72-kg person.

Changes in the metabolic and hormonal responses to the meals with time during the 90-min exercise period were assessed by using an ANOVA model for repeated measures, as were differences in substrate oxidation and energy expenditure between the different dietary conditions. To summarize the data not shown graphically, and to obtain post hoc comparisons between the dietary conditions, responses were assessed as total areas under the curve (AUCs) over the 90-min exercise period. The AUC was divided by the total exercise time period to give an average value for the 90-min exercise period. These AUCs were analyzed by using repeated-measures ANOVA, as were the "resting" values (immediately preexercise). For all statistical analyses, a level of P < 0.05 was considered to be statistically significant. For values attaining this criterion, post hoc analysis was performed by using Tukey's honestly significant difference test, to identify which dietary conditions were significantly different.

RESULTS

Nutritional analysis. Mean values and SEs for the three macronutrients during the 2 days before each trial (expressed as a percentage of total energy) were 61.5 ± 3.2% carbohydrate, 24.0 ± 4.6% fat, and 14.5 ± 2.3% protein. Absolute amounts were 445 ± 23 g carbohydrate, 77 ± 5 g fat, and 104 ± 5 g protein per day with a mean daily energy intake of 11.9 ± 0.6 MJ. There were no significant differences among the three trials.

Blood glucose and plasma insulin concentrations. For all trials the blood glucose concentration decreased during the first 15 min of exercise and then remained almost constant for the next 45 min before declining during the final 30 min of exercise (Fig. 2). Similarly, plasma insulin concentrations declined during the first 15 min in all trials and then decreased gradually toward the end of the exercise period (Fig. 2). Blood glucose concentrations in the high-fat trial were greater than in the high-carbohydrate trial, and plasma insulin concentrations in the high-carbohydrate trial were significantly greater than in the no-meal trial (statistics in Fig. 2).

Plasma metabolite concentrations. The plasma TAG concentration was greater before (P < 0.05) and during exercise period. These AUCs were analyzed by using repeated-measures ANOVA, as were the "resting" values (immediately preexercise). For all statistical analyses, a level of P < 0.05 was considered to be statistically significant. For values attaining this criterion, post hoc analysis was performed by using Tukey's honestly significant difference test, to identify which dietary conditions were significantly different.

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Plasma metabolite concentrations. The plasma TAG concentration was greater before (P < 0.05) and during
exercise in the high-fat trial compared with the no-meal trial (Fig. 3). Similarly, the plasma chylomicron-TAG concentration was significantly greater in the high-fat trial compared with the other two trials (statistics in Fig. 3).

Plasma NEFA concentrations (Fig. 2) and plasma glycerol concentrations (Fig. 3) were significantly greater before exercise in the high-fat and no-meal trials compared with the high-carbohydrate trial ($P < 0.01$). During exercise both plasma NEFA and plasma glycerol concentrations were significantly greater in the high-fat and no-meal trials than in the high-carbohydrate trial ($P < 0.01$). For plasma glycerol, there were significant effects of time and of meal type and interaction between time and meal type (all $P < 0.001$), with a significant difference between both high-fat and no-meal trials and high-carbohydrate trial ($P < 0.01$ and $P < 0.001$, respectively, on post hoc testing). For plasma 3-OHB there were significant effects of time ($P < 0.01$) and of meal type ($P < 0.05$) on repeated-measures ANOVA but no significant post hoc differences between trials.

Plasma lactate concentrations (not shown in figure form) increased during the first 15 min of exercise and then declined. There were no significant differences in plasma lactate concentrations among the three trials (Table 3).

Plasma hormone concentrations (not shown in figure form). Plasma norepinephrine and epinephrine concentrations increased throughout the exercise period for all trials. This rise in plasma epinephrine was significantly greater in the high-carbohydrate trial compared with the other two trials. Plasma growth hormone concentration was significantly greater throughout the exercise period in the high-carbohydrate and no-meal trials compared with the high-fat trial (Table 3).

Plasma cortisol concentrations remained almost constant in the no-meal and high-fat trials, whereas they

![Figure 3. Plasma triacylglycerol (TAG), chylomicron-TAG, glycerol, and 3-hydroxybutyrate (3-OHB) concentrations during 90 min of exercise after the 3 different test meals (see Table 2 for meal composition): no meal (●), high-fat meal (▲); high-carbohydrate meal (●). Values are means with SE represented by vertical bars; $n = 8$ subjects for all 3 meals. Repeated-measures ANOVA for plasma TAG showed significant effects of time ($P < 0.001$) and of meal type ($P < 0.05$) and interaction between time and meal type ($P < 0.001$). Post hoc testing showed a significant difference between high-fat and no-meal trials ($P < 0.05$). For chylomicron-TAG, there were significant effects of time ($P < 0.01$) and of meal type ($P < 0.005$) and interaction between time and meal type ($P < 0.001$). Post hoc testing showed a significant difference between high-fat and the other 2 trials ($P < 0.01$). For plasma glycerol, there were significant effects of time and of meal type and interaction between time and meal type (all $P < 0.001$), with a significant difference between both high-fat and no-meal trials and high-carbohydrate trial ($P < 0.01$ and $P < 0.001$, respectively, on post hoc testing). For plasma 3-OHB there were significant effects of time ($P < 0.01$) and of meal type ($P < 0.05$) on repeated-measures ANOVA but no significant post hoc differences between trials.

### Table 3. Areas under the curve for plasma lactate and hormone concentrations against time during the 90 min of exercise at 70% $V_{\text{O}_2\text{max}}$

<table>
<thead>
<tr>
<th>Condition</th>
<th>Lactate, µmol/l</th>
<th>Norepinephrine, nmol/l</th>
<th>Epinephrine, nmol/l</th>
<th>Growth Hormone, mU/l</th>
<th>Cortisol, nmol/l</th>
</tr>
</thead>
<tbody>
<tr>
<td>No meal</td>
<td>2.432 ± 263</td>
<td>11.8 ± 1.69</td>
<td>1.31 ± 0.20</td>
<td>66.2 ± 10.7</td>
<td>620 ± 77.1</td>
</tr>
<tr>
<td>High-fat meal</td>
<td>2.392 ± 320</td>
<td>12.5 ± 1.73</td>
<td>1.29 ± 0.19</td>
<td>39.0 ± 7.02*</td>
<td>583 ± 80.0</td>
</tr>
<tr>
<td>High-CHO meal</td>
<td>2.760 ± 350</td>
<td>12.5 ± 2.14</td>
<td>2.00 ± 0.36†</td>
<td>62.0 ± 8.78</td>
<td>613 ± 78.1</td>
</tr>
</tbody>
</table>

Values are means ± SE for 8 subjects for all 3 conditions. Total areas under the curve were divided by time baseline to represent average value over 90-min exercise period. CHO, carbohydrate. Significant difference among the 3 meals: *$P < 0.05$; †$P < 0.01$. 

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progressively increased in the high-carbohydrate trial. No significant differences were observed among the three trials (Table 3).

Indirect calorimetry. The respiratory exchange ratio (RER) was significantly greater before exercise in the high-carbohydrate trial compared with the other two trials (P < 0.01; Fig. 4), reflecting an increase in the proportion of carbohydrate oxidized. During the exercise period the RER gradually declined below preexercise values in the high-carbohydrate trial, whereas the RER in the high-fat and no-meal trials rose over the first 15 min to approach the value in the high-carbohydrate trial and then remained relatively constant throughout the exercise period. Before exercise, the rate of carbohydrate oxidation was also greatest after the high-carbohydrate meal (P < 0.01), but carbohydrate oxidation rose markedly, to similar values in all trials, during the 90-min exercise period (Table 4). In contrast, fat oxidation was greater before exercise in the high-fat and no-meal trials compared with the high-carbohydrate trial (P < 0.01). During the exercise period, fat oxidation progressively increased in the high-carbohydrate trial, whereas fat oxidation increased for the first 15 min and then remained relatively stable in the high-fat and no-meal trials (Table 4).

For all trials, energy expenditure increased significantly above preexercise values during the first 15 min of exercise. It then remained relatively stable throughout the exercise period and was not different among the three dietary conditions (Table 4).

Heart rate and RPE. Heart rate increased significantly above preexercise values for all trials during the first 15 min of exercise and then gradually increased toward the end of the exercise period. Equally, RPE values increased progressively throughout the exercise period for all trials. No significant differences in heart rate and RPE were observed among the three trials during the 90-min exercise period (data not shown).

Performance measures for the 10-km time trial. Time to complete the 10-km performance test was not significantly different among the three conditions, although there was considerable between-subject variability (Table 5, Fig. 5). Mean power output and heart rate (not shown) during the 10-km performance test were also not significantly different among the three trials (Table 5).

## DISCUSSION

The present study confirms the well-known observation that preexercise meals can profoundly affect the pattern of substrate availability in plasma. In the present study a large high-carbohydrate meal (215 g carbohydrate and 3 g fat) eaten 4 h before exercise resulted in a significant suppression in plasma NEFA concentrations during 90 min of endurance exercise compared with maintenance of plasma NEFA concentra-

### Table 4. Areas under the curve for substrate oxidation and energy expenditure against time during the 90 min of exercise at 70% VO2max

<table>
<thead>
<tr>
<th>Condition</th>
<th>CHO oxidation, mg·kg⁻¹·min⁻¹</th>
<th>Fat oxidation, mg·kg⁻¹·min⁻¹</th>
<th>Energy expenditure, kJ·kg⁻¹·min⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>No meal</td>
<td>22.2 ± 2.20</td>
<td>5.55 ± 0.80</td>
<td>0.58 ± 0.03</td>
</tr>
<tr>
<td>High-fat meal</td>
<td>22.3 ± 1.35</td>
<td>4.83 ± 0.65</td>
<td>0.56 ± 0.02</td>
</tr>
<tr>
<td>High-CHO meal</td>
<td>27.8 ± 1.70</td>
<td>5.50 ± 0.74</td>
<td>0.57 ± 0.02</td>
</tr>
</tbody>
</table>

Values are means ± SE for 8 subjects for all 3 meals. Areas under the curve were divided by time baseline to represent average value over respective exercise period. *Significant difference among the 3 meals; P < 0.05. Total area under the curve was divided by time baseline to represent average value over 90-min exercise period.

### Table 5. Performance measures for 10-km time trial

<table>
<thead>
<tr>
<th>Condition</th>
<th>Time to Completion, s</th>
<th>Mean Power, W</th>
</tr>
</thead>
<tbody>
<tr>
<td>No meal</td>
<td>874 ± 48</td>
<td>279 ± 31</td>
</tr>
<tr>
<td>High-fat meal</td>
<td>854 ± 37</td>
<td>290 ± 29</td>
</tr>
<tr>
<td>High-CHO meal</td>
<td>878 ± 44</td>
<td>276 ± 33</td>
</tr>
</tbody>
</table>

Values are means ± SD for 8 subjects for all 3 meals. Mean power was calculated as average power output during 10-km time trial.
Despite the marked alterations in substrate availability in plasma, our results show that the pattern of substrate oxidation during exercise is remarkably resistant to alteration by dietary means under these conditions. Total carbohydrate oxidation during the 90-min exercise period preceding the time trial was 227 g in the no-meal trial, 238 g in the high-fat trial, and 274 g in the high-carbohydrate trial, despite very different substrate concentrations in plasma. Only during the first 15 min of exercise were there differences in substrate oxidation between the trials. This is similar to the observation of Ravussin et al. (29) that marked elevation of plasma NEFA concentrations by means of Intralipid and heparin infusion affected the pattern of substrate oxidation only during the early part of exercise. These results contrast with those observed after isoenergetic meals of different macronutrient composition at rest, when relative rates of fat and carbohydrate oxidation vary according to meal composition (2, 36).

Given that the high-carbohydrate meal provided 165 g more carbohydrate than did the high-fat meal and 215 g more than did no meal, body carbohydrate stores will have been considerably higher at the beginning of the time trial after the high-carbohydrate meal than in the other two trials. Despite this, we observed no performance advantage with either meal compared with the fasting state. In this respect our results differ markedly from those of a number of studies that have shown beneficial effects on performance of a large carbohydrate load ingested 3–4 h before exercise (26, 30, 38; reviewed in Ref. 6). A possible reason for the fact that no consistent differences were observed in performance on the time trial may be that substrate availability is not the limiting factor in such a situation, in which lactate accumulation may be more important (8). Thus consideration of the appropriate performance test is important in the evaluation of preexercise feeding regimes.

In summary, the present study demonstrates that feeding isoenergetic meals containing different proportions of carbohydrate and fat can markedly affect the contributions of carbohydrate and fat to energy expenditure at rest, as long as 4 h after the meals. However, the pattern of substrate oxidation during exercise is very resistant to alteration despite variations in substrate availability in plasma.

Because we believed it important to study isoenergetic meals, the high-carbohydrate meal necessarily provided considerably more carbohydrate than did the high-fat meal. This must have affected the results because total body carbohydrate stores, as argued above, would have been greater at the start of exercise. It would be interesting in subsequent research to investigate the effect on substrate supply and exercise performance of a preexercise high-fat meal (as in this study) followed by additional carbohydrate taken at intervals during exercise, as the latter is common practice in competition among elite athletes.

The authors thank Mo Clark for valuable technical assistance during this study and Dr. John Dutton (Dept. of Clinical Chemistry.
REFERENCES


