Dietary Effects on Liver and Muscle Glycogen Repletion in Exhaustively Exercised Rats: Energy Composition and Type of Complex Carbohydrates

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Summary Previous reports have indicated that administration of a glucose-citrate (G-C) drink after a bout of exhaustive exercise results in more effective glycogen repletion in liver and skeletal muscle in rats as compared with administration of glucose alone. The present studies report the effects of the energy pattern and the type of carbohydrates, dextrin or starch from rice, in diet given following the G-C drink after exercise, on further glycogen repletion in the tissues of rats. Rats were adapted to meal-feeding 3 times a day and trained with light swimming for 7 to 10 days. On the final day of experiments, rats received the G-C drink after 2 h of exhaustive swimming and were then fed on diets with different energy patterns or carbohydrate types. Results showed that a high-carbohydrate diet is more effective than a high-fat diet for further glycogen repletion in liver and skeletal muscle. In addition, dextrin was revealed to be superior to starch as a carbohydrate source in tissue glycogen repletion. As compared with the high-fat diet, the high-carbohydrate diet, however, resulted in a lower serum free fatty acid concentration 4 h after ingestion of food possibly by decreasing adipose tissue lipolysis.

Key Words exhaustive swimming, glucose-citrate drink, energy pattern, dextrin, starch, glycogen repletion, liver, skeletal muscle, serum free fatty acid, lipolysis

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We have recently demonstrated that the post-exercise administration of glucose with citrate can stimulate glycogen repletion significantly in liver and skeletal muscle of rats during the early period of recovery, as compared with the feeding of glucose alone (1).

Sullivan (2) has reported that after competitive running, 25% of runners have troublesome abdominal pain or diarrhea, and that 50% have anorexia lasting for 0.5–2.5 h. Therefore, in order to achieve favorable physiological recovery, it is important to consider the composition of a meal which is served after exhaustive exercise. The nutritional consequence of such a meal becomes especially important when another competition is scheduled within several hours of the first.

The present investigation was conducted to explore the effects of diet given as lunch on liver and muscle glycogen repletion over several hours of recovery following exhaustive exercise. For the purpose of the present studies, the energy pattern as well as the type of dietary carbohydrates were investigated using rats adapted to a meal-feeding system of 3 meals equivalent to breakfast, lunch and supper. This feeding system has been suggested previously by Suzuki and Chiba (3) to be applicable to nutritional studies in rats.

This paper shows that a high carbohydrate diet can enhance more considerably glycogen repletion in liver and skeletal muscle than can a high-fat diet. In addition, dextrin as a carbohydrate source for diet was revealed to replenish the tissue glycogen more effectively than starch.

EXPERIMENTAL

Study on energy pattern of diet (experiment 1). Male Sprague-Dawley rats of 5 weeks of age (29 rats; Doken Co., Ibaraki) were used. The lights in the temperature-regulated room (26 ± 2°C) used were on from 07:00 to 19:00. Rats were individually housed in ordinary cages and automatically meal-fed three times per day with the Suzuki-Imamura feeding system (4). Rats were meal-fed on a basal diet (Table 1) at 18:30–18:50, 01:30–01:50 and 07:00–07:20. Water was given freely. This feeding schedule was continued for 7 days.

Swimming exercise was given at 21:30–22:00 every day during the 7-day feeding period. Swimming was performed in a plastic barrel (53 cm diameter and 50 cm deep with 30–35°C water) with a water-stream generated by compressed air and an air draining system (4). Rats had a load corresponding to 2–3% of body weight tied to their necks during swimming (1). The food intake was measured twice during the training period.

The outlines of the schedule for the final bout of exercise and the administration of drink and meal are shown in Fig. 1. On the final day of the experiment, rats were fed 23 g of the basal diet per kg body weight at 18:30–18:50 and were then fasted for 2.5 h prior to a final bout of exercise. Two hours of exhaustive swimming in streamed water was started at 21:30 with a load, corresponding to 4% of body weight, tied to the rats’ necks. Just before and after the exhaustive swimming, 6 rats...
Table 1. Compositions of basal, high-carbohydrate and high-fat diets (experiment 1).

|                   | Basal       | High-carbohydrate | High-fat    |
|-------------------|-------------|-------------------|-------------|
| (g/100 g)         |             |                   |             |
| Corn starch       | 51.0        | 58.0              | 43.0        |
| Sucrose           | 17.0        | 20.0              | 14.0        |
| Soybean oil       | 11.0        | 2.0               | 22.0        |
| Casein            | 16.0        | 15.0              | 18.0        |
| Salt mixturea     | 4.0         | 4.0               | 4.0         |
| Choline chloride  | 0.15        | 0.15              | 0.15        |
| Vitamin mixturea  | 0.85        | 0.85              | 0.85        |
| Fat-soluble vitamina | 0.044    | 0.044             | 0.044       |
| (kcal/100 g)      | 435         | 390               | 480         |
| Carbohydrate      | 62.5        | 80.0              | 45.0        |
| Fat               | 22.5        | 5.0               | 40.0        |
| Protein           | 15.0        | 15.0              | 15.0        |

aPurchased from CLEA Japan Inc., Tokyo.

Fig. 1. Experimental schedules for experiments 1 and 2. After adaptation to meal-feeding and training exercise for 7 days (experiment 1) or 10 days (experiment 2), rats were given 23 g and 20 g of the respective basal diets (Tables 1 and 2) per kg body weight at 18:30–18:50 and 18:30–19:00, respectively. Exhaustively loaded swimming from 21:30 to 23:30 was undertaken in both experiments. Just after exercise, rats were orally given a glucose-citrate drink at the level of 3.0 g of glucose and 0.5 g of citrate per kg body weight. Rats were given a high-carbohydrate diet or a high-fat diet (99 kcal/kg body weight, Table 1) at 01:30–01:50 (experiment 1) and Hinex-R-Dextrin® diet or Hinex-R-Starch® diet (105 kcal/kg body weight, Table 2) at 01:30–02:00 (experiment 2). Rats were killed at the indicated times. B and L, meal; G+C, glucose-citrate drink.
were killed. The remaining 17 rats were orally given a 2 ml solution containing 3.0 g of glucose and 0.5 g of citrate per kg body weight (G-C drink) in the same manner as described previously (1), and allowed to recover in their own cages. No water was given up to 01:30. Six rats were killed at 01:30. The remaining 11 rats were divided into 2 groups and given either the isocaloric (99 kcal/kg body weight) high-carbohydrate diet or high-fat diet (Table 1) at 01:30–01:50. Finally, 5 or 6 rats of each dietary group were killed at 06:00. Energy content of the final meal was about 90% of the average energy intake at 01:30–01:50 during the feeding period.

Rats were killed by decapitation. Blood was collected and serum was separated. Liver, heart, kidneys, soleus muscles and epididymal fat pads were removed as quickly as possible. These tissues, except for epididymal fat pads, were immediately frozen in liquid nitrogen and stored at −80°C until the assay of glycogen. Epididymal fat pads were weighed and dissected into several pieces for the assay of lipolytic activity and glycogen contents. Serum was determined for concentrations of glucose (5) and free fatty acids (6). Tissue glycogen contents were determined according to Lo et al. (7). Lipolytic activity of adipose tissue was measured as described elsewhere (8). Pieces of epididymal fat pads, weighing 100–120 mg, were incubated with mild shaking at 37°C for 60 min in 2 ml of Krebs-Ringer bicarbonate buffer, containing 3% bovine serum albumin (Fraction V, essentially fatty acid free; Sigma Co., St. Louis), pH 7.4. (-)Epinephrine (+)bitartrate (Sigma Co., St. Louis) was either not added (basal lipolysis) or added (epinephrine-stimulated lipolysis) at 5 μg/ml in the incubation medium. After incubation, the reaction was stopped by cooling the flasks in ice water for 5 min, and free fatty acid concentrations in the incubation medium were determined (6). The difference between epinephrine-stimulated lipolysis and basal lipolysis was considered to be epinephrine-induced lipolysis.

Study on the type of carbohydrates of diet (experiment 2). Thirty-five male Sprague-Dawley rats of 4 weeks of age (CLEA Japan Inc., Tokyo) were used. Feeding conditions were almost the same with those described in experiment 1. Rats were meal-fed on a basal diet (Table 2) at 18:30–19:00, 01:30–02:00 and 08:00–08:30 for 10 days. Drinking water was given freely.

Rats were loaded daily for 30 min swimming exercise in streamed water at 21:30–22:00 with sinkers around their necks as described in experiment 1.

On the final day of the exercise loading experiment, rats were given the basal diet of 20 g (78 kcal) per kg body weight at 18:30–19:00. Seven out of 35 rats were killed at 21:30. At this time, a 2-h period of exhaustive swimming for the remaining rats was started, with weights corresponding to 2–4% of body weight tied to the rats' necks.

Seven rats were killed immediately after the exhaustive swimming. The remaining rats were orally given the G-C drink as described in experiment 1, and then allowed to recover in their cages. Seven rats were killed at 01:30. The remaining 14 rats were divided into 2 groups and given either Hinex-R-Dextrin® (Dextrin) or Hinex-R-Starch® (Starch) (Otsuka Pharmaceutical Co., Ltd., Tokyo)
Table 2. Compositions of basal, Hinex-R-Dextrin® and Hinex-R-Starch® diets (experiment 2).

| Diets                | Basal  | Hinex-R-Dextrin® | Hinex-R-Starch® |
|----------------------|--------|------------------|-----------------|
|                      | (g/100 g) |                  |                 |
| Rice starch          | 55.0   | 70.1             |                 |
| Rice dextrin         |        |                  |                 |
| Sucrose              | 2.45   |                  |                 |
| Lactose              | 21.4   |                  |                 |
| Casein               | 14.0   | 14.0b            | 14.0b           |
| Soybean oil          | 2.0    | 9.3c             | 9.3c            |
| Salt mixture         | 4.0a   | *                | *               |
| Choline chloride     | 0.15   |                  |                 |
| Vitamin mixture      | 0.85a  | **               | **              |
| Fat-soluble vitamin  | 0.044a |                  |                 |
| (kcal/100 g diet)    | 390    | 420              | 420             |
| ( % of total calorie) | 80     | 67               | 67              |
| Carbohydrate         |        |                  |                 |
| Fat                  | 5      | 20               | 20              |
| Protein              | 15     | 13               | 13              |

*a Purchased from CLEA Japan Inc., Tokyo. *b Milk, soybean and wheat proteins. *c Margarine and butter. *: Ca 165 mg, Fe 2.8 mg, K 321 mg, Na 594 mg, Mg 63 mg, P 222 mg. **: A 1,900 IU, B1 0.85 mg, B2 1.27 mg, B6 2.11 mg, B12 6.34 mg, C 52.8 mg, D 158 IU, E 42 mg, Ni 13.7 mg, folic acid 0.63 mg, pantothenic acid 10.6 mg.

diets of 25 g (105 kcal) per kg body weight at 01:30–02:00. Seven rats of each dietary group were killed at 05:00.

Animals were killed and samples of serum, liver, heart, kidneys, soleus muscles and epididymal fat pads were obtained, stored and analyzed as described in experiment 1. Lipolysis study on adipose tissue, however, was not conducted in experiment 2.

Hinex-R-Dextrin® is a preparation for enteral hyperalimentation of patients. Hinex-R-Starch® was specially prepared for the present study. Both dextrin and starch were prepared from rice.

Statistical analysis of the data was done by means of Student’s t-test.

RESULTS

Experiment 1
Serum glucose and free fatty acid concentrations (Fig. 2)

With 2 h of exhaustive swimming, serum glucose concentrations were signifi-
Fig. 2. Changes in concentrations of serum glucose (A) and serum free fatty acids (B) (experiment 1). Each point and vertical line represents mean and SEM for 5-6 rats, respectively. ○, pre-exercise, post-exercise, or pre-meal; △, high-carbohydrate diet; ●, high-fat diet. B, L and S, meal; Ex, swimming exercise. *, **, *** Significant difference between the two adjacent points (*p<0.05, **p<0.01, ***p<0.001).

Glycogen stores in liver, soleus muscle, heart, kidney and epididymal fat pad (Fig. 3)

The 2 h of exhaustive swimming resulted in a significant reduction of glycogen stores in liver (p<0.001), soleus muscle (p<0.01) and epididymal fat pad (p<0.05). The administration of the G-C drink immediately after the exercise caused a significant repletion of glycogen stores in liver (p<0.001), soleus muscle (p<0.01) and heart (p<0.001). During the 4-h post-meal period, significant repletion of glycogen stores in liver (p<0.001), soleus muscle (p<0.01), and epididymal fat pad (p<0.01) was observed in the high-carbohydrate diet fed group. In the high-fat diet fed group, similar increases in glycogen stores were found in these three tissues, which were not significant. Consequently, the difference in glycogen stores at 06:00 between the high-carbohydrate diet and high-fat diet fed groups was significant in liver (p<0.001), soleus muscle (p<0.05) and epididymal fat pad (p<0.01).

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Fig. 3. Changes in glycogen contents of liver (A), soleus muscle (B), heart (C), kidney (D) and epididymal fat pad (E) (experiment 1). Each point and vertical line represents mean and SEM for 5–6 rats, respectively. ○, pre-exercise, post-exercise or pre-meal; △, high-carbohydrate diet; ●, high-fat diet. a,b,c Significantly different from the high-fat diet fed group (*p<0.05, **p<0.01, ***p<0.001). Other legends are the same as for Fig. 2.

In contrast to these tissues, heart did not show an increase in glycogen stores after the high-carbohydrate diet and showed a decrease after the high-fat diet. There was a significant difference in heart glycogen stores between the two diet groups at the 4-h post-meal time (p<0.05). Kidney glycogen stores showed only slight depletion and repletion during exercise and recovery periods, respectively.

Lipolytic activity of epididymal fat pad (Fig. 4)

Basal lipolytic activity was not affected significantly by experimental treatment.
Fig. 4. Changes in basal and epinephrine-stimulated lipolysis (A) and epinephrine-induced lipolysis (B) (experiment 1). Each point and vertical line represents mean and SEM for 5–6 rats, respectively. ○, pre-exercise, post-exercise or pre-meal; Δ, high-carbohydrate diet; ●, high-fat diet. Other legends are the same as for Fig. 2.

Fig. 5. Changes in concentrations of serum glucose (A) and serum free fatty acids (B) (experiment 2). Each point and vertical line represents mean and SEM for 7 rats, respectively. ○, pre-exercise, post-exercise or pre-meal; ●, Hinex-R-Dextrin®; Δ, Hinex-R-Starch®. ***, *** Significant difference between the two adjacent points (*p<0.05, **p<0.01, ***p<0.001). Other legends are the same as for Fig. 2.

such as exercise and the administration of the G-C drink and meal. Epinephrine-stimulated lipolytic activity was slightly elevated with the exercise and remained constant for 2 h after the administration of the G-C drink. During the 4-h post-meal period, epinephrine-stimulated lipolytic activity remained constant in the high-carbohydrate diet fed group, whereas it was slightly elevated in the high-fat diet fed group. However, the difference between the two groups was not significant. At 06:00 epinephrine-induced lipolytic activity was higher in the high-fat diet fed group than in the high-carbohydrate diet fed group, but this was not a significant difference.
Experiment 2

Serum glucose and free fatty acid concentrations (Fig. 5)

Serum glucose was slightly elevated by 2 h of exhaustive swimming, and serum free fatty acids were increased 8-fold as compared with the pre-exercise value (pre- vs. post-exercise, 76 ± 14 vs. 588 ± 89 μeq/liter; \( p < 0.001 \)). The administration of the G-C drink immediately after the exhaustive exercise caused a slight reduction in both serum glucose and free fatty acid concentrations. Serum concentrations of glucose remained constant but those of free fatty acids decreased significantly.

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![Graphs showing changes in glycogen contents of liver (A), soleus muscle (B), heart (C), kidney (D) and epididymal fat pad (E) (experiment 2). Each point and vertical line represents mean and SEM for 7 rats, respectively. ○, pre-exercise, post-exercise or pre-meal; ●, Hinex-R-Dextrin®; △, Hinex-R-Starch®. a,b Significantly different from the Hinex-R-Starch® diet fed group (\(^* p < 0.05, ^{b} p < 0.01 \)). Other legends are the same as for Fig. 2.](image-url)
Glycogen stores in liver, soleus muscle, heart, kidney and epididymal fat pad (Fig. 6)

The 2-h exhaustive exercise session resulted in a significant reduction of glycogen stores in liver ($p<0.001$), soleus muscle ($p<0.01$), kidney ($p<0.01$) and epididymal fat pad ($p<0.01$). The administration of the G-C drink after exercise caused a significant repletion of glycogen stores in both soleus muscle ($p<0.05$) and heart ($p<0.001$). Liver glycogen stores also increased considerably after the G-C drink. A significant repletion of glycogen stores in liver ($p<0.05$ for the Starch diet and $p<0.001$ for the Dextrin diet), soleus muscle ($p<0.05$ and $p<0.001$) and kidney ($p<0.05$ and $p<0.01$) occurred 4 h after either the Starch or Dextrin diet. Glycogen stores in epididymal fat pads did not show a pronounced increase during the post-meal period in both groups. Heart glycogen stores decreased significantly after the Starch diet ($p<0.05$). As compared with the Starch diet, the Dextrin diet produced significantly higher glycogen stores in liver ($p<0.01$), soleus muscle ($p<0.05$) and heart ($p<0.05$) at 05:00.

DISCUSSION

The effectiveness of the G-C drink on glycogen repletion in animal tissues after exhaustive exercise (1) was confirmed in the present studies. In liver and soleus muscle, an increase in glycogen stores caused by the drink was further enhanced by the feeding of the high-carbohydrate diet (experiment 1) regardless of the type of carbohydrates, dextrin or starch (experiment 2). This was specially significant in soleus muscle, in which markedly large glycogen stores above the pre-exercise glycogen levels were observed. Although a high-carbohydrate diet has been reported in rats (9–12) to be effective in the recovery of tissue glycogen stores after exercise, our study differs in setting the diet at “lunch” time after exhaustive exercise.

Only a few reports (13) have described the types of carbohydrate present in a meal and its effect on glycogen repletion in animal tissues after exhaustive exercise. The present study is the first demonstration that the repletion of liver and skeletal muscle glycogen stores is much faster when a high-dextrin diet rather than a high-starch diet is fed during the early recovery period.

Serum glucose and insulin are known to influence the rate of glycogen synthesis in animal tissues (14). Unfortunately, in the present studies, consecutive changes in serum glucose and insulin after ingestion of the Dextrin or Starch diet were not measured. In addition, there is little information available on the digestibility of dextrin and starch. Wahlqvist et al. (15) showed that the rate of changes in blood glucose concentration in healthy subjects was the same after ingestion of either corn starch or dextrin “Caloreen®” with a mean chain length of 5 glucose units. However, changes in glucose concentrations of peripheral blood, with the exception

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of portal blood, may not directly reflect the digestibility of saccharides. Recently, ingestion of dextrin "Polycose®" with almost the same mean chain length as Caloreen® has been observed by Costill (16) to provide quite similar responses in serum glucose and insulin in humans as those obtained after ingestion of free glucose.

Snow and O'Dea (17) have reported that physical factors, grain or powder, considerably affect digestibility of starch in cooked rice. They (18) have also demonstrated a greater postprandial glucose and insulin response to cooked ground rice rather than to cooked whole rice in humans. Usually, rice is consumed in the form of cooked whole rice by humans. Therefore, the difference between the Dextrin and Starch diet in tissue glycogen repletion may become larger when powdered rice starch in Hinex-R-Starch® is replaced with whole rice starch. The above suggests the superiority of the Dextrin meal to ordinary rice meal consumed by Japanese for rapid glycogen repletion in liver and skeletal muscle during the recovery period.

Thus, besides the probable concern of digestibility, other possibilities such as biochemical, sympathetic and/or endocrine controls of tissue glycogen synthesis must be considered to evaluate the results of experiment 2. However, there is no information available on the difference between effects of dextrin and starch on these points.

Glycogen repletion in heart after prolonged exercise has been reported to be more rapid than in liver and skeletal muscle of rats (19). Segel and Mason (20) and others (21, 22) have shown that when rats are given food during the recovery period, glycogen supercompensation in heart is observed within 1 to 2h. This was also observed in experiments 1 and 2 in this paper. This phenomenon arises because the increased uptake of plasma free fatty acids and their oxidation by the heart during the post-exercise recovery period favors the accumulation of intracellular glucose and in turn increases conversion of glucose to glycogen (23). In the present studies, serum free fatty acid levels at the end of exercise and 2h after the administration of the G-C drink were higher than those obtained before exercise. High levels of serum free fatty acids as well as the administration of citrate, which is known to be a phosphofructokinase inhibitor (24), might contribute to stimulate fatty acid oxidation and consequently enhance the conversion of glucose to glycogen in heart. These explanations may be also applicable to the glycogen supercompensation occurring in soleus muscle in experiments 1 and 2.

Shafrir et al. (25) have reported that the increment in adipose tissue glycogen stores promotes a concomitant increase in free fatty acid re-esterification and inhibits free fatty acid release from adipose tissue. In addition, lipogenesis activity and glycogen stores in adipose tissue of rats have been reported to be positively related (26). In experiment 1, the high-carbohydrate diet enhanced glycogen repletion in adipose tissue but significantly decreased serum free fatty acid concentrations as compared with the high-fat diet. The activity of epinephrine-induced lipolysis in the high-carbohydrate diet fed rats was lower than that in the high-fat
diet fed rats. These results seem to indicate that, in the adipose tissue, the high-carbohydrate diet increases the rate of glucose uptake and free fatty acid re-esterification, and consequently inhibits free fatty acid release and enhances glycogen repletion.

It has been reported that elevated plasma free fatty acid concentrations prior to exercise decrease the rate of glycogen depletion in liver and/or in skeletal muscles with increasing fat oxidation during exercise in rats (27) and humans (28). Hickson et al. (29) have reported that rats with plasma free fatty acid levels raised by the feeding of corn oil 3 h before exercise and the injection of heparin 20 min prior to exercise were able to run for a longer time than control rats. In experiment 1, the rats fed on the high-carbohydrate diet showed significantly lower serum free fatty acid concentrations and also slightly lower epinephrine-induced lipolytic activity of adipose tissue than the rats fed on the high-fat diet. These physiological conditions brought about by the feeding of the high-carbohydrate diet seem to be undesirable for endurance sports programmed for several hours after the meal, because endurance sports are thought to be favorably undertaken under the increased oxidation of fatty acids in tissues.

In conclusion, the present studies have shown that a high-carbohydrate diet is more effective than a high-fat diet for glycogen repletion in liver and skeletal muscle after exhaustive exercise in rats. Dextrin has been demonstrated to be superior to starch as a carbohydrate source for the high-carbohydrate diet. Additionally, our results also suggest that a high-carbohydrate diet seems to be less effective for keeping high levels in either serum free fatty acid concentrations or adipose tissue lipolytic activity than a high-fat diet.

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