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The role of dietary carbohydrates in muscle glycogen resynthesis after strenuous running^{1, 2}

D. L. Costill,³ W. M. Sherman, W. J. Fink, C. Maresh, M. Witten, and J. M. Miller

ABSTRACT This study examined the effect of the type, amount, and the frequency of feeding of carbohydrates on muscle glycogen resynthesis after running. Trained male runners performed a 16.1 km run at 80% $\dot{V}O_2$ max to decrease gastrocnemius glycogen levels. A complex or simple carbohydrate diet (~3000 kcal) resulted in similar muscle glycogen levels 24 h after exercise. Forty-eight hours after exercise the complex carbohydrate diet resulted in significantly higher ($p < 0.05$) muscle glycogen levels. Consuming increasing amounts of carbohydrate, between 188 to 648 g carbohydrate/day, resulted in increasingly larger amounts of muscle glycogen resynthesis (24 h) after exercise. Frequent feedings of a high carbohydrate diet did not enhance muscle glycogen synthesis when compared to equal amounts of carbohydrates in two meals. It appears that muscle glycogen can be normalized between daily strenuous running activity. *Am. J. Clin. Nutr.* 34: 1831-1836, 1981.

KEY WORDS Dietary carbohydrate, glycogen, physical exertion

The importance of muscle glycogen for prolonged strenuous exercise is well documented (1-3), and various studies have examined exercise-dietary regimens to enhance muscle glycogen stores before performance (1, 3). None of these studies, however, has examined the influence of the amount or type of dietary carbohydrate consumed on glycogen resynthesis during the 24 h after strenuous running. Therefore, the purpose of this study was to determine the following: 1) What effect does the form of carbohydrate have on glycogen resynthesis following exercise? 2) What effect does consuming different quantities of carbohydrate have on muscle glycogen resynthesis during the 24 h after strenuous exercise? 3) What effect does the frequency of carbohydrate feedings have on glycogen resynthesis during the 24 h after exercise? In addition, the effect of muscle glycogen levels on muscle metabolism during sprint and endurance activity was examined. Answers to these questions will provide guidelines for the management of the nutrition of athletes who engage in daily strenuous exercise.

Methods

Subjects

Six trained male runners participated in phase 1 of this study, whereas four trained male runners partici-

pated in phase 2. The physical characteristics of both groups of runners appear in **Table 1**. The subjects consumed the same diet (50% of calories derived from carbohydrate) and performed the same activity (30 min running) the 2 days preceding each trial. The subjects were fully informed of all risks associated with participation in this study before giving their written consent to participate. A flow chart of the experimental protocol for phase 1 and 2 appears in **Figure 1**.

Phase 1

To determine the effects of different forms of carbohydrate on muscle glycogen resynthesis after strenuous running, the subjects were fed isocaloric diets containing either simple sugars (glucose, sucrose, fructose) or complex carbohydrate (starches). The exercise consisted of a 16.1 km run at 80% $\dot{V}O_2$ max immediately followed by five 1-min sprint runs (3 min rest intervals) on the treadmill at speeds requiring 130% $\dot{V}O_2$ max. After this exercise, the subjects consumed one of two randomly assigned carbohydrate diets (two meals per 24 h) for the next 48 h and were restricted from any vigorous activity. During the first 24 h the subjects consumed 3700 kcal, which was calculated to meet the day's caloric expenditure; similarly, during the second 24 h the subjects consumed 2383 kcal. The carbohydrate, fat, and protein content represented 70:20:10% of the calories consumed, respectively, and totaled 648 and 415 g of carbohydrate for the 1st and 2nd days, respectively. The amount of kcal consumed was calculated to meet only the subjects'

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energy expenditure in order to elucidate differences in glycogen resynthesis as a result of the two forms of carbohydrate. We did not wish to examine the differential effect of the two forms of carbohydrate on supercompensating muscle glycogen stores.

Muscle samples were obtained by percutaneous needle biopsy from the gastrocnemius immediately after and at 24 and 48 h after exercise. These samples, weighing 15 to 30 mg, were dissected into three samples, weighed and frozen at -180°C . The muscle sample weights were corrected for evaporative water and analyzed for muscle glycogen according to the method of Passonneau and Lauderdale (4). The average glycogen value determined from the dissected samples was used for statistical analysis and the standard error of duplicate samples was $\pm 1.5\%$.

Phase 2

The influence of the frequency of feedings and the amount of carbohydrate consumed on glycogen resynthesis during the 24 h after exercise was investigated using the following dietary treatments (3000 kcal): 1) low carbohydrate (CHO), 188 g CHO/day in two meals; 2) mixed diet, 375 g CHO/day in two meals; 3) high carbohydrate, 525 g CHO/day in seven feedings (high -7); 4) high carbohydrate, 525 g CHO/day in two meals (high -2). The exercise was that described earlier and the order of the diets was randomized with at least one week separating each trial. Since the subjects could differentiate between high and low carbohydrate diets, randomization of trials eliminates any systematic effect on subsequent measurements due to the "nonblindedness" of the diet.

Muscle biopsies were obtained from the gastrocnemius immediately after exercise and 24 h later. These tissue samples were handled and analyzed for muscle

glycogen as previously described. In addition, the effect of the glycogen levels (after the dietary treatments) on 300 m sprint performance was examined. Total time and split times for 100 and 200 m were recorded, and 5 min after the sprint a blood sample was obtained and analyzed for lactic acid (5). In addition, the subjects performed a 30 min treadmill run at $70\% \dot{V}\text{O}_2 \text{ max}$ 1 h after the 300 m sprint. At 10-min intervals samples of expired gases were collected via the semiautomated gas collection system described by Wilmore and Costill (6). From this measurement the respiratory exchange ratio was calculated. Heart rate and perceived exertion (7) were also taken at 10-min intervals. Immediately after the run, a blood sample was obtained and analyzed for lactic acid (5).

Statistical analysis

Phase 1—mean values for all variables were tested for significance using the Student's *t* test for paired observations (8). Phase 2—a one-way analysis of variance was used to determine significant treatment effects. When a significant *F* was observed, multiple range testing was used to determine significant differences between treatments (8). The level of probability was set at $p < 0.05$.

Results

Phase 1

The strenuous running resulted in mean (\pm SE) muscle glycogen of 53.4 ± 7.5 and 56.1 ± 7.1 mmol/kg wet tissue before consuming the complex and simple carbohydrate diets, respectively. Glycogen restoration during the first 24 h period was similar for both the complex and simple carbohydrate diets (Fig. 2). The next 24 h (24 to 48 h), however, resulted in a significantly greater muscle glycogen storage ($p < 0.05$) with the complex carbohydrate diet (Fig. 2). The mean (\pm SE) change in muscle glycogen during this period was 22.1 ± 13.1 and 7.8 ± 11.5 for the complex and simple carbohydrate diets, respectively.

Phase 2

Mean (\pm SE) muscle glycogen content after the running exercise was 71.3 ± 14.3 , 49.3 ± 9.4 , 55.3 ± 12.0 , and 46.8 ± 9.4 mmol/kg wet tissue for the low, mixed high 2 and high -7 carbohydrate diet trials, respectively. There is no significant difference ($p > 0.05$) between these mean glycogen values. Twenty-four hours later, muscle glycogen levels were 66.6 ± 7.8 , 74.2 ± 3.9 , 125.6

TABLE 1
Mean (\pm SD) characteristics of the subjects in phases 1 and 2

	Age	Ht	Wt	$\dot{V}\text{O}_2 \text{ max}$	ST
	yr	cm	kg	ml/kg min	%
Phase 1 (n = 6)	24.5 (2.7)	179 (7.4)	71.8 (4.0)	56.1 (3.1)	59.6 (11.0)
Phase 2 (n = 4)	25.5 (4.4)	184 (6.1)	79.7 (6.8)	59.7 (4.6)	57.6 (3.7)

* Percentage slow twitch fibers.

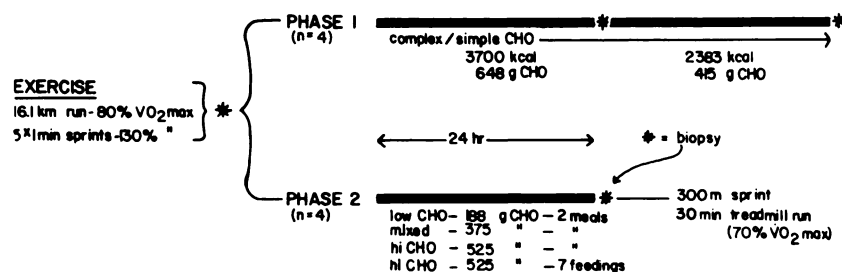


FIG. 1. Flow chart depicting the sequence of depletion and dietary intake for phase 1 and 2.



± 10.9 , and 101.2 ± 20.9 mmol/kg wet tissue for the low, mixed, high-2 and high-7 carbohydrate diet trials, respectively. The change in muscle glycogen during the 24-h feeding periods for each trial is depicted in Figure 3. The low carbohydrate diet resulted in a significant reduction ($p < 0.05$) of muscle glycogen while the high-2 carbohydrate diet resulted in a significant gain ($p < 0.05$) in muscle glycogen when compared to the mixed diet trial.

The different initial muscle glycogen levels had no effect on either the 300 m sprint performance or the 100 and 200 m splits. In addition, there was no significant difference ($p > 0.05$) in lactate levels measured 5 min after each sprint (Table 2).

During the treadmill performance runs there was no

significant difference ($p > 0.05$) in either the calculated oxygen uptake and total caloric cost or the measured heart rate and blood lactate accumulation between the trials (Table 2). The calculated oxidation of carbohydrate and fat, however, was affected by the diets. After the low carbohydrate diet the respiratory exchange ratio was lower ($p < 0.05$) and the grams of fat combusted were higher ($p < 0.05$) than the respiratory exchange ratio and the grams of fat combusted after the mixed diet. On the other hand, the high-7 diet resulted in a higher ($p < 0.5$) respiratory exchange ratio and larger ($p < 0.05$) gram carbohydrate oxidation than did the mixed diet trial (Table 2).

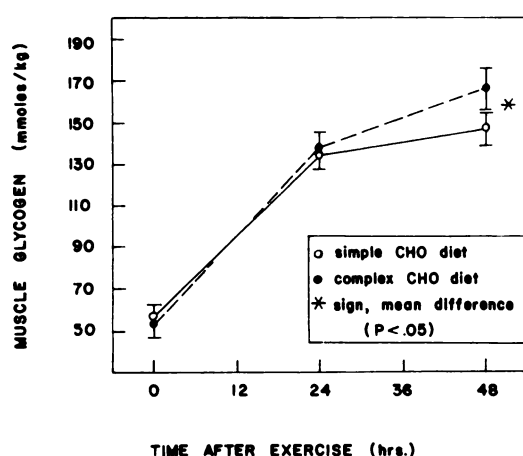


FIG. 2. Muscle glycogen levels (means \pm SE) after exhaustive exercise with diets composed of 70% simple (i.e., glucose, fructose and sucrose) and complex (i.e., starch) CHO.

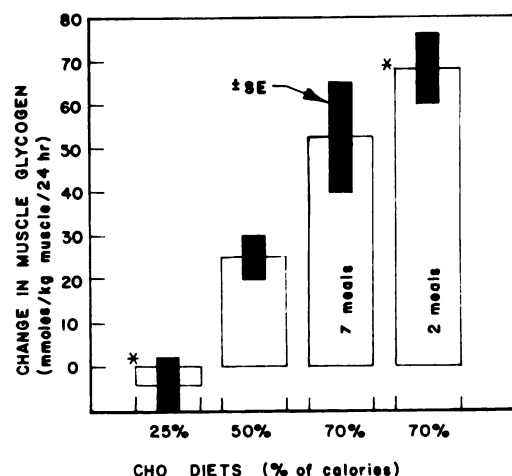


FIG. 3. Effects of varied CHO diets on the restorage of muscle glycogen. Asterisk denotes a significant difference between that mean and the mean change in muscle glycogen observed during the mixed diet (50% of cal from CHO).

TABLE 2
Mean (\pm SE) data obtained during the 300 m and 30 min treadmill runs after each of the diets*

	Low CHO	Mixed	High CHO (2 meals)	High CHO (7 meals)
300 m (s)	47.8 (2.1)	48.1 (2.2)	47.8 (1.7)	47.5 (1.8)
HLa (mM)	9.6 (0.6)	9.1 (0.4)	9.0 (0.6)	8.6 (0.5)
$\dot{V}O_2$	3.39 (0.17)	3.25 (0.18)	3.37 (0.14)	3.39 (0.37)
R ($\dot{V}CO_2/\dot{V}O_2$)	0.801† (0.006)	0.843 (0.007)	0.844 (0.011)	0.873† (0.002)
HR (beats/min)	154 (1.6)	156 (2.3)	155 (2.0)	156 (1.4)
PE	10.6† (0.6)	9.7 (0.5)	8.6† (0.6)	9.3‡ (0.6)
HLa (mM)	1.8 (0.1)	1.3 (0.1)	1.6 (0.1)	1.5 (0.1)

* $\dot{V}O_2$, oxygen consumption; R, respiratory exchange ratio; HR, heart rate; PE, perceived exertion (Borg scale); HLa, blood lactate.

† Denotes significant difference ($p < 0.05$) between identified mean and the "mixed" (50% CHO) diet.

‡ Denotes significant difference ($p < 0.05$) between identified mean and the high CHO (two meals) diet.

Discussion

Phase 1 examined the effect of the type of dietary carbohydrate on muscle glycogen re-synthesis during the 48-h period after strenuous running. The type of carbohydrate, simple or complex, had no differential effect on the change in muscle glycogen during the first 24 h after exercise. Reasons for the significantly ($p < 0.05$) larger change in muscle glycogen, and higher levels of muscle glycogen after the complex carbohydrate diet during the second 24 h, is presently unknown and might be explained by other factors.

The different responses in insulin and glucose as a result of the complex and simple carbohydrate diets has been reported by other investigators (11, 12). Hodges and Krehl (11) demonstrated that the insulin levels after a starch feeding were lower but remained elevated longer when compared to an equivalent g/g glucose meal. In addition, the activation of glycogen synthetase by insulin is well documented (13). Therefore, it is possible that maintained elevation of serum insulin occurring as a result of the complex carbohydrate diet is responsible for the enhanced muscle glycogen storage during the second 24-h period.

The strenuous bout of running exercise was sufficient to reduce muscle glycogen levels to an average of 55 mmol/kg wet tissue. This represents about 1 g/100 g of muscle glycogen and is slightly higher than the levels of muscle glycogen reported following cycling to exhaustion (1, 9). The recruitment pattern of muscle fibers as determined by periodic acid-Schiff staining has shown glycogen-filled fast twitch fibers after 2 h of running at 80% $\dot{V}O_2$ max (10). Thus, the glycogen remaining in the muscle sample in nonrecruited fibers following the strenuous bout of running might account for these slightly higher muscle glycogen levels.

As was anticipated, increasing amounts of carbohydrate 24 h after reduction of muscle glycogen resulted in increasing amounts of glycogen stored in the gastrocnemius (Fig. 3). This relationship was found to be significant $r = 0.84$, ($p < 0.05$) when data from phase 1 (first 24-h period) and phase 2 were combined. It is obvious that a plateauing of the change in muscle glycogen/24 h was not demonstrated up to 648 g CHO/day and that larger carbohydrate meals might maximize

muscle glycogen storage during the 24 h after strenuous running. Indeed, Blom et al. (14) reported that maximal glycogen storage was attained when exercise-exhausted subjects (cycling) consumed between 1.4 to 2.0 g glucose/kg body weight every 2 h. They did not report muscle glycogen levels, but this amounts to 588 to 840 g CHO/day if a subject weighed 70 kg and consumed glucose for 12 h.


O'Dea and Puls (15) demonstrated that nibbling-fed rats incorporated more labeled glucose into glycogen and had higher muscle glycogen levels than meal-fed rats. This suggests that carbohydrate ingested at intervals after exercise might result in a greater glycogen storage than carbohydrate consumed in only two meals and indicates that an optimal glucose load might exist for glycogen synthesis during recovery from exercise. This, however, did not occur since the change in muscle glycogen during the high-7 trial was not significantly different ($p > 0.05$) from the mixed diet trial.

Bergström and Hultman (9) and Kochan et al. (16) reported normal muscle glycogen levels 24 h after exhaustive cycling exercise. Therefore, consistent with previous findings, both phase one (glucose and starch) and phase two (high-2) normalized muscle glycogen levels in 24 h. This is based on the fact that depletion levels averaged 55 mmol/kg wet tissue and the subsequent change in muscle glycogen was 81 and 70 mmol/kg wet tissue for the two diets, respectively. This would bring muscle glycogen levels to approximately 130 mmol/kg wet tissue, which is normal for rested, well-trained runners (17, 18). Thus, it appears that consuming between 525 to 648 g of carbohydrate during the 24 h after strenuous running will result in normal muscle glycogen levels.

Although muscle glycogen storage is known to play a critical role in activities lasting longer than 1 h (19), its significance in short term highly anaerobic exercise has not been examined during running. Anaerobic metabolism predominates as the energy producing system in events of high intensity lasting 0.75 to 3.0 min (20), and muscle glycogen is the substrate oxidized during such an exercise bout. Studies have demonstrated higher blood lactate levels during submaximal workloads when muscle glycogen was elevated as compared to lower levels of mus-



cle glycogen (21, 22). Therefore, higher levels of muscle glycogen preceding anaerobic activity might result in impaired performance resulting from enhanced lactate production. Table 3 illustrates that the mean performance time and blood lactate concentrations were not significantly different between any of the trials. Differences in initial muscle glycogen levels, therefore, had no effect on flux through the anaerobic energy producing systems which might impair performance.

The influence of dietary carbohydrate during exercise was first reported by Christensen and Hansen in 1939 (23). Although the mechanisms regulating a substrate shift with high and low carbohydrate diets have not been fully explained, the current data suggest that the amount of time between the final carbohydrate meal and the onset of exercise may have some bearing on the use of carbohydrate by muscle. This is supported by the fact that, although muscle glycogen was elevated after both high carbohydrate diets (two meals and seven feedings), only the seven feeding regimen produced an increase in carbohydrate oxidation during exercise. When the carbohydrate was taken in only two meals, nearly 15 h had elapsed between the second feeding and the 30-min treadmill run. In the seven feeding regimen, however, the final meal was consumed only 8 h before the exercise. Since carbohydrate availability, as measured by glucose levels (D. L. Costill, W. M. Sherman, W. J. Fink, C. Maresch, M. Witten, and J. M. Miller, unpublished data) and muscle glycogen content did not differ between the trials, the enhanced rate of carbohydrate oxidation may be related to a greater insulin sensitivity and/or activity after the seven feedings trial. This concept is supported by studies with juvenile diabetic runners who show normal muscle glycogen use, increased glucose uptake and an accelerated rate of carbohydrate oxidation when insulin is administered 3 h before exercise (24). When deprived of insulin for 24 h these men oxidized the same amount of muscle glycogen but experienced a marked reduction in glucose uptake and total carbohydrate metabolism during exercise. 

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