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Muscle glycogen utilization during exhaustive running

DAVID L. COSTILL, KENNETH SPARKS, ROBERT GREGOR, AND CRAIG TURNER
Human Performance Laboratory, Ball State University, Muncie, Indiana 47306

COSTILL, DAVID L., KENNETH SPARKS, ROBERT GREGOR, AND CRAIG TURNER. *Muscle glycogen utilization during exhaustive running.* J. Appl. Physiol. 31(3): 353–356. 1971.—The purpose of this investigation was to make serial observations of the content and utilization of glycogen in selected leg muscles at rest and after both short and prolonged bouts of exhaustive running. Five well-trained men performed a 16.1-km (10-mile) treadmill run at 80% maximal oxygen uptake ($\dot{V}O_{2\,max}$) and a continuously run $\dot{V}O_{2\,max}$ test, 45 min after the 10-mile run. Muscle biopsies were obtained from the vastus lateralis, gastrocnemius, and/or soleus before and after the 16.1-km and $\dot{V}O_{2\,max}$ runs. At rest the glycogen storage was greater in the soleus than the gastrocnemius or vastus lateralis. Prolonged exhaustive running caused a greater glycogen decrease from the soleus (−1.06 g/100 g) than either the vastus lateralis or gastrocnemius. Compared with cycling, running at 80% $\dot{V}O_{2\,max}$ for over 1 hr produced much less glycogen depletion from the vastus lateralis. It was concluded that glycogen depletion was an unlikely explanation for the fatigue experienced by the subjects. The reduced capacity to perform anaerobic work after prolonged exertion seems to involve more than muscle glycogen concentration.

maximal lactate; prolonged exertion; maximal oxygen uptake

MUSCLE BIOPSY STUDIES by Bergstrom, Hultman, and others (4, 5, 12, 13) have established a direct relationship between the depletion of working muscle glycogen and muscular exhaustion. Exercising at approximately 80% of their aerobic capacities ($\dot{V}O_{2\,max}$) men have been shown to nearly exhaust the glycogen content of the m. quadriceps femoris in slightly more than 1 hr. However, it must be noted that the exercise was performed on a bicycle ergometer which tends to isolate the metabolic demands to a relatively small muscle mass. On the other hand, running would seem to involve several muscle groups, thereby, sharing the metabolic responsibilities during exercise.

Past research has relied heavily on respiratory exchange to estimate the role of carbohydrate metabolism during exhaustive work. Muscle biopsy procedures now permit the opportunity to study carbohydrate utilization in the working musculature. The studies employing this procedure have been limited to cycling. The objective of our research, therefore, was to make serial determinations of the content and depletion of glycogen in selected leg muscles at rest and after both short and prolonged bouts of exhaustive running.

METHODS

The five men examined in this study were well trained and accustomed to running a minimum of 5 miles/day. Some of their characteristics are presented in Table 1. All testing was preceded by 2 days of rest with the subjects ingesting a normally mixed diet. All trials were performed with the men in a 12-hr postabsorptive state.

Muscle biopsies were obtained as described by Bergstrom (3) from the vastus lateralis of the quadriceps femoris, gastrocnemius, and soleus. After removing all excess blood, fat, and connective tissue, the samples were weighed on a Roller-Smith precision torsion balance and frozen with Dry Ice and alcohol. Samples were kept deep frozen until ready for assay. Muscle glycogen was determined by the phenol-sulfuric acid method described by Lo, Russell, and Taylor (17). The reproducibility of this procedure has been shown to yield a reliability coefficient of 0.93 (unpublished data). Hultman (13) has reported that the standard error of this method was 0.05 g/100 g, representing 3.5% of the mean preexercise value.

Due to the muscle trauma associated with this technique *subject RB* was the only runner to have samples taken from all three sites. Samples were obtained from the vastus lateralis and gastrocnemius of *subjects KS* and *CT*; and from the lateralis and soleus of *subjects RG* and *DC*. Muscle biopsies were taken at rest, immediately after a 16.1-km (10-mile) treadmill run, and after a continuously run $\dot{V}O_{2\,max}$ test. The $\dot{V}O_{2\,max}$ test was performed 45 min after the 16.1-km trial. This testing procedure has been reported earlier (7). A similar $\dot{V}O_{2\,max}$ trial was performed several days before the 16.1-km run.

During the 16.1-km treadmill runs, heart rates and rectal temperatures were monitored at 5-min intervals, and respiratory exchange was measured every 10 min. Venous blood samples obtained before and at 10, 30, and 60 min of exercise were analyzed for lactate by the enzyme method (18). Heart rates were recorded electrocardiographically, respiratory exchange was measured by the Douglas bag method, and core temperatures determined with a YSI telethermometer and rectal probe. Respiratory gas samples were analyzed with the Beckman E2 (oxygen) and LB-1 (carbon dioxide) gas analyzers.

In addition to the gas samples and heart rates measured during the $\dot{V}O_{2\,max}$ trials, venous blood samples were obtained 5 min after the run for lactate concentration.

TABLE 1. *Characteristics of subjects*

Subj	Age, yr	Ht, cm	Wt, kg	Body Fat,* %	$\dot{V}O_{2\ max}$, L/min	Max HR, beats/min	Max Lactate, mg/100 ml
RG	26	178	70.6	10.4	3.96	187	91.6
DC	34	183	75.7	13.0	3.82	184	100.9
KS	26	177	64.2	4.6	4.25	172	132.4
CT	27	179	67.9	9.4	3.17	192	102.4
RB	32	180	76.4	13.7	4.09	180	101.4

* Body fat determined by underwater weight.

TABLE 2. *Average running speed, $\dot{V}E_{STPD}$, $\dot{V}O_2$, % $\dot{V}O_{2\ max}$, and blood lactate during 16.1-km treadmill runs, and $\dot{V}O_{2\ max}$, HR, and lactic acid during post-16.1-km $\dot{V}O_{2\ max}$ test*

Subj	During 16.1-km Run							Post-16.1-km Run $\dot{V}O_{2\ max}$ Test		
	Speed, m/min	$\dot{V}E_{STPD}$, L/min	$\dot{V}O_2$, L/mi	% $\dot{V}O_{2\ max}$	Lactate, mg/100 ml			$\dot{V}O_{2\ max}$, L/min	Max HR, beats/min	Lactate, mg/100 ml
					10 min	30 min	60 min			
RG	247	93.6	3.02	79	28.8	24.7	24.5	3.65	190	45.2
DC	201	92.2	2.92	77	22.3	39.0	36.5	3.48	184	44.4
KS	295	126.5	3.42	80	19.1	19.5	21.9	4.04	172	94.7
CT	200	96.2	2.48	80	26.6	24.4	20.4	2.74	192	37.1
RB	217	77.0	3.04	79	16.6	19.0	27.2	3.81	183	40.6

$\dot{V}E_{STPD}$ = pulmonary ventilation; $\dot{V}O_2$ = oxygen consumption; % $\dot{V}O_{2\ max}$ = percent of maximal oxygen uptake; HR = heart rate.

RESULTS AND DISCUSSION

The 16.1-km runs were performed at about 77–80% of the runners $\dot{V}O_{2\ max}$. The average speed, pulmonary ventilation ($\dot{V}E_{BTPS}$), oxygen consumption ($\dot{V}O_2$), % $\dot{V}O_{2\ max}$, and blood lactate during the 16.1-km run are presented in Table 2. Based on the $\dot{V}O_2$ and R values, the total estimated energy expenditures for the 16.1-km runs varied from 13.7 to 15.0 kcal/kg. These values are in close agreement with the data of Costill and Fox (7) and Kollias et al. (16), and when combined with the extreme sensations of fatigue experienced at the end of the runs suggest that the men were performing near their maximal capacity for that duration.

Respiratory exchange ratios (R value), heart rates, and rectal temperatures during the 16.1-km runs are presented in Fig. 1. After the first few minutes of the run, the subjects reached nearly constant levels of $\dot{V}O_2$ and lactate. It seems justifiable, therefore, to use the nonprotein R value to represent the proportion of carbohydrate and fat used (9). All of the men, with the exception of *subject KS*, demonstrated a gradual decline in the R value after the first 15–20 min of the run. These data suggest a shift toward greater lipid mobilization and utilization during the latter portion of the exercise session. During the early minutes of the run approximately 87% of the oxygen consumption was used to metabolize carbohydrates. This value declined to about 67% during the final minutes of exercise. Since the energy expenditure remained fairly constant during the runs, the rate of glycogen utilization was probably on the decline during much of the exercise. These observations are supported by Bergstrom and Hultman (5) who noted that the disappearance curve of glycogen seemed to follow a semilogarithmic course. They suggest, however, that this curve is actually triphasic, implying an initial rapid disappearance, followed by a constant fall, and, finally, during the last minutes of work a slower disappearance.

All of the men, with the exception of *subject CT*, demonstrated a leveling of heart rate after the first 10–15 min of the run. It should be noted that *subject CT* showed the most distinct symptoms of exhaustion during the final 15 min. The rapid increase in rectal temperature during the first 30–40 min of running was followed by a gradual elevation until the end. Since all of the men experienced core temperatures above 39° C for the final 20–45 min, hyperthermia might partially explain the subjective sensations of fatigue reported by the subjects (8, 20).

Resting muscle glycogen. Muscle glycogen values measured before and after the 16.1-km run and after the $\dot{V}O_{2\ max}$ test are presented in Table 3. Saltin and Hermansen (19) have reported that preexercise muscle (vastus lateralis) glycogen values of men on a mixed diet varied from 1.5 to 2.5 g/100 g of wet muscle. These findings are in close agreement with our values measured prior to the 16.1-km run (range = 1.54–2.16 g/100 g muscle).

It is known that red and white muscle fibers differ with respect to their glycogen content, and that the proportion of these fibers is not the same in different muscle groups

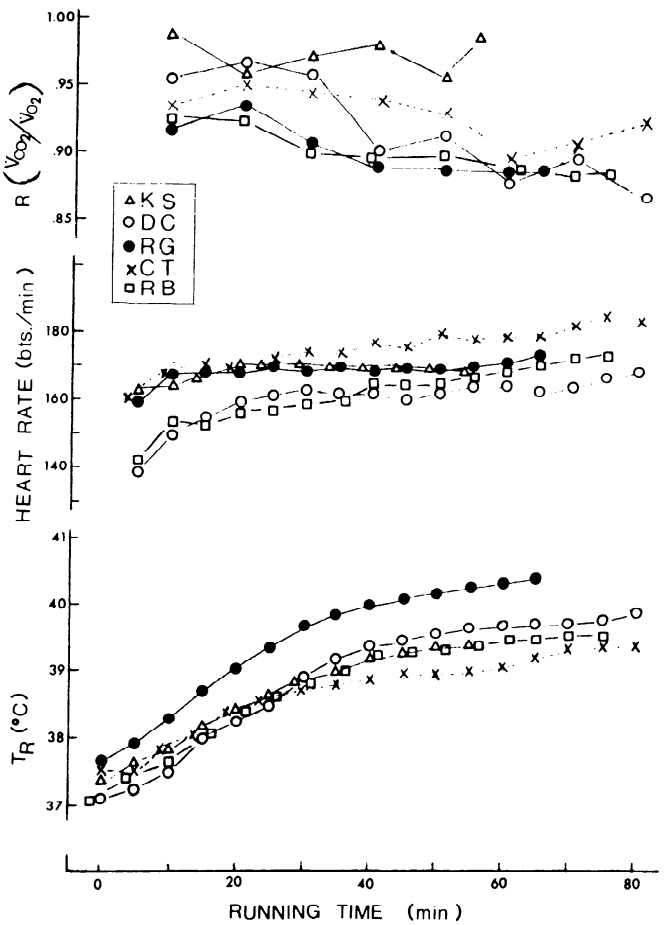

FIG. 1. Respiratory exchange ratios (R), heart rates, and rectal temperatures (T_R) for all subjects during 16.1-km run.

(2). In trained rats, glycogen concentrations are higher in red than in white muscle. This might explain the differences between the muscle glycogen concentrations of the soleus, vastus lateralis, and gastrocnemius.

Resting samples from the soleus showed a greater glycogen content than either the vastus lateralis or gastrocnemius. In contrast to *subjects RB* and *CT*, *subject KS* had a greater glycogen storage in the gastrocnemius than in the vastus lateralis. This individual variation in the relative concentrations of muscle glycogen might be explained by differences in muscular training and/or variations in running mechanics. *Subjects CT* and *RB* train at relatively slow speed for 30- to 60-min periods daily. *Subject KS*, on the other hand, is a nationally ranked sprint and middle distance runner. Much of his training is performed in an interval method at sprinting speeds.

Postexercise muscle glycogen. Previous studies by Bergstrom and Hultman (5, 6, 14) and Saltin and Hermansen (19) have shown nearly total glycogen depletion following 45–90 min of cycling exercise at approximately 75–85% of $\dot{V}O_{2\,max}$. During that period glycogen content was seen to decrease by 1.30–1.60 g/100 g tissue. In the present study the average muscle glycogen reduction from the lateralis was 0.74 g/100 g wet tissue. In an earlier investigation we observed a similar decrease (0.78 g/100 g muscle) among five men after a 16.1-km run (unpublished data). Since both the intensity and duration of the exercise in Saltin and Hermansen's study (19) and the present study are comparable one might have anticipated similar levels of glycogen utilization. The observed differences between glycogen utilization in the two studies might be explained by the larger muscle mass involved in running. Cycling, on the other hand, seems to involve a smaller portion of the total muscle mass. Consequently, in order for the cyclist to perform at the same % $\dot{V}O_{2\,max}$ a greater stress has to be accommodated by the quadriceps, as well as other active musculature. This might account for the greater degree of glycogen utilization during cycling.

Saltin and Hermansen (19) reported constant R values above 0.95 throughout 90 min of cycling. Hedman (10) has suggested that, during activities which involve a larger part of the muscle mass, a higher relative work load can be maintained for a longer period of time with somewhat lower R values than during cycling. This is accomplished by greater mobilization and utilization of free fatty acids. The current data support this concept, since the R values show a steady decline after the first 15–20 min of treadmill running (Fig. 1).

Although it is likely that the rate of glycogen utilization may be influenced by individual variations in running mechanics during the 16.1-km and $\dot{V}O_{2\,max}$ runs, the soleus appears to phosphorylate more glycogen than either the lateralis or gastrocnemius. However, the soleus seems to compensate for such energy demands by storing relatively more glycogen, thereby, reducing the likelihood of isolated muscle fatigue (Table 3).

Lactate accumulation. Maximal lactic acid values measured after the preliminary $\dot{V}O_{2\,max}$ test averaged 107.7 mg/100 ml (Table 1) in contrast to the peak lactate values observed after the post-16.1-km $\dot{V}O_{2\,max}$ test which were significantly lower (Table 2). Åstrand et al. (1) have suggested that the inability to produce lactate after prolonged heavy work may be caused by a lack of glycogen. The present study indicates that sufficient glycogen is present during the $\dot{V}O_{2\,max}$ run for anaerobic metabolism (Table 3). Recent studies by Hermansen (11) have shown that blood lactate levels attain the same relative maximal value over a wide range of muscle glycogen content. Blood lactate levels were 55–64 mg/100 ml even when the muscle glycogen content had fallen to zero. Karlsson et al. (15) suggest that the reduction in maximal lactate concentration in blood after prolonged exertion may be due to rate-limiting steps in glycolysis.

TABLE 3. *Muscle glycogen (g/100 g wet tissue) before and after 16.1-km run and $\dot{V}O_{2\,max}$ run to exhaustion*

Muscle	Subj	16.1-km Running			$\dot{V}O_{2\,max}$ Test		
		Prerun	Postrun	Decrease	Pre-max*	Post-max	Decrease
Lateralis	*RG*	1.87	1.07	−0.80	1.07	0.91	−0.16
	DC	1.54	0.81	−0.74	0.81	0.64	−0.17
	KS	2.16	1.50	−0.66	1.50	1.25	−0.25
	CT	1.77	0.90	−0.87	0.90	0.68	−0.14
	RB	2.03	1.40	−0.63	1.40	1.14	−0.26
Gastrocnemius	*KS*	2.75	2.07	−0.68	2.07	1.94	−0.13
	CT	1.64	0.92	−0.72	0.92	0.78	−0.14
	RB	1.66	1.07	−0.59	1.07	1.04	−0.03
Soleus	*RG*	2.51	1.37	−1.14	1.37	0.97	−0.40
	DC	2.42	1.12	−1.17	1.12	0.83	−0.34
	RB	3.04	2.17	−0.87	2.17	1.81	−0.36

* Premax run glycogen values were assumed to be the same as those measured immediately after the 16.1-km run (10).

The $\dot{V}O_{2\,max}$ after the 16.1-km run was about 8% lower than the $\dot{V}O_{2\,max}$ measured in a preliminary test. The subjects' inability to perform anaerobic work, as indicated by the lower lactate values after the post-16.1-km $\dot{V}O_{2\,max}$ test, might prevent the men from attaining work levels essential to stimulate the oxygen transport system maximally. Since the maximal heart rate was unaffected by the prolonged run (Tables 1 and 2), further information is needed to establish the cause for this reduction in the aerobic capacity.

Conclusions. Since substantial quantities of muscle glycogen were found after both the prolonged and short exhaustive runs, glycogen depletion is an unlikely explanation for the fatigue experienced by the subjects in this investigation. However, these data illustrate varied concentrations and rates of glycogen utilization among selected leg muscles during running. When compared to cycling, running seems to permit longer periods of work at about 80% of $\dot{V}O_{2\,max}$ without total muscle glycogen depletion. The reduced capacity to perform anaerobic work after prolonged exhaustive exertion seems to involve more than muscle glycogen concentration and may be explained by future studies of muscle enzymes and metabolites after prolonged exercise.

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