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Diet, Muscle Glycogen and Physical Performance

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Abstract

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The muscle glycogen content of the quadriceps femoris muscle was determined in 9 healthy subjects with the aid of the needle biopsy technique. The glycogen content could be varied in the individual subjects by instituting different diets after exhaustion of the glycogen store by hard exercise. Thus, the glycogen content after a fat + protein (P) and a carbohydrate-rich (C) diet varied maximally from 0.6 g/100 g muscle to 4.7 g. In all subjects, the glycogen content after the C diet was higher than the normal range for muscle glycogen, determined after the mixed (M) diet. After each diet period, the subjects worked on a bicycle ergometer at a work load corresponding to 75 per cent of their maximal O_2 uptake, to complete exhaustion. The average work time was 59, 126 and 189 min after diets P, M and C, and a good correlation was noted between work time and the initial muscle glycogen content. The total carbohydrate utilization during the work periods (54—798 g) was well correlated to the decrease in glycogen content. It is therefore concluded that the glycogen content of the working muscle is a determinant for the capacity to perform long-term heavy exercise. Moreover, it has been shown that the glycogen content and, consequently, the long-term work capacity can be appreciably varied by instituting different diets after glycogen depletion.

It was shown in previous studies that the muscle glycogen content decreased during work (Bergström and Hultman 1966 a), and that during exhaustive exercise the glycogen stores were almost completely emptied (Bergström and Hultman 1967). In a study by Hermansen, Hultman and Saltin (1967), it was found that the rate of combustion of carbohydrates was extremely high and constant throughout the whole work period. In this study, as well as in that of Ahlborg *et al.* (1967a), there were some indications that the initial muscle glycogen concentration was related to the ability to perform prolonged, heavy exercise (measured as the work time), provided that the subjects worked with the same relative load.

The muscle glycogen concentration in man can be considerably increased by first emptying the glycogen stores through hard work, and then giving a carbohydrate-rich diet. The enhancement of glycogen synthesis is localized to the muscles that have worked, and does not affect other muscle groups (Bergström and Hultman

TABLE I. Pertinent data in the nine subjects

Subject	Age yrs	Ht cm	B.W. kg	Max. oxygen uptake l/min
T.P.	22	179	76	4.93
B.T.	22	176	69	4.03
Å.L.	26	173	62	3.37
R.S	20	174	75	3.94
S.P.	25	179	67	3.77
S.-O.J.	23	182	72	4.96
C.F.	24	184	71	4.62
R.E.	23	173	62	3.57
K.-G.G.	24	177	73	4.46

1966 b). On the other hand, a fat + protein diet after exercise induces only a slow, incomplete resynthesis of glycogen, and if carbohydrate is given without previous exercise, only a moderate increase in muscle glycogen takes place (Hultman and Bergström 1967). Thus, by varying the type of diet after exhaustive exercise, it is possible to obtain different muscle glycogen levels in the same individual.

As early as 1939, Christensen and Hansen showed that the capacity for prolonged exercise can be markedly varied by varying the subject's diet. After 3—7 days of predominantly carbohydrate intake, the work time was 210 min on a fixed load, compared to only 80 min after an equal time on a fat diet.

The aim of the present study was to determine the extent to which the muscle glycogen content could be altered in individual subjects by varying the dietary regime after depletion of the glycogen store, and subsequently to ascertain the relation between the initial glycogen content and the capacity for prolonged hard exercise.

Material and methods

Nine physical education students participated in this study; some pertinent data regarding them are given in Table I.

The methods used are described in the previous article (Hermansen, Hultman and Saltin 1967), except for the blood glucose determination which, in this study, was made by a glucose oxidase method (Hjelm and de Verdier 1963). These experiments were performed at the Department of Physiology, Gymnastik- och Idrottshögskolan. The sequence of the measurements is shown in Fig. 1. The determination of the glycogen content in needle biopsy specimens from the lateral portion of the quadriceps femoris was made according to the method described by Hultman (1967). Muscle biopsy specimens were taken before exercise started, and immediately after the subjects were exhausted.

The week schedule for both diet and work is illustrated at the top of Fig. 1. The subjects were given a mixed, uncontrolled diet prior to the first measurements of muscle glycogen and work time. The work consisted of pedalling a bicycle to exhaustion at a work load corresponding to an oxygen uptake of 3.15 (2.4—3.7) l/min, which equals 75 (71—82) per cent of the subjects' maximal oxygen uptake. On the day of the experiment, the subjects had no breakfast before the exercise test. Six of the 9 subjects were then given a fat + protein (P) diet for 3 days before the next work period. The work again consisted of pedalling to exhaustion at the 75 per cent work load. On the next 3 days, the subjects were limited to a predominantly carbohydrate (C) diet before the last work experiment. The remaining three subjects also followed the aforementioned schedule, except that they were first given the carbohydrate diet, followed by the fat + protein diet. All the food

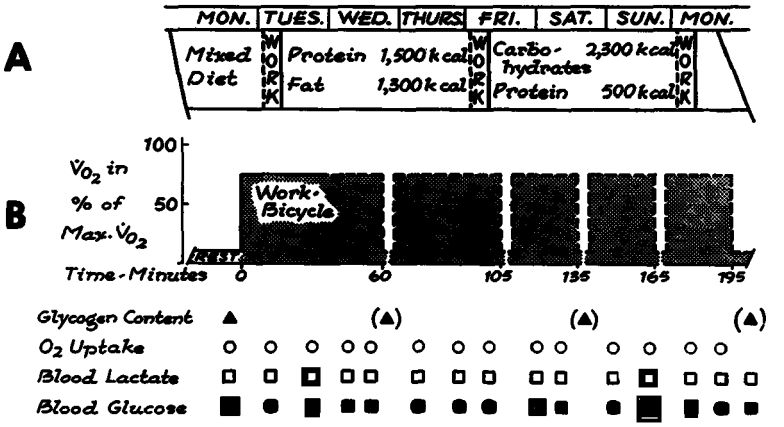

Fig. 1. A. Week schedule for diet and work programme in 6 subjects. In 3 subjects the two last diet periods were interchanged.
B. Schedule for the measurements in connexion with the exercise test.
The second biopsy for glycogen determination (▲) was made immediately after the work period, which was of different length depending on the type of diet.

eaten by the subjects when they were on the controlled diet was prepared and served at the laboratory. During work, the subjects drank water with some electrolytes, to minimize the effect of sweating. For psychological reasons, a 5-min rest period was inserted in the continuous exercise at fixed intervals (Fig. 1 b).

TABLE II. Prolonged physical exercise after three periods of different diets (mixed = M; fat = F; protein = P; carbohydrate (CH g); oxygen uptake (O_2 l/min)

Subject	After M diet					After P diet	
	Muscle glycogen		WT min	Used CH g	O_2 l/min	Muscle glycogen	
	Before	After				Before	After
T.P.	2.51	0.07	113.4	413	3.86	1.29	0.08
B.T.	1.19	0.35	148.5	375	2.99	0.60	0.32
R.S.	1.63	0.10	121.5	266	2.94	0.42	0.20
Å.L.	1.91	0.10	130.5	194	2.47	0.58	0.25
S.P.	2.20	0.53	117.3	292	2.93	0.31	0.20
S-O.J.	2.11	0.06	124.3	423	3.67	0.91	0.10
Mean	1.93	0.20	125.8	327	3.14	0.69	0.19
C.F.[1]	1.32	0.11	94.5	279	3.61	0.48	0.03
R.E.[1]	1.50	0.16	84.7	210	3.11	0.48	0.00
K-G.G.[1]	1.35	0.04	88.0	306	3.55	0.56	0.02
Total mean	1.75	0.17	113.6	306.4	3.24	0.63	0.13
± S.E.	±0.15	±0.05	±5.3	±27.4	±0.15	±0.10	±0.05

[1] In these 3 subjects the diet schedule was M, C, and P; not as in the 6 others (M, P and C).

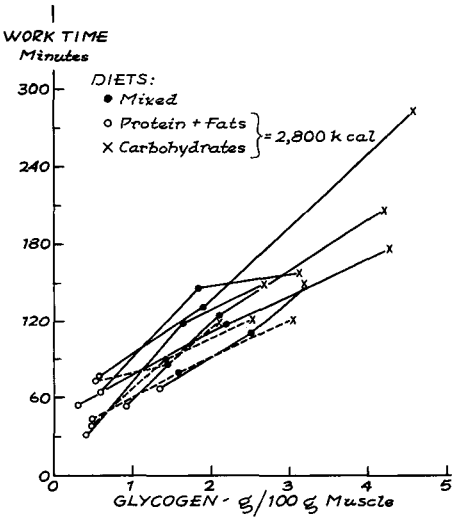

Fig. 2. Relation between initial glycogen content in quadriceps femoris and work time. Equation for regression line: $y = 41.6x + 36.8$, $r = 0.92$, $p < 0.001$. — — — the 3 subjects with carbohydrate diet prior to the fat + protein one.

Results

In Table II and Fig. 2, the individual values are given for the *muscle glycogen content* in relation to the maximal work time on a work load corresponding to 75 per cent of the maximal oxygen uptake. A good correlation is present between the

tein = P; carbohydrate = C). Muscle glycogen (g/100 g muscle); work time (W T min); used

			After C diet				
W T min	Used CH g	O_2 l/min	Muscle glycogen		W T min	Used CH g	O_2 l/min
			Before	After			
68.5	159	3.86	3.18	0.27	150.0	544	3.75
66.6	88	3.12	3.11	0.53	160.6	429	3.02
30.3	54	2.76	2.66	0.60	150.3	329	2.80
75.3	71	2.41	4.68	0.30	285.0	574	2.44
56.1	88	3.00	4.31	0.56	180.0	535	3.06
56.0	67	3.41	4.24	0.43	210.0	798	3.54
58.8	88	3.09	3.70	0.45	189.3	535	3.10
41.6	77	3.70	2.48	0.59	123.8	348	3.61
43.5	71	3.05	3.00	0.53	119.0	360	2.92
75.0	91	3.22	2.10	0.07	120.0	416	3.30
56.9	85.1	3.17	3.31	0.43	166.5	481.5	3.16
±1.7	±10.1	±0.15	±0.30	±0.06	±17.8	±47.1	±0.14

TABLE III. Statistical treatment: mean values of data (Table II and Fig. 3) obtained before, during, differences after the three diets (C, M, P)

C = carbohydrate diet
M = mixed diet
P = fat + protein diet

		n	C	M
			mean ± S.E.	mean ± S.E.
Muscle glycogen g/100 g	before work	9	3.31 ± 0.30	1.75 ± 0.15
	after work	9	0.43 ± 0.06	0.17 ± 0.05
Work time min		9	166.5 ± 17.8	113.6 ± 5.3
Utilized carbohydrate g	during work	9	481.5 ± 47.1	306.4 ± 27.4
Oxygen uptake l/min		9	3.16 ± 0.14	3.24 ± 0.15
Blood pyruvate mM/l	at rest	6	0.163 ± 0.011	0.120 ± 0.003
	after 30 min work	6	0.238 ± 0.025	0.237 ± 0.011
	at end of work	6	0.228 ± 0.038	0.178 ± 0.017
Blood lactate mM/l	at rest	6	1.73 ± 0.17	1.02 ± 0.16
	after 30 min work	6	4.92 ± 0.74	5.22 ± 0.91
	at end of work	6	3.61 ± 0.74	2.65 ± 0.53
Respiratory quotient	at rest	6	0.943 ± 0.024	0.815 ± 0.004
	after 30 min work	6	0.942 ± 0.009	0.915 ± 0.007
	at end of work	6	0.918 ± 0.012	0.882 ± 0.020
Blood glucose mg/100 ml	at rest	6	91.7 ± 5.9	76.8 ± 4.5
	after 45 min work	5	77.3 ± 5.4	76.3 ± 8.6
	at end of work	6	63.3 ± 2.1	53.8 ± 6.2

initial muscle glycogen concentration and the maximal work time over the whole range of initial glycogen values, as well as in each subject. The muscle glycogen averaged 1.75, 0.63 and 3.31 g/100 g wet muscle after the M, P and C diet, respectively. The mean maximal work times in the corresponding situations were 114, 57 and 167 min, respectively. The mean decrease during exercise in muscle glycogen (mg/100 g tissue/min) was 14.2 ± 1.40, 8.78 ± 1.70 and 17.4 ± 0.85 after diets M, P and C. The differences in decrease M—P and C—M had p values of <0.05 and < 0.005, respectively (paired t test).

The three subjects (C. F., R. E. and K.-G. G.) given the C diet prior to the P one had markedly lower values for the muscle glycogen content after the C diet, compared to the other six subjects (*cf.* Table II and Fig. 2). Therefore, only six subjects following the main procedure are included in Figs. 3 and 6, where a comparison is made between the average values for blood pyruvate, blood lactate, RQ, blood glucose (Fig. 3), heart rate and oxygen uptake (Fig. 6) after the three diets. These values are also used for calculation of the statistics (*cf.* the lower part of Table III).

The mean *blood pyruvate* at rest was 0.12, 0.09 and 0.16 mmole/l after the M, P and the C diet, respectively. During the first 30 min of exercise, the pyruvate level

and after work following the three diets. Probability calculated on paired *t* test of intra-individual

P	C—M	C—P	M—P
mean ± S.E.	p	p	p
0.63 ± 0.10	<0.001	<0.001	<0.001
0.13 ± 0.05	<0.01	<0.01	>0.1
56.9 ± 1.7	<0.01	<0.001	<0.001
85.1 ±10.1	<0.005	<0.001	<0.001
3.17 ± 0.15	>0.1	>0.1	>0.1
0.092± 0.008	<0.05	<0.01	<0.05
0.187± 0.017	>0.1	<0.05	<0.05
0.185± 0.020	>0.1	>0.1	>0.1
0.75 ± 0.17	<0.05	<0.01	>0.1
2.45 ± 0.18	>0.1	<0.01	<0.01
2.38 ± 0.24	<0.05	<0.05	>0.1
0.743± 0.029	<0.01	<0.01	<0.05
0.813± 0.009	<0.01	<0.01	<0.01
0.795± 0.014	<0.01	<0.01	<0.01
84.3 ± 4.0	>0.1	>0.1	>0.1
52.6 ± 2.6	>0.1	<0.05	<0.05
50.7 ±10.8	>0.1	>0.1	>0.1

was significantly lower after the P diet than after the M and C diets (*cf.* Table III and Fig. 3).

The *blood lactate* at rest was 1.0, 0.8 and 1.7 mmole/l (*cf.* Fig. 3) after the respective diets (M. P and C). It increased during the first 30 min of exercise to 5.2, 2.5 and 4.9 mmoles/l. At the end of exercise, immediately before exhaustion, the blood lactate concentration had fallen to 3.7 mmoles/l after the C diet, and to 2.7 mmoles/l after the M diet. The last reduction was significant. After the P diet, the blood lactate was essentially unchanged during exercise. Statistical treatment of intra-individual differences after the three diets is given in Table III.

The *RQ* at rest was 0.81, 0.74 and 0.94 after the respective diets (*cf.* Fig. 3). It increased during the first 15 min of exercise to 0.93, 0.84 and 0.97, respectively. When the exercise proceeded, there was a slight reduction in the mean for the RQ with all diets, but the decrease was not significant. The probability of differences in RQ after the three diets is given in Table III.

The mean *blood glucose* values are given in Table III and Fig. 3. During exercise there was a fall in blood glucose from the beginning of exercise, except after the M diet, when a transient increase was first noted. At 45 min exercise, the concentrations after the C and the M diets were almost significantly higher than the cor-

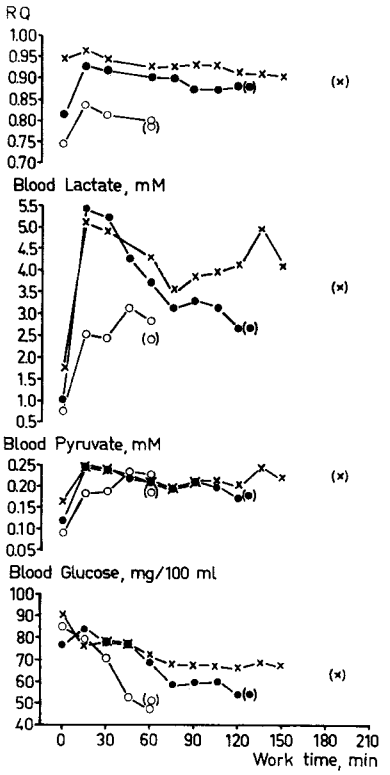

Fig. 3. Mean values of RQ, blood lactate, pyruvate and glucose in connexion with exercise after different diets in 6 subjects. × carbohydrate diet, ● mixed diet, ○ fat + protein diet, ( ) denotes the value at end of exercise.

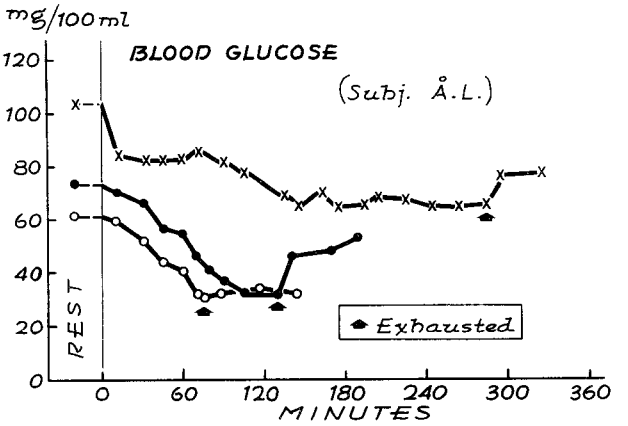

Fig. 4. Blood glucose concentration in connexion with exercise after different diets in subject Å.L. × carbohydrate diet, ● mixed diet, ○ fat + protein diet.

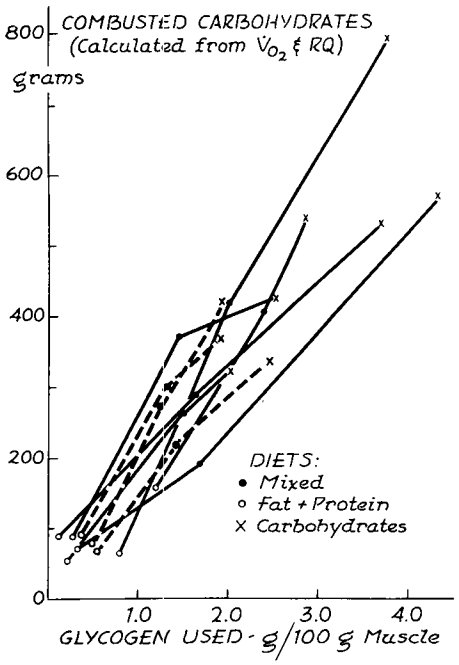

Fig. 5.

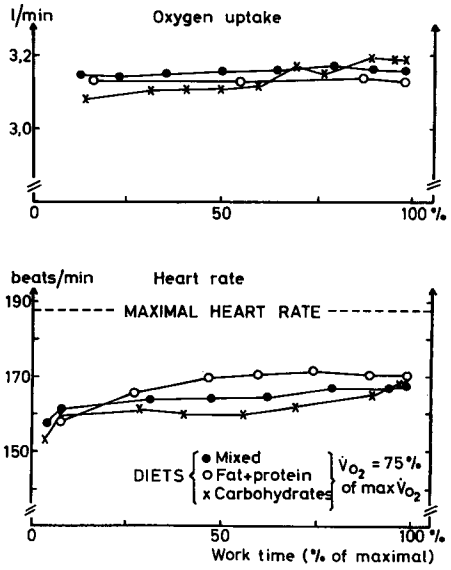

Fig. 6.

Fig. 5. Relation between used muscle glycogen and total utilization of carbohydrates during exhaustive exercise. Symbols as in Fig. 2. Equation of regression line: $y = 148.52\,x + 43.8$, $r = 0.92$, $p < 0.001$.

Fig. 6. Heart rate and oxygen uptake during exercise. Mean values in 6 subjects.

responding values after the P diet (*cf.* Table III). A slow recovery in the blood glucose concentration was marked in some subjects after the P diet. In subject Å.L. (*cf.* Fig. 4), the blood glucose concentration at exhaustion after the P diet was 32 mg/100 ml, and after 60 min recovery it was still only 34 mg/100 ml.

The *total amount of carbohydrate* combusted during the work period, calculated from the oxygen uptake and RQ, is related to the amount of glycogen utilized, *i.e.*, the difference between the muscle glycogen content before and after exercise (*cf.* Tables II and III, Fig. 5).

The calculated values for utilized carbohydrates during exercise ranged from 54 g to 798 g. In all instances there was a good correlation to the glycogen reduction in the quadriceps, which ranged from 0.11 to 4.38 g/100 g wet muscle. The mean decrease in muscle glycogen (mg/100 g tissue/g used carbohydrate) was 5.41 ± 0.65, 5.71 ± 1.02 and 6.02 ± 0.33 after the respective diets (M, P and C). The differences between the groups were not significant.

Fig. 6 illustrates the *heart rate* during exercise after the different diets. The differences were small and not significant.

The *oxygen uptake* during exercise was, on the average, 3.15 l/min, regardless of

the diet preceding the experiment. Nor were any significant changes noted in a comparison between the beginning and end of exercise.

The three subjects given the carbohydrate diet before the fat + protein diet showed similar results to those presented for the six subjects in Figs. 3 and 6, except that the differences between the M and C diet were smaller.

Discussion

The results of the present experiments demonstrate that the muscle glycogen concentration can be varied within a wide range, provided that different diets are administered after exhaustive exercise causing depletion of the local muscle glycogen stores. This is in agreement with previous studies (Bergström and Hultman 1966 b, Hultman and Bergström 1967). Thus, three days of fat + protein diet after exhaustive work did not resynthetize the muscle glycogen content to more than about 50 per cent of the initial value, whereas the carbohydrate diet raised the concentration to far above the normal range (0.95—2.0 g/100 g muscle) (Hultman 1967). Three subjects reached values above 4 g/100 g muscle, which are the highest ever reported in healthy males. It should be recalled that the three subjects given a C diet after the M diet did not reach as high muscle glycogen values as the 6 subjects given the P diet before the C one. Thus, a period of carbohydrate-free diet (*i.e.*, a period with low muscle glycogen) seems to further stimulate glycogen synthesis when carbohydrates are given (Ahlborg *et al.* 1967 b, Saltin and Hermansen 1967). It should be pointed out that the effect of the M diet on the muscle glycogen formation is not comparable to that of the P and C diet, as the M diet period was not preceded by glycogen-depleting exercise.

It is well established that the capacity for exercise is directly dependent on the individual's maximal oxygen uptake (Åstrand 1956). To minimize the inter-individual variation in work time during prolonged exercise, the work load for each subject was selected so that it represented about 75 per cent of his maximal oxygen uptake. All the subjects were somewhat trained (*cf.* maximal oxygen uptake in Table I), which implies that the exercise performed during the first part of the study should not have improved their performance in the last experiment. In subject Å.L., who had the lowest maximal oxygen uptake, measurements of his maximal uptake before and after the experimental period showed identical values (3.35 and 3.36 l/min).

The good correlation between initial glycogen concentration and work time (Fig. 2) demonstrates that the individual's ability to sustain prolonged exercise is highly dependent on the glycogen content of the muscles which, in turn, is dependent on the type of diet before exercise. It is improbable that the degree of fitness plays an essential role, either in the variation in muscle glycogen concentration or in its importance for the performance capacity, since the best-trained subject (S.-O.J.) and the least trained one (Å.L.) behaved similarly. These two subjects had the most marked increase in muscle glycogen concentration after the C diet, and they could also perform the longest on the 75 per cent work load.

Christensen and Hansen (1939) have earlier shown that the ability to perform prolonged exercise on a given work load is dependent on the type of diet before exercise. They concluded that carbohydrates were the most essential fuel during heavy muscular work. The results of the present study fully confirm this conclusion. It is of special interest that the performance time on a given load can be increased by more than 100 per cent by instituting a carbohydrate-rich diet after exhaustive exercise, and that the muscle glycogen concentration seems to be the key factor for the increase in performance capacity for prolonged work. This method of increasing the performance capacity may have practical applications in such situations as manual labour, military activities and athletics.

The output of glucose from the liver during prolonged exercise has been found to amount to 300 mg/min (Rowell, Masoro and Spencer 1965). At the end of prolonged severe exercise, a marked further increase in the glucose output was observed (Hultman, to be published). The blood glucose concentration during and after exercise fell to extremely low levels only after the P diet. In this situation the subjects experienced fatigue, not only localized to the legs but also generally. Some subjects suffered from headache and dizziness. The low blood sugar values at the end of exercise and the slow increase in blood sugar after exercise, especially after the P diet, might indicate a relative depletion of the glycogen stores in the liver in this situation.

It has been shown earlier that the diet can influence the relative role of fat and carbohydrate as fuel at rest and during exercise (Christensen and Hansen 1939). This was also manifested in the present study by a significantly higher RQ, both at rest and during exercise, after the M and C diets on the one hand, than after the P diet on the other hand. Furthermore, the calculated consumption of glycogen per time unit is lower after the P diet than after M and C diets. After the C diet both the RQ and the glycogen consumption per time unit were highest. This is in accordance with the observation that the regression line between performance time and initial muscle glycogen does not pass through zero (Fig. 2).

Blood lactate and pyruvate levels at rest and during the first part of exercise were also significantly lower after the P diet. These data suggest that the muscle cells have an ability to adapt to oxidizing more fat also at extremely high work loads, provided that the carbohydrate supply is low during the days before exercise. In contrast to this, the constantly high RQ throughout the period of prolonged heavy exercise after the carbohydrate and mixed diets indicates that the carbohydrate supply must, in fact, be limited for some time before exercise to permit the adaptation to fat combustion to take place.

As illustrated in Fig. 5, a good correlation is present between the glycogen used in the working muscles and the amount of carbohydrate utilized, calculated from the oxygen uptake and RQ. This applies over a wide range of RQ values and muscle glycogen concentrations. The glycogen decrease in relation to total carbohydrate consumption was not significantly different in the three diet groups. This indicates that the muscle glycogen store is the most important carbohydrate source during

heavy exercise. After the C diet, some subjects had available carbohydrate stores up to 700—800 g, *i.e.*, almost twice the figure presented by Hedman (1957) during cross-country skiing. His values are, however, compatible with those obtained by us after the M diet. Assuming that 20 kg of muscle are involved in the bicycle exercise, the exceedingly high figures after the carbohydrate diet noted in the present study are reasonable, since the reduction in glycogen concentration in the quadriceps femoris muscle during exercise was up to 4 g/100 g muscle.

The higher muscle glycogen concentration at exhaustion after the C diet may indicate that other factors ultimately limit the performance in this situation. Although psychological factors may have been of importance, it cannot be concluded that this is the only explanation.

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References

AHLBORG, B., J. BERGSTRÖM, J. BROHULT, L.-G. EKELUND and E. HULTMAN, Human muscle glycogen content and capacity for prolonged exercise after different diets. *Försvarsmedicin* 1967 (b). *3*. In press.

AHLBORG, B., J. BERGSTRÖM, L.-G. EKELUND and E. HULTMAN, Muscle glycogen and muscle electrolytes during prolonged physical exercise. *Acta physiol. scand.* 1967 (a). *70*. 129—142.

ÅSTRAND, P. O., Human physical fitness with special reference to sex and age. *Physiol. Rev.* 1956. *36*. 307—335.

BERGSTRÖM, J. and E. HULTMAN, The effect of exercise on muscle glycogen and electrolytes in normals. *Scand. J. clin. Lab. Invest.* 1966 (a). *18*. 16—20.

BERGSTRÖM, J. and E. HULTMAN, Muscle glycogen synthesis after exercise. An enhancing factor localized to the muscle cells in man. *Nature (Lond.)* 1966 (b). *210*. 309—310.

BERGSTRÖM, J. and E. HULTMAN, A study of the glycogen metabolism during exercise in man. *Scand. J. clin. Lab. Invest.* 1967. *19*. In press.

CHRISTENSEN, E. H. and O. HANSEN, Arbeitsfähigkeit und Ernährung. *Skand. Arch. Physiol.* 1939. *81*. 160—171.

HEDMAN, R., The available glycogen in man and the connection between rate of oxygen intake and carbohydrate usage. *Acta physiol. scand.* 1957. *40*. 305—321.

HERMANSEN, L., E. HULTMAN and B. SALTIN, Muscle glycogen during prolonged severe exercise. *Acta physiol. scand.* 1967. *71*. 129—139.

HJELM, M. and C. H. DE VERDIER, A methodological study of the enzymatic determination of glucose in blood. *Scand. J. clin. Lab. Invest.* 1963. *15*. 415—428.

HULTMAN, E. Muscle glycogen in man determined in needle biopsy specimens. Method and normal values. *Scand. J. clin. Lab. Invest.* 1967. *19*. In press.

HULTMAN, E. and J. BERGSTRÖM, Muscle glycogen synthesis in relation to diet studied in normal subjects. *Acta med. scand.* 1967. In press.

ROWELL, L. B., E. J. MASORO and M. J. SPENCER, Splanchnic metabolism in exercising man. *J. appl. Physiol.* 1965. *20*. 1032—1037.

SALTIN, B. and L. HERMANSEN, Glycogen stores and prolonged severe exercise. *Symposia of the Swedish Nutrition Foundation*. Ed. G. Blixt. Almquist and Wicksell, Uppsala, Sweden. 1967. *4*.