Glycogen Synthesis During Exercise and Rest with Carbohydrate Feeding in Males and Females

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Abstract


Since it has been demonstrated that endurance-trained cyclists are able to synthesize glycogen during mild exercise, glycogen synthesis was investigated in non-endurance-trained males and females as well. Seven males and nine females exercised on a cycle ergometer to deplete muscle glycogen. After the exhaustive exercise and taking a muscle biopsy, the males either exercised 2.5 h at 40% of maximal work load (trial A) or rested for 2.5 h (trial B). In both trials the subjects drank a 25% maltodextrin-fructose solution. After 2.5 h of exercise or rest, a second muscle biopsy was taken for determination of glycogen and for histochemistry (ATPase and PAS). In the females glycogen synthesis was only studied during 2.5 h rest, after prior glycogen depletion. In the male subjects, during mild exercise with carbohydrate feeding muscle glycogen did not increase. During rest muscle glycogen increased in the males from 123 ± 49 mmol/kg DW at exhaustion to 229 ± 70 mmol/kg DW (P < 0.001), resulting in a net increase of 42 mmol/kg DW/h. Glycogen synthesis during rest occurred both in type I and type II fibers. In the females, during 2.5 h of rest, muscle glycogen increased from 130 ± 56 mmol/kg DW at exhaustion to 224 ± 51 mmol/kg DW, resulting in a net increase of 37 mmol/kg DW/h. The results demonstrate that glycogen synthesis during mild exercise does not occur in non-endurance-trained athletes, whereas in the resting state glycogen synthesis in non-endurance-trained males is not different from endurance-trained cyclists. In addition, glycogen synthesis during rest is similar in males and females.

Key words

carbohydrate, glycogen synthesis, exercise, gender, muscle fiber type

Introduction

It is well established that glycogen is the major source of substrate in long-lasting exercise with high intensity while endurance is enhanced by high pre-exercise glycogen levels. In addition, exhaustion from glycogen depletion can be postponed by carbohydrate feeding during exercise. Research on carbohydrate feeding during exercise indicates that the major portion of the exogenous carbohydrate is oxidized by the working muscles (5, 14, 15, 17, 19). Studies by Hultman (10) and Van Handel (26) in man indicated that the glycogen sparing effect of carbohydrate feeding during exercise may also be attributed to glycogen synthesis in the working muscle. Constable and co-workers (3) and Kuipers et al. (12) demonstrated that muscle glycogen can be synthesized in the working muscles after prior glycogen depletion, in endurance-trained rats. In addition, Kuipers and co-workers (13) demonstrated that endurance-trained cyclists are able to synthesize glycogen in the type IIb fibers of the quadriceps muscle during mild exercise. This latter study did not provide an answer to the question of whether individuals who are not endurance-trained are able to synthesize glycogen during mild exercise as well. Therefore, the purpose of the present study was to study glycogen synthesis both during mild exercise and in the resting state in active, but not endurance-trained individuals. Since it was suggested from a study in marathon runners (unpublished data) that glycogen synthesis may differ in males and females, females were included in the study as well.

Materials and Methods

Subjects

Seven fit and physically active males and nine fit and physically active females participated in the study. All subjects were involved in non-endurance-type sports such as soccer, tennis, handball, gymnastics, and power lifting, for at least 6 h/week. In some subjects running was part of the training, but they ran maximally twice a week 20 min at the time at an easy pace. The mean age of the male subjects was 26 ± 6 years (x ± SD) and the mean body weight was 77 ± 6 kg.

The mean age of the female subjects was 21 ± 1 years and the mean body weight was 55 ± 4 kg. All female subjects were college students, studying physical education and had a normal regular menstrual cycle and did not take oral contraceptives. To standardize the experiment with

* This study was supported by research grants of Wunder Ltd., Bern, Switzerland.
relation to the menstrual cycle, all females were studied on the 6th or 7th day of the cycle (day 1 is the first day of the menses).

Before giving written consent, the subjects were fully informed about the purpose of the study and the stresses and risks involved.

Procedure

The male subjects were subjected to two different trials, i.e., A and B, whereas the female subjects only underwent trial B. Trial A consisted of glycogen depletion by heavy exercise, followed by 2.5 h cycling at 40% of maximal work load (W_{max}), while in trial B the glycogen depletion ride was followed by 2.5 h rest. Thus, in trial A glycogen synthesis was investigated during mild exercise, whereas in trial B glycogen synthesis was studied in the resting state. The order of the trials A and B were randomized and at least 3 weeks separated the two trials.

In each trial the subjects had their usual breakfast at home 1.5 h before reporting to the laboratory at 8:00 AM. After dressing in sportswear, the subjects mounted a cycle ergometer (Lode, NL). In trials A and B cycle exercise was employed to deplete muscle glycogen in the quadriceps muscles. The exercise started at 100 W for 5 min in the males and at 50 W for 5 min in the females. After the first 5 min the work load was increased by 50 W each 3 min. However, from a heart rate of 155 bts/min, the work load was increased by 25 W each 3 min. The exercise was terminated when the revolution rate dropped below 50 rpm in spite of encouragement. The highest work load attained was defined as:

\[ W_{\text{max}} = \frac{W_{\text{out}} + (t/180) \times \Delta W}{t} \]

in which \( W_{\text{out}} \) is the highest work load completed for 3 min, \( t \) the number of seconds the final uncompleted work load was sustained, and \( \Delta W \) the load increment. The subjects were allowed to recover for 5 min, whereupon intermittent exercise was employed. This consisted of 2-min bouts at 90% \( W_{\text{max}} \), interspersed with 2 min at 50% \( W_{\text{max}} \). When the subjects were unable to complete the 2 min at 90% \( W_{\text{max}} \), the intensive work load was lowered, subsequently to 80%, 70%, and 60% \( W_{\text{max}} \). The exercise was stopped when the 2 min at 60% \( W_{\text{max}} \) could not be completed any more. During the exercise the subjects were only allowed to consume water ad libitum.

In all trials, after stopping the intermittent exercise to deplete glycogen, a percutaneous needle biopsy was taken from the vastus lateralis muscle (8). After taking the biopsy the subjects either continued to cycle for 2.5 h at 40% \( W_{\text{max}} \) (trial A) or rested for 2.5 h (trial B). In the females glycogen synthesis was only studied in the resting state, after prior glycogen depletion (trial B). From the moment the biopsy was taken, the subjects started to drink a 25% maltodextrin-fructose solution (Perform, Wander, Bern, Switzerland; 85% maltodextrin, 15% fructose), in the resting state as well as during exercise. The temperature of the drink was kept between 4° and 7° C, because of its enhancing effect on gastric emptying (4). To provide immediate substrate for muscle tissue, from the moment the subjects started the 40% \( W_{\text{max}} \), on the average 40 g of glucose were infused intravenously during the first 60 min. In addition, the subjects were encouraged to drink 2 liters of the carbohydrate drink, divided over 130 min. The subjects stopped drinking 20 min before taking another biopsy to keep the gastric residue low.

In trial A, during the 2.5 h at 40% \( W_{\text{max}} \), oxygen uptake and respiratory exchange ratio (R value) were measured (Ergoscreen, Fennyus & Guth, Switzerland) for calculating the amount of carbohydrate oxidized during exercise (16).

In trial B, after the glycogen-depleting exercise and taking the first biopsy, the subjects rested, sitting in a comfortable chair for 2.5 h. They were asked to consume as much as possible of the aforementioned carbohydrate drink.

In both trials, after 2.5 h at 40% \( W_{\text{max}} \) (trial A) as well as after 2.5 h rest (trial B), a second biopsy was taken from the contralateral vastus lateralis muscle for histochemical use and analysis of glycogen.

Biochemical and Histochemical Analysis

The muscle biopsy sample was divided into two portions. One portion for histochemistry was mounted on a cork and frozen in isopentane, cooled to melting temperature in liquid nitrogen. The second portion was frozen in liquid nitrogen for analysis of glycogen. After freeze-drying (Leybold-Heraeus, GT2, FRG), glycogen was determined fluorimetrically after HCI hydrolysis (18) and expressed as mmol of glycose units per kilogram dry weight (kg DW).

From the portion selected for histochemistry 8-μm thick sections were cut in a cryostat at −20° C and mounted on cover glasses for histochemical staining. Serial sections were stained for ATPase, after preincubation at pH 4.2 and pH 4.6 (7), and classified into type 1, 1a, and 1b, and PAS-stained (7) to visualize glycogen depletion and/or repletion in different fiber types. For identification and counting of muscle fibers, color pictures were made (Zeiss photo microscope). The PAS-stained fibers were qualified as negative (−), light (±), moderate (+), or dark (+++). The fiber typing and qualification of the PAS stain was done by one person who was ignorant of the codes used on the cover glasses to avoid any bias.

Statistical Analysis

The data were analyzed using ANOVA for repeated measures. Differences between males and females were analyzed with Student's t test. Differences were considered statistically significant at \( P < 0.05 \).

Results

Carbohydrate Intake

The male subjects consumed 410 ± 44 g (mean ± SD) of carbohydrate during the 2.5-h exercise at 40% \( W_{\text{max}} \). In addition 40 g (range 35–49 g) of glucose were infused intravenously during the first 60 min of exercise. During the 2.5 h rest (trial B) the male subjects consumed on the average 471 ± 65 g (range 325–500) of carbohydrate. The female subjects consumed on the average 407 ± 44 g (range 325–450) of carbohydrate during 2.5 h rest (trial B).
Carbohydrate Oxidation

Using the oxygen uptake data (range 1.7–2.3 
1/min) and R values (range 0.78–0.84), it was calculated that on the average 150 g (range 92–241) of carbohydrate was oxidized in the males during 2.5 h cycling.

Muscle Glycogen

Muscle glycogen in males after the depletion ride was on the average (mean ± SD) 107 ± 44 mmol/kg DW in trial A and 123 ± 49 mmol/kg DW in trial B (Table 1). Mean glycogen concentration after 2.5 h of exercise at 40% Wmax with carbohydrate feeding was 112 ± 41 mmol/kg DW, which was not significantly different from the starting level.

After 2.5 h of rest (trial B) muscle glycogen in the male subjects increased significantly from 123 ± 49 to 229 ± 70 mmol/kg DW (P < 0.001), which results in a net increase of 42 mmol/kg DW/h. In the female subjects mean muscle glycogen concentration increased from 130 ± 46 mmol/kg DW at exhaustion to 224 ± 51 mmol/kg DW after 2.5 h rest (P < 0.001), which on results in a net increase of 37 mmol/kg DW/h.

As can be seen from the individual data in Table 2, some subjects demonstrated a further decrease in muscle glycogen levels during exercise, whereas in one subject an increase was observed. Histochemical analysis demonstrated that at exhaustion glycogen is lost mainly from type I and type IIa fibers (Table 2). The histochemical data further suggest that during exercise type I fibers demonstrated a further loss of glycogen, whereas type IIa fibers increased their glycogen content. After prior glycogen depletion, during rest and carbohydrate feeding glycogen synthesis is suggested to occur in all fiber types (Table 3).

Discussion

During exercise the male subjects were able to consume on the average 410 g of carbohydrate. Since none of the subjects encountered any gastrointestinal complaints, it is suggested that the solution was emptied from the stomach and absorbed adequately. In terms of gastric emptying this would mean that 1.6 liter of a 25% carbohydrate solution passed the stomach, resulting in an emptying rate of 11 ml/min. This is in line with the results of Costill and co-workers (4), taking the osmolality (470 mOsmol) into account. Preliminary results on gastric emptying in our laboratory seem to be in line with this estimation.

In each subject carbohydrate oxidation was estimated, using oxygen uptakes and R values. On the average 135 ± 26 g of carbohydrate were oxidized during the 2.5 h exercise at 40% Wmax. Taking the intake into account, approximately 300 g of carbohydrate have neither been oxidized nor incorporated into glycogen in the vastus lateralis muscles. The data of the present study do not allow conclusions about this unoxidized amount of the ingested carbohydrate, but are in line with the findings of Van Handel and co-workers (27), who observed that a great proportion of the 14C-labeled carbohydrate, consumed during exercise, was not recovered in the expired CO2, but remained in an “unoxidized pool.” Animal data suggest that the contribution of the liver in clearing blood glucose during exercise is of minor importance (12). However, the relative amount of glucose was much lower in the animal study (12). It is unknown whether the same is true in man and whether the contribution of the liver in clearing blood glucose with a surplus of carbohydrate is low as well.

The non-endurance-trained athletes in the present study did not increase muscle glycogen during exercise. This finding is different from a previous study in which endurance-trained cyclists demonstrated an increase in muscle glycogen during 2.5 h of mild exercise (13). The difference cannot be explained by differences in work load since the average work load during the 2.5-h cycling was 140 ± 23 W in the cyclists vs 139 ± 19 W in the present study. The carbohydrate intake between the cyclists and the athletes in the present study were similar as well. From Table 2 it can be seen that in some subjects in the present study muscle glycogen further decreased during mild exercise, mainly from type I fibers. The histochemical data suggest that in spite of a further decrease of glycogen in type I fibers, in type IIa fibers there is an increase in glycogen content, which, however, does not compensate for the amount oxidized since the total glycogen concentration decreased. This may be explained by differences in recruitment pattern during this exercise intensity in which type IIa fibers may be less involved. Only in one subject was a net increase in total muscle glycogen observed. The histochemical data (Table 2) demonstrate that the increase in total muscle glycogen in this particular subject resulted from glycogen increase in type I as well as type II fibers. It turned out that he had successfully competed in triathlons during the previous year but he had been out of training for several months prior to the study. It cannot be ruled out that training effects of the endurance training were still present.

The present data do not explain the difference in glycogen balance during exercise in endurance-trained and non-endurance-trained individuals and cannot be attributed to differences in work load, amount of carbohydrate intake, or amount of carbohydrate oxidation during exercise. A factor that has to be considered is catecholamine levels during exercise since catecholamines depress glycogen synthesis (9, 21, 25). However, exercise at 40% Wmax was not experienced as being stressful by the subjects. If the catecholamine levels would be increased for a longer period of time after exhaustion, a decreased glycogen synthesis was to be expected in the resting state as well. Since this was not the case, it is unlikely that the difference in glycogen synthesis between endurance-trained and non-endurance-trained males can be explained by catecholamine levels. Another factor which might influence
Table 2 Individual glycojen (Gly) values (mmol/kg DW) and the relative fiber number (%) with the intensity of the PAS stain at exhaustion (a) and after 2.5 h of mild exercise (b). The PAS stain is qualified as intensive (+ +), moderate (+), light (+, ±), or negative (–).

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Table 3 Individual glycojen data (mmol/kg DW) in trail B and the relative fiber number (%) and the PAS stain at exhaustion (a) and after 3 h rest (b).

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Glycojen metabolism during exercise are differences in muscle fiber types. However, the proportion of type I and type IIa fibers was not different between the endurance-trained cyclists and the non-endurance-trained males. Differences in glycojen metabolism may also be explained by training effects. Regular endurance exercise challenging glycojen stores may elicit adaptations in carbohydrate metabolism in muscle tissue (11, 24). The data from a previous study in cyclists (13) and those from the present study in non-endurance-trained individuals do support the assumption that a net glycojen synthesis during mild exercise in cyclists is indeed an effect of endurance training. The mechanism, however, remains to be clarified although some evidence exists that the initial activation of phosphorylase b-kinase at the onset of exercise can be reversed during prolonged work, creating favorable conditions for glycojen synthesis (2, 20, 22).

In the resting state a net glycojen increase in male subjects is 42 mmol/kg DW/h, which is comparable to the resting synthesis rate in cyclists [37 mmol/kg DW/h (13)]. This suggests that endurance training in cyclists does not influence maximal synthesis rates in the resting state, provided that sufficient carbohydrate is available.

The results of the present study demonstrate that glycojen synthesis in the resting state after prior depletion is similar in males and females. From previous observations (unpublished data) in males and females, it was suggested that glycojen synthesis after exertion was slower in females. However, calculations of average glycojen increase should be cautioned since glycojen synthesis rates attain the highest values within 2 h after exercise and level off after this period of time (1, 8, 23).

In conclusion, in contrast to endurance-trained cyclists, non-endurance-trained, glycojen-depleted subjects are unable to increase muscle glycojen during mild exercise in spite of high carbohydrate intake. In the resting state glycojen synthesis in endurance-trained males is not different from non-endurance-trained males and females.
Acknowledgment

The technical assistance of Peter Gurten and Gerrit van Kranenburg is greatly acknowledged.

References