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Muscle glycogen resynthesis rate in humans after supplementation of drinks containing carbohydrates with low and high molecular masses

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Abstract The rate of muscle glycogen synthesis during 2 and 4 h of recovery after depletion by exercise was studied using two energy equivalent carbohydrate drinks, one containing a polyglucoside with a mean molecular mass of 500 000–700 000 (C drink), and one containing monomers and oligomers of glucose with a mean molecular mass of approximately 500 (G drink). The osmolality was 84 and 350 mosmol · l⁻¹, respectively. A group of 13 healthy well-trained men ingested the drinks after glycogen depleting exercise, one drink at each test occasion. The total amount of carbohydrates consumed was 300 g (4.2 g · kg⁻¹) body mass given as 75 g in 500 ml water immediately after exercise and again 30, 60 and 90-min post exercise. Blood glucose and insulin concentrations were recorded at rest and every 30 min throughout the 4-h recovery period. Muscle biopsies were obtained at the end of exercise and after 2 and 4 h of recovery. Mean muscle glycogen contents after exercise were 52.9 (SD 27.4) mmol glycosyl units · kg⁻¹ (dry mass) in the C group and 58.3 (SD 35.4) mmol glycosyl units · kg⁻¹ (dry mass) in the G group. Mean glycogen synthesis rate was significantly higher during the initial 2 h for the C drink compared to the G drink: 50.2 (SD 13.7) mmol · kg⁻¹ (dry mass) · h⁻¹ in the C group and 29.9 (SD 12.5) mmol · kg⁻¹ (dry mass) · h⁻¹ in the G group. During the last 2 h the mean synthesis rate was 18.8 (SD 33.3) and 23.3 (SD 22.4) mmol · kg⁻¹ (dry mass) · h⁻¹ in the C and G

group, respectively (n.s.). Mean blood glucose and insulin concentrations did not differ between the two drinks. Our data indicated that the osmolality of the carbohydrate drink may influence the rate of resynthesis of glycogen in muscle after its depletion by exercise.

Key words Carbohydrate · Osmolality · Glycogen · Insulin · Glucose

Introduction

It has generally been accepted that prolonged submaximal exercise is limited by the availability of muscle and liver glycogen stores and that these stores increase when carbohydrate intake is high (Bergström and Hultman 1967; Bergström et al. 1967). It has also been shown that the rate of glycogen synthesis is highest in muscles in which the glycogen stores have been depleted by exercise (Bergström and Hultman 1966).

The rate of glycogen synthesis following exercise is of importance for athletes during training sessions with repeated periods of heavy or submaximal exercise as well as during competition especially when several periods of intense exercise are performed. Synthesis of muscle glycogen from ingested carbohydrates is dependant on the transport of glucose across the intestinal mucosa and the muscle cell membrane and on the enzymes responsible for glycogen phosphorylation and synthesis.

Blood glucose concentrations are influenced by the flux of glucose from the stomach, via the intestine and into the blood. It has been shown that the osmolality of an ingested solution can interfere with the emptying rate from the stomach (Hunt et al. 1985; Vist and Maughan 1995). Thus a high osmolality may delay gastric emptying which could delay the release of glucose from the intestine. It has also been shown that the rate of synthesis of muscle glycogen is highest during the first 2 h after exercise (Kiens et al. 1990). In the present study, the aim was to compare the rate of synthesis of muscle glycogen during the first 2 and 4 h after ingestion of two

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energy equivalent carbohydrate solutions, one with high osmolality the other with low osmolality.

Methods

Subjects

A group of 13 healthy and well-trained male physical education students, regularly training in cycling, running, swimming and football, participated in the study. Mean age was 26 years (range 21–33 years), mean height 190 cm (range 175–200 cm) and mean body mass 82.1 kg (range 65–96 kg). They all gave their oral and written consent and the Ethics Committee at the Karolinska Institute approved the study.

Protocol

The participants were instructed not to do any intense exercise during the 2 days prior to the experiment and were asked to eat a standardised diet the day before each experiment. At 8 o'clock in the morning, after having had a standardised breakfast consisting of coffee or tea with bread, cheese and orange juice, the subjects reported to the laboratory on two occasions, at least 1 week apart. On each occasion they performed a standard exercise routine followed by ingestion of one of two drinks. Each subject consumed a total of 300 g of carbohydrates corresponding to a mean value of $4.2 \text{ g} \cdot \text{kg}^{-1}$ body mass (range $3.1\text{--}4.6 \text{ g} \cdot \text{kg}^{-1}$ body mass). The G drink contained, in each 500 ml of water, 75 g of monomeric and oligomeric glucose from maize starch with a molecular mass of approximately 500 giving an osmolality of $350 \text{ mosmol} \cdot \text{l}^{-1}$. The C drink contained, in each 500 ml of water, 75 g of a large glucose polymer from potato starch with a molecular mass between 500 000–700 000 giving an osmolality of $84 \text{ mosmol} \cdot \text{l}^{-1}$. None of the drinks contained sodium. The subjects were randomly selected to start with either the G or the C drink. The G drink carbohydrate (Glucidex IT 38) is available from Roquette, Lille Cedex, France. The C drink carbohydrate (PU 24-002) is available from Carbamyl AB, Kristianstad, Sweden.

Procedure

The exercise consisted of a 60-min run on a treadmill or outdoors followed by 60 min of submaximal cycle ergometer exercise and a series of short sprints on the cycle to exhaustion. The exercise was designed to deplete as many different fibre types as possible. After finishing the exercise a catheter was inserted into an arm vein and blood samples for determination of insulin and glucose concentrations were taken every 30 min during a 4-h resting recovery as indicated in Fig. 1. A muscle biopsy from vastus lateralis muscle was taken within 5 min of the end of exercise, using the technique described by Henriksson (1979). After having taken the initial blood and muscle samples and within 5–10 min of the end of exercise, the subjects consumed 75-g carbohydrate dissolved in 500 ml of sugar-free lemonade (room temperature) and the same amount again was consumed at 30, 60 and 90 min post exercise and an additional 50 ml of water was allowed. Muscle samples were taken again after 2 h from the opposite leg and after 4 h from the

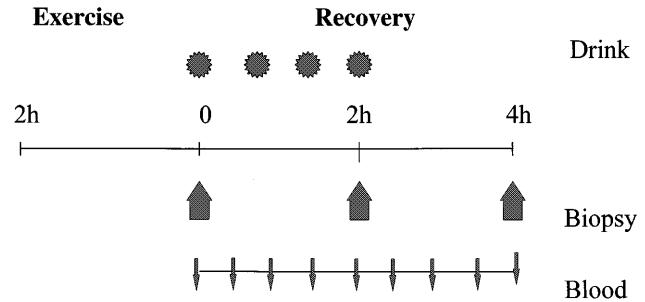


Fig. 1 Experimental design. Blood samples were taken every 30th min throughout the recovery period

same leg as the first biopsy with the second sampling site located distal to the first (see Costill et al. 1988).

The tissue samples were immediately frozen in liquid nitrogen and then freeze-dried and stored at -80°C until analysed. Muscle content of glycogen was determined using the method modified by Harris et al. (1974). Glycogen synthase activity was determined by measuring the incorporation of uridine diphosphate $\text{UDP-}^{14}\text{C}$ -glucose into glycogen (Danforth 1965). The glycogen synthase activity was expressed in terms of total activity in the presence of $6.0 \text{ mmol} \cdot \text{l}^{-1}$ G-6-P and the I form in the presence of $0.3 \text{ mmol} \cdot \text{l}^{-1}$ G-6-P, expressed as a percentage of total activity. Urine samples were analysed for glucose concentration throughout the study by using a laboratory stick (Boehringer Mannheim). Blood samples were immediately centrifuged in cold conditions and serum stored at -80°C until subsequently analysed for glucose and insulin concentrations. Blood glucose concentration was analysed using a fluorimetric method according to Lowry and Passonneau (1972). (Farrand Optical co., Inc., Ratio fluorimeter-2) and insulin concentration with a radioimmunoassay kit 10-6414-01 (Pharmacia-Upjohn). The osmolality of the C and G drink was measured using an osmometer (model 3D3, Advanced Instruments Incorporated).

Statistical analysis

Wilcoxon's signed ranks test was used in the calculations between paired items. A P value <0.05 was considered significant. Simple linear regression was calculated according to Pearson.

Results

In all the subjects exercise caused a reduction in muscle glycogen content and the mean values post exercise were 52.9 (SD 27.4) $\text{mmol glycosyl units} \cdot \text{kg}^{-1}$ (dry mass) and 58.3 (SD 35.4) $\text{mmol glycosyl units} \cdot \text{kg}^{-1}$ (dry mass) in the C and the G groups respectively (Table 1). At 2 h after exercise, and after consumption of 300 g of carbohydrates the mean muscle glycogen contents were significantly elevated ($P < 0.05$) in both groups and

Table 1 Mean (SD) muscle glycogen content and synthesis rate post exercise (0 h) and after 2 and 4 h and glycogen synthesis rate during 2 and 4 h

	Glycogen, $\text{mmol} \cdot \text{kg}^{-1}$ (dry mass)			Synthesis rate, $\text{mmol} \cdot \text{kg}^{-1}$ (dry mass) $\cdot \text{h}^{-1}$	
	0 h	2 h	4 h	0–2 h	2–4 h
C group	52.9 (27.4)	153.3 (27.4)*	190.8 (61.5)	50.2 (13.7) [#]	18.8 (33.3)
G group	58.3 (35.4)	118.1 (38.9)*	164.7 (49.9)	29.9 (12.5)	23.3 (22.4)

* $P < 0.06$, [#] $P < 0.06$

Fig. 2 Muscle glycogen resynthesis 2 and 4 h after exercise after consumption of the C and G drinks (for details see text). Mean and SD. * $P < 0.05$

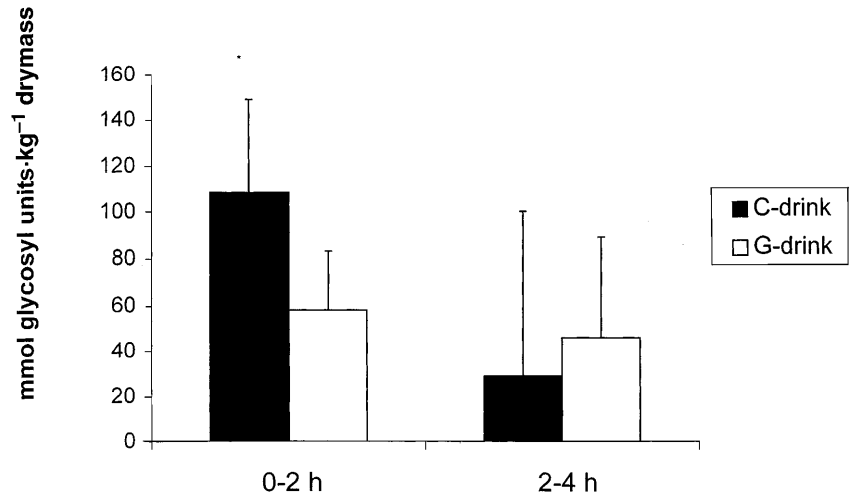
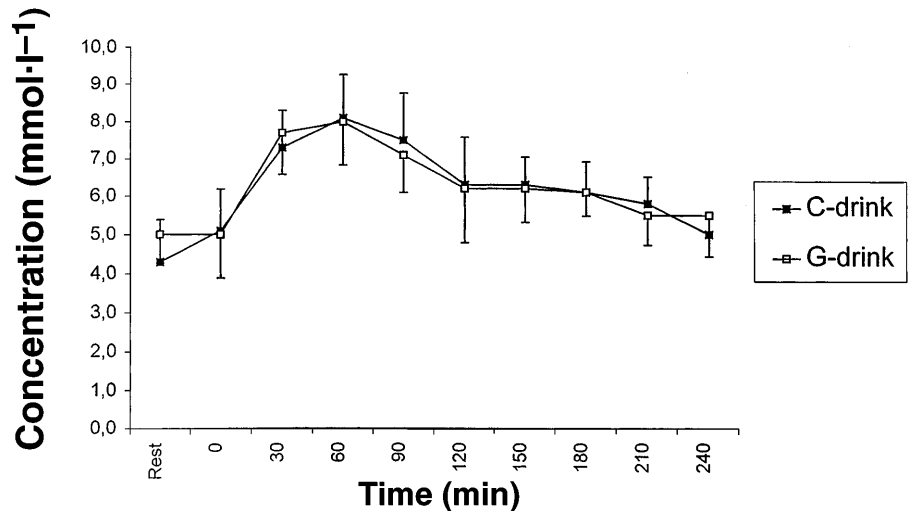


Table 2 Mean (SD) glycogen synthesis activity after exercise (0 h) and after 2 h and 4 h of recovery in the C and G group

	Glycogen synthase activity, I+D $\mu\text{mol} \cdot \text{g}^{-1} (\text{dry mass}) \cdot \text{min}^{-1}$			Synthase I activity % of total activity		
	0 h	2 h	4 h	0 h	2 h	4 h
C group	6.45 (2.66)	8.13 (2.60)	8.65 (2.49)	39.76 (12.21)	37.22 (10.08)	34.72 (10.10)
G group	6.00 (2.79)	8.82 (2.16)	8.26 (2.71)	40.96 (8.71)	38.85 (5.52)	35.51 (8.31)

Fig. 3 Blood glucose concentrations before and during ingestion of the C and G drinks (for details see text). Mean and SD



were significantly higher ($P < 0.05$) in the C group: 153.3 (SD 27.4) $\text{mmol glycosyl units} \cdot \text{kg}^{-1} (\text{dry mass})$ compared to 118.1 (SD 38.9) $\text{mmol glycosyl units} \cdot \text{kg}^{-1} (\text{dry mass})$ the G group. Mean muscle glycogen contents were further elevated (n.s.) after 4 h of recovery with no differences between the two groups.

Mean rate of glycogen synthesis during the 1st h in the C group was 50.2 (SD 13.7) $\text{mmol glycosyl units} \cdot \text{kg}^{-1} (\text{dry mass}) \cdot \text{h}^{-1}$ and 29.9 (SD 12.5) $\text{mmol glycosyl units} \cdot \text{kg}^{-1} (\text{dry mass}) \cdot \text{h}^{-1}$ in the G group (Fig. 2, Table 1). Mean rates during the remaining 2–4 h were 18.8 (SD 33.3) and 23.2 (SD 22.4) $\text{mmol glycosyl units} \cdot \text{kg}^{-1} (\text{dry mass}) \cdot \text{h}^{-1}$ for the C and G drinks respectively (Table 1). Mean total glycogen synthase activity and I form as a percentage of total activity are

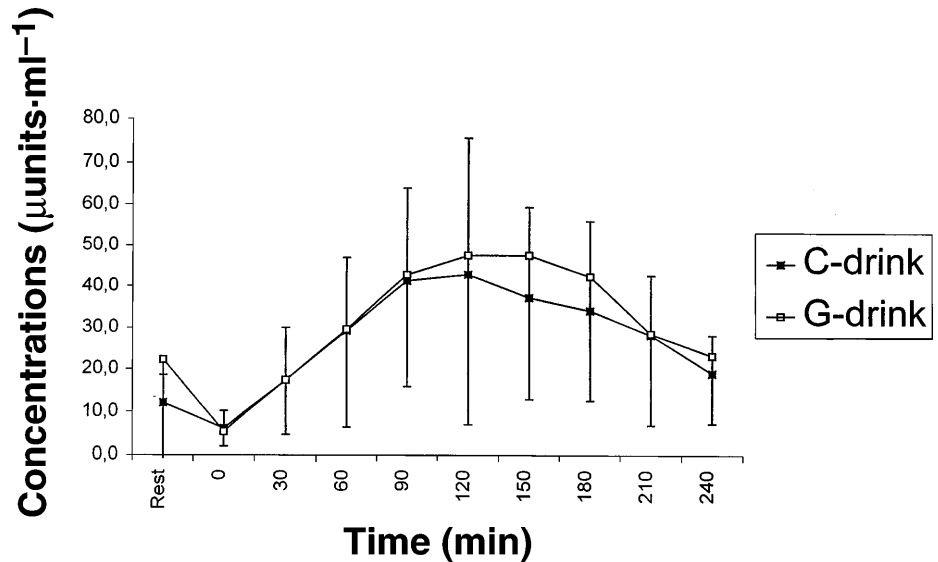
presented in Table 2. There was a tendency towards a decrease in the I form with increasing glycogen contents.

Blood glucose and insulin concentrations in the C and G groups did not differ significantly at any point during the study as shown in Figs. 3 and 4. There were great individual differences in insulin concentrations seen most markedly at 120 min. No urine sample contained glucose at any point in the study.

Discussion

In the present study, the rate of synthesis of muscle glycogen during the first 2 h post exercise, when consuming a carbohydrate solution with low osmolality was

Fig. 4 Insulin concentrations before and during consumption of the C and G drinks (for details see text). Mean and SD



significantly higher compared to an energy equivalent carbohydrate solution with high osmolality. To our knowledge there have been no studies looking at the rate of resynthesis of muscle glycogen after exercise when consuming isoenergetic carbohydrate drinks composed of predominantly glucose monomers compared to large glucose polymers.

Earlier studies have shown a rapid synthesis of glycogen in glycogen depleted muscle after carbohydrate feeding (Bergström and Hultman 1966, 1967; Bergström et al. 1967; Piehl 1974; Kiens et al. 1990). A brief summary of previous studies regarding the rate of glycogen synthesis after exercise after 2 and 4 h of recovery post exercise is given in Table 3. In most studies carbohydrates were administered orally in amounts varying from 0.7 to 3.0 g glucose equivalents per kilogram body mass

given as a solution consisting of a mixture of glucose and glucose polymers with relatively short glucose chains or as an unspecified carbohydrate meal. The mean rate of glycogen synthesis during the first 2 h has varied from 22.3 mmol · kg⁻¹ (dry mass) · h⁻¹ to 38.7 mmol · kg⁻¹ (dry mass) · h⁻¹ (Maehlum et al. 1977, Blom et al. 1987; Ivy et al. 1988a, b; Reed et al. 1989). 1978; There have been only minor differences in the rate of synthesis when the carbohydrate load was increased from 0.7 g · kg⁻¹ (body mass) to 1.4 g · kg⁻¹ body mass (Blom et al. 1987).

In our study, when providing a sufficient amount of carbohydrate with the G drink, the rate of glycogen storage and blood glucose and plasma insulin concentrations were in agreement with earlier studies. However, after ingestion of the C drink, composed of

Table 3 Summary of previous data regarding muscle glycogen synthesis rate 2–4 h post exercise. Data are converted to dry mass using a factor of 4.3 based on the assumption of 77% water content

Authors	Type, concentration and dose of carbohydrate given	Type of administration and time interval.	Total amount given, g	Muscle glycogen synthesis rate, mmol · kg ⁻¹ (dry mass) h ⁻¹	
				0–2 h	0–4 h
Maehlum et al. (1977)	Solid food	Meal, after exercise			30.9
Maehlum et al. (1978)	Glucose monomer 59%, 1.4 g · kg ⁻¹ bw	Solution, 15 min after exercise	100	30.5	
Blom et al. (1987)	Glucose monomer 30%, 0.7 g · kg ⁻¹ bw	Solution, 0 and 2 h after exercise	103	32.2	29.0
	Glucose monomer 30%, 1.4 g · kg ⁻¹ bw	Solution, 0 and 2 h after exercise	207	38.7	29.0
Ivy et al. (1988a)	Glucose polymer 25%, 2.0 g · kg ⁻¹ bw	Solution, 0 h after exercise	140	33.1	25.6
Ivy et al. (1988b)	Glucose polymer 50%, 1.5 g · kg ⁻¹ bw	Solution, 0 and 2 h after exercise	225	22.3	
	Glucose polymer 50%, 3.0 g · kg ⁻¹ bw	Solution, 0 and 2 h after exercise	450	24.9	
Reed et al. (1989)	Glucose polymer 50%, 3.0 g · kg ⁻¹ bw	Solution, 0 and 2 h after exercise	223	26.2	21.9
	Solid food, 3.0 g · kg ⁻¹ bw	Rice/banana cake, 0 and 2 h after exercise	223	27.0	23.6
	Glucose monomer 20%, 0.8 g · kg ⁻¹ bw h ⁻¹	Continuous infusion for 4 h	223	30.1	24.0
Piehl-Aulin et al. (present study)	Glucose monomer 15%, 4.2 g · kg ⁻¹ bw	Solution, 0, 30, 60, 90 and 120 min	300	29.9	26.6
	Glucose polymer 15%, 4.2 g · kg ⁻¹ bw	Solution, 0, 30, 60, 90 and 120 min	300	50.2	33.0

predominantly glucose polymers, a significantly higher rate of synthesis of glycogen in muscle was seen during the first 2 h post exercise, without further increased blood glucose and plasma insulin concentrations.

The blood glucose concentration after administration of carbohydrates by mouth is dependant on the release of glucose to the intestine, the transport over the intestinal mucosa to the blood and glucose uptake into the muscle cell. Hunt et al. (1985) have described a faster rate of gastric emptying 20 min after ingestion of a starch solution than when ingesting an energy equivalent glucose solution. Foster et al. (1980) have found that a 5% glucose polymer solution emptied from the stomach at a faster rate than an energy equivalent glucose monomeric solution whereas more concentrated solutions of glucose polymers and glucose emptied at similar rates. Sole and Noakes (1989) have demonstrated a significantly faster gastric emptying rate when consuming a 15% glucose polymer solution compared to an 15% glucose monomer solution. These last authors have also calculated a significantly higher carbohydrate delivery to the intestine with the polymer solution.

After intake of a 10% glucose polymer solution compared to a 3% monomeric solution Näveri et al. (1989) have demonstrated an equally steep rise in the blood glucose and serum insulin concentrations with higher maximal levels seen for the polymeric solution. However, no comparisons with energy equivalent solutions were undertaken. Vist and Maughan (1994) have found a concentrated glucose polymer solution (18%; 237 mosmol · kg⁻¹) to leave the stomach at a higher rate than a corresponding isoenergetic glucose solution (1300 mosmol · kg⁻¹). These findings suggest that a polymer carbohydrate solution will empty more rapidly from the stomach into the intestine than an isoenergetic monomer solution, resulting in a faster delivery of carbohydrate to the intestine. Our results may therefore be explained in part by a faster gastric emptying and a faster delivery of carbohydrate to the intestine.

Glucose in the blood has been shown to be taken up into the muscle cell by insulin-stimulated transport related to the GLUT-4 protein content of the muscle membrane (Henriksson et al. 1990; Kern et al. 1990; Brozinick et al. 1994; McCoy et al. 1996). It has been reported that exercise stimulated glucose uptake (non-insulin-dependent) is also related to the GLUT-4 protein content of the plasma membrane (McCoy et al. 1996). The duration of this increased non-insulin-dependent transport after exercise is uncertain in human muscle, but in rat muscle there have been reports of a progressive decline during 2–2½ h after exercise. Ivy et al. (1988a) have shown that a 2-h delay after the end of exercise, before ingesting a 25% glucose polymer solution, revealed a glycogen synthesis rate that was only one-third as fast as if the solution was ingested immediately after exercise. This was seen in spite of similar blood glucose and insulin concentrations and activity of the enzyme glycogen synthase under the two conditions. The reason for this solvent rate of glycogen synthesis

after 2 h was proposed to be a reduction in the non-insulin-dependent uptake of glucose across the cell membrane. These data indicate that the non-insulin-dependent exercise-induced uptake of glucose may be highest immediately at the end of glycogen depleting exercise which may contribute to our present findings. Taken together, if a faster delivery of glucose to the intestine is combined with a faster glucose uptake by the muscle cell immediately post exercise, this may mask an increase in delivery of glucose to the blood from the intestine and result in only minor changes in blood glucose concentration.

Glycogen synthase activity has been supposed to be a rate-limiting factor in muscle glycogen synthesis. This could not be demonstrated in the present study. However, Ivy et al. (1988a) and Greiwe et al. (1999) have shown an enhanced rate of glycogen synthesis without differences in the activity of glycogen synthase. The enzyme exists in two interconvertible forms – the D form dependant on glucose-6-phosphate and the I form, dependant on glucose-6-phosphate. Danforth (1965) has shown that synthase I activity was inversely related to the glycogen content which has also been demonstrated by Hultman et al. 1971 both of which studies support the present findings.

The increased blood flow to the muscle during exercise has been found to decrease rapidly after the end of exercise and to reach pre-exercise values after 15 to 45 min of recovery (Saltin 1984). However, an increased blood flow during the first few minutes after exercise, together with a faster gastric emptying rate may have contributed to an enhanced glucose delivery to the muscle after the C drink.

In summary, our results indicated that consumption of a carbohydrate solution containing glucose polymers giving a low osmolality will restore the muscle glycogen at a faster rate, compared to an energy equivalent solution containing monomers with a high osmolality during the first 2 h after exercise when muscle glycogen content is low. The hypothesis of a more rapid gastric emptying and glucose delivery to the intestine together with a postexercise stimulated non-insulin-dependent glucose uptake into the muscle cell as part of the possible mechanisms for the present findings merits further investigations.

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