Exogenous carbohydrate oxidation from different carbohydrate sources during exercise

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SARIS, W. H. M., B. H. GOODPASTER, A. E. JEUKENDRUP, F. BROUNIS, D. HALLIDAY, AND A. J. M. WAGENMAKERS. Exogenous carbohydrate oxidation from different carbohydrate sources during exercise. J. Appl. Physiol. 70(5): 2168–2172, 1991. —The exogenous carbohydrate (CHO) oxidation of naturally enriched [13C]CHO sources with different solubilities was studied during cycling exercise (150 min, 80% maximum work output). Moreover, the effect of adding a 13C tracer with different physical properties than the tracer on exogenous CHO oxidation was investigated. Test solutions (28.5 ml/kg body wt) were water for control of 13C background, 15% soluble partially hydrolyzed corn starch (SOL), 15% insoluble corn starch (InSOL), and 15% InSOL with [13C6]glucose as tracer. Both the mean and peak exogenous oxidation rates were significantly greater (P < 0.05) in the SOL trial than in the InSOL trial (mean oxidation rate, 0.84 ± 0.21 and 0.50 ± 0.15 g/min, respectively; peak oxidation rate, 1.10 ± 0.18 and 0.51 ± 0.25 g/min, respectively). The amount of the ingested CHO that was oxidized was significantly higher (P < 0.05) in the SOL trial (126 ± 31 g) than in the InSOL trial (75 ± 25 g). When we added an extrinsic tracer ([13C6]glucose), the apparent mean and peak oxidation rates of the trial with InSOL and [13C6]glucose were significantly (P < 0.05) higher (0.91 ± 0.30 and 1.23 ± 0.41, respectively) than the InSOL values. These results indicate that the addition of the soluble [13C6]glucose tracer to an insoluble starch tracer leads to overestimation of the exogenous CHO oxidation rates and 2) suggest that soluble CHO is oxidized at a higher rate during exercise than isocaloric insoluble CHO.

soluble vs. insoluble carbohydrate; carbon-13 carbohydrate; tracer vs. tracee

CARBOHYDRATE (CHO) supplementation during prolonged endurance exercise has been shown to delay fatigue and thus improve performance in endurance-trained subjects (2). It is thought that CHO ingested during strenuous exercise maintains blood glucose availability late in exercise when muscle glycogen content is low, thereby providing CHO for oxidation and allowing subjects to exercise longer (2, 5). Because it is now known that CHO ingestion during exercise provides a CHO source to the exercising muscles, it is important to consider how much ingested CHO can be effectively oxidized during exercise. Coggan and Coyle (3) have shown that total CHO oxidation can occur at a rate up to 2 and 1.5 g/min late in prolonged exercise by glucose infusion and ingestion, respectively. With the use of the 13C labeling technique, oxidation of exogenous CHO given during exercise has been shown to be between 0.6 and 1.0 g/min late in exercise (11–13, 21, 25).

However, Hawley et al. (10), using a 14C tracer method, found very high (1.8 g/min) exogenous CHO oxidation rates near the end of prolonged exercise for a mixture of amylose and amylpectin, which was twice the oxidation rate for an isocaloric glucose polymer solution. Moreover, a more rapid appearance of the 14C label in the blood for the insoluble starch was found. The authors suggested that the greater oxidation rates of the insoluble oral CHO seen were because the number of 1,4-α-glycosidic bonds cleaved by a single molecule of α-amylase are increased when the enzyme acts on solid particles rather than in solution. In their study, however, [14C]glucose was added to the insoluble starch to estimate its oxidation rate. It is questioned whether this technique reflects true exogenous oxidation rates because of the possibility that the [14C]glucose label may be preferentially taken up and subsequently oxidized at different rates, depending on the solubility characteristics of the CHO solutions employed.

The first aim of the present study was to reexamine the oxidation rates reported by Hawley et al. (10). Therefore, we used exactly the same CHO sources that were naturally 13C enriched to measure the exogenous 13CO2 production during 150 min of exercise.

The second aim was to investigate whether adding a tracer with different solubility characteristics than the tracee leads to erroneous calculation of oxidation rates. We therefore added [13C]glucose to an insoluble starch and compared the apparent oxidation rate obtained with this mixture with the true oxidation rate obtained with the naturally and therefore uniformly enriched 13C source.

METHODS

Subjects

Eight male competitive cyclists or triathletes participated in this study. They were given complete verbal and written explanation of the nature of the study and the risks of the experimental procedures before written consent was obtained. Mean age, height, weight, maximum work output (Wmax), and maximum VO2 uptake (VO2max) were 25 ± 4.8 (SD) yr, 183 ± 6 cm, 74.0 ± 6.7 kg, 387 ± 18 W, and 4.81 ± 0.61 l/min, respectively.
EXOGENOUS CARBOHYDRATE OXIDATION DURING EXERCISE

Preliminary Procedures

Preliminary testing. Subjects were tested for $\dot{V}O_2^{\text{max}}$ and $w_{\text{max}}$ by using an incremental exertion test on an electronically braked bicycle ergometer (Lode, Groningen, The Netherlands). $\dot{V}O_2^{\text{max}}$ and $w_{\text{max}}$ were determined by first having the subjects warm up at 100 W for 5 min. The work load was then increased 50 W every 2.5 min until the heart rate exceeded 160 beats/min. The work load was then increased 25 W every 2.5 min until exhaustion. The results of this test were used to determine the work load that corresponded to 60% of the subject's $w_{\text{max}}$ (68% $\dot{V}O_2^{\text{max}}$), which was used in the experimental trials. Expired gases were analyzed using a SensorMedics 2900 open-circuit system (Anaheim, CA).

Experimental trials. Exercise tests were conducted with repeated beverage ingestion during which measurements of CHO oxidation and gastric emptying were made. Each subject performed four exercise trials in a random order. To prevent carry-over of the $^{13}C$ label given during the trials, at least 1 wk separated the tests with one exhaustive training session 2 days before the next exercise trial. Subjects were encouraged to continue their normal training and competition schedules. They were instructed to carefully refrain from consuming foodstuffs containing naturally enriched $[^{13}C]$:CHO such as corn products, commercial sport drinks, and candy bars at least 1 wk before and during the experimental period (26).

Protocol. Subjects reported to the laboratory at 8:00 A.M. after an overnight fast. Resting expired breath samples were analyzed for $O_2$ uptake, $CO_2$ elimination ($\dot{V}CO_2$), and $^{13}C/^{12}C$ ratio in expired $CO_2$. The $CO_2$ for $^{13}C/^{12}C$ determination was drawn directly from expired air in the mixing chamber of the open-circuit system. After resting measures were obtained, subjects mounted the cycle ergometer and commenced a 10-min warm-up at 100 W. After warming up, the subjects consumed an initial bolus of 6 ml/kg body wt of the test solution. During all trials subjects consumed a total quantity of 28.5 ml/kg body wt of four different test solutions: water (control for background $^{13}C$), a 15% (by wt) naturally enriched $^{13}C$:soluble CHO (SOL), a 15% naturally enriched insoluble CHO (InSOL), and the same 15% insoluble CHO to which 1 g of $[^{13}C]$:glucose (99 atom % excess) per kilogram was added (InSOL $[^{13}C]$:Glc). The soluble CHO was derived from partially hydrolyzed waxy corn starch, which contains only amylopectin with the majority of the polymers >30 glucose units and a dextrose equivalent <2 (Glucidex 2B, Roquette, Bern, Switzerland). The insoluble CHO (SAARCHEM, Krugersdorp, South Africa) was derived from corn starch containing 24% amylose and 76% amylopectin. The enrichments of the CHO were expressed relative to the international standard Pee Dee Belemnitella (PDB). Enrichments ($\delta^{13}C$PDB) of the CHO samples were −10.45 and −10.90 per mil for SOL and InSOL, respectively.

After the subjects warmed up and drank the initial bolus, they began the 150 min of exercise at 60% $w_{\text{max}}$. They ingested 2.5 ml/kg body wt of the test solution every 15 min (9 feedings of 2.5 ml/kg body wt/feeding). The drinks were kept at room temperature, and the subjects were instructed to consume the drink within 1 min. The drinks contained 25 mg/l of phenol red, a nonabsorbable marker, for analysis of gastric residue at the end of the exercise period (1).

Sample analysis. Total CHO oxidation was calculated from $O_2$ uptake and the respiratory exchange ratio. Exogenous CHO oxidation was calculated on the basis of $^{13}C/^{12}C$ ratios in the ingested CHO and in the expired $CO_2$. This procedure can be done because $^{13}CO_2$ is expired when $^{13}C$:enriched CHO is oxidized (9). Breath samples were taken for 5 min at rest before exercise and for 3 min every 15 min during exercise. Breath samples were collected in duplicate from the mixing chamber into evacuated 20-ml tubes (Vacutainer) and were analyzed for $^{13}CO_2$ isotope enrichment in a Finnigan Delta S isotope ratio mass spectrometer (Bremen, Germany) (23).

Exogenous CHO oxidation was calculated using the computation procedure developed by Mosera et al. (15). Exogenous CHO oxidation was calculated each 15 min. Exogenous CHO oxidation was computed from $\dot{V}CO_2$, $\delta^{13}C$ from the expired air during exercise ($\delta^{13}C_{\text{exp}}$) and at rest ($\delta^{13}C_{\text{rest}}$), and $\delta^{13}C$ from the ingested CHO ($\delta^{13}C_{\text{inc}}$). Background $^{13}C$ enrichment values at rest were subtracted from values during exercise with ingestion of $^{13}C$-enriched CHO (15)

$$VCO_2 = \frac{\dot{V}CO_2 (\delta^{13}C_{\text{rest}} - \delta^{13}C_{\text{exp}})}{(\delta^{13}C_{\text{rest}} - \delta^{13}C_{\text{inc}})}$$

from exogenous CHO

exogenous CHO oxidized (g) = $VCO_2$

Immediately on cessation of the exercise, the gastric contents remaining in the stomach were aspirated using a 50-ml syringe, and the beverage volume remaining as well as the gastric secretions were estimated using the double labeling technique of George as applied by Beckers et al. (1).

Statistics. A repeated-measures (2-way) analysis of variance was used to compare differences in CHO oxidized during 150 min of exercise, differences in peak oxidation rates, and the amount of CHO emptied from the stomach as well as differences in the proportions of the amount of CHO emptied that was oxidized. A level of significance was set at 0.05. All results are expressed as means ± SD.

RESULTS

Figure 1 shows the rise in exogenous CHO oxidation over the 150 min of exercise for the three trials with CHO ingestion. Both the mean (over 150 min of exercise) and peak (at the end of 150 min of exercise) exogenous oxidation rates were significantly greater ($P < 0.05$) in the SOL trial than in the InSOL trial (Table 1). Mean and peak oxidation rates during the InSOL $[^{13}C]$Glc trial were significantly higher ($P < 0.05$) than mean and peak exogenous oxidation rates during the InSOL trial. These findings imply that the addition of the soluble $[^{13}C]$Glc to the insoluble starch leads to artificially higher exogenous CHO oxidation rates, thus overestimating true oxidation. Therefore, data for the InSOL $[^{13}C]$Glc...
trial have not been used for further analysis of the total and endogenous CHO oxidation rates.

Figure 2 shows that the amount of CHO ingested in each trial during 150 min of exercise was the same (516 ± 70 g). The amount of CHO delivered to the intestine was 265 ± 45 and 258 ± 53 g for the SOL and InSOL trials, respectively, and was not significantly different in the two trials. The amount of the ingested CHO that was oxidized was significantly greater \((P < 0.05)\) in the SOL trial \((128 ± 31 g)\) than in the InSOL trial \((75 ± 25 g)\). The amount of ingested CHO oxidized in proportion to the amount of CHO delivered to the intestine was also significantly greater \((P < 0.05)\) in the SOL trial than in the InSOL trial, the proportions being 47.8 and 32.3%, respectively.

Total CHO utilization was not different between the trials with SOL and InSOL ingestion, although total CHO utilization did decrease significantly \((P < 0.05)\) throughout the exercise period in each of the two tests (Fig. 3). The relative proportion of exogenous CHO to the total CHO utilized increased during the exercise trials with this proportion being significantly greater \((P < 0.05)\) in the SOL trial than in the InSOL trial (Fig. 3). Moreover, the amount of endogenous CHO utilized during the SOL trial was significantly less \((P < 0.05)\) than the endogenous CHO utilized during the InSOL trial (252 and 299 g, respectively, over the 150 min of exercise).

Each subject also performed a fourth exercise trial in which he ingested only water. The \(^{13}\text{C}\) enrichment of the expired air in the test with water ingestion did not differ significantly at any time point from that of the rest sample in the same trial. This finding is in accordance with previous observations in Dutch subjects refraining from eating foodstuffs with a high abundance of \(^{13}\text{C}\) enrichments from naturally \(^{13}\text{C}\)-enriched foodstuffs (Table 2) (26). The total amount of CHO utilized during the water trial \((2.24 \text{ g/min})\) was not significantly different from the amount of CHO utilized during the exercise trials with CHO ingestion \((2.52 \text{ and } 2.49 \text{ g/min for SOL and InSOL trials, respectively; Table 1})\). Consequently, the amount of endogenous CHO utilized was significantly greater \((P < 0.05)\) with water ingestion than during either CHO trial.

### DISCUSSION

Highly trained endurance athletes are capable of oxidizing blood-borne glucose at high rates when fed CHO (4). Quantifying the oxidation rate of ingested CHO by using naturally enriched \(^{13}\text{C}\)CHO has been regularly reported (6, 8, 11–14, 17, 19–21). In these studies, oxidation rates of ingested CHO for glucose and glucose polymers have never exceeded 1.2 g/min near the end of exercise, when endogenous CHO stores are presumably low. A previous study by Guennene et al. (8), using naturally enriched \(^{13}\text{C}\)CHO, showed that starch was oxidized at a lower rate than glucose and glucose polymers in solution. Recently, however, Hawley et al. (10), using a \(^{13}\text{C}\)-glucose or starch label, reported that an insoluble starch could be oxidized at a rate of 1.8 g/min after 90 min of exercise. This rate was twice that found for a glucose polymer solution of the same concentration in the same study.

These observations taken together led us to hypothesize that the estimated oxidation rate of 1.8 g/min reported by Hawley et al. (10) was erroneous because of problems of adding a tracer of different physical properties to the tracer to quantify oxidation rates of the ingested CHO.
The first purpose of the present study was to determine, using naturally enriched [$^{13}$C]CHO labeling techniques, the oxidation rates of two different CHO solutions (true soluble vs. insoluble) that were used by Hawley et al. (10). The results of this study indicate a greater oxidation rate of the SOL than that of the InSOL solution (Figs. 1 and 3, Table 1). The exogenous oxidation rates presented here are similar to those of others who used glucose or glucose polymers during exercise with intensities similar to that used in the present study (11–14, 21, 25). Our results also confirm that an insoluble starch is oxidized more slowly than glucose, as reported by Guezennec et al. (8). Our results are in contrast, however, with those of Hawley et al., even though the amount and type of CHO ingested in their study was identical to that used here.

Results from this study (Fig. 2) indicate that the amount of CHO delivered to the intestine was not significantly different in the solutions examined. The amount of CHO oxidized relative to the amount that was delivered to the intestines was greater in the SOL trial than in the InSOL trial, indicating that gastric emptying influences but does not limit exogenous oxidation of CHO. These results are in agreement with results from other studies, showing that gastric emptying does not limit oxidation of the ingested CHO (10, 21).

The soluble CHO used in the present study was a partially hydrolyzed waxy corn starch containing 100% amylopectin. The insoluble corn starch consisted of 24% amylose and 76% amylopectin. Because the amount of CHO delivered to the intestine from the two CHO solutions was not different, it is possible that digestion and absorption could have limited oxidation. It has been shown that amylose is digested less rapidly than amylopectin (7, 22). Therefore, the physical characteristics of the two starches could possibly account for the differences in oxidation rates. The straight glucose chains of amylose are bonded more tightly than the branched glucose chains in amylopectin, making hydrolysis of the insoluble starch containing amylose by α-amylase more difficult. The higher surface area of the amylopectin could additionally increase its rate of hydrolysis. It has been shown that a higher surface area of a starch does indeed increase its rate of hydrolysis (16, 24).

The second purpose of the present study was to determine whether adding a [$^{13}$C]glucose tracer to an insoluble starch solution artificially increases the oxidation rates of the starch solution. Our results (Fig. 1, Table 1) show that both mean and peak oxidation rates with the [$^{13}$C]glucose tracer added (InSOL [$^{13}$C]Glc) were significantly higher than the oxidation rates of the starch alone (InSOL). These results clearly indicate that the [$^{13}$C]glucose tracer added to the starch solution falsely indicates a high oxidation rate for the insoluble starch solution. This observation is further evidence that the solubility of CHO affects oxidation rates. This phenomenon also explains the higher oxidation rate reported for an insoluble starch reported by Hawley et al. (10). The $^{14}$C tracer they used also had a higher solubility than the trace. This issue was recently addressed by Peronnet et al. (18). In

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<th>TABLE 2. Results of water trial</th>
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Values are differences in $^{13}$C enrichment (δ per mill vs. PDB) at different time points vs. rest sample in same trial.
EXOGENOUS CARBOHYDRATE OXIDATION DURING EXERCISE

reply. Hawley et al. confirmed the failure of the used [U-14C]starch label to track the ingested starch by comparing the ratios of plasma glucose (plus lactate) to ingested hexose disintegrations per minute per millimole specific activity. After the ingestion of glucose labeled with [U-14C]glucose and maltose labeled with [U-14C]-maltose, plasma specific activity ratios rose consistently to values of 1.2 ± 0.01 (SR). In contrast, plasma specific activity rose to values of ~3.4 ± 0.21 after the ingestion of starch containing 24% amylose and 76% amylopectin labeled with a [U-14C]amylopectin starch tracer, leading to an overestimation of starch oxidation.

In summary, the results of this study clearly indicate the problems associated with adding a tracer to an insoluble starch solution of different physical characteristics to quantify the starch solution’s oxidation rate. We suggest that the tracer employed must have physical characteristics identical to that of the tracer. This would always be the case when 14CO2 production is measured from naturally enriched CHO (labeling occurs in nature during biosynthesis of CHO by C4 plants). Moreover, it was shown that the physical characteristics of the CHO solutions themselves, namely their solubility in solution, influence exogenous CHO oxidation rates during exercise. The soluble CHO, being oxidized at a higher rate during exercise than an isocaloric insoluble CHO, should be preferred for use by endurance athletes since the ingested soluble CHO represents a larger proportion of the total CHO utilized during exercise, thus saving endogenous CHO stores.

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REFERENCES


