Gastric emptying, absorption, and carbohydrate oxidation during prolonged exercise


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REHRER, N. J., A. J. M. WAGENMAKERS, E. J. BECKERS, D. HALLIDAY, J. B. LEIPER, F. BROUNS, R. J. MAUGHAN, K. WESTERTERP, AND W. H. M. SARIS. Gastric emptying, absorption, and carbohydrate oxidation during prolonged exercise. J. Appl. Physiol. 72(2): 468-475, 1992.—This study was designed to examine aspects of digestive function that may limit assimilation of water and oxidation of orally ingested carbohydrate (CHO) during exercise. Eight males completed a crossover study in which each cycled on four occasions for 80 min at 70% maximal O2 consumption. Beverage was consumed at 0, 20, 40, and 60 min. Beverages were water, 4.5% glucose (4.5G), 17% glucose (17G), and 17% maltodextrin (17MD). CHO beverages contained 20 meq/l NaCl and were 13C enriched to measure exogenous CHO oxidation. Gastric (beverage) volume was measured at 80 min. Water uptake was estimated by including 4H2O in the beverage and measuring 4H accumulation in blood. Jejunal perfusion tests were conducted at rest with the same subjects and beverages. In 80 min, 1.29±.31 (SE) ml were ingested; at 80 min, volumes emptied with H2O (1.257±.32 ml) and 4.5G (1.223±.32 ml) were greater than with 17G (0.71±.56 ml) and 17MD (0.86±.71 ml; P<0.05). Total CHO oxidised was similar with all beverages, but there was a greater increase in exogenous CHO oxidation over time with 17G and 17MD than with 4.5G; 54.19, and 18% of the CHO ingested with 4.5G, 17G, and 17MD, respectively, was oxidised. This represents 57, 32, and 27%, respectively, of the CHO emptied from the stomach. 4H accumulation in the blood was more rapid with H2O and 4.5G than with 17G or 17MD. Net jejunal water absorption was greater from 4.5G than from water. Net water absorption was also observed from 17MD, whereas net secretion was observed with 17G. In conclusion, neither gastric emptying nor intestinal absorption appears to limit exogenous CHO oxidation, and differences in net water absorption are not necessarily reflected in gastric emptying rates.

carbohydrate metabolism; intestinal absorption

SUPPLEMENTATION with carbohydrate (CHO) solutions has been advocated during intense endurance exercise to replace fluid losses and to provide additional CHO in situations where endogenous reserves may become limiting. During the past two decades, many individual aspects of the availability of fluids ingested during exercise have been investigated using a variety of techniques. We (27) and others (3, 4) have estimated availability of fluid (water) and CHO on the basis of gastric emptying (GE) rates. Measurements of the oxidation of orally ingested CHO have been made using both radioactive (2, 30) and stable carbon isotopes (22, 24). The appearance of isotopically labeled CHO (25) and water (7, 8, 12, 20, 26, 31) in blood has also been used to reflect availability of CHO and fluid. The triple-lumen perfusion technique has been used to investigate the exchange of water, electrolytes, and CHO in jejunal segments (12, 16). The present study is the first attempt to perform a complete analysis of GE, fluid availability, water and CHO absorption, and CHO oxidation by application of all the techniques in one series of experiments on eight human volunteers. This approach was chosen in an attempt to identify the factors that limit availability of water and CHO during prolonged exercise at 70% maximal O2 uptake (VO2 max).

Two properties of CHO-containing beverages are known to influence GE rates: osmolality and CHO (glucose) concentration. In most situations both increase or decrease simultaneously. However, different forms of CHO (disaccharide and, to a greater degree, oligo- and polysaccharide) make it possible to have a solution of lower osmolality with similar CHO concentration compared with a monosaccharide solution. From published results it is not clear which of these factors is more critical in delaying GE, nor is it apparent whether these factors have a similar role in determining intestinal absorption and to what degree these processes determine the rates of incorporation of water into body water and oxidation of orally ingested CHO. The present study was designed to question the premise that GE is the limiting factor for incorporation of water into body pools and for the oxidation of orally ingested CHO. Furthermore the effects of CHO concentration and osmolality on GE rate, absorption, and exogenous CHO oxidation rates were examined.

METHODS

Subjects

Eight trained male athletes participated in this study. Subjects were given full oral and written explanation of the procedures before giving written consent. The study
was approved by the Medical Ethical Committee of the University of Limburg. The subjects were triathletes or competitive cyclists aged 28.5 ± 2.8 (SE) yr (range 20-39) with body mass of 76.1 ± 1.8 kg (range 70-82) and \( \text{VO}_{2 \text{max}} \) 5.0 ± 0.1 l/min (range 4.7-5.4; 66.1 ± 0.8 ml·kg\(^{-1}\)·min\(^{-1}\), range 61.0-68.6).

**Experimental Procedures**

**Pretrial.** All subjects came to the laboratory for a preliminary trial 1-2 wk before the first experimental session. \( \text{VO}_{2 \text{max}} \) was determined by an incremental exertion test (for details see Ref. 15) on an electronically braked bicycle ergometer (Lode, Groningen, The Netherlands). The highest \( \text{O}_2 \) consumption value recorded was considered the \( \text{VO}_{2 \text{max}} \). \( \text{O}_2 \) consumption was measured with a SensorMedics 2900 (Anaheim, CA) gas monitor. After the maximal work load test, a nasogastric tube was placed so that subjects could make a decision as to participation with full knowledge of the procedure and to reduce anxiety on the first study day.

**Treatment trials.** Exercise studies were conducted for 80 min with repeated beverage ingestion. Fluid balance, GE, fluid absorption, and CHO oxidation were measured. The order of treatment was randomized. To prevent any carryover of \( ^{13} \text{C} \) label, tests were separated by at least 2 wk and one or more long-lasting training sessions after a test in which \( ^{13} \text{C} \)-labeled CHO was ingested. Otherwise tests were separated by at least 48 h. Subjects were asked to train easily and eat a CHO-rich diet for 48 h before experimentation. Subjects were carefully instructed to refrain from consuming foodstuffs potentially containing naturally enriched \( ^{13} \text{C} \)-labeled CHO (e.g., corn flakes, candy bars, commercial sport drinks) for 2 wk before and during the experimental period. All exercise trials were conducted within a 10-wk period. Perfusion studies were done in a 2-wk period ~1 mo after completion of exercise trials.

**Protocol**

At 8:00 a.m., after an overnight fast, a standardized liquid breakfast was provided (6 ml/kg body wt, Powerplay). At 9:00 a.m., subjects were weighed (naked), and thereafter an indwelling catheter was placed in a forearm vein and a resting blood sample was taken (3 ml). At 9:30 a.m., resting breath samples were taken for measurement of the baseline \( ^{13} \text{C}/^{12} \text{C} \) ratio in expired \( \text{CO}_2 \). Samples were drawn directly from the mixing chamber of the gas-exchange analyzer. At 9:50 a.m., a 10-min warm-up began that consisted of 5 min of cycling at 30% \( \text{VO}_{2 \text{max}} \) followed by 5 min at 50% \( \text{VO}_{2 \text{max}} \). At 10:00 a.m. the first beverage bolus (8 ml/kg body wt) was ingested while the work load was increased to an intensity requiring 70% \( \text{VO}_{2 \text{max}} \). All beverages were given at a temperature of 15°C. At 20, 40, and 60 min additional beverage (3 ml/kg body wt) was given. Two subjects were tested on the same day in most instances, with subjects starting the protocol 5 min apart. Breath samples were collected alternately in each subject throughout exercise.

After 80 min, subjects discontinued exercise, a nasogastric tube was placed, and gastric samples were taken to determine remaining beverage volume. In two individuals after completion of the 80-min protocol and 1 h of rest, exercise was restarted at 70% \( \text{VO}_{2 \text{max}} \) for 30 min while intermittent breath samples were collected for gas exchange and oxidation measurements. In the laboratory the ambient temperature was 19-21°C and the relative humidity was 50-55%.

**Experimental Techniques**

**Gastric emptying.** Beverage volume remaining in the stomach was measured using George’s double-sampling technique as applied by Beckers et al. (1) immediately after the 80-min exercise protocol.

**Fluid balance.** To obtain information concerning fluid balance, body weight, and plasma volume changes were measured before and after exercise. Nude body weight was taken before and directly after exercise. Plasma volume changes were calculated from changes in hematocrit and hemoglobin according to Dill and Costill (9).

**Fluid absorption and deuterium accumulation.** Appearance of deuterium in the blood after oral ingestion of the different beverages labeled with \( ^{2} \text{H}_2 \text{O} \) was used to obtain a relative estimate of water uptake. Accumulation in the circulation is the result of the rate of GE, intestinal absorption, and movement between water compartments. After 40 min of exercise at 70% \( \text{VO}_{2 \text{max}} \) when subjects were essentially in steady state, a 1.5-l dose of 99.8% \( ^{2} \text{H}_2 \text{O} \) (Academy of Sciences, Leipzig, FRG) was included in the beverage bolus ingested.

At rest (baseline sample) and at 42, 50, 60, and 80 min of exercise blood samples (3 ml) were taken. Deuterium was measured in the plasma with mass spectrometry as described previously (33). Excess deuterium values (actual minus baseline enrichment) were used for making comparisons. Statistics were conducted using values at 80 min and the slopes of the accumulation curves determined by least-squares regression (representing rate of accumulation of deuterium).

**Carbohydrate oxidation.** Total oxidation of CHO (exogenous and endogenous) was calculated from the rate of \( \text{O}_2 \) consumption and respiratory exchange ratio with the assumption that the protein contribution was negligible. To measure exogenous CHO oxidation, use was made of the fact that \( ^{14} \text{CO}_2 \) is released when \( ^{13} \text{C} \)-enriched sugars are oxidized (13). Exogenous CHO oxidation can thus be determined using \( ^{13} \text{C} \)-labeled sugars in a CHO load. Breath samples were made for 5 min at rest before exercise and every 7.5 min during exercise for 2.5 min. Breath samples were collected in duplicate directly from the mixing chamber of the gas monitor into evacuated 20-ml tubes (Vacutainers) and were analyzed for \( ^{13} \text{C}_2 \) isotope enrichment in a Finnigan Delta S isotope ratio mass spectrometer (Bremen, FRG) as previously described (28).

A small portion of the free glucose solutions was made up of D-glucose 99 atom% \( ^{13} \text{C}_4 \) (Isotec, Miamisburg, OH). This was added to glucose obtained from potato starch (Avebe, Foxhol, The Netherlands) to give \( ^{13} \text{C} \) of \(-13.69 \) (4.5% glucose) and \(-13.57 \) (% vPDB standard) (17% glucose). The maltodextrin used for 17% maltodextrin was naturally enriched with \( ^{13} \text{C} \) of \(-7.91 \) % (Amylum, Aalst, Belgium). Identical exercise tests were done to determine background, or endogenous, \( ^{13} \text{C} \) levels while}
the subjects were ingesting 4.5% glucose without $^{13}$C glucose addition or while they were ingesting water. Background $^{8}$C in exhaled CO$_2$ was not different in the CHO trial vs. the water trial.

CHO oxidation was calculated in 15-min blocks. To calculate exogenous CHO oxidation, background $^{13}$CO$_2$ enrichment values from the control run (4.5 g/l glucose, nonenriched) were subtracted from corresponding values during ingestion of $^{13}$C-enriched CHO. $^{13}$C enrichment of breath CO$_2$ corrected in this way was divided by $^{13}$C enrichment of the oral CHO to calculate the proportion of CO$_2$ derived from oxidation of exogenous CHO. This proportion was multiplied by the rate of CO$_2$ production to obtain the amount of CO$_2$ derived from exogenous CHO per minute.

**Triple-lumen perfusion.** Seven of the eight subjects returned to the laboratory for a separate set of experiments at rest, in which the triple-lumen perfusion technique was employed to measure net intestinal absorption of fluid and solutes. Perfusion was conducted within 10 cm distal from the duodenoejejunal junction, and samples were extracted 15 cm (mixing segment) and 45 cm (test segment) distal to the perfusion site. Values for absorption of water and solutes were calculated from samples obtained after steady state was achieved. [For details of the perfusion technique, including analyses of solutes and calculations, see Leiper and Maughan (17).] The same beverages as those used in the exercise experiments were tested. Additionally, all beverages contained 500 mg/l polyethylene glycol 4000 as a nonabsorbable marker. This method gives absolute values for intestinal absorption (or secretion) of water and CHO from the various solutions once they are present in the intestinal lumen. To assess glucose absorption when the 17% maltodextrin solution was perfused, acid hydrolysis of the original perfusion solution and luminal samples was carried out before measurement of the glucose concentrations.

**Beverage composition analyses.** Osmolality of the beverages was measured using freezing-point depression (Osmomat 003, Gonotec, Berlin, FRG). A double check on the concentrations of the beverages was conducted by freeze-drying a liquid sample and performing bomb calorimetry. Freeze-dried portions of the beverages were also analyzed for $^{13}$C enrichment after combustion.

### Table 1. Heart rate and O$_2$ consumption in exercise trials

<table>
<thead>
<tr>
<th>Beverage</th>
<th>Heart Rate, beats/min</th>
<th>O$_2$ Consumption, ml/min</th>
</tr>
</thead>
<tbody>
<tr>
<td>H$_2$O</td>
<td>153±3</td>
<td>3.515±86</td>
</tr>
<tr>
<td>4.5G</td>
<td>152±3</td>
<td>3.641±118</td>
</tr>
<tr>
<td>17G</td>
<td>149±2</td>
<td>3.644±114</td>
</tr>
<tr>
<td>17MD</td>
<td>154±3</td>
<td>3.446±77</td>
</tr>
</tbody>
</table>

Values are means ± SE. 4.5G, 4.5% glucose; 17G, 17% glucose; 17MD, 17% maltodextrin.

### Statistics

Friedman analysis of variance (ANOVA) was used to compare differences in the volumes of beverage and the amounts of CHO emptied from the stomach, the amounts of exogenous and total CHO oxidized in 80 min, the rates of deuterium accumulation, net absorption of water and glucose, and plasma volume and body weight changes. The amounts of exogenous and total CHO oxidized over time were compared with a repeated measures (2-way) ANOVA. Individual treatment mean comparisons were made with Wilcoxon’s signed-rank analysis. Multiple linear regression was performed to evaluate relative influences of CHO and intestinal absorption on incorporation of ingested water into body water and oxidation of ingested CHO.

### Results

**Exercise Intensity**

Verification that the stress was similar in all exercise treatments can be deduced from the fact that both mean heart rate and oxygen consumption were similar in all treatment (beverage) trials (Table 1).

**Gastric Emptying**

Mean volume ingested in all exercise trials was 1,294 ± 31 (SE) ml. Mean volumes emptied for the various treatments were 1,257 ± 32 ml (H$_2$O), 1,223 ± 32 ml (4.5G), 781 ± 56 ml (17G), and 864 ± 71 ml (17MD), giving mean emptying rates of 16, 15, 10, and 11 ml/min, respectively. There were no differences in mean volume emptied in 80 min between 4.5G and H$_2$O or between 17G and 17MD. Both 4.5G and H$_2$O emptied faster than both 17% solutions ($P < 0.05$). The mean amounts of CHO ingested and emptied with the different beverages are displayed in Fig. 1. The amount of CHO emptied after 80 min with both 17G and 17MD was greater than with 4.5G. However, the proportion of the total amount of CHO ingested that was emptied was less with 17G (60%) and 17MD (67%) than with 4.5G (95%).

**Carbohydrate Oxidation**

The total amount of CHO oxidized was similar with all beverages (Fig. 2). There was a trend for the rate of total CHO oxidation to decrease with time. The mean amounts of exogenous CHO oxidized in 80 min are also displayed in Fig. 1. The amounts of exogenous CHO oxidized in 80 min were not significantly different between CHO treatments: 31.5 ± 2.7 g (4.5G), 42.0 ± 4.6 g (17G),

**Treatments**

Exercise tests were repeated by each subject for the five different beverages: H$_2$O, 4.5 g/100 ml $^{13}$C-enriched glucose (4.5G), 17 g/100 ml $^{13}$C-enriched glucose (17G), 17 g/100 ml naturally $^{13}$C-enriched maltodextrin (17MD) and 4.5 g/100 ml potato starch-derived glucose (control for background $^{13}$C). During this control run with nonenriched CHO, only breath samples were taken. All CHO-containing beverages also had 29 meq/l NaCl. For triple-lumen perfusion trials 4.5G, 17G, and 17MD were made up with the same ingredients as for the exercise trials, but no $^{13}$C-enriched glucose was added to 4.5G and 17G. Osmolarities of the beverages were 313, 1,223, and 301 mosmol/kg for 4.5G, 17G, and 17MD, respectively.
Deuterium Accumulation

Accumulation of deuterium in the blood after ingestion of the labeled bolus at 40 min resulted in accumulation curves shown in Fig. 3. Analysis of the 80-min blood values and of slopes of the accumulation curves revealed similar differences between treatments. When deuterium accumulation was expressed as a percentage of a 6-h postexercise urine value (which represents complete

and 39.1 ± 2.9 g (17MD). CHO oxidation, divided into exogenous and endogenous contributions, is also depicted in Fig. 2. The amount of exogenous CHO oxidized increased with time and with the amount of CHO fed. When repeated-measures (2-way) ANOVA was performed on the amounts of exogenous CHO oxidized each 15 min, through 75 min, for the different CHO-containing beverages, a significant beverage × time interaction was observed ($P < 0.01$). This indicates that as the exercise time increased, the proportional contribution of orally provided CHO to total CHO oxidized varied significantly between treatments. When Wilcoxon's signed-rank analysis was performed, the amounts of exogenous CHO oxidized at 30–45, 45–60, and 60–75 min were greater with 17MD and 17G than with 4.5G ($P < 0.05$).

Much of the ingested CHO was not oxidized (Fig. 1); multilinear regression revealed a significant correlation ($r = 0.784$) between total exogenous CHO oxidized and CHO emptied from the stomach ($P < 0.01$). The discrepancy between amounts ingested and amounts oxidized cannot, however, be totally accounted for by the delay in GE. There were large differences in the total amount of CHO being emptied from the stomach with the different treatments, but the differences in total exogenous CHO utilized were trivial in comparison.

When the oxidation data are described in terms of percent CHO ingested that was emptied, the discrepancy between the amount of CHO emptied and the amount oxidized was greatest in the 17% solutions. With 4.5G, 57% of the CHO that was emptied was oxidized, whereas with 17G and 17MD only 32 and 27%, respectively, of the amount emptied was oxidized.

After the initial 80 min of exercise, two subjects conducted an additional 30 min of 70% $V_{\text{O}}_{\text{max}}$ cycling after a 1-h rest period in the 17G trial. This brought about large increases in the proportion of exogenous CHO that was oxidized (Table 2). The total amount of CHO oxidized per 15 min was similar with 70% $V_{\text{O}}_{\text{max}}$ exercise before and after 1 h of rest.

FIG. 2. Mean amounts of exogenous and endogenous carbohydrate oxidized with different beverages.
TABLE 2. Carbohydrate oxidation during initial regimen and in second exercise bout of 30 min after 1 h of rest

<table>
<thead>
<tr>
<th>Time, min</th>
<th>CHO Oxidation, g</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total</td>
<td>Exogenous</td>
<td></td>
</tr>
<tr>
<td>0-15</td>
<td>41.1±2.5</td>
<td>1.3±0.8</td>
<td></td>
</tr>
<tr>
<td>15-30</td>
<td>38.8±2.2</td>
<td>7.1±2.5</td>
<td></td>
</tr>
<tr>
<td>30-45</td>
<td>42.2±4.8</td>
<td>10.6±1.7</td>
<td></td>
</tr>
<tr>
<td>45-60</td>
<td>42.0±0.8</td>
<td>12.2±1.4</td>
<td></td>
</tr>
<tr>
<td>60-75</td>
<td>39.8±2.5</td>
<td>12.8±0.8</td>
<td></td>
</tr>
<tr>
<td>Rest</td>
<td>42.3±0.3</td>
<td>25.8±1.1</td>
<td></td>
</tr>
<tr>
<td>140-155</td>
<td>39.3±1.0</td>
<td>19.8±1.0</td>
<td></td>
</tr>
</tbody>
</table>

Values are means ± SE for 2 subjects. 17G was used as beverage.

Equilibration of the ingested tracer with body water, the same treatment differences were observed. With H$_2$O and 4.5G treatments, 100% of the dose given was absorbed in 40 min, whereas with 17G and 17MD only 45 and 54%, respectively, of the dose was absorbed in 40 min. The rate of accumulation, as well as the degree of accumulation at 80 min, was greater with H$_2$O and 4.5G than with 17G and 17MD. Mean slopes were 0.82 ± 0.12 (H$_2$O), 0.66 ± 0.02 (4.5G), 0.27 ± 0.02 (17G), and 0.31 ± 0.04 (17MD). When linear regression was performed, a significant correlation (r = 0.827) was observed between the rate of deuterium accumulation in the blood (slope) and the GB rate (P < 0.01).

**Plasma Volume and Body Weight Changes**

Changes in plasma volume and body weight, as a result of the 80-min exercise bout, are given in Table 3. Weight changes were negligible, with no significant treatment effect. Friedman ANOVA revealed no significant beverage effect on plasma volume changes. There was, however, a trend for ingestion of 17G and 17MD during exercise to result in greater plasma volume decreases. When multilinear regression analysis was performed with plasma volume change as the dependent variable and deuterium accumulation rate and subjects as the independent variables, the multiple r was 0.715. Deuterium accumulation did not make a significant contribution to the regression. A similar regression analysis was performed with volume of beverage emptied, water absorption (jejunal perfusion), and subjects as independent variables. In this instance the multiple r was 0.722, and the volume emptied did make a significant contribution to the regression (P < 0.04).

**Triple-Lumen Perfusion**

Only six of the subjects completed all four treatments. Water absorption across the jejunal mucosa was affected by the composition of the beverage infused (Fig. 4). One-way ANOVA showed a significant treatment (beverage) effect on water absorption (P < 0.05). Differences in treatment means were significant for all paired comparisons (P < 0.05). Net secretion was observed with 17G perfusion (-50.2 ml·cm$^{-1}$·h$^{-1}$; negative values indicate secretion), whereas perfusion with the other beverages

![FIG. 3. Deuterium accumulation in blood after 1.5-ml dose of 99 atom% H$_2$O was given in 40-min beverage bolus.](image)

![FIG. 4. Net water absorption with triple-lumen perfusion at rest. Negative values represent net efflux into jejunum.](image)

TABLE 3. Plasma volume and body weight changes after 80 min of 70% VO$_2$max cycling

<table>
<thead>
<tr>
<th>Beverage</th>
<th>∆PV, %</th>
<th>∆BW, kg</th>
<th>∆BW, %</th>
<th>∆BW - Beverage Wt</th>
</tr>
</thead>
<tbody>
<tr>
<td>H$_2$O</td>
<td>-10.2±1.3</td>
<td>-0.70±0.12</td>
<td>0.9±0.2</td>
<td>-1.29±0.31</td>
</tr>
<tr>
<td>4.5G</td>
<td>-9.8±1.5</td>
<td>-0.44±0.10</td>
<td>0.6±0.1</td>
<td>-1.30±0.34</td>
</tr>
<tr>
<td>17G</td>
<td>-14.2±1.3</td>
<td>-0.58±0.16</td>
<td>0.8±0.2</td>
<td>-1.47±0.32</td>
</tr>
<tr>
<td>17MD</td>
<td>-14.1±3.0</td>
<td>-0.56±0.16</td>
<td>0.8±0.2</td>
<td>-1.35±0.31</td>
</tr>
</tbody>
</table>

Values are means ± SE. VO$_2$ max, maximal O$_2$ consumption; PV, plasma volume; BW, body weight.
resulted in net water absorption. There were, however, large individual differences.

Mean steady-state glucose absorption rates with triple-lumen perfusion were 2,198 ± 382 (4.5G), 7,150 ± 2,177 (17G), and 326 ± 291 μmol·cm⁻¹·h⁻¹ (17MD). ANOVA revealed a significant difference in glucose absorption with treatment (P < 0.01). Wilcoxon’s signed-rank comparisons between individual treatment means demonstrated significant differences in absorption of glucose between all treatments (P < 0.05).

DISCUSSION

The volume of beverage emptied was significantly influenced by beverage composition, as would be expected on the basis of our earlier results (27) and those of others (for review, see Ref. 23). Specifically, CHO concentration was found to be of particular importance. Type of CHO (e.g., glucose vs. glucose polymer) was found to be of no importance in terms of emptying rate of beverage.

Total CHO oxidation was not different between CHO treatments. The rate of oxidation of exogenous CHO increased with time for all the CHO-containing beverages. The significant interaction of time × beverage indicates that there was a difference in the magnitude of this increase, with the increase being greater with both 17% CHO solutions than with the 4.5% CHO solution. Because glucose transport is related to the metabolic needs of the cell, one may theorize that as endogenous reserves become depleted transport and oxidation of blood-borne glucose are increased, and it is only at this point that a more concentrated solution makes a larger contribution to CHO oxidation. In support of this are results from experiments of longer duration in which total exogenous glucose oxidation is proportional to the glucose load (22, 32).

In the present study, 17G and 4.5G beverages provided 220 and 55 g of CHO, respectively, in 80 min, whereas only 42.0 (17G) and 31.5 g (4.5G) were oxidized. Although the 17G drink provided 3.8 times more CHO, only 1.3 times more CHO was oxidized. Several factors appear to form physical and metabolic barriers such that the proportion of orally ingested CHO available for oxidation is less with 17G than with 4.5G. In this respect, the stomach appears to be an important moderating barrier, in that it retains 88 g CHO with 17G and only 3 g with 4.5G. It is assumed that the relative rates of CHO absorption observed with jejunal perfusion also apply to the exercise situation, then the jejunum would not be an important moderating barrier, because the absorption rate of CHO from 17G was 3.3 times faster than the absorption rate of 4.5G, while 3.8 times more CHO was provided. However, it is not certain whether this assumption is valid. Exercise may delay intestinal absorption, and the possibility that this occurs differentially with the ingestion of beverages of varying CHO content cannot be eliminated. The increase observed in oxidation of exogenous CHO with additional exercise after 1 h of rest and no further CHO ingestion might be interpreted as meaning that a large portion of CHO was not yet absorbed and became so during the rest phase. However, it is equally possible that the increase in exogenous CHO oxidation was not a result of an increase in CHO availability through increased absorption but rather a result of an incorporation of the exogenous CHO into skeletal muscle stores and subsequent oxidation with renewed exercise.

If relative absorption rates from the perfusion experiments can be extended to the exercise studies, then a third modulating effect must exist that more or less equalizes the amount of CHO oxidized with 17G and 4.5G. In support of the conclusion that intestinal absorption is not limiting for the oxidation of exogenous CHO are results from a study by Coyle et al. (5). In this study, hyperglycemia was induced via a glucose infusion in humans during exercise, and a "gap" was also observed between the amount of CHO infused and that which was oxidized. Oxidation of the exogenous glucose and the increase in blood glucose could not account for all the glucose infused. It is possible that the large amounts of CHO that enter the blood with 17G are converted to glycogen instead of being oxidized. Glycogen synthesis may occur in the nonexercising muscles, and glycogen synthesis also cannot be excluded in certain fibers of the exercising muscles (type II fibers) (14). The possibility of fat synthesis can also not be ruled out when massive amounts of CHO are given.

The other question raised by this study concerned fluid availability. In the present study, the measured GE rates correlated with deuterium accumulation rates (r = 0.63; P < 0.01). However, no difference was observed between accumulation of deuterium from H₂O and 4.5G, whereas triple-lumen perfusion demonstrated significantly greater water absorption from 4.5G than from H₂O. Gisolfi et al. (12) have also observed no difference in deuterium accumulation in blood after intestinal perfusion with a 6% carbohydrate-electrolyte solution and water (both containing deuterium), yet they have observed greater net water absorption from the carbohydrate-electrolyte solution on the basis of direct measurement of water absorption with triple-lumen perfusion. On the basis of these results they suggested that the difference in results can be due to the fact that deuterium accumulation represents unidirectional flow (absorption, not secretion) and as such is not representative of net intestinal absorption.

One other problem with interpretation of the perfusion data in the present study is the fact that deuterium uptake and oxidation data were collected during exercise, whereas perfusion data were collected at rest. Although Fordtran and Saltin (11) found no effect of exercise on net intestinal absorption measured with perfusion, results of Maughan et al. (21) have demonstrated differences in deuterium accumulation with exercise at various intensities (19), which necessitates similar physiological state when comparing intestinal absorption of different solutions. Furthermore, absolute deuterium accumulation values may give erroneous results in rest if the rate of disappearance from the bloodstream is not measured and corrected for. The rate of disappearance from the blood is relatively slow at rest (21) and increases substantially during exercise (20; N. J. Rehrrer et al., unpublished observations). During exercise, mixture with total body water is practically instantaneous, and the different body water compartments may be treated as one pool.
Despite potential problems with extrapolation to an exercise situation of results collected at rest, there are no data to suggest that relative differences in GE or absorption between solutions found at rest would not persist during exercise. Therefore the assumption is made that although absolute amounts absorbed and secreted may be altered during exercise, relative differences in GE and absorption resulting from differences in beverage composition would still be present during exercise.

Advantages of a glucose-polymer over a free-glucose solution are not obvious when one looks at GE rate, water uptake as measured by deuterium accumulation, or oxidation rate. However, one observes an apparent advantage with a glucose polymer when comparing the net water flux. Net water absorption is observed with the polymer (17MD), whereas net secretion is observed with the hypertonic-free-glucose solution (17G). These results are supported by those of others in which water movement across the intestine has been shown to be related to the osmolality of the sucus within the test segment (11). Intestinal secretion is increased with hypertonic intestinal perfusion (17, 29), and a decrease in plasma volume has also been observed with intestinal perfusion (29) as well as with ingestion of hypertonic solutions (20). Neither deuterium uptake values nor plasma volume changes reflect the difference in net water absorption between 17G and 17MD, as measured with triple-lumen perfusion. This discrepancy may again be explained by the fact that deuterium measures only unidirectional flow or by the possibility that although there is net secretion at one point, absorption can take place further down the intestine. Also, plasma volume changes at 80 min may not be representative of changes that occurred earlier after ingestion. It is possible that more of the maltodextrin was hydrolyzed in the deuterium 17MD experiment than in the perfusion experiment, leading to a greater intraluminal osmolality than in the perfusion study. However, in a study in rats by Daum and coworkers (6) in which the entire intestine was perfused, a much lower intraluminal osmolality was maintained with a glucose-polymer solution than with a similarly concentrated glucose solution.

Another inconsistency with the triple-lumen results is that net absorption of glucose from 17MD was significantly less than with 17G or 4.5G. However, no difference in oxidation of orally ingested CHO between similarly concentrated glucose (17G) and glucose-polymer (17MD) solutions was observed, as previously reported by Massicotte et al. (18). The discrepancy between apparent absorption of glucose and oxidation may be an artifact of the triple-lumen technique.

Although the perfusion technique gives a measure of the absorption capacity, the physiological rate at which absorption may occur is unknown, because fluid is provided to the jejunum at a constant rate (10 ml·min⁻¹·cm⁻²). This rate is similar to the mean rates of emptying observed in this study (10–16 ml/min); however, the naturally occurring and variable delay in GE is absent here.

Furthermore, these absorption, or secretion, rates represent only this one section of the intestine, and different areas of the intestine have different absorptive and secretory capacities. Also, in the case of oligo- and polysaccharides, the absorption of glucose is dependent on the presence of the hydrolyzing enzymes that are not uniformly distributed throughout the intestine. Because the triple-lumen perfusion technique involves perfusion of only a very small segment of the intestine, the net absorption of a glucose polymer may be underestimated. It may be that the membrane surface area required to hydrolyze the amount of carbohydrate presented as oligosaccharides was simply not sufficient to allow the absorption that could occur over the entire intestine.

In conclusion, oxidation rates of CHO given as dilute (4.5%) and concentrated (17%) solutions were similar during 80 min of 70% VO₂max exercise, despite the fact that more CHO is emptied from the stomach with the 17% solutions. This implies that factors other than GE limit exogenous CHO oxidation. The glucose absorption data, obtained with triple-lumen perfusion at rest, demonstrate a difference in absorption rates between the two solutions that is of the same magnitude as the difference in CHO concentration, making it unlikely that intestinal storage of CHO has a substantial role in minimizing the difference in CHO oxidation between these two solutions. Other steps in metabolism may limit exogenous CHO oxidation and storage sites besides or in addition to the intestines (e.g., muscle and liver glycogen), which appear to retain excess glucose during and after exercise. GE rates are similar for a dilute (4.5%) glucose sodium-containing solution and water, yet net water absorption, measured at rest, is significantly greater with the dilute glucose solution. This may imply an advantage to consumption of fluids containing glucose (or glucose polymer) and sodium during exercise, even when hydration and not CHO provision is the primary objective.

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REFERENCES


EXERCISE, GI FUNCTION, AND CARBOHYDRATE OXIDATION


