

Carbohydrate Intake During Exercise and Performance

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It is generally accepted that carbohydrate (CHO) feeding during exercise can improve endurance capacity (time to exhaustion) and exercise performance during prolonged exercise (>2 h). More recently, studies have also shown ergogenic effects of CHO feeding during shorter exercise of high intensity (~1 h at >75% of maximum oxygen consumption). During prolonged exercise the mechanism behind this performance improvement is likely to be related to maintenance of high rates of CHO oxidation and the prevention of hypoglycemia. Nevertheless, other mechanisms may play a role, depending on the type of exercise and the specific conditions. The mechanism for performance improvements during higher-intensity exercise is less clear, but there is some evidence that CHO can have central effects. In the past few years, studies have investigated ways to optimize CHO delivery and bioavailability. An analysis of all studies available shows that a single CHO ingested during exercise will be oxidized at rates up to about 1 g/min, even when large amounts of CHO are ingested. Combinations of CHO that use different intestinal transporters for absorption (e.g., glucose and fructose) have been shown to result in higher oxidation rates, and this seems to be a way to increase exogenous CHO oxidation rates by 20% to 50%. The search will continue for ways to further improve CHO delivery and to improve the oxidation efficiency resulting in less accumulation of CHO in the gastrointestinal tract and potentially decreasing gastrointestinal problems during prolonged exercise. *Nutrition* 2004;20:669–677. ©Elsevier Inc. 2004

KEY WORDS: carbohydrate feeding, exercise performance, exogenous oxidation, carbohydrate absorption

INTRODUCTION

Whereas 100 y ago beef (protein) was believed to be the most important component of an athlete's diet, nowadays it seems to be pasta (carbohydrate [CHO]). Athletes are often advised to eat a high-CHO diet, consume CHO before exercise, ensure adequate CHO intake during exercise, and replenish CHO stores as soon as possible after exercise. In the most recent position statement of the International Olympic Committee (IOC) on nutrition for athletes, it was stated: "A high carbohydrate diet in the days before competition will help enhance performance, particularly when exercise lasts longer than about 60 min" and "Athletes should aim to achieve carbohydrate intakes that meet the fuel requirements of their training programs and also adequately replace their carbohydrate stores during recovery between training sessions and competition. This can be achieved when athletes eat carbohydrate-rich snacks and meals that also provide a good source of protein and other nutrients." These recommendations have also been discussed in detail in reviews resulting from this IOC consensus meeting in 2003.^{1,2} CHO also played a central role in a joint position statement³ of the American College of Sports Medicine, the American Dietetic Association, and the Canadian Dietetic Association on nutrition for athletic performance, and several recommendations were made specifically for CHO.

Research on the effects of CHO feeding before and during exercise has accumulated since the beginning of the 20th century. Krogh and Lindhardt⁴ were probably the first to recognize the importance of CHO as a fuel source during exercise. They reported that subjects found exercise easier if they had consumed a CHO-

rich diet compared with a high-fat diet, and this was accompanied by higher respiratory exchange ratios during exercise. Important observations were also made by Levine et al.⁵ who measured blood glucose in some of the participants after the 1923 Boston Marathon. They found that most runners had reduced blood glucose concentrations after the race. Levine et al.⁵ suggested that these low blood glucose levels were a cause of fatigue. To test that hypothesis they encouraged several participants of the same marathon 1 y later to consume CHO during the race.⁵ This practice, in combination with a high-CHO diet before the race, prevented hypoglycemia and significantly improved running performance (i.e., time to complete the race). In 1932 Christensen⁶ showed that with increasing exercise intensity the proportion of CHO utilized increased. This work was expanded in the late 1960s with the reintroduction of the muscle biopsy technique by a group of Scandinavian scientists.^{7,8} These studies indicated for the first time the critical role of muscle glycogen. The improved performance after a high-CHO diet was linked with the higher muscle glycogen concentrations observed after such a diet. A high-CHO diet (~70% of dietary energy from CHO) and elevated muscle glycogen stores seemed to enhance endurance capacity compared with a normal (~50%) and a low (~10%) CHO diet. In the late 1970s and early 1980s the effects of CHO feeding during exercise on exercise performance and metabolism was further investigated.^{9–11} In the following years, more and more studies provided evidence of an ergogenic effect of CHO ingested during exercise, and slowly this practice of consuming CHO during exercise became a habit in many sports, especially endurance sports. During the 1980s so-called sports drinks became commercially available. Now CHO drinks are deeply embedded in the "culture" of endurance sports.

Despite the general acceptance of the ergogenic effects of CHO supplementation during exercise, there is a need to evaluate the existing evidence critically because some of the results may have been exaggerated by the choice of the experimental protocols,

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which were not always comparable to the situation of competition. This review discusses the effects of CHO on endurance capacity and endurance performance when ingested *during* exercise and the underlying mechanisms for the observed performance effects. The second part of this review discusses ways to improve the bioavailability of CHO and directions for future research.

CHO DURING EXERCISE AND PERFORMANCE

Although early studies^{5,12} had suggested a role for hypoglycemia in the development of fatigue, when researchers started to study this in more detail in the early 1980s they initially could not confirm a role for hypoglycemia.¹⁰ There did not seem to be a clear relation between hypoglycemia and performance, and the effects of CHO feeding on perceptions of effort and general fatigue were inconsistent.¹¹ These findings were also consistent with recent studies on rebound hypoglycemia.^{13–16} In these studies there was no evidence of a relation between the degree of hypoglycemia and exercise performance.

Nevertheless, the beneficial effects of CHO feeding on endurance capacity were consistently demonstrated by researchers led by David Costill^{11,17–20} or researchers who had been his students.^{21–23} The ergogenic effects were also confirmed by several other research groups,^{24–26} although not all studies found effects of CHO feeding on performance.^{9,10,27,28} For a summary of studies, see Table I.

Although initial studies investigated the effects of CHO feeding on endurance capacity or performance during prolonged exercise lasting 2 h or longer, more recent studies have also found positive effects of CHO feeding during exercise of relatively high intensity (>75% of maximum oxygen consumption [$\text{VO}_{2\text{max}}$]) lasting approximately 1 h. Jeukendrup et al.²⁹ investigated the effects of CHO ingestion during the equivalent of a 40-km time trial in well-trained cyclists and found that performance was improved by 2.3%. Several studies have reported similar results,^{30–33} although not all studies have found an ergogenic effect.^{34–36} When Palmer et al.³⁷ investigated the effects of CHO ingestion during a 20-km time trial (~30 min), no effect on performance was found.

Whether or not performance differences were observed might be related to the way performance was evaluated or by the type and amount of CHO that was provided. Some studies have measured performance by a short time trial or a sprint at the end of 3 to 4 h of continuous exercise, whereas others have measured endurance capacity by time to exhaustion (Table I). More researchers have studied the effect of CHO feeding on prolonged time trial performance (100 to 128 km).^{28,38} There are clear differences in the reproducibility of these protocols,⁸⁷ and it is likely that some measures of performance are more sensitive than others to the effects of CHO feeding. The control of external variables such as diet, conditions during the experimental trials, feedback given to subjects, and motivation of subjects is also different between studies, and these factors are likely to play an important role. Some have argued that the reason for a lack of an ergogenic effect of CHO ingested during exercise was related to the duration of the exercise that may have been too short, the intensity of exercise that may have been too low to cause CHO depletion, or the amount of CHO ingested may have been insufficient. The balance of studies, however, is convincingly in favor of the ones that show ergogenic effects of CHO feeding during exercise.

THE MINIMAL AMOUNT OF CHO NEEDED

Mitchell et al.⁴⁰ observed that 12 min of isokinetic time trial performance was enhanced at the end of 2 h of intermittent exercise. The improvements were similar with ingestion of 34, 39, or 50 g of CHO per hour compared with a water trial. Based on a study by Fielding et al.,¹⁷ it is usually believed that a minimum of

22 g of CHO per hour is required to observe a performance benefit. In that study subjects exercised for 4 h and performed a sprint at the end. Performance improvements were observed when 22 g of CHO was ingested every hour, whereas no effects were observed when half this dose was consumed (11 g/h). In a study by Maughan et al.,⁴¹ the intake of 16 g of glucose per hour resulted in an improved endurance capacity by 14% compared with water (no placebo was given in this study). Most other studies that have found positive results used ingestion rates that were higher than this. However, Mitchell et al.⁴⁰ found no effect of CHO ingestion on 12 min of all-out isokinetic cycling when 6% was ingested, but performance was enhanced when a 12% CHO solution was ingested. Interestingly, ingestion of an 18% CHO solution did not improve performance. In an earlier study the same investigators found no effect of 6% and 7.5% CHO solutions, but performance was improved with a 5% CHO solution. In this study, however, the amount and type of CHO ingested were varied. Flynn et al.²⁷ found no differences in performance with the ingestion of 5% or 10% CHO solutions. In that study, however, these drinks were similar to placebo in the resulting performance. Most of these studies provided 40 to 75 g of CHO per hour and observed performance benefits. Ingesting CHO at a rate higher than 75 g/h did not appear to be any more effective at improving performance than ingesting CHO at a rate of 40 to 75 g/h. It has been suggested that this is because ingestion of 40 to 75 g of CHO per hour already results in optimal CHO availability and ingesting CHO at higher rates may not increase the bioavailability.⁴² It is also possible that the current performance measurements are not sensitive enough to identify the small differences in performance that may exist when comparing two different CHO solutions. The overall conclusion seems to be that performance benefits can be observed with relative small amounts of CHO (16 g/h), but no further improvement has been observed with the ingestion of larger amounts of CHO.

FORM OF CHO

The form in which the CHO is provided during exercise (solid or liquid) does not seem to affect the ergogenic potential. Hargreaves et al.¹⁸ studied the effects of ingestion of a candy bar (43 g of CHO, 9 g of fat, and 3 g of protein) and observed a 46% improvement in sprint capacity after 4 h of exercise compared with placebo ingestion. Others confirmed these findings and reported that liquid and solid CHO feedings improved exercise performance to a similar degree.^{43,44}

More recently, Murdoch et al.⁴⁵ investigated the effects of an artificially sweetened placebo with slurried bananas or solid bananas and observed improved performance after 3 h of exercise at 70% of $\text{VO}_{2\text{max}}$ with both types of bananas compared with placebo. In addition, the type of CHO seemed to have little or no effect on performance (Table I).

CRITICAL ANALYSIS

It must be noted that most of the early studies were performed after an overnight fast. This means that the subjects started the exercise with suboptimal glycogen stores, and it has been shown that after an overnight fast liver glycogen stores may be considerably reduced.^{46,47} It seems obvious that exogenous CHO would have an effect in these conditions because it can provide an alternative substrate to compensate for the reduced endogenous CHO availability. Whether CHO feeding can also improve performance when endogenous CHO stores are optimal at the start of exercise has been investigated in later studies. This is highly relevant because athletes will rarely ever start a race with suboptimal glycogen stores.

Another concern is that it is currently much more difficult to perform a blinded study because subjects are no longer naive to the

TABLE I.

| EFFECT OF CARBOHYDRATE FEEDING DURING EXERCISE ON EXERCISE PERFORMANCE OR EXERCISE CAPACITY | | | | | | | | |
|---|------|------------|------------------------|---|---|-------------|--|------------------|
| Study | Year | n | Mean intake rate (g/h) | Exercise | CHO type | Fast period | Effect versus placebo | Effect |
| Bonen et al. ⁹ | 1981 | 8 G 8 P | 234 | Cycling at 80% $\text{VO}_{2\text{max}}$ to exhaustion | 20% Glucose | 36–44 h | 26.1 min (G) versus 29.9 (P) | N |
| Ivy et al. ²³ | 1983 | 10 | 24–29 | Walking to exhaustion at 45% $\text{VO}_{2\text{max}}$ | Glucose polymer | 12 h | 299 min (GP) versus 268 min (P) | Y |
| Coyle et al. ²² | 1983 | 10 | 124 | Cycling at 74% $\text{VO}_{2\text{max}}$ to exhaustion | Glucose | Overnight | 157 min (C) versus 134 min (P) | Y |
| Hargreaves et al. ¹⁸ | 1984 | 10 | 43 | 4-h intermittent intensity cycling followed by 100% $\text{VO}_{2\text{max}}$ to exhaustion | Candy bar 43 g sucrose, 6 g fat, 3 g protein | Overnight | 127 s (S) versus 87 (P) s | Y |
| Bjorkman et al. ²⁴ | 1984 | 8 | 53 | Cycling at 68% $\text{VO}_{2\text{max}}$ to exhaustion | 7% Glucose, 7% fructose | Overnight | 137 min (G) versus 116 min (P) 116 min (F) versus 116 min (P) | Y Y |
| Fielding et al. ¹⁷ | 1985 | 9 | 22 | 240-min cycling followed by sprint at 100% $\text{VO}_{2\text{max}}$ | 5% CHO | Overnight | 121 s (C) versus 81 s (P) | Y |
| Coyle et al. ²¹ | 1986 | 7 | 100 | Cycling at 71% $\text{VO}_{2\text{max}}$ to exhaustion | Glucose polymer | Overnight | 4.02 h (GP) versus 3.02 h (P) | Y |
| Coggan and Coyle ⁸⁹ | 1987 | 7 | 3 after first bout | Cycling to exhaustion at 73% $\text{VO}_{2\text{max}}$ followed by 20-min recovery and again cycling to exhaustion at 73% $\text{VO}_{2\text{max}}$ | Glucose | Overnight | 26 min (G) versus 10 min (P) | Y |
| Flynn et al. ²⁷ | 1987 | 8 | 45 90 90 | Cycling for 120 min trying to produce as much work as possible | 3% Glucose polymer + 2% glucose 5% Glucose polymer + 5% fructose 7.7% Glucose polymer + 2.3% high-fructose corn syrup (>60% fructose) | | 184 W versus 186 W 178 W versus 186 W 189 W versus 186 W | N N N |
| Murray et al. ⁹⁰ | 1987 | 13 | 24 29 34 | Intermittent cycling (55–65% $\text{VO}_{2\text{max}}$) followed by a sprint | 5% Glucose polymer 4% Sucrose + 2% glucose 5% Glucose polymer + 2% fructose | 8 h | 400 s (GP) versus 432 s (P) 384 s (S + G) versus 432 s (P) 375 s (GP + F) versus 432 s (P) | N Y Y |
| Murray et al. ²⁵ | 1989 | 12 | 31 41 52 | 3 × 20-min cycling at 65% $\text{VO}_{2\text{max}}$ with 5-min rest followed by a sprint | 6% Sucrose 8% Sucrose 10% Sucrose | 4 h | 13.03 s (6%) versus 13.62 s (P) 13.30 s (8%) versus 13.62 s (P) 13.57 s (10%) versus 13.62 s (P) | Y N N |
| Maughan et al. ⁹¹ | 1989 | 6 | 24 | Running at 70% $\text{VO}_{2\text{max}}$ to exhaustion | 4% Glucose 19% Glucose, 15% fructose, 7% maltose, 8% glucose polymers 11% Glucose, 6% maltose, 19% glucose polymers 34% Fructose, 2% glucose | Overnight | 90.8 min (C) versus 70.2 min (P) 79.5 min (C) versus 70.2 min (P) 79.0 min (C) versus 70.2 min (P) 65.6 min (C) versus 70.2 min (P) | Y N N N |
| Mitchell et al. ⁴⁰ | 1989 | 10 | 37 74 111 | 105-min cycling at 70% $\text{VO}_{2\text{max}}$ followed by 15 min time trial | 6% CHO 12% CHO 18% CHO | 10 h | 213 kJ versus 201 kJ 228 kJ versus 201 kJ 217 kJ versus 201 kJ | N Y N |
| Wright et al. ⁹² | 1991 | 9 | 35 | Cycling at 70% $\text{VO}_{2\text{max}}$ to exhaustion | 5% Glucose polymer + 3% sucrose | 10 h 3 h | 201 min (C) versus 266 min (P) 289 min (C) versus 237 min (P) | Y Y |
| Zachwieja et al. ⁹³ | 1992 | 8 | 63 | 105-min cycling at 70% $\text{VO}_{2\text{max}}$ followed by a 15-min time trial | 4% Glucose + 6% fructose | Overnight | 264 W (G + F) versus 242 W (P) | Y |
| Wilber and Moffat ⁹⁴ | 1992 | 10 | 41 | Running at 80% $\text{VO}_{2\text{max}}$ to exhaustion | 7% Glucose | Overnight | 115.4 min (G) versus 92.0 min (P) | Y |
| Tsintzas et al. ⁹⁵ | 1993 | 7 | 50 only first hour | 30-km road race (running) | 5.5% CHO (glucose polymer + glucose + fructose) | | 128.3 min (C) versus 131.2 min (P) | Y |
| Langenfeld et al. ⁹⁶ | 1994 | 14 | 37 | 80-mile (128-km) cycle time trial on windload simulator | 5% MD + 2% fructose | 3–4 h | 64.7% $\text{VO}_{2\text{max}}$ versus 55.3% $\text{VO}_{2\text{max}}$ | Y |
| Maughan et al. ⁴¹ | 1996 | 12 | 22 16 | Cycling at 70% $\text{VO}_{2\text{max}}$ to exhaustion | Glucose Glucose | Overnight | 110 min (G) versus 93 (P) 107 min (G) versus 93 (P) | Y Y |
| Tsintzas et al. ⁵⁶ | 1996 | 8 | 45 | Running at 76% $\text{VO}_{2\text{max}}$ to exhaustion | 5.5% CHO (glucose polymer + glucose + fructose) | 12–16 h | 132 min (C) versus 114 min (P) | Y |
| Madsen et al. ²⁸ | 1996 | 9 | 66 | 100-km time trial on magnetic braked simulator | 5% (MD plus glucose 1:1) | 4 h | 160 min versus 160 min | N |
| Angus et al. ⁹⁷ | 2000 | 8 | 60 | 100-km time trial on cycle ergometer | 6% (glucose plus sucrose; Gatorade) | 2–3 h | 166 min versus 178 min | Y |

C, carbohydrate; CHO, carbohydrate; F, fructose; G, glucose; GP, glucose polymer; MD, maltodextrin; N, no; P, placebo; S, sucrose; $\text{VO}_{2\text{max}}$, maximal oxygen consumption; W, watts; Y, yes

treatments and there are strong expectations that CHO feeding improves endurance performance, especially when many subjects are also familiar with the taste of artificial sweeteners and can distinguish between sweeteners and CHO. Unless placebos are prepared by dedicated laboratories, the results may be influenced by expectations. An elegant study by Clark et al.³⁴ demonstrated this point in an attempt to distinguish between a placebo effect of CHO and a real physiologic effect. They examined 42 cyclists who performed two 40-km time trials. During the first time trial they ingested water and for the second trial they were randomized into six different groups. The researchers gave CHO to three of the groups and placebo to other three groups. They told one group on CHO that it was placebo, they told the second group that it was CHO, and they provided the third group with no information. Similarly in the placebo groups, one group was told it was placebo, one group that it was CHO, and the third group was not told. The study confirmed the existence of a placebo effect. Changes in mean power in the second trial were 4.3% when subjects were told they were ingesting CHO and 0.5% when they were told they were ingesting placebo. The real effect of CHO in this study was reported to be a slight reduction of 0.3%. Although this study illustrates the importance of a placebo effect, this study did not use a cross-over design and there appeared to be considerable differences between groups in their ability (especially peak power).

MECHANISM BY WHICH CHO FEEDING IMPROVES PERFORMANCE

There are several mechanisms by which CHO feeding during exercise may improve endurance performance. These include maintaining blood glucose and high levels of CHO oxidation, sparing endogenous glycogen, synthesizing glycogen during low-intensity exercise, or a central effect of CHO. The mechanisms may be different for relatively short-duration (~1 h) high-intensity exercise (80% to 85% of $\dot{V}O_{2max}$) than for long-duration (>2 h) low- to moderate-intensity exercise (60% to 75% of $\dot{V}O_{2max}$).

Coyle et al.²¹ found that CHO feeding during exercise at 70% of $\dot{V}O_{2max}$ prevented the drop in blood glucose that was observed when water (placebo) was ingested. In the placebo trials the glucose concentration started to drop after 1 h and reached extremely low concentrations (2.5 mM/L) at exhaustion after 3 h of exercise. With CHO feeding, euglycemia was maintained and subjects continued for 4 h at the same intensity. Total CHO oxidation rates followed a similar pattern. There was a drop in CHO oxidation after about 1.5 h of exercise with placebo, and high rates of CHO oxidation were maintained with CHO feeding.

In a follow-up study subjects exercised to exhaustion at 73% of $\dot{V}O_{2max}$ (~170 min) on three occasions separated by a week. During these trials, plasma glucose declined from 5.0 to 3.1 mM/L. After resting for 20 min, the subjects attempted to continue exercise 1) after ingesting a placebo, 2) after ingesting glucose polymers (3 g/kg), or 3) when glucose was infused intravenously to maintain plasma glucose concentrations of 11 mM/L. Interestingly, when subjects exercised to exhaustion with water, they were able to continue when glucose was ingested or infused intravenously. Time to fatigue during this second exercise bout was significantly longer with CHO ingestion (26 min) or glucose infusion (43 min) than with placebo (10 min). These studies support the idea that plasma glucose is an important substrate during prolonged exercise. It is interesting that some studies found improvements in performance with CHO ingestion without a drop in plasma glucose concentration.

It has been shown that CHO feeding during exercise "saves" liver glycogen.^{48,49} Hepatic glucose output is tightly regulated, ensuring a relatively constant glucose output in the presence or absence of CHO feeding. Although the total rate of appearance of glucose increases somewhat with increasing rates of CHO intake,

there is a progressive decrease in endogenous glucose production (liver glycogenolysis and gluconeogenesis) with increasing rates of CHO intake.⁴⁹ Some studies have reported that with high rates of CHO intake liver glucose production returns to its basal levels,⁵⁰ whereas others have observed complete blocking of hepatic glucose output by CHO feeding.⁴⁹ This liver glycogen sparing means that there is still CHO in the liver toward the end of exercise, which could be beneficial if, for whatever reason, CHO intake cannot supply enough CHO to maintain plasma glucose concentrations and high rates of total CHO oxidation.

Whether CHO feeding during exercise has an effect on muscle glycogen breakdown has been the subject of considerable debate. An early study by Bergstrom and Hultman⁵¹ showed a 25% reduction in muscle glycogen breakdown during exhaustive one-legged cycling when glucose was infused intravenously to achieve hyperglycemic values of 21 mM/L. However, such high plasma glucose concentrations are rather non-physiologic and impossible to achieve during exercise with CHO feeding. With CHO feeding during cycling exercise plasma glucose concentrations are usually elevated by about 0.5 to 1.0 mM/L,^{18,21,22,52} whereas plasma insulin concentrations are similar to water ingestion.^{18,21} Several studies have reported that CHO ingestion does not result in a reduced net breakdown of muscle glycogen measured with the muscle biopsy technique^{21,27,40,53} or the indirect stable isotope technique.^{49,54} There are, however, a few studies that reported reduced muscle glycogen breakdown with CHO intake during cycling.^{52,55} Tsintzas et al.⁵⁶ studied muscle glycogen breakdown during running at 70% of $\dot{V}O_{2max}$ and observed that with CHO feeding there was a reduction in net muscle glycogen breakdown in type I muscle fibers after 60 min, whereas type II fibers seemed unaffected. In a follow-up study similar results were obtained.⁵⁷ A reduction in muscle glycogen breakdown was observed with CHO feeding, and the depletion of type I muscle fibers coincided with the point of exhaustion.

After intermittent exercise muscle glycogen concentrations were higher when CHO was ingested than when water was ingested.⁵⁵ This could indicate that there was reduced rate of muscle glycogenolysis. However, it is also possible that during the low intensity of exercise periods the ingested CHO was used to synthesize muscle glycogen.^{58,59}

During continuous cycling exercise at moderate exercise intensities CHO ingestion has little effect on plasma glucose concentrations, but without CHO ingestion plasma glucose concentrations may drop after approximately 2 h of exercise. The majority of the evidence shows that in these conditions CHO ingestion seems to improve endurance capacity (or performance) by maintaining euglycemia and high rates of CHO oxidation. In contrast, during constant pace running CHO ingestion has been shown to reduce net muscle glycogen breakdown in type I fibers. In intermittent exercise (cycling and running) CHO ingestion during exercise seems to reduce the net breakdown of muscle glycogen. An excellent review by Tzintzas and Williams⁶⁰ summarized the evidence for a glycogen sparing effect of CHO, and the interested reader is referred to this report for more details.

CHO may also have central effects. The ergogenic effect of CHO feeding during relatively short (60 min) high-intensity exercise (>75% of $\dot{V}O_{2max}$) has now been confirmed by several studies,²⁹⁻³³ although others did not find such an effect.^{34,35} It is difficult to understand why CHO ingestion would benefit such exercise because the proportional contribution of muscle glycogen to energy expenditure far exceeds the contribution of blood glucose at these high intensities,^{61,62} and muscle glycogen is not fully depleted after such exercise.⁶³ In addition, the amount of CHO that can be absorbed in the short period is small and was estimated to be approximately 15 g,²⁹ and absorption of exogenous glucose may even be lower at approximately 85% of $\dot{V}O_{2max}$ than at approximately 70% of $\dot{V}O_{2max}$. Further, blood glucose concentration tended to increase even when no CHO was ingested during exercise at 80% to 85% of $\dot{V}O_{2max}$.³¹ Recently Carter et al.⁶⁴

infused glucose at a rate of 1 g/min (in saline) or just saline during an approximately 60-min time trial. The infusion of glucose resulted in a marked elevation of plasma glucose concentrations and an increase in the rate of disappearance of glucose. However, performance was not different from saline infusion. This suggests that the mechanism by which glucose improves performance during this type of exercise is not metabolic but rather central. To investigate this possibility further Carter et al.⁶⁵ designed a study in which trained cyclists received a CHO solution or an identical-tasting placebo. The subjects were asked to use the solution as a mouth rinse and spit it out rather than swallow the solution. Similar, additional time trials of approximately 60-min duration were performed, and it was found that the CHO solution improved performance by 2.8%. These results suggest that receptors exist in the oral cavity that communicate with the brain. Although direct evidence for such an effect is lacking, it is clear that the brain can sense changes in the composition of the mouth and stomach contents. Oropharyngeal mechanisms, including those situated in the oral cavity, have important roles in perceptual responses during rehydration and exercise in the heat.^{66,67} In these studies, oral hydration resulted in reduced values for rating of perceived exertion (RPE) and thirst sensation compared with intravenous hydration. These findings are supported by reports of temporary reductions in thirst due to the gargling of tap water.⁶⁸ Although somewhat speculative, it cannot be excluded that triggering of stimuli within the oral cavity by the CHO solution initiated a chain of neural messages in the central nervous system, resulting in the stimulation of the reward and/or pleasure centers in the brain.

OXIDATION OF INGESTED CHO

Several factors have been suggested to influence exogenous CHO oxidation including feeding schedule, type and amount of CHO ingested, and exercise intensity, and these have been intensively investigated (Figure 1). Some of these factors have only small effects and other factors have major effects on exogenous CHO oxidation. For example, the timing of CHO ingestion seems to have relatively little effect on exogenous CHO oxidation rates. Studies in which a large bolus (100 g) of a CHO in solution was given⁶⁹ seemed to result in similar exogenous CHO oxidation rates to studies in which 100 g of glucose was ingested at regular intervals. With increasing exercise intensity, the active muscle mass becomes more and more dependent on CHO as a source of energy. Increased muscle glycogenolysis and increased plasma glucose oxidation contribute to the increased energy demands.⁶¹ It is therefore reasonable to expect that exogenous CHO oxidation will increase with increasing exercise intensities. An early study by Pirnay et al.⁷⁰ reported lower exogenous CHO oxidation rates at low exercise intensities compared with moderate intensities, but exogenous CHO oxidation tended to level off between 51% and 64% of $\text{VO}_{2\text{max}}$. When the exercise intensity was increased from 60% to 75% of $\text{VO}_{2\text{max}}$ exogenous CHO oxidation, no increase in exogenous CHO oxidation was observed.⁷¹

Therefore, it is possible that lower exogenous CHO oxidation rates are observed only at very low exercise intensities when the reliance on CHO as an energy source is minimal. In this situation, part of the ingested CHO may be directed toward non-oxidative glucose disposal (storage in the liver or muscle) rather than toward oxidation. Studies with CHO ingestion during intermittent exercise have suggested that during low intensity exercise glycogen can be resynthesized.⁷²

It seems fair to conclude that at exercise intensities below 50% to 60% of $\text{VO}_{2\text{max}}$ exogenous CHO oxidation will increase; with increasing total CHO oxidation rates, usually above approximately 50% to 60% of $\text{VO}_{2\text{max}}$, oxidation rates will not increase further.

Numerous studies have compared the oxidation rates of various types of CHO with the oxidation of ingested glucose during exercise.⁷³

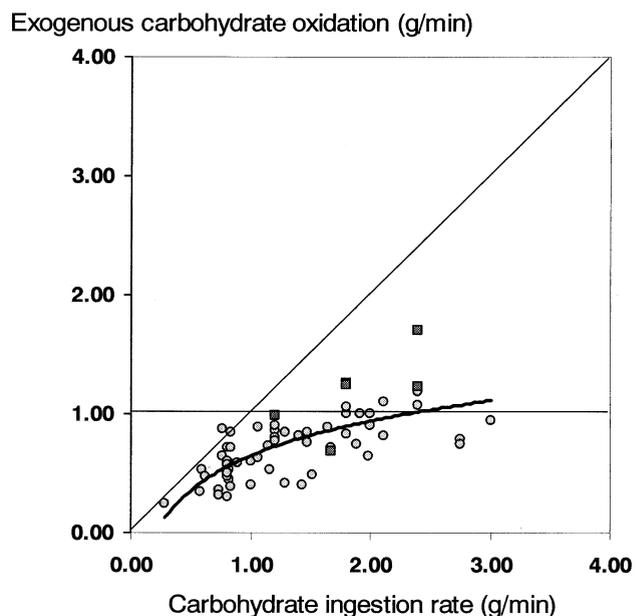


FIG. 1. Peak exogenous carbohydrate oxidation during exercise as a function of the rate of carbohydrate intake. Each dot represents the peak oxidation rate observed with one type of carbohydrate. The dotted line represents the line of identity where oxidation equals the ingestion rate. In general, there is an increase in oxidation with increasing intake, but this seems to level off with higher rates of intake (>1.2 g/min). Peak oxidation rates for a single carbohydrate (circles) are typically 1.0 to 1.1 g/min. However, when multiple carbohydrates that use different intestinal transporters are ingested, oxidation rates can increase by 20% to 50% (squares). This figure is based on data from many studies that measured exogenous carbohydrate oxidation during exercise.^{15,39,74–76,83,88,98–113}

Glucose is found to be oxidized at relatively high rates (up to ~1 g/min). The other two monosaccharides, fructose and galactose, are oxidized at much lower rates during exercise.^{74,75} This has been attributed to the fact that fructose and galactose must be converted into glucose in the liver before they can be metabolized.

The exogenous CHO oxidation rates of maltose, sucrose, and glucose polymers (maltodextrin) are comparable to those of glucose. Starches with a relatively large amount of amylopectin are rapidly digested and absorbed, whereas those with a high amylose content have a relatively slow rate of hydrolysis. Ingested amylopectin is oxidized at very high rates (similar to glucose), whereas amylose is oxidized at very low rates.⁷⁶

In summary, CHOs can be divided into two categories according to the rate at which they are oxidized. One group is oxidized at relatively high rates up to about 1 g/min, and another group is oxidized at much lower rates up to about 0.6 g/min.

The optimal amount is likely to be the amount of CHO that results in maximal exogenous CHO oxidation rates without causing gastrointestinal problems. Rehrer et al.⁷⁷ studied the oxidation of different amounts of CHO ingested during 80 min of cycling exercise at 70% of $\text{VO}_{2\text{max}}$. Subjects received a 4.5% glucose solution (a total of 58 g glucose during 80 min of exercise) or a 17% glucose solution (220 g during 80 min of exercise). Total exogenous CHO oxidation was measured, which was slightly higher (42 g versus 32 g in 80 min) with the larger CHO dose. Thus, even though the amount of CHO ingested was increased almost four-fold, the oxidation rate was barely affected. More recently Jeukendrup et al.⁴⁹ investigated the oxidation rates of even larger CHO intakes of up to 3.00 g/min and found that this resulted in oxidation rates of up to 0.94 g/min at the end of 120 min of cycling exercise.

The results from a large number of studies were used to construct the graph shown in Figure 1. The peak exogenous CHO oxidation rates are plotted against the rate of ingestion. It must be concluded that the maximal rate at which a single ingested CHO can be oxidized is about 1.0 g/min. The horizontal line depicts the absolute maximum around 1.0 g/min. The dotted line represents the line of identity where the rate of CHO ingestion equals the rate of exogenous CHO oxidation. From this graph it can be concluded that oxidation of orally ingested CHO may be optimal at ingestion rates near 1.0 to 1.2 g/min. This implies that athletes should ensure a CHO intake of about 60 to 70 g/h for optimal CHO delivery. Ingesting more than this will not result in higher CHO oxidation rates and is more likely to be associated with gastrointestinal discomfort.

BIOAVAILABILITY OF INGESTED CHO

The results of studies with different dosages of CHO suggest that with increasing intake the bioavailability does not necessarily increase. Several factors may reduce the bioavailability of ingested CHO, including gastric emptying and intestinal absorption. It has also been suggested that the liver plays an important role and that muscle glucose uptake could be a limiting factor.

There is, however, accumulating evidence that gastric emptying is not an important limitation to exogenous CHO oxidation, at least at low to moderate intensities (up to ~70% of VO_{2max}).

Several studies that measured gastric emptying and exogenous CHO oxidation concluded that only 32% to 48% of the CHO delivered to the intestine was oxidized and that therefore gastric emptying did not limit exogenous CHO oxidation.^{76,78} Massicotte et al.⁷⁵ performed a study in which subjects exercised for 120 min at 65% of VO_{2max} and ingested CHO at regular intervals during exercise with or without metoclopramide, a drug known to stimulate gastric emptying. Metoclopramide, however, had no enhancing effect on exogenous CHO oxidation. Surely, gastric emptying can limit the delivery of CHO to the intestine, especially at high-intensity or intermittent exercise,⁷⁹ but generally this does not seem to be a major limiting factor for exogenous CHO oxidation during prolonged moderate-intensity exercise.

More and more evidence is suggesting that the most important rate-limiting factor is the rate of absorption of CHO from the small intestine into the systemic circulation. Studies using a triple-lumen technique have measured glucose absorption and estimated whole-body intestinal absorption rates of a 6% glucose-electrolyte solution.⁸⁰ It was estimated that the maximal absorption rate of the intestine ranged from 1.2 to 1.7 g/min. Such measurements are usually made over 40 cm of the small intestine and extrapolations to whole-body absorption rates are problematic, especially because various sections of the gut have different absorptive capacities. Because of limitations of the techniques that measure absorption directly, there is only indirect evidence for limitations at the level of absorption. Probably the strongest evidence is from studies using CHO types that use different transport proteins for absorption across the intestinal epithelial membrane.

A study by Shi et al.⁸¹ suggested that the inclusion of two or three different CHOs (glucose, fructose, and sucrose) in a drink may increase water and CHO absorption despite the increased osmolality. This effect was attributed to the separate transport mechanisms across the intestinal wall for glucose, fructose, and sucrose.⁸¹ The monosaccharides glucose and galactose are transported across the luminal membrane by a glucose transporter called sodium dependent glucose transporter 1 (SGLT1); fructose is transported by glucose transporter 5 (GLUT5). It was hypothesized that a mixture of these CHOs may reduce competition for transport and increase total CHO absorption.

Adopo et al.⁸² were the first to show that the ingestion of a glucose and fructose mixture results in higher exogenous CHO oxidation rates compared with ingestion of an isoenergetic amount

of glucose. The cumulative amount of exogenous hexoses oxidized was 21% larger with glucose and fructose than when only glucose was ingested.

However, in that study relatively small amounts of CHO were ingested and exogenous CHO oxidation was relatively low; therefore, it could not be investigated whether saturation of the SGLT1 transporter is the factor that limits exogenous CHO oxidation. A recent study by Jentjens et al.⁸³ using ¹⁴C-labeled glucose and ¹³C-labeled fructose demonstrated that, with the ingestion of glucose at a rate of 1.8 g glucose per minute, exogenous CHO oxidation rates peaked at 0.83 g/min toward the end of 120 min of exercise. However, when a mixture of glucose and fructose was ingested (isoenergetic), total exogenous CHO oxidation rates peaked at 1.26 g/min, 55% higher compared with glucose only. Higher exogenous CHO oxidation rates were also observed when glucose and sucrose were ingested in combination, possibly because the fructose released after hydrolysis of sucrose used a different transport mechanism.⁸³ When glucose was ingested in combination with maltose (which after hydrolysis results in two glucose molecules that will also compete for transport by SGLT1), this did not result in higher exogenous CHO oxidation rates. These results provide indirect evidence for an important role of absorption. A follow-up study investigated the exogenous CHO oxidation rates of combined ingestion of glucose, fructose, and sucrose at relatively high rates (2.4 g/min).⁸⁴ Peak exogenous CHO oxidation rates were approximately 44% higher with this combination of CHO than with an isoenergetic amount of glucose and reached values as high as 1.7 g/min.

In theory uptake by skeletal muscle could also be a limiting factor for exogenous CHO oxidation, but it has been observed that glucose appearing in the systemic circulation was taken up at similar rates to its rate of appearance, and 90% to 95% of this glucose was oxidized during exercise. When a larger dose of CHO was ingested (3 g/min), rate of appearance gut (entrance of CHO from the gut into the systemic circulation) was one-third of the rate of CHO ingestion (0.96 to 1.04 g/min). Thus, only part of the ingested CHO entered the systemic circulation. However, a large proportion of the glucose appearing in the blood was taken up by tissues (presumably mainly by the muscle) and 90% to 95% was oxidized. It was concluded that entrance into the systemic circulation is a limiting factor for exogenous glucose oxidation, rather than intramuscular factors. This is further supported by glucose infusion studies. Hawley et al.⁸⁵ bypassed intestinal absorption and hepatic glucose uptake by infusing glucose into the circulation of subjects exercising at 70% of VO_{2max} . When large amounts of glucose were infused and subjects were hyperglycemic (10 mM/L), it was possible to raise blood glucose oxidation rate substantially above 1 g/min.

These studies provide evidence that exogenous CHO oxidation is limited by the rate of digestion, absorption, and subsequent transport of glucose into the systemic circulation rather than by the rate of uptake from the blood and subsequent oxidation by the muscle. It is important to note that during high-intensity exercise (e.g., >80% of VO_{2max}), a reduced blood flow to the gut may result in a decreased absorption of glucose and water⁸⁶ and, hence, a low rate of appearance gut relative to the rate of ingestion. Taken together, this suggests that intestinal absorption is a factor contributing to the limitation to oxidize ingested CHO at rates higher than 1.0 to 1.1 g/min, but it may not be the sole factor. The liver may play another important role. Hepatic glucose output is highly regulated, and it is possible that the glucose output derived from the intestine and from hepatic glycogenolysis and gluconeogenesis will not exceed 1.0 to 1.1 g/min, even though the rate of absorption is slightly in excess of this rate. If supply from the intestine is too large (>1.0 g/min), glycogen synthesis may be stimulated in the liver.

IMPORTANCE OF HIGH EXOGENOUS CHO OXIDATION RATES

A greater contribution of exogenous (external) fuel sources (CHO) will spare endogenous sources (liver and possibly muscle glycogen in some conditions), and it is tempting to believe that a greater contribution from exogenous sources will increase endurance capacity and/or exercise performance. Although many studies (including our own) are based on this assumption, the evidence for this is lacking. To our knowledge no studies have demonstrated that ingesting larger amounts of CHO that will result in higher exogenous CHO oxidation rates will also enhance performance. Studies have shown effects of CHO feeding even with relatively low rates of intake (as low as 16 g/h), but generally no greater improvements have been observed with higher intake rates. However, as discussed elsewhere, the measurement of performance is very difficult, and performance or endurance capacity is dependent on many external variables that, if not adequately controlled, can influence performance measurements. It is known that there is considerable day-to-day variation in endurance performance and especially endurance capacity.⁸⁷ It is therefore not unlikely that the tests currently being used to measure performance or endurance capacity are not sensitive enough to pick up smaller differences. It may be possible to detect the difference between water placebo and CHO feeding (although not all studies were able to pick up this difference), but it may be more problematic to pick up the smaller effect of one type of CHO feeding versus another.

In an earlier review we introduced the term *oxidation efficiency*, which refers to the percentage of the ingested CHO that is oxidized.⁷³ High oxidation efficiency means that smaller amounts of CHO remain in the gastrointestinal tract, and it is likely that this will reduce the risk of developing gastrointestinal complaints during prolonged exercise.^{77,86} The oxidation efficiency of drinks containing CHO that use different transporters for intestinal absorption is higher than that of drinks with a single CHO. This means that, for instance, drinks containing glucose and fructose are less likely to cause gastrointestinal distress. Interestingly, this is a consistent finding in studies that have attempted to register gastrointestinal discomfort during exercise.^{13,88}

Although the search will continue for ways to further improve CHO delivery and to improve the oxidation efficiency, resulting in less accumulation of CHO in the gastrointestinal tract, thereby potentially reducing gastrointestinal problems during prolonged exercise, studies should be performed to investigate the effects of high exogenous CHO oxidation rates on exercise performance.

REFERENCES

- Coyle EF. Fluid and fuel intake during exercise. *J Sports Sci* 2004;22:39
- Hargreaves M, Hawley JA, Jeukendrup A. Pre-exercise carbohydrate and fat ingestion: effects on metabolism and performance. *J Sports Sci* 2004;22:31
- American College of Sports Medicine, American Dietetic Association, and Dietitians of Canada. Joint position statement. Nutrition and athletic performance. *Med Sci Sports Exerc* 2000;32:2130
- Krogh A, Lindhard J. The relative value of fat and carbohydrate as sources of muscular energy. *Bioch J* 1920;14:290
- Levine SA, Gordon B, Derick CL. Some changes in chemical constituents of blood following a marathon race. *JAMA* 1924;82:1778
- Christensen EH. Der Stoffwechsel und die Respiratorischen Funktionen bei schwerer körperlicher Arbeit. *Scand Arch Physiol* 1932;81:160
- Bergstrom J, Hultman E. Muscle glycogen synthesis after exercise: an enhancing factor localized in muscle cells in man. *Nature* 1966;210:309
- Bergstrom J, Hultman E. A study of glycogen metabolism during exercise in man. *Scand J Clin Invest* 1967;19:218
- Bonen A, Malcolm SA, Kilgour RD, MacIntyre KP, Belcastro AN. Glucose ingestion before and during intense exercise. *J Appl Physiol* 1981;50:766
- Felig P, Cherif A, Minagawa A, Wahren J. Hypoglycemia during prolonged exercise in normal men. *N Engl J Med* 1982;306:895
- Ivy JL, Costill DL, Fink WJ, Lower RW. Influence of caffeine and carbohydrate feedings on endurance performance. *Med Sci Sports* 1979;11:6
- Christensen EH, Hansen O. Arbeitsfähigkeit und ernährung. *Scand Arch Physiol* 1939;81:160
- Jentjens RL, Venables MC, Jeukendrup AE. Oxidation of exogenous glucose, sucrose and maltose during prolonged cycling exercise. *J Appl Physiol* 2004; 96:1285
- Jentjens RL, Jeukendrup AE. Prevalence of hypoglycemia following pre-exercise carbohydrate ingestion is not accompanied by higher insulin sensitivity. *Int J Sport Nutr Exerc Metab* 2002;12:398
- Jentjens RL, Jeukendrup AE. Effects of pre-exercise ingestion of trehalose, galactose and glucose on subsequent metabolism and cycling performance. *Eur J Appl Physiol* 2003;88:459
- Moseley L, Lancaster GI, Jentjens RLPG, Achten J, Jeukendrup AE. The effect of timing of pre-exercise carbohydrate feedings on metabolism and cycling performance. *Med Sci Sports Exerc* 2001;34:S203
- Fielding RA, Costill DL, Fink WJ, King DS, Hargreaves M, Kovaleski JE. Effect of carbohydrate feeding frequencies and dosage on muscle glycogen use during exercise. *Med Sci Sports Exerc* 1985;17:472
- Hargreaves M, Costill DL, Coggan A, Fink WJ, Nishibata I. Effect of carbohydrate feedings on muscle glycogen utilisation and exercise performance. *Med Sci Sports Exerc* 1984;16:219
- Mitchell JB, Costill DL, Houmard JA, Flynn MG, Fink WJ, Beltz JD. Effects of carbohydrate ingestion on gastric emptying and exercise performance. *Med Sci Sports exerc* 1988;20:110
- Neufer PD, Costill DL, Flynn MG, Kirwan JP, Mitchell JB, Houmard J. Improvements in exercise performance: effects of carbohydrate feedings and diet. *J Appl Physiol* 1987;62:983
- Coyle EF, Coggan AR, Hemmert MK, Ivy JL. Muscle glycogen utilization during prolonged strenuous exercise when fed carbohydrate. *J Appl Physiol* 1986;61:165
- Coyle EF, Hagberg JM, Hurley BF, Martin WH, Ehsani AA, Holloszy JO. Carbohydrate feeding during prolonged strenuous exercise. *J Appl Physiol* 1983;55:230
- Ivy JL, Miller W, Dover V, et al. Endurance improved by ingestion of a glucose polymer supplement. *Med Sci Sports Exerc* 1983;15:466
- Bjorkman O, Sahlin K, Hagenfeldt L, Wahren J. Influence of glucose and fructose ingestion on the capacity for long term exercise in well trained men. *Clin Physiol* 1984;4:483
- Murray R, Seifert JG, Eddy DE, Paul GL, Halaby GA. Carbohydrate feeding and exercise: effect of beverage carbohydrate content. *Eur J Appl Physiol* 1989;59:152
- Sasaki H, Maeda J, Usui S, Ishiko T. Effect of sucrose and caffeine ingestion on performance of prolonged strenuous running. *Int J Sports Med* 1987;8:261
- Flynn MG, Costill DL, Hawley JA, et al. Influence of selected carbohydrate drinks on cycling performance and glycogen use. *Med Sci Sports Exerc* 1987; 19:37
- Madsen K, MacLean DA, Kiens B, Christensen D. Effects of glucose, glucose plus branched-chain amino acids, or placebo on bike performance over 100 km. *J Appl Physiol* 1996;81:2644
- Jeukendrup A, Brouns F, Wagenmakers AJ, Saris WH. Carbohydrate-electrolyte feedings improve 1 h time trial cycling performance. *Int J Sports Med* 1997; 18:125
- Anantaraman R, Carmines AA, Gaesser GA, Weltman A. Effects of carbohydrate supplementation on performance during 1 h of high intensity exercise. *Int J Sports Med* 1995;16:461
- Below PR, Mora-Rodríguez R, González Alonso J, Coyle EF. Fluid and carbohydrate ingestion independently improve performance during 1 h of intense exercise. *Med Sci Sports Exerc* 1995;27:200
- Carter J, Jeukendrup AE, Mundel T, Jones DA. Carbohydrate supplementation improves moderate and high-intensity exercise in the heat. *Pflugers Arch* 2003; 446:211
- el-Sayed MS, Balmer J, Rattu AJ. Carbohydrate ingestion improves endurance performance during a 1 h simulated time trial. *J Sports Sci* 1997;15:223
- Clark VR, Hopkins WG, Hawley JA, Burke LM. Placebo effect of carbohydrate feedings during a 40-km cycling time trial (in process citation). *Med Sci Sports Exerc* 2000;32:1642
- McConnell GK, Canny BJ, Daddo MC, Nance MJ, Snow RJ. Effect of carbohydrate ingestion on glucose kinetics and muscle metabolism during intense endurance exercise. *J Appl Physiol* 2000;89:1690
- Powers SK, Lawler J, Dodd S, Tulley R, Landry G, Wheeler K. Fluid replacement drinks during high intensity exercise: effects on minimizing exercise-induced disturbances in homeostasis. *Eur J Appl Physiol* 1990;60:54
- Palmer GS, Clancy MC, Hawley JA, Rodger IM, Burke LM, Noakes TD. Carbohydrate ingestion immediately before exercise does not improve 20km time trial performance in well trained cyclists. *Int J Sports Med* 1998;19:415

38. Angus DJ, Hargreaves M, Dancy J, Febbraio MA. Effect of carbohydrate or carbohydrate plus medium-chain triglyceride ingestion on cycling time trial performance. *J Appl Physiol* 2000;88:113
39. Jeukendrup AE, Borghouts L, Saris WHM, Wagenmakers AJM. Reduced oxidation rates of orally ingested glucose during exercise after low CHO intake and low muscle glycogen. *J Appl Physiol* 1996;81:1952
40. Mitchell JB, Costill DL, Houmard JA, Fink WJ, Pascoe DD, Pearson DR. Influence of carbohydrate dosage on exercise performance and glycogen use. *J Appl Physiol* 1989;67:1843
41. Maughan RJ, Bethell LR, Leiper JB. Effects of ingested fluids on exercise capacity and on cardiovascular and metabolic responses to prolonged exercise in man. *Exp Physiol* 1996;81:847
42. Coggan AR, Swanson SC. Nutritional manipulations before and during endurance exercise: effects on performance. *Med Sci Sports Exerc* 1992;24(suppl):S5331
43. Lugo M, Sherman WM, Wimer GS, Garleb K. Metabolic responses when different forms of carbohydrate energy are consumed during cycling. *Int J Sport Nutr* 1993;3:398
44. Neuffer PD, Costill DL, Fink WJ, Kirwan JP, Fielding RA, Flynn MG. Effects of exercise and carbohydrate composition on gastric emptying. *Med Sci Sports Exerc* 1986;18:658
45. Murdoch SD, Bazzarre TL, Snider IP, Goldfarb AH. Differences in the effects of carbohydrate food form on endurance performance to exhaustion. *Int J Sports Nutrition* 1993;3:41
46. Hultman E, Nilsson LH. Liver glycogen in man: effects of different diets and muscular exercise. In: Pernow B, Saltin B, eds. *Muscle metabolism during exercise, Vol II*. New York: Plenum, 1971:143
47. Nilsson LH, Hultman E. Liver glycogen in man; the effects of total starvation or a carbohydrate-poor diet followed by carbohydrate feeding. *Scand J Clin Lab Invest* 1973;32:325
48. Bosch AN, Dennis SC, Noakes TD. Influence of carbohydrate ingestion on fuel substrate turnover and oxidation during prolonged exercise. *J Appl Physiol* 1994;76:2364
49. Jeukendrup AE, Raben A, Gijsen A, et al. Glucose kinetics during prolonged exercise in highly trained human subjects: effect of glucose ingestion. *J Physiol (Lond)* 1999;515(pt 2):579
50. Howlett K, Angus D, Proietto J, Hargreaves M. Effect of increased blood glucose availability on glucose kinetics during exercise. *J Appl Physiol* 1998;84:1413
51. Bergstrom J, Hultman E. Synthesis of muscle glycogen in man after glucose and fructose infusion. *Acta Med Scand* 1967;182:93
52. Erickson MA, Schwarzkopf RJ, McKenzie RD. Effects of caffeine, fructose, and glucose ingestion on muscle glycogen utilization during exercise. *Med Sci Sports Exerc* 1987;19:579
53. Hargreaves M, Briggs CA. Effect of carbohydrate ingestion on exercise metabolism. *J Appl Physiol* 1988;65:1553
54. Jeukendrup AE, Wagenmakers AJ, Stegen JH, Gijsen AP, Brouns F, Saris WH. Carbohydrate ingestion can completely suppress endogenous glucose production during exercise. *Am J Physiol* 1999;276(pt 1):E672
55. Yaspelkis BB, Patterson JG, Anderla PA, Ding Z, Ivy JL. Carbohydrate supplementation spares muscle glycogen during variable-intensity exercise. *J Appl Physiol* 1993;75:1477
56. Tsintzas OK, Williams C, Boobis L, Greenhaff P. Carbohydrate ingestion and glycogen utilisation in different muscle fibre types in man. *J Physiol* 1995;489:243
57. Tsintzas OK, Williams C, Boobis L, Greenhaff P. Carbohydrate ingestion and single muscle fiber glycogen metabolism during prolonged running in men. *J Appl Physiol* 1996;81:801
58. Keizer HA, Kuipers H, van Kranenburg G, Geurten P. Influence of liquid and solid meals on glycogen resynthesis, plasma fuel hormone response, and maximal physical working capacity. *Int J Sports Med* 1987;8:99
59. Kuipers H, Costill DL, Porter DA, Fink WJ, Morse WM. Glucose feeding and exercise in trained rats: mechanisms for glycogen sparing. *J Appl Physiol* 1986;61:859
60. Tsintzas K, Williams C. Human muscle glycogen metabolism during exercise: effect of carbohydrate supplementation. *Sports Med* 1998;25:7
61. Romijn JA, Coyle EF, Sidossis LS, et al. Regulation of endogenous fat and carbohydrate metabolism in relation to exercise intensity. *Am J Physiol* 1993;265:E380
62. van Loon LJ, Greenhaff PL, Constantin-Teodosiu D, Saris WH, Wagenmakers AJ. The effects of increasing exercise intensity on muscle fuel utilisation in humans. *J Physiol* 2001;536(pt 1):295
63. Gollnick PD, Piehl K, Saltin B. Selective glycogen depletion pattern in human muscle fibers after exercise at varying pedalling rates. *J Physiol* 1974;241:45
64. Carter J, Jeukendrup AE, Jones DA. The effect of carbohydrate mouth-rinse on 1 h cycle time-trial performance. 2004 (in press)
65. Carter J, Jeukendrup AE, Mann CH, Jones DA. The effect of glucose infusion on glucose kinetics during a 1h time trial. *Med Sci Sports Exerc* 2004;36
66. Maresh CM, Herrera-Soto JA, Armstrong LE, et al. Perceptual responses in the heat after brief intravenous versus oral rehydration. *Med Sci Sports Exerc* 2001;33:1039
67. Riebe D, Maresh CM, Armstrong LE, et al. Effects of oral and intravenous rehydration on ratings of perceived exertion and thirst. *Med Sci Sports Exerc* 1997;29:117
68. Seckl JR, Williams TD, Lightman SL. Oral hypertonic saline causes transient fall of vasopressin in humans. *Am J Physiol* 1986;251(pt 2):R214
69. Pallikarakis N, Jandrain B, Pirnay F, et al. Remarkable metabolic availability of oral glucose during long-duration exercise in humans. *J Appl Physiol* 1986;60:1035
70. Pirnay F, Crielard JM, Pallikarakis N, et al. Fate of exogenous glucose during exercise of different intensities in humans. *J Appl Physiol* 1982;53:1620
71. Pirnay F, Scheen AJ, Gautier JF, Lacroix M, Lefebvre PJ. Exogenous glucose oxidation during exercise in relation to the power output. *Int J Sports Med* 1995;16:456
72. Kuipers H, Saris WHM, Brouns F, Keizer HA, ten Bosch C. Glycogen synthesis during exercise and rest with carbohydrate feeding in males and females. *Int J Sports Med* 1989;10(suppl 1):S63
73. Jeukendrup AE, Jentjens R. Oxidation of carbohydrate feedings during prolonged exercise: current thoughts, guidelines and directions for future research. *Sports Med* 2000;29:407
74. Leijssen DP, Saris WH, Jeukendrup AE, Wagenmakers AJ. Oxidation of exogenous [¹³C]galactose and [¹³C]glucose during exercise. *J Appl Physiol* 1995;79:720
75. Massicotte D, Péronnet F, Adopo E, Brisson GR, Hillaire-Marcel C. Effect of metabolic rate on the oxidation of ingested glucose and fructose during exercise. *Int J Sports Med* 1994;15:177
76. Saris WHM, Goodpaster BH, Jeukendrup AE, Brouns F, Halliday D, Wagenmakers AJM. Exogenous carbohydrate oxidation from different carbohydrate sources during exercise. *J Appl Physiol* 1993;75:2168
77. Rehrer NJ, van Kemenade M, Meester W, Brouns F, Saris WH. Gastrointestinal complaints in relation to dietary intake in triathletes. *Int J Sport Nutr* 1992;2:48
78. Rehrer NJ, Wagenmakers AJM, Beckers EJ, et al. Gastric emptying, absorption and carbohydrate oxidation during prolonged exercise. *J Appl Physiol* 1992;72:468
79. Leiper JB, Broad NP, Maughan RJ. Effect of intermittent high-intensity exercise on gastric emptying in man. *Med Sci Sports Exerc* 2001;33:1270
80. Duchman SM, Ryan AJ, Schedl HP, Summers RW, Bleiler TL, Gisolfi CV. Upper limit for intestinal absorption of a dilute glucose solution in men at rest. *Med Sci Sports Exerc* 1997;29:482
81. Shi X, Summers RW, Schedl HP, Flanagan SW, Chang R, Gisolfi CV. Effects of carbohydrate type and concentration and solution osmolality on water absorption. *Med Sci Sports Exerc* 1995;27:1607
82. Adopo E, Peronnet F, Massicotte D, Brisson GR, Hillaire-Marcel C. Respective oxidation of exogenous glucose and fructose given in the same drink during exercise. *J Appl Physiol* 1994;76:1014
83. Jentjens RL, Moseley L, Waring RH, Harding LK, Jeukendrup AE. Oxidation of combined ingestion of glucose and fructose during exercise. *J Appl Physiol* 2003
84. Jentjens RLPG, Achten J, Jeukendrup AE. High oxidation rates from a mixture of glucose, sucrose and fructose ingested during prolonged exercise. *Med Sci Sport Exerc* 2004;36
85. Hawley JA, Bosch AN, Weltan SM, Dennis SC, Noakes TD. Effects of glucose ingestion or glucose infusion on fuel substrate kinetics during prolonged exercise. *Eur J Appl Physiol* 1994;64:381
86. Brouns F, Beckers E. Is the gut an athletic organ? Digestion, absorption and exercise. *Sports Med* 1993;15:242
87. Jeukendrup AE, Saris WHM, Brouns F, Kester ADM. A new validated endurance performance test. *Med Sci Sport Exerc* 1996;28:266
88. Jentjens RL, Wagenmakers AJ, Jeukendrup AE. Heat stress increases muscle glycogen use but reduces the oxidation of ingested carbohydrates during exercise. *J Appl Physiol* 2002;92:1562
89. Coggan AR, Coyle EF. Reversal of fatigue during prolonged exercise by carbohydrate infusion or ingestion. *J Appl Physiol* 1987;63:2388
90. Murray R, Eddy DE, Murray TW, Seifert JG, Paul GL, Halaby GA. The effect of fluid and carbohydrate feedings during intermittent cycling exercise. *Med Sci Sports Exerc* 1987;19:597
91. Maughan RJ, Fenn CE, Leiper JB. Effects of fluid, electrolyte and substrate ingestion on endurance capacity. *Eur J Appl Physiol* 1989;58:481
92. Wright DA, Sherman WM, Dernbach AR. Carbohydrate feedings before, during, or in combination improve cycling endurance performance. *J Appl Physiol* 1991;71:1082

93. Zachwieja JJ, Costill DL, Beard GC, Robergs RA, Pascoe DD, Anderson DE. The effects of a carbonated carbohydrate drink on gastric emptying, gastrointestinal distress, and exercise performance. *Int J Sport Nutr* 1992;2:229
94. Wilber RL, Moffatt RJ. Influence of carbohydrate ingestion on blood glucose and performance in runners. *Int J Sport Nutr* 1992;2:317
95. Tsintzas K, Liu R, Williams C, et al. The effect of carbohydrate ingestion on performance during a 30-km race. *Int J Sport Nutr* 1993;3:127
96. Langenfeld ME, Seifert JG, Rudge SR, Bucher RJ. Effect of carbohydrate ingestion on performance of non-fasted cyclists during a simulated 80-mile time trial. *J Sports Med Phys Fitness* 1994;34:263
97. Angus DJ, Hargreaves M, Dancey J, Febbraio MA. Effect of carbohydrate or carbohydrate plus medium-chain triglyceride ingestion on cycling time trial performance. *J Appl Physiol* 2000;88:113
98. Bosch AN, Weltan SM, Dennis SC, Noakes TD. Fuel substrate kinetics of carbohydrate loading differs from that of carbohydrate ingestion during prolonged exercise. *Metabolism* 1996;45:415
99. Decombaz J, Sartori D, Arnaud M, Thelin A, Schurz P, Howald H. Oxidation and metabolic effects of fructose or glucose ingested before exercise. *Int J Sports Med* 1985;6:282
100. Galloway SD, Wootton SA, Murphy JL, Maughan RJ. Exogenous carbohydrate oxidation from drinks ingested during prolonged exercise in a cold environment in humans. *J Appl Physiol* 2001;91:654
101. Hawley JA, Bosch AN, Weltan SM, Dennis SC, Noakes TD. Glucose kinetics during prolonged exercise in euglycemic and hyperglycemic subjects. *Pflugers Arch* 1994;426:378
102. Jentjens RL, Cale C, Gutch C, Jeukendrup AE. Effects of pre-exercise ingestion of differing amounts of carbohydrate on subsequent metabolism and cycling performance. *Eur J Appl Physiol* 2003;88:444
103. Jeukendrup AE, Saris WHM, Van Diesen R, Brouns F, Wagenmakers AJM. Effect of endogenous carbohydrate availability on oral medium-chain triglyceride oxidation during prolonged exercise. *J Appl Physiol* 1996;80:949
104. Massicotte D, Peronnet F, Brisson G, Bakkouch K, Hillaire-Marcel C. Oxidation of a glucose polymer during exercise: comparison with glucose and fructose. *J Appl Physiol* 1989;66:179
105. Massicotte D, Péronnet F, Brisson G, Bakkouch K, Hillaire-Marcel C. Oxidation of a glucose polymer during exercise: comparison with glucose and fructose. *J Appl Physiol* 1989;66:179
106. Massicotte D, Péronnet F, Brisson G, Boivin L, Hillaire-Marcel C. Oxidation of exogenous carbohydrate during prolonged exercise in fed and fasted conditions. *Int J Sports Med* 1990;11:253
107. Moodley D, Noakes TD, Bosch AN, Hawley JH, Schall R, Dennis SC. Oxidation of exogenous carbohydrate during prolonged exercise: the effects of the carbohydrate type and its concentration. *Eur J Appl Physiol* 1992;64:328
108. Peronnet F, Burelle Y, Massicotte D, Lavoie C, Hillaire-Marcel C. Respective oxidation of ¹³C-labeled lactate and glucose ingested simultaneously during exercise. *J Appl Physiol* 1997;82:440
109. Peronnet F, Rheaume N, Lavoie C, Hillaire-Marcel C, Massicotte D. Oral [¹³C]glucose oxidation during prolonged exercise after high- and low-carbohydrate diets. *J Appl Physiol* 1998;85:723
110. Riddell MC, Bar-Or O, Schwarcz HP, Heigenhauser GJ. Substrate utilization in boys during exercise with [¹³C]-glucose ingestion. *Eur J Appl Physiol* 2000; 83:441
111. Riddell MC, Bar-Or O, Wilk B, Parolin ML, Heigenhauser GJ. Substrate utilization during exercise with glucose and glucose plus fructose ingestion in boys ages 10–14 yr. *J Appl Physiol* 2001;90:903
112. Timmons BW, Bar-Or O, Riddell MC. Oxidation rate of exogenous carbohydrate during exercise is higher in boys than in men. *J Appl Physiol* 2003;94:278
113. Wagenmakers AJM, Brouns F, Saris WHM, Halliday D. Oxidation rates of orally ingested carbohydrates during prolonged exercise in man. *J Appl Physiol* 1993;75:2774