Human Muscle Glycogen Metabolism During Exercise
Effect of Carbohydrate Supplementation

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Summary

Carbohydrate (CHO) ingestion during exercise, in the form of CHO-electrolyte beverages, leads to performance benefits during prolonged submaximal and variable intensity exercise. However, the mechanism underlying this ergogenic effect is less clear. Euglycaemia and oxidation of blood glucose at high rates late in exercise and a decreased rate of muscle glycogen utilisation (i.e. glycogen ‘sparring’) have been proposed as possible mechanisms underlying the ergogenic effect of CHO ingestion. The prevalence of one or the other mechanism depends on factors such as the type and intensity of exercise, amount, type and timing of CHO ingestion, and pre-exercise nutritional and training status of study participants. The type and intensity of exercise and the effect of these on blood glucose, plasma insulin and catecholamine levels, may play a major role in determining the rate of muscle glycogen utilisation when CHO is ingested during exercise. The ingestion of CHO (except fructose) at a rate of >45 g/h, accompanied by a significant increase in plasma insulin levels, could lead to decreased muscle glycogen utilisation (particularly in type I fibres) during exercise. Endurance training and alterations in pre-exercise muscle glycogen levels do not seem to affect exogenous glucose oxidation during submaximal exercise. Thus, at least during low intensity or intermittent exercise, CHO ingestion could result in reduced muscle glycogen utilisation in well trained individuals with high resting muscle glycogen levels. Further research needs to concentrate on factors that regulate glucose uptake and energy metabolism in different types of muscle fibres during exercise with and without CHO ingestion.
Fatigue during prolonged intense exercise in a thermoneutral environment appears to be associated with either glycogen depletion in working muscles\(^1\) or hypoglycaemia.\(^2\) Although body carbohydrate (CHO) stores are limited, diet can increase these stores and training temper their utilisation. It is not surprising, therefore, that CHO ingestion during exercise in the form of CHO-electrolyte beverages has become a very popular practice among both recreational and endurance athletes. The rationale underpinning the ingestion of any CHO solution during exercise is that, in preventing hypoglycaemia and providing a fuel source which is immediately usable by the working muscles, the onset of fatigue might be delayed. An additional aim of ingesting CHO and electrolytes in a liquid form is to help offset body fluid losses from sweating during exercise in an attempt to attenuate the cardiovascular stress and hyperthermia associated with exercise-induced dehydration.\(^3\) In addition to these thermoregulatory and cardiovascular benefits, recent evidence suggests that the ingestion of fluid has profound metabolic effects. Indeed, the ingestion of water during prolonged exercise has been shown to reduce muscle glycogen utilisation compared with no fluid intake.\(^4\)

The performance benefits of drinking CHO-electrolyte solutions during prolonged submaximal cycling and running have been clearly confirmed in several studies. Indeed, CHO ingestion has been shown to prolong the time to exhaustion when exercising at a constant speed or power output\(^5-8\) and improve the performance during a high intensity exercise test performed immediately after a prolonged period of intermittent or continuous exercise.\(^9-11\) It also improves performance times during road races in moderate and high environmental temperatures.\(^12,13\) The effect of CHO ingestion on exercise capacity and performance has been reviewed extensively elsewhere.\(^14\) However, the mechanism(s) underlying the ergogenic effect of ingesting CHO during exercise are less clear and have received little attention. It has been suggested that CHO ingestion delays the onset of fatigue by maintaining euglycaemia (i.e. normal blood glucose level) and oxidation of blood glucose at high rates late in exercise.\(^6,10,14,15\) Other studies, however, have observed a decreased rate of muscle glycogen utilisation (i.e. glycogen ‘sparing’) as a result of CHO ingestion.\(^9,16-20\) Recently, CHO ingestion and its effect on the ratio of plasma free tryptophan levels to branched chain amino acid levels has been linked with factors relating to the central/mental aspect of fatigue during prolonged exercise.\(^21\) This topic, however, is beyond the scope of this review which will focus on the peripheral metabolic effects of CHO ingestion.

One of the explanations for the lack of consistency in the results from different studies on the metabolic responses to CHO ingestion is that they have used a wide range of CHO solutions, exercise methodologies and analytical techniques. Therefore, this review will focus on the main factors which could modify the metabolic responses to CHO ingestion and thus affect the exogenous and endogenous CHO utilisation during exercise. The impact of each of these factors (type and intensity of exercise; amount, type and timing of CHO ingestion; pre-exercise nutritional and training status of the participants) will be discussed separately. The importance of the various analytical techniques used in different studies will also be considered.

### 1. Factors Affecting Carbohydrate Utilisation

#### 1.1 Type and Intensity of Exercise

Several different combinations of exercise intensity and duration have been used to study the effects of CHO ingestion on human energy metabolism. By far the most frequently used mode of exercise was cycling. Despite the popularity of endurance running, it is only during the past decade that the metabolic responses to CHO ingestion during running have been studied. The capacity for fluid ingestion is lower during running than cycling because of the abdominal discomfort which occurs when the stomach is full. There are also a number
of different physiological, metabolic and ergogenic responses to cycling and running.\textsuperscript{22-24}

1.1.1 Constant Intensity Cycling

In most of the cycling studies that have examined metabolic responses during prolonged exercise, blood glucose levels and the rate of total CHO oxidation gradually decrease. However, they are maintained at higher levels when CHO is ingested during exercise.\textsuperscript{5,6,15,25} These observations led to the proposition that only those individuals who demonstrate a fall in blood glucose would improve their endurance capacity when they ingested CHO.\textsuperscript{5,25}

The ingestion of large amounts of CHO (120 to 300g) during continuous cycling at \(\approx 70\% \text{ VO}_{2\text{max}}\) produced modest increases in blood glucose levels (0.5 to 1.5 mmol/L) and no substantial increases in plasma insulin levels.\textsuperscript{6,10,15} Furthermore, similar muscle glycogen utilisation rates were observed with or without CHO ingestion.\textsuperscript{6,10,15,26}

In the study by Coyle et al.,\textsuperscript{6} 7 well trained individuals cycled at 71\% \text{ VO}_{2\text{max}} to exhaustion with and without CHO ingestion. The control trial (placebo ingestion) occurred first. On the second occasion, the participants ingested 130g of glucose polymer in a 50\% solution, 20 minutes into exercise, and 27g in a 10\% solution every 20 minutes thereafter. Muscle biopsies for glycogen determination were obtained at rest, after 2 hours of cycling and the point of exhaustion (3 hours) in the placebo trial and at rest, 2 and 3 hours and exhaustion (4 hours) in the CHO trial. The onset of fatigue was delayed by 1 hour in the CHO trial. The total utilisation of muscle glycogen was similar both with and without CHO ingestion after 3 hours of exercise ([440 mmol/kg dry mass (dm)]. What was more surprising, however, was the observation that no further glycogen was used in the CHO trial during the additional hour of exercise. This is despite the fact that a considerable amount of glycogen (=160 mmol/kg dm) remained in the muscles after 3 hours of exercise. It can be calculated that, in the control trial of the above study and for the period between 2 to 3 hours of exercise, endogenous blood glucose oxidation was about 0.7 g/min. This value agrees with the figure of 0.5 g/min which was obtained during a similar type of exercise using a \(^1\text{C}\)-labelled glucose tracer.\textsuperscript{27} However, according to the findings from the latter study, the endogenous glucose oxidation is lower when CHO is ingested during exercise compared with placebo. Thus, in the CHO trial of the study by Coyle et al.,\textsuperscript{6} the endogenous blood glucose oxidation would have been lower than 0.7 g/min. It was further calculated that during the same time interval, total blood glucose oxidation exceeded 2 g/min.\textsuperscript{6} This implies that the exogenous blood glucose oxidation was >1.5 g/min. However, determination of blood glucose oxidation during the latter stages of prolonged exercise using either the euglycaemic clamp technique or \(^1\text{C}\)-labelled glucose feeding does not support such high rates of exogenous blood glucose oxidation.\textsuperscript{28,29}

Bearing in mind the modest increase in blood glucose levels, the absence of an increase in plasma insulin levels and the delayed increase in the CHO oxidation rate in the study by Coyle et al.,\textsuperscript{6} it is possible that the ingested CHO was not available to the working muscles until after the second hour of exercise. The delayed availability of CHO to the muscles and the fact that no additional muscle glycogen use was observed between hours 3 and 4 of exercise suggests that sparing of muscle glycogen might have occurred during that period. Interestingly, 2 out of the 7 individuals in this study had increased muscle glycogen levels at exhaustion when they ingested CHO. Histochemical analysis of the biopsy samples revealed that this was probably the result of less glycogen having been utilised within some of the muscle fibres.\textsuperscript{6}

In a subsequent study, glucose infusion was used to elevate blood glucose levels to 11 mmol/L (5 to 6 mmol/L above control), achieving and maintaining a hyperglycaemic state during 2 hours of cycling at 73\% \text{ VO}_{2\text{max}}.\textsuperscript{30} Despite a stable infusion of glucose at a rate of 1.6 g/min in order to maintain this hyperglycaemic state, plasma insulin levels did not increase during the first hour of exercise, but were elevated during the second (peak value at 80 minutes) compared with the control
However, muscle glycogen utilisation was unaffected by glucose infusion. In addition, histochemical analysis of the muscle samples did not reveal any differences between trials in the glycogen depletion patterns in different fibre types. It appears, therefore, that both mild and modest hyperglycaemia (blood glucose levels up to 11 mmol/L) cannot induce any changes in muscle glycogen utilisation during cycling at 70% $\text{VO}_{2\text{max}}$ if hyperinsulinaemia does not occur, at least during the first hour of exercise.

In an early study by Bergstrom and Hultman,[31] intravenous infusion of glucose at a very high rate (up to 3.5 g/min) during 1 hour of exhaustive 1-leg cycling produced a marked hyperglycaemia (blood glucose levels averaged 21 mmol/L; range 13 to 30 mmol/L) and a 25% reduction in muscle glycogen utilisation in moderately trained individuals. The hyperglycaemia observed in this study was non-physiological and much higher than the one achieved in the study by Coyle et al.,[30] in which sparing of muscle glycogen was not observed. It cannot be excluded, however, that apart from the extent of hyperglycaemia, the different type of exercise employed by the 2 studies (moderate continuous 2-leg cycling vs high intensity 1-leg cycling) might have affected the rate of glycogen utilisation when glucose was infused. Indeed, one would expect higher glucose uptake and oxidation in 1-leg compared with 2-leg cycling, since less muscle mass is involved in the former.[29] Nevertheless, on the basis of the results from 2-leg cycling studies, it has been suggested that CHO ingestion during such exercise delays the onset of fatigue by maintaining euglycaemia (i.e. normal blood glucose level) and oxidation of blood glucose at high rates late in exercise rather than reducing the rate of muscle glycogen utilisation.[14]

The link between an increased oxidation of blood glucose and the delay in the onset of fatigue is not clear. Recently, CHO ingestion [0.27g CHO/kg bodyweight (BW) every 15 minutes] during 135 minutes of cycling at 70% $\text{VO}_{2\text{max}}$ attenuated the decrease in hexosemonophosphates and tricarboxylic acid cycle intermediates, and the accumulation of inosine monophosphate (IMP) in the working muscles compared with placebo ingestion.[32] Both blood glucose and plasma insulin levels were elevated above control levels when CHO was ingested. Thus, it could be argued that CHO ingestion contributes to oxidative adenosine triphosphate (ATP) production and by doing so improves exercise capacity. Indeed, in a subsequent bout of exercise in the same study, the participants were able to exercise for an additional 22 minutes compared with 0.6 minutes in the placebo trial. It should be noted that, despite the similar muscle glycogen utilisation rates observed with and without CHO ingestion, higher muscle glycogen levels were reported at 135 minutes in the CHO trial.[32] It is not clear, therefore, whether the improvement in the exercise capacity was the result of an increased muscle glycogen availability per se or an increased blood glucose availability.

In some cycling studies, however, CHO ingestion during exercise improved endurance capacity and performance in individuals who did not demonstrate a fall in blood glucose levels and CHO oxidation rates in the control trial.[33,34] Moreover, CHO ingestion did not consistently increase total CHO oxidation rates.[16,33] In addition, some studies have observed a decreased rate of muscle glycogen utilisation (i.e. a glycogen-sparing effect) as a result of CHO ingestion compared with water ingestion.[16,25] Glycogen sparing occurred either in the presence[25] or the absence[16] of declining blood glucose levels and an increased CHO oxidation rate. It should be pointed out, however, that the unequal exercise duration in the study by Bjorkman et al.[25] could have masked the real effect of CHO ingestion on muscle glycogen utilisation.

Although the effect of both fluid and CHO ingestion on high intensity cycling performance ($\approx 80\% \text{VO}_{2\text{max}}$) has been found to be additive rather than synergistic,[35] it appears that no study to date has examined the relative influence of fluid and CHO ingestion on muscle metabolism during prolonged exercise. Drinking water during cycling of moderate intensity has recently been shown to reduce muscle glucogen utilisation compared with
This sparing of muscle glycogen when water was ingested is thought to be brought about by a decreased plasma catecholamine response and/or muscle and core temperature. This sparing of muscle glycogen could also account for the improved endurance capacity observed when fluid was ingested compared with no fluid ingestion. When CHO is added to the fluid, a further improvement in exercise capacity is observed. However, no difference in core temperature and plasma catecholamines was found when a fluid solution containing CHO was ingested during exercise compared with plain water. Thus, although the ingestion of fluid per se has profound metabolic and thermoregulatory effects, the addition of CHO has the potential to enhance the metabolic, rather than the thermoregulatory, aspect of this effect during prolonged submaximal exercise.

### 1.1.2 Constant Pace Running

During prolonged running without CHO ingestion, blood glucose levels do not appear to decrease to the same extent as during cycling. In fact, in most running studies, blood glucose levels do not even decline. In most of these studies, CHO ingestion resulted in increased blood glucose levels compared with control conditions. When water or a placebo solution is ingested, CHO oxidation rates are maintained throughout exercise in most, but not all, studies. Moreover, when CHO is ingested, CHO oxidation rates are either similar or higher compared with control.

Carbohydrate ingestion has been shown to improve endurance capacity and performance in most, but not all, studies in the absence of declining blood glucose and CHO oxidation rates. Unfortunately, none of these studies examined the effect of CHO ingestion on muscle glycogen utilisation and so do not provide us with any information about the underlying mechanism(s).

In a recent study from our laboratory, the direct effect of CHO ingestion on muscle glycogen utilisation during running at 70% V\(_{\text{O}2\text{max}}\) was examined while the pre-exercise glycogen levels (350 mmol/kg dm) and the duration of exercise (60 min) were kept the same. As a result of ingesting 50g CHO in a 5.5% solution, a 28% sparing of glycogen in the vastus lateralis muscle was observed. This glycogen sparing was accompanied by an increase in blood glucose levels and, more importantly, by a significant increase in serum insulin levels within the first 20 minutes of exercise (fig. 1). Glycogen determination in type I and type II muscle fibres, using a biochemical method, revealed that the ingestion of the CHO solution resulted in a 42% sparing of glycogen in type I (slow twitch) fibres only; type II (fast twitch) fibres were unaffected during the 60 minutes of exercise. A linear relationship (r = 0.69) was observed between the amount of glycogen spared in type I fibres and the magnitude of the increase of serum insulin within the first 20 minutes of exercise when CHO was ingested. When one participant, who exhibited a decrease rather than an increase in serum insulin level, was excluded, an even higher correlation was obtained (r = 0.93).

In addition, since CHO oxidation rate was also unaffected by CHO ingestion, a decreased glycogen utilisation would reflect a greater oxidation of blood glucose by the type I fibres of the working muscles. The suppressed plasma free fatty acids (FFA) levels observed during the CHO trial would also favour an enhanced glucose uptake. It seems, therefore, that skeletal muscle fibres are capable of increasing blood glucose uptake not only during the latter stages of exercise but also within the initial 60 minutes of exercise, resulting in a reduced muscle glycogen utilisation.

Furthermore, most type I muscle fibres are recruited during exercise at an intensity of \(\approx 70\% \text{ V}O_2\text{max}\), whereas type II fibres are relatively inactive during the early stages of this type of exercise. Furthermore, the ingestion of a CHO solution results in sparing of glycogen in type I, but not type II, fibres. This suggests that, during constant intensity running, a reduced glycogenolysis in the active fibres and not an increased glycogen...
synthesis in inactive fibres could account for the observed glycogen sparing.

The link between this sparing of muscle glycogen early in exercise and an improvement in exercise capacity was examined in a separate study. Eleven recreational runners ran to exhaustion at 70% $V_{\text{O}2\text{max}}$ with and without CHO ingestion. As in the previous study, the same 5.5% CHO solution was ingested and the same drinking pattern was followed resulting in the ingestion of CHO =48g within the first hour of the run. After the first 60 minutes, water was ingested for the remainder of the run to exhaustion. The participants improved their time to exhaustion by 14% compared with the control trial, in which water was ingested for the whole of the run. It was reasonable, therefore, to suggest that the consumption of 50g CHO during the first hour of running at 70% $V_{\text{O}2\text{max}}$ delays the onset of fatigue by sparing glycogen utilisation in the type I fibres of the working muscles. 

This suggestion, however, is based on the assumption that muscle glycogen depletion is associated with fatigue during prolonged running and, thus, any reduction in the rate of its utilisation would delay the onset of fatigue. In order to test the validity of this assumption, a separate study was conducted in our laboratory. Eight male recreational runners ran at 70% $V_{\text{O}2\text{max}}$ to exhaustion on a motorised treadmill on 2 occasions. The participants ingested either placebo or a 5.5% CHO solution. Needle biopsy samples were obtained from the vastus lateralis muscle before and after each trial for glycogen determinations, and also at the time coinciding with placebo exhaustion (TPE) in the CHO trial. As expected, running time to exhaustion was longer in the CHO trial compared with the placebo trial (132 ± 12 vs 104 ± 9 minutes, respectively). The resting muscle glycogen levels were the same before the start of each run. A 24% reduction in glycogen utilisation was observed in the CHO trial after 104 ± 9 minutes. At the respective points of exhaustion, very low values of muscle glycogen levels were observed in both trials (59.8 ± 7.9 vs 49.2 ± 8.1 mmol/kg dm).

Confirming our previous findings, the use of a quantitative biochemical method to measure glycogen levels in single muscle fibres revealed that this reduction in glycogen utilisation was confined to type I fibres (fig. 2). Moreover, a very high correlation ($r = 0.95$) was observed between the amount of glycogen spared ($=70$ mmol/kg dm) and the amount of glycogen used ($=60$ mmol/kg dm).
type I fibres to sustain the exercise intensity for an additional 28 minutes in the CHO trial compared with placebo.

Interestingly, in both the placebo and CHO trials, the type I fibres were glycogen depleted at the point of exhaustion (31.6 ± 10.3 and 28.1 ± 7.1 mmol/kg dm, respectively). Thus, under the circumstances of this experiment and irrespective of the prevailing rates of blood glucose and total CHO oxidation, fatigue coincided with glycogen depletion in type I fibres. This finding supports the proposition that CHO ingestion improves running capacity by delaying the development of glycogen depletion in exercising type I muscle fibres. It is possible that this is the result of an increased contribution of the ingested CHO to oxidative ATP production. Indeed, the better maintained mixed muscle ATP and phosphocreatine (PCr) levels and the lower muscle lactate levels observed when CHO is ingested during exercise\(^{[19,20]}\) could be an indication of an enhanced contribution to aerobic ATP resynthesis.

### 1.1.3 Intermittent Cycling

A number of studies in the literature have examined the effect of CHO ingestion on muscle metabolism during intermittent exercise; that is, moderate to high intensity bouts of exercise interspersed with low intensity bouts or complete rest periods. Indeed, when 43g of solid CHO (in 400ml of water) was ingested by trained individuals prior to, and every hour during, 4 hours of intermittent cycling, a 20% reduction in utilisation of muscle glycogen was observed compared with placebo ingestion.\(^{[9]}\) In the CHO trial, blood glucose was increased 20 minutes after each ingestion by 0.5 to 1 mmol/L above control levels and it returned to those levels before the next ingestion. Unfortunately, plasma insulin levels were not reported. The protocol in this study consisted of 8 repeated 30-minute exercise periods. Each period consisted of 20 minutes cycling at 50% VO\(_{2\text{max}}\) and 10 minutes of four 30-second bouts at 100% VO\(_{2\text{max}}\) with 2-minute rest periods between each bout. It is possible that the long periods of low intensity exercise allowed for either muscle glycogen resynthesis to occur in non-contracting type II fibres\(^{[49]}\) or a reduced glycogen breakdown rate to occur in the contracting type I fibres.\(^{[18,19]}\)

In a subsequent study, using an exercise protocol identical to the one used by Hargreaves et al.,\(^{[9]}\) the ingestion of CHO 21.5g every hour failed to affect muscle glycogen utilisation despite elevated blood glucose levels following each ingestion.\(^{[50]}\) It appeared that the amount of ingested CHO was not sufficient to alter the utilisation of muscle glycogen. The effect of the amount of ingested CHO on muscle glycogen metabolism is discussed in section 1.2.

In another study by Mitchell et al.,\(^{[10]}\) the effect of ingesting a 12% CHO solution at a rate of 74g per hour on muscle glycogen utilisation was studied during 105 minutes of cycling at 70% VO\(_{2\text{max}}\), performed either continuously or intermittently (15-minute bouts at 70% VO\(_{2\text{max}}\) with 3-minute rest periods between each bout). In the control trial, a water placebo solution was ingested during 105 minutes of continuous cycling at the same intensity. The blood glucose levels in both CHO trials were significantly elevated (=0.5 to 1.5 mmol/L) compared with control levels. However, no differences in insulin levels were observed between trials at any sampling time, and the amount of muscle

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**Fig. 2.** Muscle glycogen levels in type I and type II fibres during running to exhaustion with placebo and CHO ingestion. Muscle samples were obtained at rest, placebo exhaustion (104 ± 9 min) and CHO exhaustion (132 ± 12 min). Values are mean ± SEM; n = 6.\(^{[50]}\), Abbreviations and symbols: CHO = carbohydrate; dm = dry mass; *p < 0.05 from placebo; **p < 0.01 from type I fibres; †p < 0.01 from 104 ± 9 min.
glycogen utilised in the 3 trials was similar. It should be noted that the intermittent exercise protocol used by Mitchell et al.\[10\] consisted of repeated exercise bouts of similar intensity (70%) with 3-minute rest periods between bouts. The absence of low intensity exercise bouts, and the very brief rest periods, possibly precluded any measurable resynthesis of muscle glycogen in non-contracting muscle fibres as has been suggested by Kuipers et al.\[49\]

In a more recent study by Yaspelkis et al.,\[18\] using cycling exercise that varied between low (45% \(\text{VO}_{2\text{max}}\)) and moderate (75% \(\text{VO}_{2\text{max}}\)) intensities, the ingestion of CHO 65g immediately before exercise and a further ingestion of CHO 54g per hour for a total of 190 minutes of exercise resulted in a marked elevation of both blood glucose (up to 2.5 mmol/L above control levels) and plasma insulin levels (up to 3.5 times the values observed in the control trial). These changes were accompanied by a 30% reduction in muscle glycogen utilisation.\[18\] It was suggested that both hyperglycaemia and hyperinsulinaemia of sufficient magnitude are required to reduce muscle glycogen utilisation. Furthermore, histochemical determination of glycogen in different fibre types revealed a substantially reduced glycogen utilisation in type I, but not type II, muscle fibres. On the basis of these results, it was concluded that a reduced rate of glycogen breakdown in type I fibres, and not glycogen reynthesis in inactive type II fibres, of trained individuals occurs during variable intensity exercise with CHO ingestion.

### 1.1.4 Intermittent Running

Despite the fact that variable intensity intermittent running is typical of the activity pattern of many competitive and recreational games such as soccer, football, hockey, basketball and rugby, there is a shortage of studies in the literature on the effect of CHO ingestion on muscle glycogen metabolism.

The ingestion of 35g of glucose polymer (7% solution) 10 minutes before the start of a game of soccer and the ingestion of a further 35g at half time have been shown to reduce muscle glycogen utilisation by 39% compared with placebo ingestion.\[51\] No differences in blood glucose levels were observed between the 2 trials. However, the lack of adequate experimental control was a limitation of this field study.

In a recent more controlled study, conducted in our laboratory,\[52\] CHO was ingested at a rate of about 50g per hour during 90 minutes of high intensity intermittent running, consisting of 15m maximal sprints interspersed with 90-second periods of submaximal running and walking. Carbohydrate ingestion resulted in higher serum insulin levels and slightly, but not significantly, elevated blood glucose levels during the first hour of exercise when compared with a control trial. Mixed muscle glycogen utilisation was reduced by 21%.\[52\]

Determination of glycogen in different muscle fibre types using a biochemical method,\[19,20\] revealed that drinking the 6.9% CHO solution during this type of exercise results in lower glycogen utilisation in both type I and type II muscle fibres (unpublished observation). It is possible that this sparing of muscle glycogen, at least in type II fibres, was the result of an increased resynthesis of glycogen that occurred during the low intensity exercise bouts. It cannot be excluded, however, that the sparing in type I fibres was brought about by a reduction in the rate of glycogen breakdown occurring in these exercising muscle fibres during the low and moderate intensity exercise bouts.\[18,19\]

### 1.1.5 Intensity of Exercise

It is possible that the different responses observed in muscle glycogen use between constant intensity cycling and running at moderate intensity are due to the different responses of plasma insulin and blood glucose levels to CHO ingestion. Indeed, when comparing different studies (table I), it appears that at the same relative exercise intensity (≈70% \(\text{VO}_{2\text{max}}\)), CHO ingestion during cycling results in less marked changes in blood glucose and plasma insulin levels than during running. However, factors other than the type of exercise, such as training, could alter the insulin-stimulated glucose uptake.\[53\] Unfortunately, no study has di-
rectly compared the insulin response to CHO ingestion between running and cycling at low to moderate exercise intensities (50 to 70% $V_{O2max}$). A recent study compared the metabolic effects of ingesting 105 to 150g of glucose during running and cycling at a somewhat higher exercise intensity (≈80% $V_{O2max}$) using well trained triathletes. [24] Despite the higher blood glucose levels during running compared with cycling, blood glucose oxidation and plasma insulin levels were similar between the 2 types of exercise. However, it should be noted that the plasma insulin levels in that study were very low (≈6 mIU/L) compared with studies employing an exercise intensity of ≈70% $V_{O2max}$. [19,20] The greater catecholamine stimulation at higher exercise intensities results in greater suppression of insulin secretion compared with low exercise intensities.

Indeed, one of the factors that affect the plasma insulin response to CHO ingestion is the intensity

### Table I. Metabolic responses to carbohydrate (CHO) ingestion during prolonged exercise

<table>
<thead>
<tr>
<th>Reference</th>
<th>Training status of participants</th>
<th>Type/duration of exercise</th>
<th>Intensity of exercise (%$V_{O2max}$)</th>
<th>Type and amount of CHO</th>
<th>Increase in blood glucosea</th>
<th>Increase in plasma insulina</th>
<th>Pre-exercise muscle glycogen (mmol/kg dm)</th>
<th>Muscle glycogen utilisationa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coyle et al. [5]</td>
<td>Well trained (n = 7)</td>
<td>Constant intensity cycling/120 &amp; 180 min</td>
<td>71</td>
<td>GP 100 g/h</td>
<td>No</td>
<td>No</td>
<td>&gt;720</td>
<td>Similar</td>
</tr>
<tr>
<td>Hargreaves &amp; Briggs [15]</td>
<td>Well trained (n = 5)</td>
<td>Constant intensity cycling/120 min</td>
<td>68</td>
<td>GP 60 g/h</td>
<td>Yes</td>
<td>No</td>
<td>710-765</td>
<td>Similar</td>
</tr>
<tr>
<td>Mitchell et al. [10]</td>
<td>Well trained (n = 10)</td>
<td>Constant intensity cycling/120 min</td>
<td>70</td>
<td>GP+F 74 g/h</td>
<td>No</td>
<td>No</td>
<td>580</td>
<td>Similar</td>
</tr>
<tr>
<td>Erickson et al. [16]</td>
<td>Well trained (n = 5)</td>
<td>Constant intensity cycling/90 min</td>
<td>65-70</td>
<td>G 45 g/h</td>
<td>Yes</td>
<td>No</td>
<td>600-650</td>
<td>Decreased</td>
</tr>
<tr>
<td>Yaspelkis et al. [17]</td>
<td>Well trained (n = 12)</td>
<td>Constant intensity cycling/120 min</td>
<td>49</td>
<td>MD+F 75 g/h</td>
<td>Yes</td>
<td>Yes</td>
<td>&gt;550</td>
<td>Decreased</td>
</tr>
<tr>
<td>Flynn et al. [26]</td>
<td>Well trained (n = 8)</td>
<td>Performance cycling test/90 min</td>
<td>Power output 178-186 W</td>
<td>MD+G, MD+F 22.5 &amp; 45 g/h</td>
<td>Yes</td>
<td>No</td>
<td>=750</td>
<td>Similar</td>
</tr>
<tr>
<td>Yaspelkis et al. [18]</td>
<td>Well trained (n = 7)</td>
<td>Intermittent cycling/190 min</td>
<td>45 &amp; 75</td>
<td>GP+75 g/h</td>
<td>Yes</td>
<td>Yes</td>
<td>=540</td>
<td>Decreased</td>
</tr>
<tr>
<td>Hargreaves et al. [9]</td>
<td>Trained (n = 10)</td>
<td>Intermittent cycling/240 min</td>
<td>50 &amp; 100</td>
<td>S 43 g/h</td>
<td>Yes</td>
<td>No</td>
<td>560-620</td>
<td>Decreased</td>
</tr>
<tr>
<td>Fielding et al. [50]</td>
<td>Active (n = 9)</td>
<td>Intermittent cycling/240 min</td>
<td>50 &amp; 100</td>
<td>S 21.5 g/h</td>
<td>Yes</td>
<td>No</td>
<td>450-520</td>
<td>Similar</td>
</tr>
<tr>
<td>Tsintzas et al. [19]</td>
<td>Recreational runners (n = 7)</td>
<td>Constant intensity running/60 min</td>
<td>72</td>
<td>GP+F+G 50 g/h</td>
<td>Yes</td>
<td>Yes</td>
<td>340</td>
<td>Decreased</td>
</tr>
<tr>
<td>Tsintzas et al. [20]</td>
<td>Recreational runners (n = 8)</td>
<td>Constant intensity running/100 min</td>
<td>76</td>
<td>GP+F+G 45 g/h</td>
<td>Yes</td>
<td>Yes</td>
<td>390</td>
<td>Decreased</td>
</tr>
<tr>
<td>Nicholas et al. [52]</td>
<td>Recreational games players (n = 6)</td>
<td>Intermittent running/90 min</td>
<td>55-95 + all out sprints</td>
<td>GP+G+F 47 g/h</td>
<td>No</td>
<td>Yes</td>
<td>360-400</td>
<td>Decreased</td>
</tr>
</tbody>
</table>

a Compared with placebo/water ingestion.

Abbreviations: dm = dry mass; F = fructose; G = glucose; GP = glucose polymer; n = sample size; MD = maltodextrin; S = sucrose.
of exercise. Carbohydrate ingestion during moderate to high intensity cycling (>60% VO2max) results in a modest increase in blood glucose levels and an absence in any significant increase in plasma insulin levels.16,10,15 On the other hand, CHO ingestion during low intensity cycling (30 to 50% VO2max) greatly increases both blood glucose and plasma insulin levels.54,17 The latter study examined the effect of CHO supplementation during 2 hours of cycling at 48% VO2max. The considerable increase of blood glucose and plasma insulin levels was accompanied by a 40% decrease in muscle glycogen utilisation.17 In contrast to other studies, however, the latter study was conducted in a hot (33°C) environment. Although an increase in muscle glycogen utilisation has been shown to occur during exercise in the heat in unacclimatised individuals,55 no difference in muscle glycogen and CHO metabolism has been observed when well trained, heat acclimatised individuals exercised in a high, compared with a moderate, environmental temperature.56 It appears, therefore, that CHO ingestion during exercise is quite effective in sparing muscle glycogen compared with water ingestion in both high and moderate temperature environments.17,19

Thus, although more studies are needed to directly compare the effects of CHO supplementation on both low and moderate intensity exercise using cycling and running, it appears that the intensity of exercise and its effect on blood glucose, plasma insulin and catecholamine responses may play a major role in determining the response of muscle glycogen utilisation when CHO is ingested during exercise.

### 1.2 Type, Amount and Timing of Carbohydrate Ingestion

It appears that, with the exception of fructose, all the other types of CHO (glucose, sucrose, polymers), on their own or in mixtures that could include fructose, have the potential to reduce muscle glycogen utilisation and improve exercise performance (tables II and II). When fructose is ingested on its own at a rate of 55g an hour, muscle glycogen utilisation is unaffected compared with water.25 This is not surprising since it is well established that fructose ingestion results in lower blood glucose and plasma insulin levels compared with other types of CHO and also does not improve exercise capacity.25,41,57

The amount and timing of CHO ingestion may also play an important role in determining the effect of CHO ingestion on muscle glycogen utilisation. The ingestion of a large bolus (5 to 8 ml/kg BW) of a CHO solution immediately before exercise and a subsequent ingestion of smaller volumes (2 ml/kg BW) every 15 to 20 minutes thereafter has been shown to stimulate a fast rate of gastric emptying.58 As a result of such a drinking pattern, both blood glucose and plasma insulin levels increase during the first hour of exercise and muscle glycogen utilisation is reduced.19,20 In contrast, when CHO is ingested 10 to 30 minutes after the initiation of exercise6,10 and the initial amount is too small,26,50 a glycogen-sparing effect is not observed.

As shown in table I, CHO ingestion at a rate above 45g per hour is required if any measurable changes in muscle glycogen utilisation are to be observed during constant intensity and intermittent exercise. Ingesting CHO at this rate, however, does not coincide with the minimum rate required to produce an ergogenic effect (table II). Indeed, some studies have demonstrated an enhanced exer-

<table>
<thead>
<tr>
<th>Reference</th>
<th>Rate of CHO ingestion (g/h)</th>
<th>Improvement (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Murray et al.</td>
<td>26/78</td>
<td>6/7</td>
</tr>
<tr>
<td>Mitchell et al.</td>
<td>37/74/111</td>
<td>No/13/No</td>
</tr>
<tr>
<td>Tsintzas et al.</td>
<td>50 (1st h only)</td>
<td>14</td>
</tr>
<tr>
<td>Coyle et al.</td>
<td>46</td>
<td>17</td>
</tr>
<tr>
<td>Bjorkman et al.</td>
<td>46</td>
<td>18</td>
</tr>
<tr>
<td>Tsintzas et al.</td>
<td>50 (1st h) and 25 (2nd h)</td>
<td>27</td>
</tr>
<tr>
<td>Wilber &amp; Moffat</td>
<td>48</td>
<td>29</td>
</tr>
<tr>
<td>MacArthur</td>
<td>35</td>
<td>31</td>
</tr>
<tr>
<td>Maughan et al.</td>
<td>24</td>
<td>19</td>
</tr>
<tr>
<td>Wright et al.</td>
<td>40</td>
<td>32</td>
</tr>
<tr>
<td>Coyle et al.</td>
<td>100</td>
<td>33</td>
</tr>
</tbody>
</table>
exercise capacity and performance when CHO was ingested at rates as low as 20 g per hour.\textsuperscript{[13,33,38]} On the other hand, some studies have failed to report any improvement in exercise capacity when CHO was ingested at rates as high as 60 to 80 g per hour.\textsuperscript{[41,44,59,60]} Furthermore, a dose-response relationship between CHO intake and improvement in exercise capacity does not seem to exist.\textsuperscript{[10,34]} It is obvious, therefore, that the relationship between the amount of CHO intake, the percentage improvement in exercise capacity and the extent of muscle glycogen utilisation requires further investigation.

1.3 Pre-Exercise Nutritional Status

In most of the studies that have examined the effect of CHO supplementation on muscle carbohydrate metabolism, the participants were fasted for at least 12 to 16 hours prior to the experimental trials.\textsuperscript{[6,15,19]} On the other hand, in a recent study from our laboratory,\textsuperscript{[61]} the effect of CHO ingestion on muscle glycogen utilisation was studied 3 hours after a high CHO meal that provided 2.5 g of CHO per kg bodyweight (an average of 183 ± 7 g). This pre-exercise meal increased the muscle glycogen stores by 11% 3 hours after the meal. Muscle glycogen utilisation during a subsequent 60-minute run at 70% VO\textsubscript{2max} was unaffected by CHO ingestion (a total of 50 g) compared with placebo ingestion.\textsuperscript{[61]} On both occasions, the plasma insulin levels were much higher at the start of the run compared with exercise following an overnight fast.\textsuperscript{[19]}

It is possible, however, that the pre-exercise high CHO meal \textit{per se} spares the muscle glycogen during subsequent exercise. Thus, ingesting additional CHO during exercise does not further affect glycogen utilisation under these circumstances.\textsuperscript{[61]} Some evidence for this, is provided by comparing the muscle glycogen utilisation during exercise following either a high CHO meal\textsuperscript{[61]} or an overnight fast.\textsuperscript{[19]} The experimental design, the training status of the participants and the analytical techniques used were similar in these studies. As table III shows, the glycogen use observed during exercise following a pre-exercise CHO meal\textsuperscript{[61]} was almost half of that observed during exercise performed after an overnight fast.\textsuperscript{[19]} Unfortunately, the direct effect of a high CHO meal on muscle glycogen utilisation during subsequent running has not been examined.

The ingestion of a pre-exercise meal has been shown to increase both the resting muscle glycogen levels and utilisation during cycling at 70% VO\textsubscript{2max}.\textsuperscript{[62]} However, the magnitude of the increase in resting muscle glycogen levels in this study (≈200 mmol/kg dm) cannot be explained by the amount of the ingested CHO alone (≈140 g or 780 mmol). It is possible, therefore, that the increased muscle glycogen utilisation in the fed trial of the above study was the result of the higher pre-exercise muscle glycogen levels and not due to the meal-induced metabolic responses. Thus, our hypothesis that a high CHO pre-exercise meal reduces muscle glycogen utilisation during subsequent running remains to be tested.

On the basis of this hypothesis, one might claim that ingesting additional CHO during exercise after a high CHO meal would have no further effect on exercise capacity compared with the consumption of a pre-exercise meal alone. However, 3 hours after a high CHO pre-exercise meal, the ingestion of CHO during exercise does improve endurance capacity as compared with placebo ingestion.\textsuperscript{[7,63]} Unfortunately, muscle samples for glycogen determination were not obtained at the end of the exercise tests in these studies and hence the mechanism

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Tsintzas et al.\textsuperscript{[19]}</th>
<th>Chryssanthopoulos et al.\textsuperscript{[61]}</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fast + placebo</td>
<td>Fast + CHO</td>
</tr>
<tr>
<td>Rest</td>
<td>342 ± 21</td>
<td>344 ± 27</td>
</tr>
<tr>
<td>60 min</td>
<td>191 ± 29*</td>
<td>235 ± 33</td>
</tr>
<tr>
<td>Glycogen utilisation</td>
<td>151 ± 20*</td>
<td>109 ± 16</td>
</tr>
</tbody>
</table>

\textsuperscript{a} p < 0.01 from fast + CHO.

Abbreviations: CHO = carbohydrate; dm = dry mass.
behind this improvement is not very clear. Thus, further research needs to concentrate on factors that regulate energy metabolism during exercise after the consumption of a high CHO meal.

In the study by Mitchell et al. [10], the participants also exercised 3 hours following the ingestion of a liquid dietary supplement which provided 48 g of CHO. Carbohydrate ingestion during the subsequent exercise bout did not alter the muscle glycogen utilisation compared with water ingestion. Neither pre-exercise nor exercise values for plasma insulin levels were reported by the authors. However, the amount of CHO that was ingested 3 hours before the exercise bout was much lower in this study when compared with the intake reported by Chryssanthopoulos et al. [61] (48 and 183 g, respectively). Nevertheless, it is possible that the participants started exercising on higher than normal plasma insulin levels; even if they were back to normal, the effects of insulin might have persisted. This might have affected the muscle glycogen utilisation when CHO was ingested during the exercise bout.

1.4 Pre-Exercise Muscle Glycogen Levels

In most of the cycling studies that have examined the effect of CHO ingestion on muscle metabolism, the participants had very high pre-exercise muscle glycogen levels [6,10,26] much higher than those reported in constant pace running studies, in which muscle glycogen sparing was observed. [19,20] In rats, there is a direct relationship between resting muscle glycogen levels and the rate of muscle glycogen breakdown during subsequent exercise. [64] This observation was confirmed in a more recent study in humans by Hargreaves et al. [65] in which increased pre-exercise muscle glycogen levels resulted in an increased muscle glycogenolysis during cycling at 68% VO2max, whereas the converse was true with low initial muscle glycogen levels. However, these alterations in pre-exercise glycogen levels (in the range of 230 to 536 mmol/kg dm) had no significant effect on muscle glucose uptake during exercise. Similarly, in moderately trained men, CHO loading that elevates muscle glycogen levels from 530 to 830 mmol/kg dm does not appear to influence blood glucose oxidation during prolonged cycling at 70% VO2max. [66] Collectively, the results from these 2 studies [65,66] seem to suggest that endogenous blood glucose uptake and oxidation are remarkably constant during exercise performed with initial muscle glycogen levels in the range of 230 to 830 mmol/kg dm. This is in contrast to previous studies in which high pre-exercise glycogen levels have been associated with a reduced glucose uptake by contracting muscles. [64,67]

However, the effect of pre-exercise muscle glycogen levels on exogenous CHO oxidation is less clear. In a recent study, a reduced oxidation of exogenous glucose was observed during cycling at 57% VO2max performed with low initial muscle glycogen availability, estimated to be <150 mmol/kg dm. [68] In another study, exogenous and endogenous CHO oxidation was examined during cycling at 70% VO2max in supercompensated individuals who had initial muscle glycogen levels of about 850 mmol/kg dm. [27] It was shown that, despite these high pre-exercise glycogen levels, the rate of exogenous CHO oxidation closely matched the rate of CHO ingestion (≈0.8 mg/min). In addition, similar to other cycling studies [6,10,15] muscle glycogen utilisation was unaffected by CHO ingestion. To our knowledge, however, the effect of high (>600 mmol/kg dm) compared with normal (300 to 400 mmol/kg dm) resting glycogen levels on glucose oxidation during exercise with and without CHO ingestion has not been directly tested.

Thus, it cannot be excluded that resting muscle glycogen levels in excess of 600 mmol/kg dm (see studies by Flynn et al. [26] and Hargreaves & Briggs [12]), might have resulted in a reduced and/or delayed peak of exogenous glucose oxidation during subsequent exercise, which in turn could explain the absence of muscle glycogen sparing when CHO was ingested.

It should be pointed out, however, that in real life most athletes arrive at the starting line glyco-
Carbohydrate Ingestion and Glycogen Metabolism

1.5 Training Status of Study Participants

In most of the studies that have failed to demonstrate a glycogen sparing effect as a result of CHO ingestion during continuous cycling,[6,10,15,26] the participants were well trained endurance athletes. Endurance training decreases endogenous blood glucose oxidation during prolonged exercise.[69] However, the sensitivity and responsiveness of insulin-stimulated glucose uptake is increased in the trained, compared with the untrained, human muscle.[53] Thus, when well trained endurance athletes ingest CHO at a rate of 100g per hour, an almost 3-fold increase in plasma insulin levels is observed after only 30 minutes of exercise at 70% VO$_{2_{max}}$.[70] This has been confirmed in a more recent study where it was shown that although endurance training reduces the contribution of endogenous CHO utilisation to energy expenditure, it does not diminish the exogenous glucose utilisation during sub-maximal exercise.[71]

Furthermore, little is known about the effect of training on insulin-mediated glucose uptake in different human muscle fibre types during exercise. One could argue that insulin-mediated glucose uptake would be increased in type I fibres following endurance training.[53] This, in turn, would explain the fact that in well trained endurance cyclists,[18] glycogen sparing seems to occur in type I fibres when CHO is ingested during constant intensity exercise.

No studies to date, however, have directly compared muscle glycogen utilisation during exercise with and without CHO ingestion between endurance trained and untrained individuals. The evidence so far appears to suggest that, at least during low intensity or intermittent exercise, CHO ingestion could result in a reduced muscle glycogen utilisation in well trained individuals with high pre-exercise muscle glycogen levels.[9,16-18]

2. Analytical Techniques

Caution must be exercised when drawing conclusions about muscle glycogen utilisation from analysis of glycogen in mixed muscle samples in studies involving CHO ingestion and prolonged exercise. Determination of glycogen at the mixed muscle levels might not always provide a clear or complete picture of the metabolic changes that occur in response to the oral intake of CHO during exercise. In addition, analysis of glycogen at the mixed muscle level might not be sensitive enough to detect changes that are restricted to one population of fibres (i.e. slow or fast twitch).

Some studies, therefore, have used histochemical methods, mainly periodic acid-Schiff (PAS) stain, to examine the glycogen depletion patterns in type I and type II muscle fibres, during exercise with, and without, CHO supplementation. In the study by Coyle et al.,[6] a histochemical analysis of glycogen content in individual fibres revealed a slight, but not significant, reduction in glycogen utilisation in some type II fibres in 2 of the participants when they were fed a CHO solution. Similarly, when CHO was ingested during intermittent cycling a significantly lower glycogen utilisation in type II fibres was also observed compared with placebo ingestion.[10] However, as in the study by Coyle et al.,[6] this observation was not reflected in the results of the mixed muscle glycogen analysis. In a subsequent study, no difference in glycogen depletion within type I and type II fibres was observed when glucose was infused during cycling.[30]

In other studies, however, CHO supplementation during either low intensity cycling at 48% VO$_{2_{max}}$ or intermittent cycling that varied between low (45% VO$_{2_{max}}$) and moderate (75% VO$_{2_{max}}$) intensity, resulted in substantial reduction in muscle glycogen utilisation in type I fibres only.[17,18]
It was proposed by the same authors that this decline in muscle glycogen utilisation in the active type I fibres was brought about by a reduction in the rate of glycogen breakdown rather than an increased resynthesis of glycogen.

These observations were confirmed in our recent studies when CHO was ingested during continuous running at 70 to 75% VO\textsubscript{2max} compared with placebo ingestion\cite{19,20}. Indeed, the use of a biochemical method to measure glycogen levels in single muscle fibres revealed a 42% reduction in glycogen utilisation in type I fibres after 60 minutes of exercise\cite{19} and a 25% reduction following exercise to exhaustion at similar intensity\cite{20} (figures 1 and 2). Assuming that most type I fibres are active during exercise at 70% VO\textsubscript{2max}\cite{48} and resynthesis of glycogen cannot occur in active fibres\cite{49}, it is reasonable to suggest that this sparing of muscle glycogen when CHO was ingested was entirely accounted for by a reduced rate of glycogen breakdown in type I fibres.

In another study conducted in our laboratory\cite{52}, the ingestion of a 6.9% CHO solution during 90 minutes of high intensity intermittent running, consisting of 15m maximal sprints interspersed with 90-second periods of jogging and walking, resulted in lower glycogen utilisation in both type I and type II muscle fibres (unpublished observation). It is possible that this sparing of muscle glycogen, at least in type II fibres, was the result of an increased resynthesis of glycogen that occurred during the low intensity exercise bouts (jogging and walking). It cannot be excluded, however, that a decreased rate of glycogen breakdown occurred in type I fibres during the low and moderate intensity exercise bouts.

It should be noted that in contrast to the qualitative or semi-quantitative histochemical methods used in previous studies\cite{6,10,17,18,30} the analytical method used in our recent studies\cite{19,20} for glycogen determination in different muscle fibre types is a biochemical method that is quantitative, i.e. allows for precise determination of muscle glycogen levels in different fibre types. The validity, reliability and variability of this method have been demonstrated previously\cite{72,73}.

On the basis of the above discussion, it is apparent that possible changes in energy metabolism during exercise as a result of nutritional interventions might be restricted to one population of fibres and not to the muscle as a whole. Therefore, further research needs to concentrate on energy metabolism in different types of muscle fibres to investigate the exact mechanism linking the exogenous CHO supply and possible alterations in muscle CHO metabolism.

### 3. Conclusions

The experimental evidence suggests 2 physiological/metabolic mechanisms that could explain the ergogenic effect of CHO ingestion during exercise: (i) the restoration of euglycaemia and increased oxidation of blood glucose late in exercise at a time when muscle glycogen contribution to energy metabolism is diminished; and (ii) a decreased rate of muscle glycogen utilisation, which would delay its depletion and hence the point of fatigue. The prevalence of one or the other ergogenic mechanism depends on factors such as the type and intensity of exercise, amount, type and timing of CHO ingestion, pre-exercise nutritional and training status of the participants.

During continuous cycling of moderate intensity, CHO ingestion seems to provoke a minimal change in plasma insulin levels, and an enhanced exercise capacity in those conditions is attributed to a normal blood glucose oxidation throughout exercise. In contrast, during constant pace running, CHO ingestion has been shown to affect endogenous CHO utilisation by sparing muscle glycogen early in exercise. Furthermore, it appears that CHO ingestion during running results in a reduced glycogen utilisation in type I fibres of the working muscles. During intermittent exercise which would allow for relatively long low intensity or rest periods, CHO ingestion also seems to affect endogenous CHO utilisation by sparing muscle glycogen.
Although an inverse relationship seems to exist between the intensity of exercise and the magnitude of plasma insulin response, it appears that at the same relative exercise intensity (=70% \( VO_{2\text{max}} \)), CHO ingestion during cycling results in less marked changes in blood glucose and plasma insulin levels compared with running. Thus, it is possible that the intensity and/or type of exercise and their effect on blood glucose and plasma insulin levels may play a major role in determining the response of muscle glycogen utilisation when CHO is ingested during exercise.

The experimental evidence suggests that with the exception of fructose, the ingestion of glucose, sucrose and polymers, on their own or in combination, at a rate above 45g per hour, is required if any measurable changes in muscle glycogen utilisation are to be observed during prolonged exercise. The timing of the first ingestion (i.e. a large bolus ingested immediately before exercise) might also play an important role in determining the effect of CHO ingestion on muscle glycogen utilisation.

Although the effect of normal and high pre-exercise muscle glycogen levels on exogenous CHO oxidation has not been directly tested, it appears that supercompensated individuals might still be capable of oxidising exogenous CHO at a rate high enough to closely match the rate of CHO ingestion. In addition, it seems that a pre-exercise high CHO meal on its own has the potential to spare muscle glycogen during subsequent exercise. However, ingesting CHO during exercise would not further affect glycogen utilisation under these circumstances.

Endurance training does not seem to affect the exogenous glucose oxidation during submaximal exercise. Unfortunately, the effect of CHO supplementation on muscle glycogen utilisation in endurance trained and untrained individuals has not been directly compared. There is some evidence, however, that CHO ingestion by well trained cyclists during low intensity or intermittent exercise spares muscle glycogen.

The use of histochemical, and more recently biochemical, methods to assess glycogen depletion patterns in different fibre types has shown that possible changes in energy metabolism during exercise with CHO ingestion might be restricted to one population of fibres and not to the muscle as a whole. Thus, further research needs to concentrate on factors that regulate glucose uptake and energy metabolism in different types of muscle fibres during exercise with and without CHO ingestion.

References

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