Title: Short-Term Recovery from Prolonged Exercise: Exploring the Potential for Protein Ingestion to Accentuate the Benefits of Carbohydrate Supplements.

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Running Title: Nutrition for Post-Exercise Recovery

Acknowledgments

The authors’ studies which inform this review were funded by GlaxoSmithKline, who approved submission of this manuscript.

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Word Count: 5966
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Key Words: Glycogen Resynthesis; Athletic Training; Amino Acids; Nutrition
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Figure 1: Reported rates of muscle glycogen resynthesis across the 33 published studies which have measured muscle glycogen concentrations during short-term recovery periods (i.e. 2<6 h) with varied rates of ingesting carbohydrate alone. The solid trend-line represents the correlation coefficient (r=0.7, P<0.01; n=27) for the 50% of data points in which muscle glycogen was less depleted (i.e. ≥110 mmol glucosyl units·kg dry mass\(^{-1}\)) at the onset of recovery \(^{[1-19]}\), while the broken trend-line represents the correlation coefficient (r=0.6, P<0.01; n=26) for the 50% of data points in which muscle glycogen was more depleted (i.e. <110 mmol glucosyl units·kg dry mass\(^{-1}\)) at the onset of recovery \(^{[2, 9, 20-32]}\) \(^{a}\).

Figure 2: Reported rates of muscle glycogen resynthesis across 9 studies which have measured muscle glycogen concentrations over 2<6 h post-exercise with varied carbohydrate ingestion rates either with or without protein \(^{b}\). Each individual study is represented by a different symbol, with filled data points denoting ingestion of carbohydrate alone and open data points denoting ingestion of carbohydrate plus protein \(^{[1, 15-16, 19, 25, 29, 31-32, 37]}\) \(^{c}\).

\(^{a}\)The study by Zachweija et al. is represented as data points but does not contribute to either trend-line since no absolute muscle glycogen concentrations were reported in this study \(^{[33]}\).

\(^{b}\)Any published studies which have not matched for either carbohydrate or available energy or did not measure absolute glycogen concentrations have been excluded \(^{[34-36]}\).

\(^{c}\)The apparent difference between treatments in the study by Jentjens et al. (data represented as squares) is a product of large inter-individual variation during the exercise-induced component of glycogen resynthesis and is not statistically significant \(^{[31]}\).
ABSTRACT

This review considers aspects of the optimal nutritional strategy for recovery from prolonged moderate-high intensity exercise. Dietary carbohydrate represents a central component of post-exercise nutrition. Therefore, carbohydrate should be ingested as early as possible in the post-exercise period and at frequent (i.e. 15-30 min) intervals throughout recovery to maximize the rate of muscle glycogen resynthesis. Solid and liquid carbohydrate supplements or whole-foods can achieve this aim with equal effect but should be of high glycemic index and ingested following the feeding schedule described above at a rate of at least 1 g·kg⁻¹·h⁻¹ in order to rapidly and sufficiently increase both blood glucose and insulin concentrations throughout recovery. Adding ≥0.3 g·kg⁻¹·h⁻¹ of hydrolyzed protein and/or mixed amino acids to a carbohydrate supplement results in a synergistic increase in insulin secretion that can, in some circumstances, accelerate muscle glycogen resynthesis. Specifically, if carbohydrate has not been ingested in quantities sufficient to maximize the rate of muscle glycogen resynthesis, the inclusion of protein may at least partially compensate for the limited availability of ingested carbohydrate. Some studies have reported improved physical performance with ingestion of carbohydrate-protein mixtures, both during exercise and during recovery prior to a subsequent exercise test. While not all the evidence support these ergogenic benefits, there is clearly the potential for improved performance under certain conditions, e.g. if the additional protein increases the energy content of a supplement and/or the carbohydrate fraction is ingested at below the recommended rate. The underlying mechanism for such effects may be
partly due to increased muscle glycogen resynthesis during recovery, although there is varied support for other factors such as an increased central drive to exercise, a blunting of exercise-induced muscle damage, altered metabolism during exercise subsequent to recovery or a combination of these mechanisms.
1. Introduction

Many athletes are required to train or compete on more than one occasion within a single day and therefore strive to maximize their recovery in the often relatively short interval between exercise sessions. Exercise at the intensities commonly observed in competitive sport places a high demand on the body’s finite endogenous reserves of carbohydrate such that this substrate may become progressively depleted over time \[^{38-39}\]. If such exercise is continued for a prolonged duration (i.e. ≥60-90 min), then fatigue often occurs once muscle glycogen concentrations reach critically low levels \[^{40}\]. Therefore, a logical extension of these findings is that the capacity to perform physical exercise for extended periods will be determined to a large extent by the availability of glycogen at the onset of exercise \[^{41}\].

In view of the relationships described above, it is reasonable to suggest that the rapid replenishment of depleted carbohydrate reserves will constitute an important component of effective recovery along with rehydration and repair/regeneration of damaged tissue. When recovery time is 24 hours or more, then simply ingesting carbohydrate in quantities sufficient to replace losses can completely restore the capacity for physical exertion \[^{42}\]. Conversely, when the time available for recovery is limited to 8 hours or less, neither muscle glycogen concentrations nor exercise capacity are likely to be entirely restored following exercise-induced glycogen depletion. Under these circumstances there is a greater need to identify optimal nutritional strategies to promote recovery before subsequent exercise. However, there is a related but separate question, though beyond the scope of this review, which is
whether or not adaptations to chronic training may be greater when exercise is repeated while glycogen stores remain relatively low.

This review begins with a brief overview of current evidence-based recommendations for carbohydrate intake during short-term recovery from prolonged exercise. For this, a comprehensive literature search was conducted primarily using PubMed (www.pubmed.gov) to identify studies that have reported muscle glycogen resynthesis and/or the recovery of physical performance in human participants ingesting carbohydrate alone over recovery periods of >2-6 hours in duration (see supplementary online material – Table I). Only full-articles published in scientific peer-reviewed journals met inclusion criteria and data from non-human models are used only to support certain mechanistic discussion where no human data is available. In addition to the summary of the above data, we provide specific consideration of the relative importance of and interactions between various nutritional and exercise factors in relation to carbohydrate intake and post-exercise recovery (e.g. timing/type/form/quantity of carbohydrate and the degree of muscle glycogen depletion induced prior to recovery). Thereafter, the focus is on those studies that have examined whether or not the ingestion of carbohydrate-protein mixtures can offer greater benefit during recovery from exercise than the ingestion of carbohydrate alone (with the same literature search strategy applied). Therefore, the main purpose of this review is to consider the direct effects of ingesting carbohydrate-protein mixtures on physical performance, whether or not related to muscle glycogen resynthesis. In this regard, additional novel elements of discussion include the metabolic
responses (e.g. glucose and insulin) during both recovery and subsequent exercise, along with the precise dose/type of protein that most effectively elicits these responses.

2. Ingestion of Carbohydrate

It has been consistently demonstrated that ingesting carbohydrate during short-term recovery from exercise can increase the rate of glycogen resynthesis [13, 23, 29] and also restore exercise capacity more rapidly [44] than when no carbohydrate is ingested. Over the last 50 years, a large number of well-controlled investigations have sought to better understand the metabolic consequences of carbohydrate ingestion following exercise. These studies have not only lead to a better understanding of carbohydrate metabolism after exercise but also to recommendations about the optimal timing, type/form and quantity of carbohydrate that should be ingested during recovery.

2.1 Timing of Carbohydrate Ingested

If carbohydrate is the only macronutrient ingested during recovery then it is important to begin feeding immediately after exercise, thus taking full advantage of the transient period of exercise-induced insulin sensitivity that leads to the rapid conversion of ingested carbohydrate into glycogen [45-47]. Conversely, delaying in carbohydrate ingestion by just two hours or more following exercise can result in a 50% reduction in the rate of muscle glycogen resynthesis [6].
Of course, it would be prudent to begin feeding as early as possible in recovery simply to maximize the time available to consume exogenous carbohydrates and incorporate them into endogenous glycogen stores. In addition, the consensus view is that carbohydrate supplementation should be continued throughout recovery, with more rapid rates of muscle glycogen resynthesis typically achieved when carbohydrate is provided at relatively frequent intervals (i.e. every 15-30 minutes) \cite{5, 16, 22, 31}. 

2.2 Type/Form of Carbohydrate Ingested

A number of studies have examined the types of carbohydrate that can most effectively stimulate muscle glycogen resynthesis during recovery from exercise. Insulin plays a central role in facilitating endogenous carbohydrate storage and the elevated insulin response to high glycemic index (GI) carbohydrates as opposed to low GI carbohydrates can accelerate muscle glycogen resynthesis over the first 6 hours of recovery \cite{48-49}. However, it remains debatable whether or not these differences persist over a more prolonged (i.e. ≥20 h) recovery period \cite{48-49}. Furthermore, while fructose has a lower GI than glucose and therefore results in a relatively slow rate of muscle glycogen storage \cite{2}, ingesting a mixture of glucose and fructose may provide the optimal balance of dietary carbohydrates for the effective combined resynthesis of both muscle \cite{17} and liver glycogen \cite{2, 23}. This is partly due to the preferential hepatic synthesis of glycogen from fructose \cite{50} but also because intestinal fructose absorption occurs via a different transport system than glucose, thus optimizing overall carbohydrate delivery \cite{51}. 
From a practical perspective, recent evidence also indicates that the ingestion of lower GI carbohydrates during recovery can improve the capacity for continuous exercise either later the same day [52] or on the following day [53]. Such effects may operate via an increased oxidation of lipid during exercise following feeding (thus reducing reliance on finite carbohydrate reserves and delaying glycogen depletion), which may explain why no such ergogenic benefit occurs during high-intensity intermittent exercise where sustained performance relies more heavily on carbohydrate metabolism [54].

Whether carbohydrate is ingested in solid or liquid form does not appear to influence the rate of muscle glycogen storage during recovery [9, 55]. This is consistent with the view that the gastric emptying rate of ingested carbohydrate is unlikely to limit the rate of muscle glycogen resynthesis in most situations [56-57]. However, liquid supplements can provide an exogenous source of carbohydrate while simultaneously contributing to rehydration. Whether or not the osmolality of a carbohydrate solution can influence the rate of carbohydrate delivery and muscle glycogen resynthesis is a question that is currently the focus of research [22, 58]. For example, a recent study reported improved cycling time-trial performance 2 h following exhaustive exercise during which the cyclists ingested high, as opposed to low, molecular weight glucose polymer solutions during recovery [59]. Further research is therefore warranted to extend current understanding and nutritional recommendations in relation to carbohydrate solutions with specifically modified osmolalities.
2.3 Amount of Carbohydrate Ingested

While the above considerations regarding the timing and type of carbohydrate ingested during recovery are undoubtedly of importance, it is perhaps of greater practical value to establish the optimal amount of carbohydrate to ingest following exercise. The finding that carbohydrate supplementation of any substantial magnitude during recovery can stimulate far greater rates of muscle glycogen resynthesis than when ingesting no carbohydrate at all has been well established [7, 13, 23, 29]. What is less clear are the precise effects of increasing carbohydrate intake/dose on subsequent glycogen storage rates. In particular, those factors which may limit the rate of muscle glycogen resynthesis when large quantities of carbohydrate are ingested. There are a number of factors which might explain the difficulty in ascertaining from the literature the smallest quantity of carbohydrate necessary to maximize muscle glycogen resynthesis. Not least are the confounding influences such as the timing [6, 60] and type [2, 22] of carbohydrate ingested (as discussed in Sections 2.1 & 2.2) and, perhaps most importantly, the degree of prior exercise-induced glycogen depletion [33] (see supplementary online material - Table I).

Many studies have attempted to determine the ‘optimal’ rate of carbohydrate ingestion for muscle glycogen resynthesis and, as a result, our understanding of the mechanisms involved in this anabolic process has improved. To our knowledge, there are currently 33 published studies that have reported rates of muscle glycogen resynthesis in response to ingesting varying amounts of carbohydrate during a short-term (i.e. 2<6 h) recovery in
humans. When these studies are considered collectively (Figure 1), a significant positive correlation appears between the two variables (i.e. amount ingested and rate of glycogen synthesis; r=0.6, P<0.01). The protocols adopted across this diverse number of studies have varied greatly with respect to several factors that are known to influence muscle glycogen resynthesis. For example, studies using non-exhaustive running [1, 14] or resistance-type [10, 20] exercise protocols prior to recovery are illustrated alongside the more commonly employed cycling protocols, which have been both exhaustive [2, 15-17, 21-22, 24, 26-31] and non-exhaustive [3-9, 11-13, 18-19, 23, 25, 32-33] in nature. This would account for the broad range of muscle glycogen concentrations reported at the onset of recovery (i.e. ≈16-260 mmol glucosyl units·kg dry mass$^{-1}$) [14, 20]. Given both the effective autoregulation of muscle glycogen concentration [61] and associated metabolic consequences of reduced glycogen content (e.g. increased availability and oxidation of free fatty acids [62]), it is highly likely that the large variation in glycogen resynthesis at any given rate of carbohydrate ingestion is mainly the result of these differences in glycogen concentrations at the beginning of the recovery process.

******************INSERT FIGURE 1 NEAR HERE******************

Interestingly, when the studies shown in Figure 1 are stratified according to the absolute degree of glycogen depletion prior to recovery (see trend-lines), it is apparent that the capacity for glycogen availability to mediate the glycogen storage may be less pronounced at higher rates of carbohydrate
ingestion. Of primary importance, however, is that a general dose-response relationship appears to exist between the rate of carbohydrate ingestion and muscle glycogen resynthesis, as was evident in 2003 when information on this topic was last summarised [63; Figure 2, p. 130]. Since then, it is notable that eleven further studies can now be added to this analysis [1, 4, 11-12, 14, 17, 24-26, 28, 32] and, even so, the highest reported rates of glycogen resynthesis over 2<6 hours of recovery remain in the region of 45-50 mmol glucosyl units·kg dry mass·h·1 following the ingestion of ~1 g·kg·h·1 of carbohydrate [16-17, 24, 26]. Therefore, based on current evidence, it seems that ingesting carbohydrate alone at a rate of ≥1 g·kg·h·1 may be sufficient to maximize the rate of muscle glycogen resynthesis such that additional carbohydrate intake will provide no further increase in this fuel store.

3. Ingestion of Carbohydrate with Protein

The previous sections have broadly outlined the results regarding ingestion of carbohydrate during short-term recovery from exercise. The remainder of this review will now consider the metabolic and/or ergogenic consequences of ingesting a combination of carbohydrate and protein during post-exercise recovery. In addition, studies on the effects of ingesting these supplements during exercise are also discussed in order to explore whether any ergogenic benefits of ingesting added protein in recovery may be solely due to mechanisms that can occur before a repeated bout of exercise. For example, alternative mechanisms other than accelerated muscle glycogen resynthesis during recovery may carry-over and operate during subsequent
exercise. Indeed, there appears to be a range of potentially favorable metabolic consequences of including a small quantity of protein in a post-exercise carbohydrate supplement, which may promote recovery more effectively than ingesting carbohydrate alone.

3.1 Glycemic & Insulinemic Responses to Protein/Amino Acid Ingestion

It was established over four decades ago that pancreatic insulin secretion can be induced either through intravenous infusion or oral ingestion of certain amino acids \([64-65]\). Of greater relevance to the present review are the studies to have shown a synergistic influence on insulin release when amino acids or proteins are ingested with carbohydrate \([65-67]\).

A study by van Loon et al. (2000) examined the specific magnitude of insulinemic responses following ingestion of different amino acid/protein mixtures with carbohydrate. The results suggested that the insulinemic response to a carbohydrate-protein mixture is strongly dependent on the amounts of leucine, phenylalanine and tyrosine in the mixture \([68]\). Interestingly, despite the fact that arginine is known to be highly insulinotropic when delivered intravenously \([64]\), the available evidence suggests that arginine is an ineffective means of elevating serum insulin when given orally \([69-70]\), which can cause gastrointestinal discomfort \([68]\). Finally, the study by van Loon et al. (2000) also indicated that ingestion of protein hydrolysates may increase circulating amino acid concentrations more effectively than ingestion of intact casein \([68]\). Indeed, subsequent research by these authors has now confirmed that co-ingestion of carbohydrate, protein hydrolysate,
leucine and phenylalanine provides an effective means of increasing plasma insulin concentrations during a 3 h post-exercise recovery [71].

Regarding the question of what might be the most effective mixture of amino acids to ingest during recovery, the study by van Loon et al. (2000) also found that a greater insulinemic response can be achieved through increasing the amount of protein in a given carbohydrate-protein mixture from 0.2-0.4 g·kg\(^{-1}\)·h\(^{-1}\) [71]. While an earlier study reported no significant dose-response relationship between protein intake and insulin release when assessing a range of protein intakes alongside carbohydrate, an inverse relationship between elevations in plasma glucose and protein intake was reported [72]. However, it cannot be established from these findings whether the lower blood glucose concentrations at higher rates of protein intake were the result of increased glucose uptake, reduced appearance of glucose due to a delayed rate of gastric emptying or both [73]. Recent evidence indicates that the reduced glycemic responses to the ingestion of a carbohydrate-protein mixture following exercise in healthy individuals are indeed more likely to reflect a reduced rate of glucose appearance from the gastrointestinal tract than an increased rate of glucose disposal [74]. Irrespective of whether or not glucose uptake is affected, it appears that carbohydrate-protein mixtures will be most effective in elevating circulating insulin concentrations when the protein component is ingested at rates in excess of \(~0.3\) g·kg\(^{-1}\)·h\(^{-1}\).

Compiling the results of the studies on the insulinemic responses to ingesting carbohydrate-protein protein mixtures shows that when the protein
intake is of the order of 0.3-0.5 g·kg\(^{-1}\)·h\(^{-1}\) then there is a strong trend towards higher insulin concentrations\(^\text{[1, 15-16, 19, 25, 29, 31-32, 35, 71, 74-77]}\). Conversely, those studies that have not reported any increase in insulinemic responses following ingestion of a carbohydrate-protein mixture rather than carbohydrate alone have typically provided protein in quantities closer to 0.1 g·kg\(^{-1}\)·h\(^{-1}\)\(^\text{[3, 13, 37, 78]}\). Furthermore, in agreement with previous findings\(^\text{[72]}\), thirteen of the eighteen investigations cited above have reported significantly lower blood glucose concentrations following ingestion of a carbohydrate-protein mixture rather than carbohydrate alone\(^\text{[1, 3, 15-16, 19, 29, 35, 74-78]}\). It should also be noted that, of the five remaining studies, two did not report any blood glucose data\(^\text{[25, 32]}\) and two did in fact observe a reduced glycemic response when protein was added but this difference did not attain statistical significance\(^\text{[13, 71]}\). Again, however, it is difficult to determine whether these attenuated elevations in blood glucose concentration are the consequence of decreased glucose appearance or increased glucose uptake, although the studies by Van Hall \textit{et al.} (2000) and Kaastra \textit{et al.} (2006) certainly appear to support the former explanation\(^\text{[29, 74]}\). Notwithstanding this evidence, it cannot be entirely discounted that the synergistic influence of carbohydrate and protein on insulin secretion might increase glucose uptake and thus facilitate glycogen storage during recovery, a possibility that is addressed in the following section.

\textit{3.2 Combined Carbohydrate-Protein Ingestion & Glycogen Resynthesis}

As discussed in the previous section, it appears that the greatest insulinemic response will be achieved when the protein fraction of a
carbohydrate-protein mixture is composed of hydrolyzed protein combined with certain essential amino acids \cite{68} and recent evidence from a study using laboratory rats shows that hydrolyzed whey may more effectively accelerate muscle glycogen resynthesis than either intact protein or branched chain amino acids when ingested with glucose \cite{79}. The addition of individual amino acids such as leucine, glutamine or arginine to a carbohydrate supplement has not been found to substantially increase circulating insulin concentrations, and while adding leucine to carbohydrate has been shown to enhance muscle glycogen storage in rats \cite{80}, ingestion of either glutamine or arginine in isolation has failed to accelerate muscle glycogen accumulation during recovery in humans \cite{15, 18, 81}. However, it cannot be entirely ruled out that glycogenic amino acids such as glutamine might be deaminated and converted into glycogen directly rather than promoting glycogenesis from exogenous glucose \cite{82}. In support of this, the increased availability of free fatty acids associated with muscle glycogen depletion is known to stimulate hepatic glucose production \cite{83} and recent evidence from a study using canines shows that even large increases in systemic insulin concentrations may only result in a modest inhibition of gluconeogenesis \cite{84}.

In contrast, a number of studies support the view that the augmented insulin concentrations following combined carbohydrate-protein ingestion can increase the rate of muscle glycogen resynthesis following exercise \cite{15-16, 19, 25, 34, 36-37}. In two of these studies the carbohydrate-protein mixture was assessed in relation to a carbohydrate solution which was also lower in carbohydrate content \cite{34, 36}. This raises the question about whether or not the
glycogenic effect of the carbohydrate-protein solution was due to the amino acids or to the additional carbohydrate. Of the other studies cited above, the study by Zawadzki et al. (1992) was the first to examine whether ingesting carbohydrate (~0.8 g·kg\(^{-1}\)·h\(^{-1}\)) plus protein (~0.3 g·kg\(^{-1}\)·h\(^{-1}\)) would increase the rate of muscle glycogen storage during recovery than when ingesting the carbohydrate fraction alone. Although the absolute concentrations of muscle glycogen were not different between trials by the end of recovery, the rate of muscle glycogen storage was 38% greater when protein had been included in the recovery solution \(^{[19]}\). However, it cannot be established whether this increased rate of glycogenesis was purely a result of the increased insulin response or a consequence of the 43% increase in energy provision when protein was added to the carbohydrate solution. Indeed, both the carbohydrate content and the energy content of a supplement are known to influence the rate of muscle glycogen storage during recovery from exercise \(^{[10]}\).

Another well-controlled study examined rates of glycogen resynthesis in response to the co-ingestion of carbohydrate (0.8 g·kg\(^{-1}\)·h\(^{-1}\)) and protein (0.4 g·kg\(^{-1}\)·h\(^{-1}\)) during recovery from exhaustive cycling. Importantly, the carbohydrate-protein supplement was evaluated both in comparison with a solution matched for carbohydrate content and another solution matched for available energy content (i.e. 1.2 g·kg\(^{-1}\)·h\(^{-1}\) of carbohydrate). Application of this comprehensive research design established that the rate of muscle glycogen accumulation can be increased with equal effect whether amino
acids or additional carbohydrate are added to an existing solution that provides carbohydrate in relatively moderate quantities (i.e. ≤0.8 g·kg⁻¹·h⁻¹) [16]. Interestingly, more recent evidence suggests that including protein with similarly moderate amounts of carbohydrate can increase post-exercise glycogen resynthesis even if the protein replaces some of the carbohydrate in the solution (i.e. isoenergetic supplements) [25, 37].

In contrast to the above evidence, there are also a comparable number of investigations that have observed the increase in insulinemic response when mixed amino acids have been added to a standard carbohydrate solution but have reported no concomitant increase in the rate of muscle glycogen storage during recovery [1, 15, 29-32, 35, 77]. The studies by Jentjens et al. (2001), Van Hall et al. (2000) and Howarth et al. (2009) all assessed whether the proposed ‘maximal’ rate of muscle glycogen resynthesis in response to ingesting ~1.2 g·kg⁻¹·h⁻¹ of carbohydrate could be exceeded when added protein, rather than additional carbohydrate, is ingested during a 3-4 h recovery [29, 31-32]. Notably, all these studies concluded that the added protein did not further increase the rate of glycogen resynthesis during recovery, despite some reporting a significantly increased insulin release [29, 31]. It therefore appears that the important distinction between these studies and those cited previously, in which muscle glycogen resynthesis was accelerated, is the precise quantity of carbohydrate to which the protein was added.

****************************************************INSERT FIGURE 2 NEAR HERE****************************************************
When presented graphically (Figure 2), it becomes apparent that those studies which have provided ≥1 g·kg⁻¹·h⁻¹ of carbohydrate have not observed any increase in muscle glycogen resynthesis when amino acids were added [29, 31-32]. This has prompted some authors to suggest that ingesting ≥1 g·kg⁻¹·h⁻¹ of carbohydrate during recovery may maximally stimulate glucose uptake such that further elevations in systemic insulin concentrations via the ingestion of added protein is unnecessary [3, 16, 31]. Conversely, muscle glycogen resynthesis has more commonly been accelerated when amino acids have been included in solutions providing carbohydrate at a lower ingestion rate (i.e. ≤0.8 g·kg⁻¹·h⁻¹) [15-16, 19, 25, 37].

The only studies that are inconsistent with this line of reasoning are those by Rotman et al. (2000) and Betts et al. (2008), which found similar rates of glycogen storage with a sub-optimal dose of carbohydrate (i.e. ~0.8 g·kg⁻¹·h⁻¹) compared to energy matched and carbohydrate matched carbohydrate-protein mixtures, respectively [1, 35]. The precise reasons for these apparently discrepant findings are not clear but may be related either to the methods used to quantify muscle glycogen content or the specific type of exercise that was performed prior to recovery (i.e. cycling versus running). For example, Rotman et al. (2000) employed ¹³C-MRS to quantify glycogen in their study [35] and, while this technique does correlate well with data acquired using the needle biopsy technique [85], it is impossible to determine whether or not the rates of muscle glycogen resynthesis were indeed sub-maximal given that no absolute glycogen concentrations are available (therefore precluding
the inclusion of this data in Figure 2). Equally, the study we conducted involved recovery from treadmill running \cite{1}, rather than cycling as was used by all other published studies in this area. Therefore, it is possible that compared with cycling, insulin-mediated glucose transport and glycogen resynthesis may be relatively impaired after treadmill running due to the increased eccentric muscle action and resultant myofibrillar damage associated with this type of exercise \cite{5, 86-89}. A logical extension of this reasoning is that exercise with a substantial eccentric (damaging) component might result in a lower ‘maximal’ rate of muscle glycogen storage that could be attained even when only \(\leq 0.8 \text{ g-kg}^{-1}\cdot\text{h}^{-1}\) of carbohydrate is ingested during recovery.

As discussed in Section 3.1, it is likely that ingestion of \(\geq 0.3 \text{ g-kg}^{-1}\cdot\text{h}^{-1}\) of protein is necessary to achieve a marked synergistic effect of combined carbohydrate-protein ingestion on insulin secretion \cite{71}. This finding may explain why some investigators have failed to increase glycogen storage when adding less than this critical amount of protein to carbohydrate recovery solutions, since insulin stimulated glucose transport would not be expected to differ between treatments \cite{3, 13}. However, the study by Ivy et al. (2002) demonstrated that ingestion of just \(~0.2 \text{ g-kg}^{-1}\cdot\text{h}^{-1}\) of protein can accelerate muscle glycogen resynthesis beyond that achieved when ingesting the carbohydrate fraction alone (~0.5 g-kg\(^{-1}\cdot\text{h}^{-1}\)) or even an isoenergetic supplement providing \(~0.7 \text{ g-kg}^{-1}\cdot\text{h}^{-1}\) of carbohydrate. Of further interest is that this effect was not associated with any significant increase in circulating
insulin concentrations, thus presenting the possibility that enhanced insulin-mediated glucose uptake may not be the only mechanism through which carbohydrate-protein ingestion can increase carbohydrate storage[37].

In summary, it appears that the rate of muscle glycogen resynthesis during short-term recovery can be maximized either through ingesting ≥1 g·kg⁻¹·h⁻¹ of carbohydrate or through the ingestion of a smaller quantity of carbohydrate in combination with hydrolyzed protein and/or mixed amino acids. The primary mechanism through which added amino acids increase muscle glycogen resynthesis is likely to be related to the synergistic influence of carbohydrate and protein on insulin secretion, especially when ≥0.3 g·kg⁻¹·h⁻¹ of amino acids are ingested. Irrespective of the mechanism, the potential for amino acids to accelerate glycogen resynthesis when ingested alongside carbohydrate introduces the attractive possibility that subsequent physical performance might also be enhanced. The following section will therefore review those studies which have examined the efficacy of carbohydrate-protein ingestion in terms of rapidly restoring the capacity for physical exercise within 8 h of prior exertion.

3.3 Combined Carbohydrate-Protein Ingestion & Physical Performance

As discussed above, the addition of amino acids to a carbohydrate recovery solution has the potential to increase the rate of muscle glycogen resynthesis following an initial bout of prolonged exercise. This has prompted further research into whether or not subsequent exercise capacity might also
be improved given the established association between pre-exercise muscle
glycogen availability and exercise time to fatigue\textsuperscript{[41]} (although whether or not
this association applies to short-term recovery of exercise capacity is
discussed later). Furthermore, the potential interaction of ingested amino
acids with the liver might also be relevant in terms of recovery since it has
been suggested that resynthesis of hepatic glycogen might be another crucial
factor that influences subsequent endurance capacity\textsuperscript{[23, 90]}. Some support for
this suggestion is obtained from an examination of the correlation between
recovery of exercise capacity and the resynthesis of endogenous
carbohydrate reserves as a whole (i.e. muscle and liver glycogen; \( r=0.5,\)
\( P<0.05 \)) in relation to the resynthesis of liver glycogen \textit{per se} \( (r=0.6, P<0.05)\)
\textsuperscript{[23]}.

An early example of evidence supporting the efficacy of ingesting
added protein for enhanced performance is the study by Saunders \textit{et al}. (2004). This study involved the ingestion of carbohydrate either with or
without added whey protein both during and after a prolonged bout of cycling
to exhaustion at 75\% \( \dot{V}O_2 \)\textsubscript{max}, followed 12-15 h later by another cycling
capacity test at 85\% \( \dot{V}O_2 \)\textsubscript{max}. Including protein in the solution was reported
to increase exercise time to exhaustion by 29\% during the first exercise test
and by 40\% during the second exercise test. However, while the two
solutions provided in this study were matched for carbohydrate content, the
inclusion of protein unavoidably resulted in a 20\% increase in total energy
 provision\textsuperscript{[91]}. Therefore, similar to much earlier research regarding muscle
glycogen resynthesis, it remained to be established whether the ergogenic benefit of the carbohydrate-protein solution was due to the increase in available energy or, as suggested by the authors of the study, some mechanism directly mediated by the inclusion of protein *per se* (e.g. stimulation of protein synthesis and/or repair of damaged tissue).

Indeed, the potential for carbohydrate-protein mixtures to provide a protective effect against exercise-induced muscle damage has been the focus of numerous recent studies. Many of these studies have shown that adding protein to a carbohydrate solution reduces indirect evidence of muscle damage such as serum concentrations of myoglobin [92-95], activities of both creatine kinase [91-100] and lactate dehydrogenase [97] or 3-methylhistidine excretion [101], yet many equally well-controlled studies do not support these findings [102-107]. Such discrepancies are most likely due, at least in part, to the inherent intra-individual variability that exists for indirect systemic indices of muscle damage, particularly creatine kinase [108]. This variability certainly questions the value of only using creatine kinase as a quantitative proxy measure for the degree of muscle damage sustained, particularly when using a between groups experimental design.

From this perspective, it is notable that only six extant studies have examined muscle contractile function [93, 95, 102-103, 105-106], which is believed to represent the most reliable and practical indication of the magnitude of muscle damage sustained [109]. Of these, only two have provided any evidence of improved restoration of contractile function following ingestion of supplements
containing carbohydrate and protein compared to carbohydrate alone \cite{93, 95}. Several studies have also provided evidence of an ergogenic effect of post-exercise carbohydrate-protein ingestion for prolonged whole-body exercise over repeated days of testing \cite{91, 100, 110}. It therefore remains a slight possibility that protein may facilitate functional recovery from exercise via a reduction in muscle damage over more prolonged recovery periods (i.e. ≥15 h). However, it is arguably less likely that any substantial repair of muscle tissue will occur during a more short-term recovery, at least not sufficiently to account for marked effects on physical performance within just 8 h of recovery. For example, even though the inclusion of protein in a carbohydrate supplement can result in a transition from net negative to net positive protein balance over the first 3-4 hours of recovery \cite{32, 111}, this effect has been associated with little \cite{111} or no \cite{32} increase in whole-body protein synthesis. Furthermore, any net accrual of tissue mass can be estimated at only ~0.01% (i.e. 0.1 g·kg\(^{-1}\)) over 4 hours relative to ingestion of carbohydrate alone \cite{111}. Whilst the accumulation of small changes in muscle quality and/or quantity can produce worthwhile training adaptations if sustained over weeks or months, the acute change during a single short-term recovery would not be expected to have an effect on subsequent performance.

It is possible to gain further insight into the underlying mechanisms responsible for improved performance following the ingestion of carbohydrate with added protein during recovery by considering those studies that have examined these supplements when ingested during exercise. In this way, it is interesting to view feeding during recovery as a pre-exercise nutritional
intervention with mechanisms that can be contrasted against those suggested to take effect during exercise. For example, Ivy et al. (2003) reported that time to fatigue following 3 h of variable intensity cycling was improved by 36% when their cyclists ingested a mixture of carbohydrate and protein when compared with a matched quantity of carbohydrate. The fact that this effect occurred without any prior manipulation of muscle glycogen availability therefore leads to the possibility that combined carbohydrate-protein ingestion might also operate via mechanisms other than the avoidance of muscle glycogen depletion. Interestingly, there were no significant differences in plasma insulin concentrations during the exercise, despite the intermittent periods of low intensity activity, which would tend also to argue against the possibility that muscle glycogen was spared in the carbohydrate-protein trial [78].

Alternative explanations for the differences in exercise capacity between trials may involve specific protein-mediated mechanisms such as an increased central drive for exercise [112] or anaplerotic replenishment of tricarboxylic acid (TCA) cycle intermediates [78, 113]. However, it remains debatable whether the co-ingestion of glucose along with branched-chain amino acids can actually improve performance through attenuated sensations of fatigue [114-115]. Likewise, other evidence has also challenged the hypothesis that amino acids can maintain TCA cycle flux during prolonged exercise [116-117]. Notwithstanding the absence of any clearly supported underlying mechanism, various recent studies have subsequently confirmed that including protein in a carbohydrate supplement can indeed postpone
fatigue during exhaustive exercise \cite{91, 99-100} and possibly even improve ‘late-exercise time-trial performance’ \cite{107}. However, it is difficult to entirely dissociate the latter finding from the trial order effect reported in the latter study, particularly given the potential for interactive/synergistic effects between treatment and trial order (i.e. the efficacy of protein may be trial dependant) \cite{107}.

All the studies cited above should also be considered in relation to five other studies which have reported no ergogenic effect of ingesting added protein either in terms of either exercise capacity (i.e. time to fatigue at 70-75% $\dot{V}O_2$ peak \cite{95, 97}) or exercise performance (i.e. time to complete 7 kJ·kg$^{-1}$ \cite{118}, 80 km time-trial \cite{119}, 6 km time-trial \cite{120}). Notably, while four of these studies examined supplements matched for either carbohydrate \cite{119} or available energy \cite{95, 97, 120}, the fifth identified no performance benefit of the added protein even though the carbohydrate-protein mixture also contained ~25% more carbohydrate and therefore ~51% more energy \cite{118}. Resolution of these apparently inconsistent findings may therefore lie in the central role of carbohydrate during such exercise tests. Specifically, the benefits of added protein have only been observed either when that protein increases the energy content of the supplement and/or the carbohydrate fraction is below the amount recommended to satisfy oxidative requirements during exercise. This reasoning would certainly be consistent with our observation of deteriorated exercise performance when protein replaced carbohydrate in an isocaloric carbohydrate supplement during a high-intensity exercise test \cite{120}. 
Overall, the possibility remains that an enhanced rate of post-exercise muscle
glycogen resynthesis might not be the only factor contributing to improved
recovery of performance with combined carbohydrate-protein ingestion.

In fact, there is very little evidence to support the hypothesis that an
enhanced rate of muscle glycogen resynthesis during short-term recovery
results in an improved recovery of exercise capacity. The rate of muscle
glycogen resynthesis is very low when no carbohydrate is consumed during
recovery \cite{7, 13, 29}, yet increasing the rate of muscle glycogen storage through
the provision of carbohydrate has not consistently been found to enhance
subsequent exercise capacity \cite{23, 44}. However, one of these studies may not
have provided sufficient carbohydrate throughout recovery to reveal an effect
of carbohydrate ingestion on physical performance \cite{23}. Furthermore, in
contrast to the well-documented relationship between carbohydrate ingestion
rate and muscle glycogen resynthesis (Figure 1), far fewer studies have
examined the relationship between carbohydrate intake and exercise capacity
\cite{76, 121-122}. Of these, only one study has shown increased carbohydrate intake
during recovery to translate into an enhanced capacity for physical exercise
following a short-term recovery \cite{76}.

To our knowledge, only one published investigation has demonstrated
that an increased rate of muscle glycogen resynthesis during a short-term
recovery can improve exercise capacity during subsequent exercise \cite{34}. This
investigation by Williams et al. (2003) is also of particular relevance to this
review given that it was the first study to have investigated the effect of
combined carbohydrate-protein ingestion during short-term recovery on the capacity for subsequent exercise. In this study, participants were required to cycle at 65-75% \( \dot{\text{V}}\text{O}_2\text{max} \) for >105 min in order to deplete muscle glycogen stores and reduce blood glucose concentrations below 4.0 mmol·l\(^{-1}\). Once glucose homeostasis had been sufficiently challenged, participants began a 4 h recovery during which they consumed either carbohydrate alone (0.15 g·kg\(^{-1}\)·h\(^{-1}\)) or carbohydrate (0.40 g·kg\(^{-1}\)·h\(^{-1}\)) plus protein (0.10 g·kg\(^{-1}\)·h\(^{-1}\)). Notably, the carbohydrate-protein mixture resulted in a 92% greater insulinemic response and 128% greater rate of muscle glycogen resynthesis than the solution which provided less carbohydrate and no amino acids. Of greater practical importance was the finding that participants were able to exercise 55% longer (i.e. 20 versus 31 min) during a subsequent exercise capacity test at 85% \( \dot{\text{V}}\text{O}_2\text{max} \) when mixed carbohydrate-protein rather than carbohydrate alone had been ingested during recovery \(^{[34]}\).

Interestingly, these same two supplements have also been examined in a more recent investigation in which cycling capacity was actually impaired following the ingestion of the additional carbohydrate and protein, although a separate comparison with a milk-based carbohydrate-protein mixture did not produce this negative effect \(^{[123]}\). Notwithstanding this inconsistency, the study by Williams \textit{et al.} (2003) remains as the first evidence that increased muscle glycogen resynthesis during recovery can potentially be translated into an enhanced capacity for subsequent exercise.
More recent research on this topic has subsequently attempted to establish whether an enhanced recovery of exercise capacity would also occur if a carbohydrate-protein solution were evaluated in comparison with a solution that was matched for either carbohydrate or available energy content. Of course, such a comparison would not be expected to induce differences in muscle glycogen resynthesis of the magnitude reported by Williams et al. (2003) and part of the difficulty for researchers in this area is that the application of muscle biopsy procedures can potentially influence the validity of subsequent exercise testing. One solution has been to use $^{13}\text{C}$-MRS to quantify muscle glycogen concentrations, which was applied to good effect in the study by Berardi et al. (2006). This comprehensive study compared energy matched carbohydrate-protein and carbohydrate only supplements ingested over a 6 h recovery from a 60 minute cycling test and found that, while muscle glycogen resynthesis was significantly accelerated by the addition of protein, there was no difference between treatments in terms of a second exercise performance test following recovery $^{[25]}$. This finding regarding restoration of exercise performance is consistent with two other studies which have examined recovery supplements matched for either carbohydrate or available energy content. Both studies failed to find performance benefits following the ingestion of the added protein in terms of treadmill running capacity (i.e. time to exhaustion at $\geq$85% $\bar{V}O_2\text{max}$) within 2-4 h of an initial prolonged bout of exercise $^{[75, 104]}$. 
In contrast, Berardi et al. (2008) have subsequently repeated their study with the same research design but with a more sensitive and externally valid exercise test and, consistent with another recent report \cite{124}, did observe a longer time to exhaustion with the carbohydrate-protein mixture (at least in terms of maintaining performance relative to the first bout \cite{125}). Notably, both the studies cited above by Berardi et al. incorporated a standardized lunch into the post-exercise feeding regimen, which better reflects the real life behaviour of athletes but has rarely been a feature of studies in this area \cite{13, 25, 125}. Our own work on this topic revealed no difference between isocaloric carbohydrate and carbohydrate-protein supplements. However, every participant was able to exercise for longer during the post-recovery exercise test after ingesting the carbohydrate-protein mixture when compared to a control solution of matched carbohydrate content \cite{76}. In addition, we also observed no acceleration of muscle glycogen synthesis during recovery \cite{1}, thus lending further support to the hypothesis that part of the benefit of ingesting a mixed carbohydrate-protein solution may be unrelated to increased muscle glycogen availability. In this regard, it is noteworthy that our studies on this topic have consistently found an increased rate of whole-body carbohydrate oxidation during exercise following the ingestion of a protein containing carbohydrate recovery supplement \cite{1, 75-76}, but with no alteration in the rate of muscle glycogen degradation \cite{1}. Taken together, these findings suggest that the mechanism by which the ingestion of a carbohydrate-protein solution during recovery can postpone fatigue during subsequent exercise may be at least partially related to improved maintenance of euglycemia.
and/or increased oxidation of extra-muscular carbohydrate sources during exercise (i.e. both exogenous and hepatically derived).

From this perspective, it might be speculated that even very subtle differences in blood glucose availability late in exercise could potentially account for the observed ergogenic effects of ingesting carbohydrate with added protein. This proposed mechanism would explain why the ingestion of a carbohydrate-protein solution has been shown to be most effective during the latter stages of prolonged exercise or when added to moderate quantities of carbohydrate (i.e. situations when carbohydrate availability may be compromised) [78, 91, 99]. The precise physiological mechanism through which adding protein to carbohydrate operates may therefore involve an interaction of the established fatigue mechanisms. In this way, relative muscle glycogen depletion may sensitize the central nervous system to fluctuating blood glucose availability late in exercise before a central component of fatigue ultimately determines the capacity for continued exercise. An interaction of fatigue mechanisms as described above would therefore explain how an increased rate of blood glucose oxidation can delay fatigue independent of changes in total carbohydrate oxidation [126] and is also intuitive as it relates to the preservation of homeostasis in advance of frank hypoglycaemia. However, further examination of such possibilities will require innovative research designs to isolate the relative and combined effects of each mechanism of action.
4. Conclusions & Future Directions

The weight of available evidence supports the view that muscle glycogen resynthesis over the first 8 h after prior exercise-induced glycogen depletion will be heavily dependant upon the ingestion of carbohydrate. However, the precise effects of either carbohydrate ingestion or muscle glycogen resynthesis on subsequent physical performance remain to be fully established. The most effective nutritional strategy to rapidly replenish depleted glycogen reserves is likely to involve ingesting a high GI carbohydrate source at a rate of at least 1 g·kg\(^{-1}\)·h\(^{-1}\), beginning immediately after exercise and then at frequent (i.e. 15-30 min) intervals thereafter. However, if a more moderate quantity of carbohydrate is ingested, the inclusion of a small amount of hydrolyzed protein or amino acids can accelerate muscle glycogen resynthesis and/or promote a more rapid restoration of exercise capacity (with these two outcomes not necessarily causally related). Future research is warranted to examine whether protein/amino acids can increase the rate of muscle glycogen resynthesis beyond the maximal levels that have been observed with carbohydrate alone. In addition and, perhaps more important, future investigations should aim to determine the precise causal relationships between post-exercise carbohydrate intake, muscle glycogen resynthesis and restoration of physical performance. The latter can be achieved by conducting more studies that include exercise as a measure of functional recovery within their research designs; with a more comprehensive and innovative range of assessments applied late in exercise to explore the primary mechanisms of fatigue under these conditions.
Table I. Summary of studies examining muscle glycogen resynthesis during short-term recovery (i.e. >2-6) from exercise at varied rates of ingesting carbohydrate alone.

<table>
<thead>
<tr>
<th>Mode of Exercise Prior to Recovery</th>
<th>Post-Exercise Muscle Glycogen Concentration (mmol glucosyl units·kg dm⁻¹)</th>
<th>Duration of Recovery (h)</th>
<th>Rate of Carbohydrate Ingestion during Recovery (g·kg⁻¹·h⁻¹)</th>
<th>Frequency of Carbohydrate Ingestion during Recovery</th>
<th>Type of Carbohydrate Ingested during Recovery</th>
<th>Rate of Muscle Glycogen Resynthesis during Recovery (mmol glucosyl units·kg dm⁻¹·h⁻¹)</th>
<th>Reference</th>
</tr>
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<tbody>
<tr>
<td>Exhaustive Cycling</td>
<td>50</td>
<td>6</td>
<td>0.98</td>
<td>IMPE &amp; 1 h Intervals</td>
<td>Glucose Polymer</td>
<td>49</td>
<td>Battram et al. (2004) [24]</td>
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<tr>
<td>Non-Exhaustive Cycling</td>
<td>55*</td>
<td>6</td>
<td>0.80</td>
<td>IMPE, 1, 2 &amp; 4 h</td>
<td>Glucose Polymer/meal</td>
<td>22*</td>
<td>Berardi et al. (2006) [25]</td>
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<td>0.80</td>
<td>IMPE &amp; 30 min Intervals</td>
<td>Sucrose</td>
<td>12</td>
<td>Betts et al. (2008) [1]</td>
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<td>34</td>
<td>5</td>
<td>0.35</td>
<td>IMPE &amp; 2 h Intervals</td>
<td>Sucrose</td>
<td>27</td>
<td>Blom et al. (1987) [2]</td>
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<td></td>
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<td>IMPE &amp; 2 h Intervals</td>
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<td>40</td>
<td>Blom et al. (1989) [30]</td>
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<td>IMPE &amp; 30 min Intervals</td>
<td>Glucose</td>
<td>31</td>
<td>Carrithers et al. (2000) [3]</td>
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<td>Condition</td>
<td>Time</td>
<td>Intervals</td>
<td>Time</td>
<td>IMPE</td>
<td>Glucose</td>
<td>Time</td>
<td>Placebo</td>
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<td>Glucose</td>
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<td>Casey et al. (1995)</td>
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<td>Glucose</td>
<td>33</td>
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<td>Resynthesis Rate</td>
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<td>Year</td>
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<td>2008</td>
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<td>0.50 plus ~0.6 IMPE &amp; 1 h plus lunch</td>
<td>Glucose Polymer</td>
<td>40, 3</td>
<td>1997</td>
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<td>0.15 IMPE, 20 min, 1, 1.5, 2 &amp; 3 h</td>
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<td>1.20 IMPE &amp; 30 min Intervals</td>
<td>Gluc/Fructose Glucose</td>
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<td>Glucose Polymer</td>
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IMPE = immediately post-exercise. * = glycogen concentrations in mmol·l⁻¹ and resynthesis rates in mmol·l⁻¹·h⁻¹.
REFERENCES


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Figure 1
Carbohydrate Ingestion Rate (g.kg\(^{-1}\).h\(^{-1}\))

Muscle Glycogen Synthetic Rate (mmol glucosyl units.kg dm\(^{-1}\).h\(^{-1}\))

Figure 2