Dietary macronutrient recommendations for optimal recovery post-exercise: Part I

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Abstract
Prolonged, strenuous exercise results in muscle glycogen depletion. Recovery of these stores prior to the next training session or competition is crucial to optimise exercise performance. Nutrition plays an important role during the post-exercise recovery period when processes such as muscle regeneration, glycogen and fluid restoration take place. By manipulating the timing, type and frequency of food intake the rate of recovery can be enhanced, which is of particular importance to athletes performing multiple training or competition sessions within a day, or on a day-to-day basis and recovery time is limited. Restoration of muscle glycogen stores is especially important for athletes participating in prolonged exercise, since depleted glycogen stores are associated with impaired exercise performance. Key factors affecting muscle glycogen storage are carbohydrate (CHO) availability and an increased insulin concentration, both of which are influenced by amount and timing of CHO intake, type of CHO ingested, the ratio of CHO to protein ingested, and the fat content of a food item or meal. To maximise the rate of muscle glycogen restoration during a short (< 6-hour) recovery period, 1 - 1.5 g moderate to high glycaemic index CHO/kg body weight (BW) immediately post-exercise, followed by 0.8 - 1.5 g moderate to high glycaemic index CHO/kg BW/hour (divided in smaller doses every 15 - 60 minutes) for 3 - 4 hours should be ingested. With a longer recovery period (≥ 6 hours) muscle glycogen storage is independent of type of CHO ingested but a total of 7 - 10 g CHO/kg BW should be taken in within a 24-hour period. Combining protein with an adequate amount of CHO (> 1 g/kg BW/hour) has no added advantage in terms of enhanced rate of glycogen storage, but can be of practical importance. Additionally, this combination may be beneficial since CHO and amino acid availability are important for muscle repair during the recovery period, as will be discussed in detail in Part II of this article.

Introduction
Super-compensation is the main principle in physical training aimed at improving performance. A breakdown process in skeletal muscle is followed by a recovery process, resulting in adaptation and possibly increased exercise performance.32 Exercise has a profound effect on skeletal muscle metabolism resulting in net muscle protein breakdown and glycogen depletion during exercise, followed by net protein synthesis and, depending on nutrient availability, glycogen storage post-exercise. The recovery process (muscle regeneration, glycogen and fluid restoration) is regarded as critical to successful training and adaptation, and nutrition has been identified as a major contributor in this process.35 Increasing the rate of recovery post-exercise, or decreasing the rate of catabolism during exercise, could lead to speedy and effective recovery between training sessions. An enhanced recovery process is of particular importance to athletes who do more than one training session per day, and/or engage in strenuous multi-day training or competition schedules. Macronutrients, specifically carbohydrate (CHO) and protein, have been identified as crucial dietary components in enhancing the recovery process. By regulating the timing, amount and type of these nutrients ingested, anabolism post-exercise can be reached at an earlier stage compared with unregulated ingestion of these nutrients.34,25,49

This article consists of two parts, focusing on the effect of the macronutrients, individually and in combination, on glycogen storage (Part I) and skeletal muscle repair (Part II) post-exercise. In both parts possible mechanisms will be identified and conclusions drawn. At the end of Part II one combined set of dietary recommendations for optimal recov-
er of glycogen stores and skeletal muscle repair post-exercise is provided.

Glycogen storage

Glycogen, specifically muscle glycogen, is the predominant fuel source during exercise of moderate to high intensity (> 60% maximal oxygen uptake (VO2max)). During prolonged exercise, glycogen stores become depleted and blood glucose concentrations may start to decline, a situation which is often associated with a decrease in CHO oxidation and impaired exercise performance. Hence, efficient recovery of glycogen stores (in the liver and muscles) in the post-exercise period has been identified as an important strategy to enhance subsequent exercise performance. Restoration of these stores is dependent on glucose supply originating from dietary CHO. Restoration of liver glycogen stores is important for optimal maintenance of blood glucose concentrations, which serve as the predominant fuel source to the brain and central nervous system, as well as to the working muscles when muscle glycogen becomes depleted. However, restoration of muscle glycogen in the post-exercise period takes precedence over liver glycogen restoration, which, even in the absence of dietary CHO supply, can occur at a low rate (~ 1 - 2 mmol/kg wet weight (ww)/hour), with some of the substrate being provided through gluconeogenesis. Therefore, Part I of this article focuses on aspects increasing the rate of muscle glycogen recovery specifically.

Dietary factors affecting muscle glycogen storage

The key dietary factors that can enhance the rate of muscle glycogen synthesis include: increased CHO (glucose) availability; an elevated insulin concentration; the combination of CHO and protein or amino acids to increase the insulinotrophic effect and provide substrate for glycogen and muscle protein regeneration. Non-dietary factors that may augment the rate of glycogen synthesis (for detailed review see Jentjens and Jeukendrup) include glycogen synthase activity (increased by both muscle contraction and insulin); glucose transport protein-4 (GLUT-4) availability and translocation within the muscle cell (increased by muscle contraction and insulin concentrations); training status (training increases insulin signalling and sensitivity, GLUT-4 content, and blood flow); degree of muscle glycogen depletion (glycogen depletion may increase GLUT-4 availability and glycogen synthase activity, thereby increasing the rate of muscle glycogen restoration).

CHO availability: Amount and timing of CHO ingestion

It has been established that post-exercise glycogen synthesis takes place in a biphasic manner, with a rapid, insulin-independent phase lasting between 30 and 60 minutes, and a slow, insulin-dependent phase, which, depending on CHO availability and high insulin levels, can persist for several hours. The rapid phase only occurs when post-exercise muscle glycogen concentrations are below 30 - 35 mmol/kg ww and CHO is provided immediately post-exercise. Hence, of the abovementioned dietary factors, CHO availability remains the key factor affecting both phases of post-exercise glycogen synthesis and rate of recovery.

Several studies have demonstrated very low rates of muscle glycogen synthesis when no CHO was ingested or when CHO intake was delayed (> 2 hours) compared with immediate CHO ingestion post-exercise. The mechanism behind an increased rate of glycogen synthesis with immediate post-exercise CHO ingestion might be related to an increased glycogen synthase activity (for review see Nielsen and Richter) and GLUT-4 availability immediately following exercise. However, in the absence of CHO ingestion, these exercise-induced increases in glycogen synthase and GLUT-4 availability (and hence the potential for glucose transport) may decline rapidly.

When considering the ideal amount of CHO to be ingested, Blom et al. demonstrated an increase in muscle glycogen synthesis rate of ~ 150% when post-exercise CHO intake was increased from 0.18 to 0.35 g/kg body weight (BW)/hour (provided at 2-hourly intervals post-exercise), but no further increase when CHO intake was increased to 0.7 g/kg BW/hour. Similarly, Ivy et al. found no difference in muscle glycogen synthesis rate between the ingestion of 0.75 vs. 1.5 g CHO/kg BW/hour (provided at 2-hourly intervals) over a 4-hour period post-exercise. These two studies suggested a 'glycogen synthesis threshold' and an upper limit for CHO ingestion of between ~ 0.35 - 0.7 g/kg BW/hour. However, several more recent studies have demonstrated glycogen synthesis rates beyond those reported in these two studies (~ 145 - 170% higher) when 1 - 1.7 g CHO/kg BW/hour was ingested, hence providing evidence against the existence of such an upper limit or threshold.

For example, Van Loon et al. demonstrated a ~ 200% increase in the rate of glycogen synthesis when CHO intake was increased from 0.8 to 1.2 g/kg BW/hour (~ 145% higher than Blom et al. and Ivy et al.). Several others have reported even higher rates of muscle glycogen synthesis (~ 170% higher) when 1 - 1.7 g CHO/kg BW/hour was ingested at 15 - 60-minute intervals during a 3 - 4-hour recovery period. In these studies, the CHO beverages were provided at 15 - 60-minute intervals post-exercise, as opposed to 2-hourly intervals as in the studies where no difference in rates of muscle glycogen synthesis were found. Additionally, Ivy et al. reported that if beverages are provided on a 2-hourly basis, then a CHO intake of > 0.5 g CHO/kg BW/hour is needed in order to maximise glycogen synthesis post-exercise.

Collectively taken, these results may highlight the possibility that frequent CHO ingestion in the early hours post-exercise may be better able to increase and maintain glucose availability and insulin concentrations, as opposed to when provided on a 2-hourly basis.

Although the exact amount of CHO to maximise post-exercise glycogen recovery has not been fully established yet, the abovementioned evidence suggests that optimal muscle glycogen synthesis will be achieved by the ingestion of 1 - 1.5 g CHO/kg BW immediately after exercise, followed by 0.8 - 1.5 g CHO/kg BW/hour (ideally divided into small doses every 15 - 60 minutes) for at least 3 - 4 hours thereafter, aiming for a total of 7 - 10 g CHO/kg BW over a 24-hour period.
Type of CHO ingested

The type of CHO ingested plays an important role in the rate of glycogen synthesis as it affects the rate of digestion and absorption of the CHO, and ultimately glucose availability. As mentioned earlier, glucose availability is an important determinant of glycogen synthesis. Furthermore, insulin stimulates glycogen synthase, which is considered the rate-limiting enzyme in the glycogen synthetic pathway, as well as GLUT-4 translocation which facilitates glucose uptake.

High glycemic index (GI) CHO-rich foods elicit a high glucose and insulin response within the first 2 hours after ingestion. Thus, using high GI CHO foods during the early recovery period should increase the rate of glycogen synthesis and thereby achieve a higher glycogen concentration sooner, compared with a low GI CHO food.

Blom and co-workers found that the ingestion of glucose (high GI) and sucrose (moderate GI) feedings after prolonged exercise increased the rate of glycogen synthesis significantly higher at 6 hours post-exercise compared with fructose (low GI) feeding. Surprisingly, sucrose (moderate GI), which contains equimolar amounts of fructose (low GI) and glucose (high GI), resulted in similar rates of glycogen synthesis and muscle glycogen levels than a similar amount of glucose (high GI). A possible explanation for this result may be that fructose inhibits post-exercise hepatic glucose uptake, thereby increasing the amount of glucose available for muscle glycogen synthesis.

Interestingly, Piehl Aulin and co-workers found that a post-exercise CHO drink containing glucose polymers (high GI) resulted in a significantly higher rate of glycogen synthesis 4 hours post-exercise compared with an isocaloric glucose-containing drink (high GI) (50 vs. 30 mmol/kg dry weight/hour). It was suggested that the lower osmolality of the glucose polymer drink versus the glucose drink (84 vs. 350 mOsm/l) led to greater gastric emptying rates and a faster delivery of substrate to muscle. Although there was no difference in insulin and glucose response, there could have been a greater non-insulin dependent uptake of glucose in the muscle during the early (30 - 60 minutes) post-exercise period. This hypothesis merits further investigation.

During a longer recovery period (> 6 hours) timing and type of CHO ingested seems to be of lesser importance than the amount ingested. After strenuous glycogen-depleting exercise, the ingestion of 7 - 10 g CHO/kg BW/day will be sufficient to restore glycogen stores over a 24 - 48-hour period. For athletes participating in less strenuous exercise lasting 60 - 120 minutes/day, the ingestion of 6 - 8 g CHO/kg BW/day would be sufficient to restore glycogen stores within this time frame.

There are limited data available on the role of the GI during longer recovery periods, probably due to practical difficulties, but also due to evidence suggesting that amount of CHO ingested is more important than the type (GI) of CHO itself during these periods.

In summary, for athletes who train/compete twice (or more) a day, and/or have a strenuous day-to-day training or competition schedule with limited recovery time, it is recommended to opt for CHO-rich foods of moderate to high GI within the first 6 hours post-exercise. After 6 hours, foods with low GI can be included, provided that the overall CHO requirement (~ 7 - 10 g CHO/kg BW within 24 hours) is met. For athletes who have 6 or more hours to recover before a subsequent strenuous exercise bout, the type of CHO (low or high GI) is of lesser importance, provided that the amount of CHO to be ingested within a 24-hour period be sufficient (~ 6 - 8 g CHO/kg BW per 24 hours for moderate-intensity exercise or 7 - 10 g CHO/kg BW per 24 hours for more strenuous/prolonged exercise).

Effect of combining CHO and protein on muscle glycogen storage

Though insulin secretion is mainly determined by CHO ingestion and blood glucose concentration, it has been shown that certain amino acids and/or protein peptides have a synergistic effect on insulin concentration when combined with CHO. As mentioned before, insulin stimulates glycogen synthase and muscle glucose uptake, thus enhanced insulin release post-exercise may therefore increase the rate of muscle glycogen synthesis.

Zawadski and co-workers were the first researchers to find that the addition of whey protein to a CHO supplement (112 g CHO + 40.7 g protein/serving) taken immediately and 2 hours after an hour of glycogen-depleting exercise increased the rate of glycogen synthesis during a 4-hour recovery period compared with a CHO-only supplement (112 g CHO/serving). However, the increased rate of glycogen synthesis could have been due to the added energy, since the two drinks were not isocaloric. Since then, only one other study found that muscle glycogen concentrations were higher (4 hours post-exercise) in a CHO supplement with added protein (80 g CHO + 28 g protein + 6 g fat/serving) compared with an isocaloric CHO-only (108 g CHO + 6 g fat/serving) supplement given immediately and 2 hours after a 2.5 hour glycogen-depleting cycling protocol. Unfortunately, the rate of glycogen synthesis was not reported.

Subsequently, Van Loon et al. provided beverages at 30-minute intervals up to 270 minutes post-exercise and compared the ingestion of 0.8 g CHO/kg BW/hour with 0.8 g CHO/kg BW/hour plus 0.4 g/kg BW/hour of wheat protein hydrolysate plus leucine and phenylalanine (proven to be highly insulinotrophic), and with 1.2 g CHO/kg BW/hour. Adding the protein mixture (0.4 g/kg BW/hour) to the CHO beverage (0.8 g/kg BW/hour) increased the plasma insulin response and muscle glycogen synthesis rate by ~ 113% compared with the ingestion of 0.8 g CHO/kg BW/hour only. However, increasing the CHO content by 0.4 g CHO/kg BW/hour to 1.2 g/kg BW/hour also resulted in a faster rate of muscle glycogen synthesis of ~ 170% compared with ingestion of 0.8 g CHO/kg BW/hour. This study clearly demonstrated that maximal rates of muscle glycogen synthesis are not reached when 0.8 g CHO/kg BW/hour is ingested, and that this rate can be increased by the addition of 0.4 g/kg BW/hour of either protein or more CHO. The question then arose whether the addition of protein/amino acids to a larger CHO beverage (~ 1 g CHO/kg BW/hour) would further increase the rate of muscle glycogen synthesis. In answer to this question, Jentjens et al. demonstrated that combining 0.4 g/kg BW/hour of an insulinotrophic protein-amino acid mixture with a CHO beverage containing 1.2 g CHO/kg BW/hour, given at 30-minute intervals post-exercise, does not increase the rate of muscle glycogen further, despite
much higher insulin concentrations.

The majority of studies\textsuperscript{11,12,17-19,30-32} investigating the effect of combining protein and/or amino acid mixtures with a CHO supplement have not shown an enhanced rate of glycogen synthesis when the amount of CHO ingested was above 1 g/kg BW/hour. Despite higher insulin concentrations, the rate of muscle glycogen synthesis in these studies was unaffected by the addition of protein/amino acids compared with an isocaloric CHO beverage. Furthermore, Tarnopolsky and co-workers\textsuperscript{33} found significantly higher glycogen concentrations (4 hours post-exercise) after ingesting a CHO-only (1 g CHO/kg BW/serving) compared with an isocaloric CHO-protein (0.75 g CHO + 0.1 g protein + 0.02 g fat/kg BW/serving) supplement after a glycogen-depleting exercise protocol. These results are supported Wojcik and co-workers,\textsuperscript{34} and may suggest that insulin is not the rate-limiting factor for muscle glycogen synthesis when the overall rate of CHO intake is high (> 1 g CHO/kg BW/hour).

Though the rate of glycogen synthesis might not be enhanced by adding protein and/or amino-acid mixtures to a CHO supplement, it might be of practical importance, since a lower volume supplement/drink can be ingested post-exercise, when most athletes experience loss of appetite,\textsuperscript{35} and still result in efficient recovery of glycogen stores. Furthermore, adding protein to a recovery supplement/drink might be beneficial for muscle repair post-exercise. This will be discussed in more detail in Part II.

Effect of combining CHO, protein and fat on glycogen storage

Co-ingestion of fat reduces the plasma glucose response (but not insulin secretion) to both high and low GI CHO foods, possibly due to delayed gastric emptying.\textsuperscript{36} The addition of fat and protein to a CHO meal may cause similar levels of glycogen storage at 24 hours post-exercise compared with a CHO-only diet, provided that the CHO intake is adequate.\textsuperscript{8,40}

Effect of type of exercise on glycogen storage

Type of exercise also has an effect on rate and amount of muscle glycogen stored post-exercise. The rate of glycogen synthesis after short-term high-intensity exercise is higher than after prolonged or resistance exercise.\textsuperscript{41} Possible factors contributing to this effect include higher peak blood glucose and insulin levels post-exercise, higher levels of glycolytic intermediates and lactate concentration in muscle and blood, as well as greater glycogen depletion in glycogen synthase-rich fast-twitch glycolytic muscle fibres (for review see Pascoe and Gladden\textsuperscript{42}). Additionally, eccentric exercise (usually part of resistance training) is associated with reduced rates of glycogen resynthesis.\textsuperscript{43,44} Potential mechanisms include competition between inflammatory cells and muscle cells for available glucose,\textsuperscript{45} a metabolic shift towards glycolysis induced by inflammatory cells,\textsuperscript{46} reduced GLUT-4 levels,\textsuperscript{47} and an increase in calcium which could inhibit glycogen synthase.\textsuperscript{44}

Conclusions

Prolonged, strenuous exercise results in muscle glycogen depletion. Recovery of these stores prior to the next training session or competition is crucial to optimise exercise performance. Nutrition is a major contributor to the recovery of muscle glycogen stores and the rate at which it occurs, which is especially important for athletes engaging in multi-day training or competition schedules. The rate of glycogen storage can be increased by ingesting a sufficient amount of CHO (> 0.8 g CHO/kg BW/hour) immediately post-exercise at 15 - 60-minute intervals during the first 3 - 4 hours of the recovery period. Ingesting high GI CHO during the early recovery period (≤ 6 hours) results in a higher rate of glycogen storage than low GI CHO. The total amount of glycogen stored within a 24-hour period post-exercise is, however, not dependent on the GI per se, but rather on the amount of CHO ingested during the recovery period. Thus, the GI only seems to be important when there is a short recovery period (< 6 hours) between training sessions. Finally, combining CHO and protein post-exercise does not seem to result in a higher rate of glycogen storage compared with when a high CHO-only supplement is ingested at a rate of >1 g CHO/kg BW/hour. This combination may, however, still be of benefit to the muscle recovery process since CHO and amino acid availability are important for muscle repair during the recovery period, as will be discussed in detail in Part II.

REFERENCES


