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Review article

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REGULATION OF MUSCLE GLYCOGEN REPLETION, MUSCLE PROTEIN SYNTHESIS AND REPAIR FOLLOWING EXERCISE

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ABSTRACT

Recovery from prolonged strenuous exercise requires that depleted fuel stores be replenished, that damaged tissue be repaired and that training adaptations be initiated. Critical to these processes are the type, amount and timing of nutrient intake. Muscle glycogen is an essential fuel for intense exercise, whether the exercise is of an aerobic or anaerobic nature. Glycogen synthesis is a relatively slow process, and therefore the restoration of muscle glycogen requires special considerations when there is limited time between training sessions or competition. To maximize the rate of muscle glycogen synthesis it is important to consume a carbohydrate supplement immediately post exercise, to continue to supplement at frequent intervals and to consume approximately 1.2 g carbohydrate·kg^{-1} body wt·h^{-1}. Maximizing glycogen synthesis with less frequent supplementation and less carbohydrate can be achieved with the addition of protein to the carbohydrate supplement. This will also promote protein synthesis and reduce protein degradation, thus having the added benefit of stimulating muscle tissue repair and adaptation. Moreover, recent research suggests that consuming a carbohydrate/protein supplement post exercise will have a more positive influence on subsequent exercise performance than a carbohydrate supplement.

KEY WORDS: Carbohydrate, nutrients, insulin, glucose, amino acids.

INTRODUCTION

Recovery from exercise is a complex process requiring the replenishment of the body's fuel stores, the repair of damaged muscle tissue and the initiation of training adaptations. This requires the body to switch from a predominantly catabolic state to a predominantly anabolic state. For this transition to occur efficiently and effectively requires not only that the proper nutrients be consumed, but also that they be consumed at the appropriate time.

The major source of fuel used by the skeletal muscles during prolonged aerobic exercise of a strenuous nature is muscle glycogen. The importance of muscle glycogen as a fuel source cannot be overstated. In general, it has been demonstrated that aerobic endurance is directly related to the initial muscle glycogen stores, that strenuous exercise cannot be maintained once these stores are depleted, and that perception of fatigue during prolonged intense exercise parallels the decline in muscle glycogen (Hermansen et al., 1965; Ahlborg, et al., 1967; Bergström and Hultman, 1967; Bergström et al., 1967). Because of the importance of muscle glycogen for sustaining prolonged intense exercise, there has been considerable research to establish the most efficient means for its replenishment once depleted. Early research focused on how to replenish the muscle glycogen stores on a daily basis in preparation for consecutive days of competition or exercise training. However, because many athletes may train or have to compete several times a day, more recent research has focused on how to replenishing the muscle glycogen stores within several hours after exercises. In this regard, questions that have been addressed include the most appropriate amount and frequency of carbohydrate supplementation, the most appropriate times to supplement, as well as the most appropriate supplements to use.

Aside from a reduction in the muscle glycogen stores, strenuous exercise will result in muscle tissue damage. This damage is due in part to the physical stress placed on the muscle, particularly during the eccentric phase of muscle contraction (Clarkson and Hubal, 2002; Evans, 2002), and hormonal changes that result in the breakdown of muscle protein, as well as fat and carbohydrate, to provide the fuel for powering muscle contraction (Walsh et al., 1998). However, muscle damage does not just occur during exercise, but can continue after exercise for many hours. This occurs as a result of a protracted exercise hormonal milieu, an increase in free radicals and acute inflammation. Not only will such tissue damage limit performance due to delayed onset muscle soreness, but it will also compromise the replenishment of muscle glycogen and limit muscle training adaptations (O'Reilly et al., 1987; Costill et al., 1990).

In this review the most efficient and appropriate means of rapidly replenishing the muscle glycogen stores post exercise will be discussed. Also discussed will be the means of limiting post exercise muscle damage and stimulating muscle protein synthesis. Finally, evidence will be presented that the procedures used to rapidly replenish the muscle glycogen stores and stimulate protein synthesis will favorably affect physical performance.

MUSCLE GLYCOGEN REPLENISHMENT POST EXERCISE

The competitive nature of sports today requires many athletes to cross-train and train multiple times per day. Moreover, many athletes may be required to compete in several different contests over subsequent days or even on the same day. Recent research has suggested that for these situations athletes benefit from the rapid restoration of their muscle glycogen stores. Many factors will affect the rate of muscle glycogen storage after exercise. These include the timing of carbohydrate consumption, the amount and frequency of carbohydrate consumption, and the addition of protein to a carbohydrate supplement.

Timing of Carbohydrate Consumption After Exercise

It has been found that muscle glycogen synthesis is more rapid if carbohydrate is consumed immediately following exercise as opposed to waiting several hours (Ivy et al., 1988a). When carbohydrate is consumed immediately after exercise the rate of glycogen synthesis averages between 6 to 8 $mmol \cdot kg^{-1}$ wet $wt \cdot h^{-1}$; whereas, if the supplement is delayed several hours the rate of synthesis is reduced 50% (Mæhlum et al., 1977; Blom et al., 1987; Ivy et al. 1988a). The increased synthesis immediately post exercise is due in part to a faster rate of muscle glucose uptake as a result of an increase in muscle insulin sensitivity (Garetto et al., 1984; Richter et al., 1984; Cartee et al., 1989), and an increase in the concentration of glucose transporters associated with the plasma membrane of the muscle (Goodyear et al., 1990; Etgen et al., 1996). With time, however, the increase in insulin sensitivity and membrane glucose transporter concentration declines resulting in a slower rate of muscle glucose uptake and glycogen storage. For instance, Okamura et al. (1997) infused glucose at the same rate in dogs either immediately after exercise or 2- hours after exercise. Plasma glucose and insulin levels were significantly lower in the dogs infused immediately after exercise, but their rates of hindlimb glucose uptake were significantly greater. Levenhagen et al. (2001) found that leg glucose uptake was increased 3-fold above basal when supplemented immediately after exercise with carbohydrate, and increased only 44% above basal when supplemented 3-hours after exercise. This difference in rate of uptake occurred despite no differences in leg blood flow, or blood glucose and insulin concentrations between the two treatments.

It should also be pointed out that after exercise that depletes the body's carbohydrate stores, there is little if any increase in muscle glycogen storage until adequate carbohydrate is made available (Ivy et al., 1988a; Ivy et al., 1998b; Zawadzki et al., 1992). Therefore, early intake of carbohydrate after strenuous exercise is essential because it provides an immediate source of substrate to the muscle, while also taking advantage of the increased insulin sensitivity and membrane permeability of the muscle to glucose. Furthermore, supplementing immediately after exercise appears to delay the decline in insulin sensitivity, and with frequent supplementation, a relatively rapid rate of glycogen storage can be maintained for up to 8-hours post exercise (Blom et al., 1987; Ivy et al., 1988b).

Amount of Dietary Carbohydrate

An important dietary factor affecting muscle glycogen replenishment is obviously the amount of carbohydrate consumed. When provided immediately post exercise, the rate of glycogen storage will decline as glucose availability decreases (Ivy et al., 1988a). However, Blom et al. (1987) demonstrated that this decline could be attenuated for up to 8-hours if supplements were continually provided at 2-hour intervals. They also found that supplementing with 0.7 g glucose$\cdot$kg^{-1} body wt appeared to maximize muscle glycogen storage, as there was no difference found between supplements containing 0.7 and 1.4 g glucose$\cdot$kg^{-1} body wt. Research from our laboratory, however, suggests that when providing carbohydrate supplementation at 2-hour intervals, 1.2 to 1.4 g of glucose$\cdot$kg^{-1} body wt (0.6 to 0.7 g carbohydrate$\cdot$kg^{-1} body wt$\cdot$h^{-1}) is required to maximize muscle glycogen storage (Ivy et al., 1988a; 1988b).

The rate of glycogen synthesis that is maintained by supplementing at 2-hour intervals, approximately 7 mmol$\cdot$kg^{-1} wet wt$\cdot$h^{-1}, does not appear to be the highest rate of muscle glycogen synthesis possible. Some studies have found that supplementing at increased frequency and the addition of protein to the carbohydrate supplement can positively influence the rate of synthesis (Doyle et al., 1993; Piehl-Aulin et al., 2000; van Hall et al., 2000).

Frequency of Carbohydrate Supplementation

When carbohydrate supplementation occurs at frequent intervals such as every 15 to 30 minutes and in high amounts, the rate of muscle glycogen storage has been found to be approximately 30% higher than when supplementing every 2-hours (Doyle et al., 1993; Piehl-Aulin et al., 2000; van Hall et al., 2000). Doyle et al. (1993) reported glycogen storage rates of 10 mmol$\cdot$kg^{-1} wet wt$\cdot$h^{-1}during the first 4 hours of recovery from exercise when subjects received 0.4 g carbohydrate$\cdot$kg^{-1} body wt every 15 minutes (1.6 g carbohydrate$\cdot$kg^{-1} body wt$\cdot$h^{-1}). Similar rates were reported by van Hall et al. (2000) during a 4-hour recovery period when supplementation occurred at 15-minute intervals, and by Piehl-Aulin et al. (2000) during the first two hours of recovery when supplementing at 30-minute intervals. In these studies carbohydrate was provided at a rate of approximately 1.0 to 1.2 g$\cdot$kg^{-1} body wt$\cdot$h^{-1}. These studies suggest that supplementing at 15 to 30 minutes intervals may be preferable to supplementing every 2-hours for the rapid restoration of the muscle glycogen stores post exercise. They also suggest that when supplementing at frequent intervals, the optimal amount of carbohydrate is in the range of 1.2 g$\cdot$kg^{-1} body wt$\cdot$h^{-1}. Unfortunately, there have not been any studies conducted directly comparing the frequency of supplementation on the rate of glycogen storage.

Effect of Protein on Glycogen Storage

Our laboratory was the first to study the combined effect of protein plus carbohydrate on muscle glycogen synthesis (Zawadzki et al., 1992). Comparisons were made for supplements consisting of 112 g of carbohydrate in a 21% w/v mixture and 112 g of carbohydrate with 40.7 g of protein provided immediately after and 2-hours after exercise. It was found that the addition of protein to the carbohydrate supplement increased the rate of glycogen storage by approximately 38% over the first 4-hours of recovery. The greater rate of synthesis was believe due to a greater insulin response as a result of the addition of protein to the carbohydrate supplement (Pallotta and Kennedy, 1968; Spiller et al., 1987). Controversy arouse, however, because the carbohydrate and carbohydrate/protein supplements we used were not isocaloric, and subsequent research from other laboratories failed to confirm our findings (Tarnopolsky et al., 1997; Carrithers et al., 2000; van Hall et al., 2000; Jentjens et al., 2001). The conflicting results, however, can probably be attributed to differences in experimental design such as the frequency of supplementation and the amount and types of carbohydrate and protein provided. In general, those studies that did not demonstrate a benefit of protein used more frequent feeding intervals (Tarnopolsky et al., 1997; Carrithers et al., 2000; van Hall et al., 2000; Jentjens et al., 2001), provided greater amounts of carbohydrate (van Hall et al., 2000; Jentjens et al., 2001), and in some studies less protein (Carrithers et al., 2000; Tarnopolsky et al., 1997). Support for this supposition comes from a recent study from our laboratory in which we tested the hypothesis that a carbohydrate-protein supplement would be more effective in the replenishment of muscle glycogen after exercise compared with a carbohydrate supplement of equal carbohydrate content or caloric equivalency when supplementing immediately and 2-hours post exercise (Ivy et al., 2002). After several hours of intense cycling to deplete the muscle glycogen stores, the subjects received, using a rank-ordered design, a carbohydrate protein (80 g CHO, 28 g Pro, 6 g fat), iso-carbohydrate (80 g CHO, 6 g fat), or isocaloric carbohydrate (108 g CHO, 6 g fat) supplement. After 4-hours of recovery, muscle glycogen was significantly greater for the carbohydrate/protein treatment (88.8 +/- 4.4 $mmol \cdot l^{-1}$) when compared with the iso-carbohydrate (70.0 ± 4.0 $mmol \cdot l^{-1}$) and isocaloric (75.5 ± 2.8 $mmol \cdot l^{-1}$) treatments. Glycogen storage did not differ significantly between the iso-carbohydrate and isocaloric treatments. Of interest was the very large difference in glycogen storage between treatments during the first 40 minutes of recovery. Glycogen storage was twice as fast after the carbohydrate/ protein treatment than after the isocaloric treatments, and four times faster than after the iso-carbohydrate treatment. This trend was also noted following the second feeding 2-hours into recovery.

The results indicate that the co-ingestion of protein with carbohydrate will increase the efficiency of muscle glycogen storage when supplementing at intervals greater than 1-hour apart, or when the amount of carbohydrate ingested is below the threshold for maximal glycogen synthesis. These results have important implications for athletes who wish to limit there carbohydrate intake in an effort to control body weight and for those athletes who participate in sports that have very short recovery periods during competition such as basketball, ice hockey and soccer.

LIMITING MUSCLE DAMAGE AND INITIATING MUSCLE PROTEIN ACCRETION

During strenuous exercise there is generally damage to the active muscles and this damage can continue after exercise due to acceleration in protein degradation. For complete recovery, it is important to initiate protein synthesis while limiting protein degradation. Like muscle glycogen storage, muscle protein synthesis and degradation are affected by the types, amount and timing of nutrient supplementation.

Types of Supplementation Affecting Protein Synthesis and Degradation

Although the muscle can have residual catabolic activity following exercise, it is primed to shift into an anabolic state in the presence of the right nutrients. This is due, in part, to an increased sensitivity to insulin. Insulin is one of the most anabolic hormones in the body. Insulin increases muscle amino acid uptake and protein synthesis and reduces protein degradation. Following exercise, raising the plasma insulin level is key to limiting protracted muscle damage and stimulating protein accretion.

Roy et al. (1997) investigated the effect of carbohydrate supplementation on the fractional rate of protein synthesis following resistance exercise using one leg, with the opposite leg serving as a control. The subjects received 1g of carbohydrate$\cdot kg^{-1}$ body wt immediately after and 1-hour after exercise or a placebo. Exercise alone did not result in a significant increase in protein synthesis. Carbohydrate supplementation, however, significantly elevated the plasma insulin level and increased protein synthesis by 36% in the exercised leg as compared to the none exercised leg. Furthermore, urinary nitrogen and 3-methlyhistidine were significantly reduced following carbohydrate supplementation suggesting a reduction in muscle tissue damage and protein degradation. Conversely, Levenhagen et al. (2002) found no increase in protein synthesis when a carbohydrate supplement was provided immediately post exercise. However, this finding may have been due to the lack of an appreciable insulin response resulting from the very small carbohydrate supplement (8g) provided.

Supplementation of a mixture of essential amino acids will also increase protein synthesis (Biolo et al., 1997; Tipton et al., 1999). Activation of protein synthesis by amino acids is most responsive immediately following exercise. Raising the plasma amino acid levels post exercise by infusion or oral supplementation has been reported to transition the muscle from a negative protein balance to a positive protein balance by stimulating protein synthesis (Rasmussen et al., 2000). When blood amino acid levels are reduced below normal, amino acids are released from the muscle and protein synthesis declines. Elevating the essential amino acid levels above normal, however, increases amino acid uptake and muscle protein synthesis (Wolfe, 2001).

While supplementing with either carbohydrate or amino acids post exercise may limit muscle damage and stimulate protein synthesis, there is increasing evidence that the combination can have an additive effect (Suzuki et al., 1999; Levenhagen et al., 2002; Miller et al., 2003). This is likely due to the synergist effect that a carbohydrate/amino acid or carbohydrate/protein supplement has on the plasma insulin response, and the fact that such supplements maintain an elevation in the plasma amino acid concentration. In this regard, Levenhagen et al. (2002) found that leg and whole body protein synthesis increased 6-fold and 15%, respectively, when a carbohydrate/protein supplement was provided after 60 minutes of cycling at 60% VO_2max. Net protein accretion was also positive. When a placebo or a carbohydrate supplement was provided, there was a release of muscle amino acids and protein degradation exceeded protein synthesis. In addition, Miller et al. (2002) assessed the independent and combined effects of carbohydrate and amino acid supplementation following leg resistance exercises. Supplements were provided 1- and 3-hours after exercise and protein synthesis across the leg was determined over a 3-hour recovery period. Both the plasma insulin response and protein synthesis rate were found to be greatest in response to the carbohydrate/amino acid supplement. The effect of the carbohydrate/amino acid supplement on net muscle protein synthesis was roughly equivalent to the sum of the independent effects of either the carbohydrate or amino acid supplement alone. These findings are supported by the research of Gautsch et al. (1998). These investigators found that a complete meal composed of protein and high glycemic carbohydrates provided post exercise would stimulate mRNA translation initiation for muscle protein synthesis, whereas a meal consisting of carbohydrate alone was insufficient.

Nutrient Timing on Protein Synthesis and Degradation

As with the restoration of muscle glycogen after exercise, the timing of supplementation for the stimulation of protein accretion also appears critical. Okamura et al. (1997) appear to have been the first to investigate the effect on nutrient timing on muscle protein synthesis after exercise. They measured the rate of protein synthesis and degradation in dogs after treadmill exercise. All doges were infused for 2-hours with a 10% amino acid and 10% glucose solution, with half of the dogs infused immediately after exercise and the other half infused 2-hours after exercise. During the pre-exercise period and during exercise there was a net protein breakdown. Only after initiating the infusion of the amino acids and glucose mixture did net protein balance became positive, with the increase in muscle amino acid uptake and protein synthesis greater when infused immediately after exercise compared to 2-hours after exercise.

Probably the study best illustrating the effect of nutrient timing on muscle tissue protein synthesis and accretion is that by Levenhagen et al. (2001). These researchers studied the effects of a carbohydrate/protein supplement on protein synthesis and degradation after a 60-minute moderate intensity exercise bout of cycling. Subjects were given the supplement immediately or 3-hours after exercise. Protein degradation was unaffected by supplement timing, but leg protein synthesis was increased approximately 3-fold above basal when supplementation occurred immediately post exercise. No increase in protein synthesis occurred when the supplement was delayed 3-hours, and only when the supplement was immediately provided after exercise was there a positive protein balance (the rate of protein synthesis exceeded the rate of protein degradation). It was also of interest to note that when supplementation occurred immediately compared to 3-hours after exercise, there was a greater fat oxidation. Levenhagen et al. (2001) concluded that ingesting a carbohydrate/ protein supplement early after exercise increases protein accretion as well as muscle glycogen storage.

PHYSICAL PERFORMANCE FOLLOWING RECOVERY

Research suggests that providing a carbohydrate/ protein supplement at the appropriate times after exercise will have a significant impact on subsequent exercise performance. For example, we compared the effectiveness of a carbohydrate/protein supplement (15% carbohydrate – 4% protein) designed for recovery with that of a traditional sports drink (6% carbohydrate) (Williams et al, 2003). The supplements (355 ml of each) were provided immediately after and 2-hours after exercise. Degree of recovery was assessed by having the subjects exercise to exhaustion at 80% VO_2max following a 4-hour recovery period. We found that muscle glycogen restoration was 128% greater and exercise performance 55% greater when consuming the carbohydrate/protein recovery drink as compared to the traditional sports drink. Obviously, from this study one cannot discern if the difference in performance between the two treatments was due to the type of supplement provided or the amount of carbohydrate consumed. However, the point that can be made is that a supplement designed for exercise recovery is much more effective than a traditional sports drink. Furthermore, two recent studies suggest that the addition of protein to a high carbohydrate recovery supplement is advantageous.

Niles et al. (2001) compared the effectiveness of isocaloric carbohydrate (carbohydrate, 152.7 g) and carbohydrate/protein (protein, 112 g; carbohydrate 40.4 g) supplements to promote recovery from strenuous aerobic exercise. Supplements were provided immediately and 1-hour after exercise, and recovery was assessed 3-hours after the last supplement by having the subjects run to exhaustion at an exercise intensity 10% about their anaerobic threshold. Run time to exhaustion was 21% longer when the subjects consumed the carbohydrate/protein supplement compared to the carbohydrate supplement. More remarkable are the findings of Saunders et al. (In Press). In their study, subjects received in random order 1.8 $ml \cdot kg^{-1}$ body wt of a 7.3% carbohydrate or 7.3% plus 1.85% carbohydrate/protein supplement every 15 minutes while cycling at 75% VO_2max to exhaustion, and 10 $ml \cdot kg^{-1}$ body wt immediately after exercise. Twelve to fifteen hours after the last supplement, the subjects completed a second ride to exhaustion at 85% of VO_2max. During the first cycling exercise the subjects rode 29% longer when consuming the carbohydrate/protein supplement compared with the carbohydrate supplement. Moreover, during the second ride performance was 40% longer when consuming the carbohydrate/protein supplement. Interestingly, plasma creatine phosphokinase (CPK) levels, an indication of muscle tissue damage, were 83% lower prior to the start of the second exercise in the subjects consuming the carbohydrate/protein supplement. It was concluded that the addition of protein to a carbohydrate supplement produces improvements in aerobic endurance and limits exercise muscle damage.

CONCLUSIONS

The restoration of muscle glycogen after depletion by exercise is a central component of the recovery process. To maximize the rate of muscle glycogen storage during short-term recovery, it is important to consume a carbohydrate supplement as soon after exercise as possible. If consuming only carbohydrate, supplementation should occur frequently, such as every 30 minutes, and provide about 1.2 to 1.5 g of $carbohydrate \cdot kg^{-1}$ body $wt \cdot h^{-1}$. However, the efficiency of muscle glycogen storage can be increased significantly with the addition of protein to a carbohydrate supplement. This will reduce both the amount of carbohydrate and frequency of supplementation required to maximize glycogen storage. If both carbohydrate and protein are consumed, it is recommended that 0.8 g $carbohydrate \cdot kg^{-1}$ body wt plus 0.2 g $protein \cdot kg^{-1}$ body wt be consumed immediately and 2-hours after exercise during a 4-hour recovery period. The addition of protein to a carbohydrate supplement also has the added advantage of limiting post exercise muscle damage and promoting muscle protein accretion. Along with a rapid increase in muscle glycogen, these processes can have a significant impact on subsequent exercise performance.

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Research interests

the interactions of exercise and nutrition on muscle metabolism

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KEY POINTS

- For rapid recovery from prolonged exercise, it is important to replenish muscle glycogen stores and initiate muscle tissue repair and adaptation.
- To maximize muscle glycogen replenishment, it is important to consume a carbohydrate supplement as soon after exercise as possible.
- Consume the carbohydrate frequently, such as every 30 minutes, and provide about 1.2 to 1.5 g of carbohydrate·kg^{-1} body wt·h^{-1}.
- Efficiency of muscle glycogen storage can be increased significantly with the addition of protein to a carbohydrate supplement (~4 to 1 carbohydrate to protein ratio).
- The addition of protein to a carbohydrate supplement also has the added advantage of limiting post exercise muscle damage and promoting muscle protein accretion.