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# Macronutrients and performance

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# Macronutrients and performance

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Athletes should eat a well-balanced diet made up of a wide variety of foods in sufficient quantity to cover their daily energy expenditures. Carbohydrate-containing foods should provide ~ 60-70% of their daily energy intake, protein ~ 12-15%, with the remainder being provided by fat. The higher carbohydrate intakes, however, are only recommended during preparation for, and immediate recovery from, heavy training and competition. Adopting nutritional strategies to increase muscle and liver glycogen stores before, during and after exercise can improve performance. The protein requirements of most athletes are fulfilled when their daily intake is between 1.2 and 1.7 g per kg body mass. This amount of protein is provided by a diet which covers the athlete's daily energy expenditure. Although fat metabolism contributes to energy production during exercise, and the amount increases with endurance training, there is no evidence to suggest that athletes should increase their fat intake as a means of improving their performance.

Keywords: Athletes, carbohydrate, exercise, fat, fatigue, performance, protein.

#### Introduction

The 1991 Consensus Conference on Foods, Nutrition and Sports Performance recommended the following dietary advice: 'In the optimum diet for most sports, carbohydrate is likely to contribute about 60-70% of the total energy intake and protein about 12%, with the remainder coming from fat' (Devlin and Williams, 1991). This advice is consistent with that offered by health professionals to the population at large as a means of sustaining good health. The three clear messages which emerged from the 1991 Consensus Conference after comprehensive reviews of the scientific literature were: (1) the central role played by carbohydrate nutrition in successful performance; (2) that, in general, athletes overestimate their need for dietary protein; and (3) that athletes underestimate the importance of fluid replacement and the detrimental influences on performance of even mild dehydration.

The aim of this general overview of the macronutrient needs of athletes is to draw the attention of the reader to the links between nutrition and sports performance, underlining and extending the findings of the 1991 Consensus Conference. Although not an exhaustive review of the topic, the intention is to include a selection of studies which have examined the links between nutrition and performance, recognizing that the most significant contribution of nutrition to sports performance is indirectly through its influence on helping to improve fitness.

### Carbohydrate nutrition

Athletes should consume more carbohydrate than the 50% of daily energy intake recommended for less active people. The reason for this higher level of carbohydrate consumption is that heavy exercise makes great demands on the body's carbohydrate stores and fatigue is associated with glycogen depletion (for reviews, see and Hargreaves, 1992; Coyle, Consuming foods which contain mainly carbohydrates not only provides substrate to refuel the body's glycogen stores in muscle and liver, but they also help decrease fat intake. Foods which contain carbohydrates are relatively 'bulky' in comparison with foods which are high in fat. Therefore, eating a high-carbohydrate diet helps athletes to match their energy intakes to their expenditure and control their body mass. The amount of carbohydrate recommended by the 1991 Consensus Conference is based on the assumption that athletes consume a wide range of foods in sufficient quantity to cover their daily energy expenditures. Under these conditions, the recommendation of a carbohydrate intake covering about 60% of daily energy expenditure is sufficient to match the needs of heavy training.

However, in preparation for an increase in training load or endurance competitions, the carbohydrate intake should be increased to ~ 70% of daily energy intake. Although these recommendations have general applicability, as far as macronutrient intake is concerned, there are conditions under which the recommended balanced diet is achieved but the carbohydrate intake is insufficient to replace muscle glycogen stores rapidly. For example, those athletes who restrict their overall energy intakes in preparation for competition in weight category sports or sports in which a low body mass (BM) confers an advantage on the participant, such as in endurance running and gymnastics, may consume a balanced diet but the absolute amount of carbohydrate and energy may be insufficient to support their activities. Therefore, the recommended carbohydrate intake should be extended to include the quantity of carbohydrate per unit body mass (g kg BM<sup>-1</sup>). The diets of athletes who are aware of the importance of carbohydrate contain 4.5-6.0 g kg BM<sup>-1</sup> of carbohydrate per day. When rapid recovery of endurance fitness is required, then a carbohydrate intake of 9-10 g kg BM<sup>-1</sup> day<sup>-1</sup> is needed (Fallowfield and Williams, 1993).

## Timing and type of carbohydrate

Increased carbohydrate intake is particularly important when preparing for prolonged heavy exercise or competition. Karlsson and Saltin (1971) noted the benefits of pre-exercise carbohydrate loading on running performance during a 30-km cross-country race. Their subjects undertook dietary carbohydrate loading using the original dietary and exercise manipulations of Astrand (1967). This method involves lowering muscle glycogen concentrations by prolonging exercise, and then maintaining glycogen stores at low levels by eating a low-carbohydrate diet for 3 days, followed by a highcarbohydrate diet for the 3 days before each race. Increased pre-race muscle glycogen levels improved performance by 5.4%. This was achieved not by the athletes running at faster speeds early in the race, but by being able to sustain their chosen speeds for longer. An examination of muscle glycogen concentrations at the end of the 30-km race revealed that they were higher than pre-race values for the subjects who had not undertaken carbohydrate loading (Fig. 1). Furthermore, when increases in muscle glycogen concentrations were against improvements plotted performance times, there was no clear relationship (Fig. 2). These results help to illustrate an important point about carbohydrate nutrition and performance which is often overlooked - high muscle and liver glycogen concentrations before endurance competitions

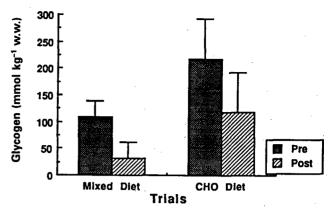


Figure 1 Muscle glycogen concentrations of runners before and after a 30-km cross-country race after two dietary preparations, namely after a normal mixed diet and after a high-carbohydrate diet (carbohydrate-loading) (Karlsson and Saltin, 1971).

are preconditions, but not necessarily predeterminants, of successful endurance performance.

In contrast, the early studies of Bergstrom et al. (1967) clearly suggested that a high pre-exercise muscle glycogen concentration is a predeterminant of endurance capacity during cycling to exhaustion (Fig. 3). Endurance capacity, assessed by constant pace running to exhaustion, is also improved after dietary carbohydrate loading for 2–3 days before exercise (Brewer et al., 1988; Goforth et al., 1980). Carbohydrate loading can be achieved simply by gradually decreasing the amount of training during the week before competition and increasing the carbohydrate

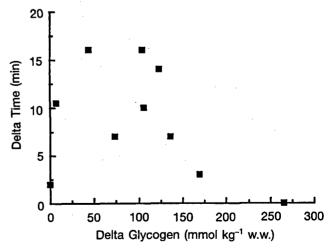


Figure 2 The relationship between increases in pre-race muscle glycogen concentrations (delta glycogen) and improvements in performance times (delta time) for the 30-km race (Karlsson and Saltin, 1971).

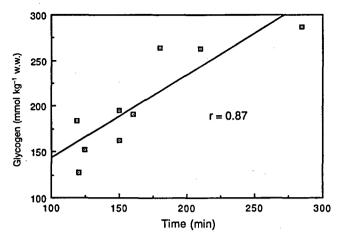


Figure 3 Relationship between pre-exercise muscle glycogen concentrations and submaximal cycling time to exhaustion (Bergstrom *et al.*, 1967).

content of the diet to ~ 70% of the daily energy intake during the 3 days before competition (Sherman et al., 1981). This method is as effective in increasing pre-exercise muscle glycogen concentrations as the traditional method of carbohydrate loading (Åstrand, 1967).

Both simple and complex carbohydrates can be used to supplement the diet in preparation for prolonged heavy exercise or competition. For example, Brewer et al. (1988) showed that rice, pasta and confectionery products were equally effective in improving endurance running capacity when used for carbohydrate loading. But beginning a race, over a shorter distance, with an elevated muscle glycogen concentration, does not necessarily improve performance. When the race distance or time is such that muscle glycogen stores are not limiting, then elevated pre-race glycogen stores will have little influence on performance times. This was the case in a study of well-trained distance runners competing over a distance of 20.9 km with and without pre-race carbohydrate loading (Sherman et al., 1981). The performance time of 83 min was not improved as a result of increasing muscle glycogen concentrations before the race. Nevertheless, high rather than low concentrations of muscle and liver glycogen are necessary for runners to sustain their optimal running speeds in races over longer distances (Karlsson and Saltin, 1971).

The influence of pre-exercise carbohydrate meals on performance has not received as much attention as the pre-exercise ingestion of carbohydrate solutions (Coleman, 1994). The type and amount of carbohydrate in a meal will influence the abdominal discomfort and blood glucose concentrations at the start of exercise 3-4 h later. In one of the few studies on pre-exercise meals, Thomas and colleagues (1991) examined the

influence of low- and high-glycaemic index foods (1 g kg BM<sup>-1</sup>) on plasma glucose concentrations and endurance capacity during prolonged cycling to exhaustion. They found that a low-glycaemic index carbohydrate (lentils) produced smaller rises in plasma glucose and insulin concentrations than a high-glycaemic index carbohydrate (potato). They concluded that these more modest responses to pre-exercise carbohydrate intake were mostly responsible for the greater endurance capacity. Nevertheless, one study showed that eating a high-carbohydrate meal, made up of high-glycaemic index carbohydrates, 3 h before prolonged constant pace running to exhaustion, increased endurance capacity by 9%. This may have been a consequence of the 10% elevation in pre-exercise muscle glycogen concentration (Chryssanthopoulos et al., unpublished results). Similar results have been reported for cycling (Neufer et al., 1987; Sherman et al., 1989).

Drinking a concentrated carbohydrate solution 30-45 min before prolonged submaximal cycling to exhaustion has been shown to decrease endurance capacity (Foster et al., 1979). This impairment in performance was attributed to an increase in glycogen degradation and transient hypoglycaemia (Costill et al., 1977). Therefore, Costill and Miller (1980) advised athletes to avoid consuming carbohydrate shortly before exercise. More recent studies, however, have shown that drinking a concentrated glucose solution shortly before exercise does not produce hypoglycaemia (blood glucose < 2.5 mm) (Seifert et al., 1994), increase the rate of glycogenolysis in skeletal muscle (Fielding et al., 1987), or increase the onset of fatigue during running to exhaustion (Chryssanthopoulos et al., 1994a). In some situations, the ingestion of carbohydrate solutions shortly before exercise does improve endurance performance (Chryssanthopoulos et al., 1994b; Sherman et al., 1991). Even consuming solid carbohydrate 30 min before prolonged submaximal cycling does not appear to have a detrimental effect on performance (Alberici et al., 1993; Devlin et al., 1986).

In contrast, drinking a carbohydrate-electrolyte solution immediately before and during prolonged running improves endurance capacity (Wilber and Moffatt, 1992; Tsintzas et al., 1994). For example, Wilber and Moffatt (1992) reported an improvement in endurance capacity of 29.4% when their subjects drank a 7% carbohydrate solution during constant pace running (80%  $\dot{V}O_2$  max). A similar improvement in endurance capacity (27%) was reported by Tsintzas et al. (1994); their subjects drank a 5.5% carbohydrate-electrolyte solution immediately before and throughout constant pace running (70%  $\dot{V}O_2$  max) to exhaustion. In this latter study, there was clear evidence of glycogen sparing in the Type I fibres of the vastus lateralis muscles when the

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runners consumed the carbohydrate-electrolyte solution. This contrasts with the results of other studies which did not find glycogen sparing in the skeletal muscles of people cycling to exhaustion (see, e.g. Coggan and Coyle, 1991). At present, the only explanation for the differences in the results of these studies is the mode of exercise studied (i.e. running rather than cycling to exhaustion). Solid carbohydrate and carbohydrate solutions have surprisingly similar influences on endurance performance and the metabolic responses to 2 h of cycling (Lugo et al., 1993).

Eating a high-carbohydrate meal 3 h before running to exhaustion (70% VO<sub>2</sub> max), and then drinking a 6.9% carbohydrate-electrolyte solution throughout exercise, improves endurance capacity to a greater extent (12%) than consuming a carbohydrate-rich preexercise meal (Chryssanthopoulos et al., 1994b). However, for those athletes who cannot tolerate eating a meal even 4 h before exercise, then drinking a carbohydrate-electrolyte solution during a race may compensate for the lack of a pre-competition meal (Chryssanthopoulos et al., 1994c). This suggestion is based on the results of a simulated 30-km race, which was run under two dietary conditions. In the first, the runners consumed a carbohydrate-rich breakfast 4 h before the race and drank only water during the 30-km time-trial; in the second, the runners had a fluid placebo, instead of breakfast, but drank a 6.9% carbohydrate-electrolyte sports drink throughout the race (Chryssanthopoulos et al., 1994c).

Endurance performance is also improved, in fasted runners, as a result of drinking carbohydrate-electrolyte solutions immediately before and throughout longdistance races (Millard-Stafford et al., 1992; Tsintzas et al., 1993, 1995). Glycogen sparing, as a consequence of drinking carbohydrate-electrolyte solutions, may be one of the reasons for such improvements in endurance running performance. Tsintzas et al. (1993) reported that glycogen concentration was increased by 28% in the vastus lateralis muscles of subjects at the end of a 60-min treadmill run if they had drunk a 5.5% carbohydrate solution throughout the run. The glycogen sparing was confined to the Type I fibres and this was also the case during exercise to exhaustion when the same carbohydrate-electrolyte solution was consumed (Tsintzas et al., 1994). In contrast, glycogen sparing did not appear to be present in the skeletal muscles of runners who had a light carbohydrate breakfast 3 h before a 60-min treadmill run, during which they drank either a 6.9% carbohydrate-electrolyte solution or water (Chryssanthopoulos, unpublished results). The effective amount of carbohydrate for improving endurance running capacity and performance appears to be 40-75 g h<sup>-1</sup>, taken in small quantities throughout prolonged exercise (Coggan and Swanson, 1992).

However, the exact mechanism(s) responsible for the delay in the onset of fatigue has yet to be established.

### Recovery from exercise

The most immediate nutritional priority after prolonged heavy exercise is rehydration, closely followed by restoration of the body's carbohydrate stores. Carbohydrate-electrolyte solutions appear to be more effective in restoring fluid balance than water per se (Gonzalez-Alonso et al., 1992). Increasing the sodium concentration of the rehydration fluid improves the restoration of fluid balance (Nose et al., 1988). Drinking a volume of a carbohydrate-electrolyte solution that is greater than the volume of sweat lost during exercise also improves rehydration during the first 3-4 h after exercise, but drinking too large a volume of fluid between exercise sessions may contribute to a decrease in subsequent performance (Costill and Sparks, 1973).

Drinking carbohydrate-electrolyte solutions immediately after exercise also contributes to the restoration of the body's carbohydrate stores. The most rapid rate of muscle and liver glycogen resynthesis occurs immediately after prolonged heavy exercise when the carbohydrate stores are low (Ivy, 1991; Morris et al., 1994). In order to exploit this phenomenon, an immediate post-exercise carbohydrate intake of between 0.7 and 1.5 g kg BM<sup>-1</sup> has been recommended (Blom et al., 1987; Ivy et al., 1988). Eating high-glycaemic index carbohydrates (see Coyle, 1991, for examples of highand low-glycaemic index foods) during a post-exercise recovery period of 24 h is more effective in replacing muscle glycogen stores than eating the same quantity of low-glycaemic index foods (Burke et al., 1993). Reed and colleagues (1989) compared the merits of consuming equal amounts of solid and liquid carbohydrate on the immediate post-exercise resynthesis of muscle glycogen. Their subjects consumed the equivalent of 3 g kg BM<sup>-1</sup> of carbohydrate in the form of a carbohydrate solution (50%) on one occasion, and in the form of rice/banana cake on another occasion. The carbohydrate was administered in two parts: half was ingested immediately after exercise and the other half was ingested after 2 h. There were no differences in the rates of resynthesis of muscle glycogen at the end of 2 h (~ 6.2 mmol kg<sup>-1</sup> h<sup>-1</sup>) or 4 h ( $\sim 4.4$  mmol kg<sup>-1</sup> h<sup>-1</sup>) of recovery (Reed et al., 1989).

Delaying carbohydrate intake immediately after exercise decreases the rate of glycogen resynthesis during the first 4 h of recovery. Ivy and colleagues (1988) reported that when they gave their subjects 2 g kg

BM<sup>-1</sup> of a liquid carbohydrate immediately after 2 h of exercise (~ 70% VO<sub>2</sub> max), the rate of muscle glycogen resynthesis was equivalent to 7.7 mmol kg<sup>-1</sup> h<sup>-1</sup> during the first 2 h of recovery. However, when carbohydrate intake was withheld, the rate of glycogen resynthesis during the first 2 h of recovery was much lower (~ 2.5 mmol kg<sup>-1</sup> h<sup>-1</sup>). When carbohydrate was ingested after 2 h of recovery, then the resynthesis rates over the following 2 h were similar for the two conditions, namely carbohydrate ingestion immediately after exercise and carbohydrate ingestion after 2 h of recovery. Providing carbohydrate and protein immediately after exercise in a ratio of 3:1 produces an even more rapid rate of glycogen resynthesis over the first 4 h of recovery (Zawadzki et al., 1992). The presence of protein increases the post-exercise plasma insulin concentration and thus improves the rate of glucose uptake by the muscles.

The obvious question is, does the delay in carbohydrate ingestion, immediately after exercise, prevent the return of muscle glycogen stores in the longer term, for example over 24 h? There is some evidence to suggest that the delay may not have a detrimental effect on the repletion of muscle glycogen over a 24-h recovery period, especially if high-glycaemic index carbohydrates are consumed. Zachwieja and colleagues (1993) examined the benefits of providing a carbohydrate solution during prolonged exercise on the rate of glycogen resynthesis over a recovery period of 24 h. Their subjects performed 2 h of cycling while drinking either a 10% carbohydrate solution or a sweet placebo. Food was withheld for the first 2 h after exercise and then 24% carbohydrate solution was provided during the second 2 h of recovery in both trials (1.4 g kg BM<sup>-1</sup>). For the remainder of the 24-h recovery period, the subjects consumed prescribed high-carbohydrate meals. The rate of muscle glycogen resynthesis was depressed during the first 2 h of recovery but similar after the second 2 h for both trials. There was also no difference between muscle glycogen concentrations between the two trials after 24 h of recovery. Therefore, it appears that consuming a carbohydrate solution during exercise has no obvious influence on glycogen resynthesis rates immediately after exercise. Furthermore, the study showed that the 2-h wait before consuming carbohydrate did not delay the muscle glycogen concentration returning to pre-exercise values at the end of the 24-h recovery period. Delaying carbohydrate consumption for 2 h after prolonged heavy exercise does not decrease muscle glycogen replenishment during the following 24 h of recovery when high-glycaemic carbohydrate index foods are consumed (Febbraio et al., 1994). Therefore, the type of carbohydrate consumed after exercise is important, if muscle glycogen stores are to be restored quickly and a slight delay in

carbohydrate feeding during the immediate recovery period can be tolerated.

The rate of glycogen resynthesis immediately after prolonged exercise is a consequence not only of substrate supply, in the form of high glycaemic index carbohydrates, but also of the effects of exercise on muscle per se. Prolonged exercise increases the insulin sensitivity of skeletal muscles and the rate of glucose transport (Klip and Paquit, 1990; Wallberg-Henriksson et al., 1988). A reduction in muscle glycogen concentration is accompanied by an increase in glycogen synthase activity during the early part of recovery from exercise (Adolfsson and Ahren, 1971; Bak and Pedersen, 1990; Zachwieja et al., 1991), and this process may also be influenced by the duration of exercise, as well as the extent to which glycogen concentrations have been reduced (Yan et al., 1992). Prolonged submaximal cycling to exhaustion depends to a large extent on the recruitment of the oxidative, slow-contracting and slow-fatiguing skeletal muscle fibres (Type 1) (Vollestad et al., 1984), and these fibres have higher glycogen synthase activity immediately after exercise than Type II fibres (Piehl et al., 1974). Nevertheless, histochemical examination of the amount of glycogen resynthesized was unable to show any differences between the two fibre populations (Piehl et al., 1974), but biochemical analyses of single muscle fibres showed a greater rate of glycogen resynthesis in Type I fibres (Casey et al., 1995; Essen and Henriksson, 1974). This differential rate of glycogen resynthesis between fibre populations may have an influence on the capacity of athletes to perform maximal exercise after a few hours of recovery from prolonged submaximal exercise.

The influence of nutrition on recovery after prolonged heavy exercise has not been as extensively studied as the post-exercise recovery of muscle glycogen stores. In one of the few studies on recovery and performance, Keizer and colleagues (1987) showed that muscle glycogen concentrations can be restored to pre-exercise values in 24 h when the amount of carbohydrate ingested is carefully prescribed for each individual. Nevertheless, even though muscle glycogen concentrations did return to pre-exercise values, their subjects were unable to match their previous day's performance during an incremental cycle ergometer test of their maximal work capacity. Similarly, Nevill and colleagues (1993b) showed that a high carbohydrate diet during a 24-h recovery period did not prevent a decline in peak power output when their subjects performed 30 sprints of 6 s duration on a non-motorized treadmill. In contrast, endurance running capacity can be restored within 24 h of recovery when athletes increase their carbohydrate intake. Fallowfield and Williams (1993) reported that when the carbohydrate intake of a group of runners was increased from about 5 to 9 g kg BM<sup>-1</sup>

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during a recovery period of 22 h, they were able to reproduce their 90-min treadmill run at  $70\% \ VO_2$  max. However, when they ate their normal amount of carbohydrate ( $\sim 5$  g kg BM<sup>-1</sup>) and additional fat and protein to achieve an energy intake equivalent to the carbohydrate recovery condition, they were unable to match their previous day's run time.

Endurance capacity during high-intensity intermittent running can also be restored and improved between daily training sessions when athletes increase their daily carbohydrate intake to about 10 g kg BM<sup>-1</sup>. In one study, university soccer players ate high (10 g kg BM<sup>-1</sup>) or normal (5 g kg BM<sup>-1</sup>) carbohydrate diets, of equal energy density, during a 22-h recovery period between two 90-min tests of endurance capacity involving intermittent running, sprinting and walking. After the high-carbohydrate diet, the soccer players were able to run for approximately 3 min longer than the day before, whereas they were unable to match their previous day's performance when they maintained their normal carbohydrate intake (Nicholas *et al.*, 1994).

Even when recovery periods last only a few hours, there appears to be a benefit in consuming carbohydrate. Fallowfield and Williams (1993) showed that when runners drank a carbohydrate-electrolyte solution equivalent to 1 g kg BM<sup>-1</sup> during a 4-h recovery period, after 90 min of treadmill running (70%  $\dot{V}O_2$  max), they were able to run for another 60 min before becoming exhausted. When the runners drank an equal volume of a sweetened placebo solution, however, their run to exhaustion lasted only 40 min. Increasing the immediate post-exercise carbohydrate intake beyond 1 g kg BM<sup>-1</sup> does not necessarily increase the rate of glycogen resynthesis (Ivy, 1991); neither does it produce further improvements in endurance running capacity (Fallowfield et al., 1993). In summary, the available evidence supports the recommendation for an increase in carbohydrate intake during recovery from prolonged exercise. It appears that to achieve the best recovery within 24 h, a carbohydrate intake of about 10 g kg BM<sup>-1</sup> is required (Sherman, 1992).

#### Protein nutrition

High-protein diets have long been associated with training for fitness because of the mistaken belief that greater gains in strength can be achieved by eating more meat than is normally part of a balanced diet. Modern-day Olympians share this mistaken belief with the Olympians of Greek antiquity (Schobel, 1965). Nevertheless, the available evidence suggests that the protein requirements of athletes are greater than the daily 0.8 g kg BM<sup>-1</sup> recommended by the World Health Organization (FAO/WHO/UNU, 1985). The amount

of protein required for strength and speed athletes is within the range 1.2-1.7 g kg BM<sup>-1</sup> day<sup>-1</sup>, whereas for endurance athletes it is within the range 1.2-1.4 g kg BM<sup>-1</sup> day<sup>-1</sup>. These recommendations can easily be achieved by consuming a normal balanced diet (Lemon, 1991a). However, strength athletes involved in very heavy training may sometimes need up to 2 g kg BM<sup>-1</sup> of protein a day (Lemon, 1991b). These are very general recommendations which ensure that athletes achieve protein balance even when they are undertaking very heavy training. There is, however, little information available to develop nutritional strategies on the type and timing of protein intake as a means of enhancing the health and fitness of athletes. Although much attention has been paid to the protein requirements of male athletes, little attention has been devoted to the protein requirements of females in particular and young athletes in general (Hickson and Wolinsky, 1989). Neither has sufficient attention been paid to the changes in protein requirements of athletes who are injured or ill. For example, during injury and illness, protein degradation increases, and so there may be nutritional strategies to offset this catabolic state by supplementing diets with selected amino acids (Newsholme et al., 1991; Reeds et al., 1994). Providing runners with glutamine (5 g) during recovery from a marathon race, as a means of supporting immune cell function, did not however prevent a decrease in circulating lymphocyte number, which persisted until the day after the marathon (Poortmans et al., 1994).

Branched-chain amino acid supplementation has been proposed as a means of indirectly decreasing the central component of fatigue during prolonged exercise (see Davis, this issue; Blomstrand et al., 1991). However, well-controlled laboratory studies have not been able to confirm the benefits of branched-chain amino acid supplementation (Lambert et al., 1994b; van Hall et al., 1994).

Another rationale that has been offered for supplementing athletes' diets with amino acids is that they may stimulate the release of growth hormone. For example, arginine and ornithine are particularly popular amino acids because they are believed to have 'anabolic' effects through their ability to stimulate a biologically significant increase in the plasma concentration of human growth hormone (Hatfield, 1987). What is usually overlooked by strength athletes and sprinters is that even brief periods of high-intensity exercise produce significant increases in the concentration of circulating growth hormone. For example, a 30-s maximal sprint on a non-motorized treadmill produced a 14-fold increase in plasma growth hormone in sprint-trained athletes and a 6-fold increase in endurance-trained athletes. The growth hormone concentrations of the sprinters were still about 11 times higher  $(44.9 \pm 27.0 \text{ mU } 1^{-1})$  than their pre-exercise values

 $(4.0 \pm 2.0 \text{ mU } 1^{-1})$  after 60 min recovery (Nevill *et al.*, 1993a). Therefore, brief periods of high-intensity exercise *per se* create the effect that athletes try to achieve by taking amino acid supplements.

#### Fat metabolism

Too much fat in the diet – rather than too little – is the problem most athletes face, because consuming too much fat makes it more difficult to consume the recommended amounts of carbohydrate. However, reducing one's fat intake to very low levels is not recommended, not only because of the important role that fat metabolism plays in energy production, but also because lipids per se contribute to general health. For example, lipids form part of the membranes of a wide variety of cells, not least of which are the membranes of neural tissue. The essential fatty acids must be a part of any diet, whereas saturated fat intake should be restricted. However, low-fat diets are difficult to achieve because so much of food manufacturing and preparation involves the use of fats in some form or other. Even if athletes are successful in achieving a lowfat diet, they may be unsuccessful in achieving the recommended balance of the different fats found in foods. For example, dietary guidelines recommend that saturated fatty acids should contribute no more than 10% of our daily energy intake, whereas the remainder of the fat intake should be provided by monounsaturated fatty acids (15%), polyunsaturated fatty acids (6%), linoleic acid (1%), linolenic acid (0.2%) and trans-fatty acids (< 2%) (Department of Health, 1991, 1994). Alphalinolenic acid is the parent fatty acid of a series of fatty acids called 'omega-3 fatty acids'. These fatty acids are of interest because they are part of the complement of essential fatty acids and there is evidence to suggest that they have a role as therapeutic and prophylactic agents, especially in relation to cardiovascular and inflammatory diseases (Sanders, 1993).

The contribution of fatty acids to energy metabolism during exercise is well known (Gollnick, 1977). However, what is less clear and hence the subject of much research is the relative contributions of fat metabolism to energy production in human skeletal muscle during exercise of varying intensities and durations. It is quite clear that carbohydrate metabolism alone cannot support energy metabolism for any significant length of time, even if biochemical pathways allowed it. Nevertheless, fatty acid metabolism plays a supporting role in energy production during heavy and high-intensity exercise, as is reflected by a premature onset of fatigue during exercise when fatty acid mobilization is reduced (Bergstrom et al., 1969; Pernow and Saltin, 1971). Intramuscular triglyceride stores also appear to make a

significant contribution to muscle metabolism during exercise and so substrate availability is rarely the cause of a decrease in fat metabolism during prolonged submaximal exercise (Romijn et al., 1993). During prolonged exercise, there is an ever-increasing reliance on the blood supply of substrates for muscle metabolism. In athletes there is an increase in the contribution of fatty acids and a decrease in the contribution of glucose to muscle metabolism as exercise continues (Turcotte et al., 1992).

Although prolonged fasting before exercise raises plasma fatty acid concentrations during exercise, the performance benefits of this practice have only been shown in rats in laboratory experiments (Dohm et al., 1983), not in humans (Nieman et al., 1987). In fact, a 24-h fast before high-intensity exercise has been shown to be detrimental to performance (Gleeson et al., 1988). Plasma fatty acids can also be raised by consuming a high-fat meal containing carbohydrate, and may lead to an increased rate of fat oxidation at rest (Griffiths et al., 1994a) and during forearm exercise (Griffiths et al., 1994b). Christensen and Hansen (1939) showed that after 3 days on a high-fat diet, energy metabolism shifted towards an increased contribution from fat during prolonged submaximal cycling. Therefore, it is not surprising that 2 weeks on a high-fat diet improved the capacity of welltrained cyclists to use a greater amount of fat during submaximal exercise (Lambert et al., 1994a). What is surprising, however, is that during cycling at 50%  $\dot{V}$ O<sub>2</sub> max, the cyclists on the high-fat diet were able to exercise longer than the group on a high-carbohydrate diet.

In contrast, there was no apparent benefit of an increased dietary fat intake on performance times of runners during a 30-km treadmill time-trial (Williams et al., 1992). Carbohydrate-loading was undertaken during the 7 days between two 30-km treadmill time-trials, using confectionery products. Daily energy intake and the amount of carbohydrate consumed were increased by approximately 30 and 52%, respectively, whereas daily fat intake was increased by 28%. The control group consumed their normal amount of carbohydrate but increased their fat and protein intake in order to match the daily energy intake of the runners on the high-carbohydrate diet. As a consequence of matching the energy intakes of the two groups in this way, the members of the control group doubled their daily fat consumption such that it represented approximately 50% of their energy intake for the 7 days before the two simulated longdistance races. The six men on the high-carbohydrate diet improved their performance times for the 30 km (127.4  $\pm$  4.9 vs 131.0  $\pm$  5.4 min), whereas the members of the control group showed no improvement in performance (Williams et al., 1992).

Endurance training increases the capacity of skeletal muscles for fat metabolism (Henriksson and Hickner, 1994). Therefore, fat metabolism will cover a greater S8 Williams

proportion of the energy production of athletes during exercise than is the case for untrained people. Nevertheless, even though fat metabolism is enhanced as a result of endurance training, and may also be increased as a consequence of eating a high-fat diet, there seems little to recommend this dietary practice for athletes preparing for competitions which involve sustained high-intensity exercise.

In summary, when athletes consume a wide range of foods, in sufficient quantity to cover their daily energy needs, paying particular attention to the carbohydrate and fat content of their diets, they will be well prepared to cope successfully with the challenges of heavy training and competition.

#### References

- Adolfsson, S. and Ahren, K. (1971). Control mechanisms for the synthesis of glycogen in striated muscle. In *Muscle Metabolism During Exercise* (edited by B. Pernow and B. Saltin), pp. 257-272. New York: Plenum Press.
- Alberici, J., Farrell, P., Kris-Etherton, P. and Shively, C. (1993).
  Effects of preexercise candy bar ingestion on glycemic response, substrate utilisation, and performance. *International Journal of Sport Nutrition*, 3, 323–333.
- Astrand, P.-O. (1967). Diet and athletic performance. Federation Proceedings, 26, 1772–1777.
- Bak, J. and Pedersen, O. (1990). Exercise-enhanced activation of glycogen synthase in human skeletal muscle. *American Journal* of *Physiology*, 248, E957–E963.
- Bergstrom, J., Hermansen, L., Hultman, E. and Saltin, B. (1967). Diet, muscle glycogen and physical performance. *Acta Physiologica Scandinavica*, 71, 140–150.
- Bergstrom, J., Hultman, E. and Jorfeldt, L. (1969). Effect of nicotinic acid on physical working capacity and on metabolism of muscle glycogen in man. *Journal of Applied Physiology*, 26, 170-176.
- Blom, P., Hostmark, A.T., Vaage, O., Kardel, K.R. and Maehlum, S. (1987). Effect of different post-exercise sugar diets on the rate of muscle glycogen synthesis. *Medicine and Science in Sports and Exercise*, 19, 491-496.
- Blomstrand, E., Hassmen, P., Ekblom, B. and Newsholme, E.A. (1991). Administration of branched-chain amino acids during sustained exercise: Effects on performance and on plasma concentration of some amino acids. *European Journal of Applied Physiology*, 63, 83–88.
- Brewer, J., Williams, C. and Patton, A. (1988). The influence of high carbohydrate diets on endurance running performance. European Journal of Applied Physiology, 57, 698-706.
- Burke, L., Collier, G. and Hargreaves, M. (1993). Muscle glycogen storage after prolonged exercise: Effect of the glycaemic index on carbohydrate feedings. *Journal of Applied Physiology*, 75, 1019-1023.
- Casey, A., Short, A., Hultman, E. and Greenhaff, P.L. (1995). Glycogen resynthesis in human muscle fibre types following

- exercise induced glycogen depletion. Journal of Physiology, 483, 265-271.
- Christensen, E.H. and Hansen, O. (1939). Arbeitsfahigkeit und Ehrnahrung. Skandinavica Archive Physiologica, 81, 160–175.
- Chryssanthopoulos, C., Hennessy, L. and Williams, C. (1994a). The influence of preexercise glucose ingestion on endurance running capacity. *British Journal of Sports Medicine*, 28, 105–119.
- Chryssanthopoulos, C., Williams, C., Nowitz, A., Kotsiopoulou, C. and Vleck, V. (1994b). Comparison between carbohydrate feedings before exercise, during, or in combination on endurance running capacity. *Clinical Science*, 87, 44A (suppl.).
- Chryssanthopoulos, C., Williams, C., Wilson, W., Asher, L. and Hearne, L. (1994c). Comparison between carbohydrate feedings before and during exercise on running performance during a 30 km treadmill time trial. *International Journal of Sport Nutrition*, 4, 374–386.
- Coggan, A. and Coyle, E. (1991). Carbohydrate ingestion during prolonged exercise: Effects on metabolism and performance. In Exercise and Sports Science Reviews (edited by J. Holloszy), pp. 1–40. London: Williams and Wilkins.
- Coggan, A. and Swanson, S. (1992). Nutritional manipulations before and during endurance exercise: Effects on performance. Medicine and Science in Sports and Exercise, 24, S331– S335.
- Coleman, E. (1994). Update on carbohydrate: Solid versus liquid. International Journal of Sport Nutrition, 4, 80-88.
- Costill, D. and Hargreaves, M. (1992). Carbohydrate nutrition and fatigue. Sports Medicine, 13, 86-92.
- Costill, D. and Miller, J. (1980). Nutrition for endurance sport: Carbohydrate and fluid balance. *International Journal of Sports Medicine*, 1, 2–14.
- Costill, D.L. and Sparks, K.E. (1973). Rapid fluid replacement following thermal dehydration. *Journal of Applied Physiology*, 34, 299-303.
- Costill, D., Coyle, E., Dalsky, G., Evans, W., Fink, W. and Hoopes, D. (1977). Effects of elevated plasma FFA and insulin on muscle glycogen usage during exercise. *Journal* of Applied Physiology, 43, 695-699.
- Coyle, E.F. (1991). Timing and method of increased carbohydrate intake to cope with heavy training, competition and recovery. *Journal of Sports Sciences*, 9, 2–24 (suppl.).
- Department of Health (1991). Dietary Reference Values for Food Energy and Nutrients for the United Kingdom. Report on Health and Social Subjects No. 41. London: HMSO.
- Department of Health (1994). Nutritional Aspects of Cardiovascular Disease. Report on Health and Social Subjects No. 46. London: HMSO.
- Devlin, J.T. and Williams, C. (1991). Foods, nutrition and sports performance: A final consensus statement. *Journal of Sports Sciences*, 9, iii (suppl.).
- Devlin, J.T., Calles-Escandon, J. and Horton, E.S. (1986). Effects of preexercise snack feeding on endurance cycle exercise. *Journal of Applied Physiology*, **60**, 980–985.
- Dohm, G., Tapscott, E., Barakat, H. and Kasparek, G. (1983). Influences of fasting on glycogen depletion in rats during exercise. *Journal of Applied Physiology*, 55, 830-833.

- Essen, B. and Henriksson, J. (1974). Glycogen content of individual muscle fibres in man. *Acta Physiologica Scandinavica*, **90**, 645-647.
- Fallowfield, J. and Williams, C. (1993). Carbohydrate intake and recovery from prolonged exercise. *International Journal of Sport Nutrition*, 3, 150–164.
- Fallowfield, J., Williams, C. and Wilson, W. (1993). Carbohydrate intake during recovery from prolonged running. *International Journal of Sports Medicine*, 14, 298A.
- FAO/WHO/UNU (1985). Energy and Protein Requirements. Report of a Joint Expert Consultation, Technical Report Series No. 724. Geneva: World Health Organization.
- Febbraio, M., Parkin, J., Martin, I., Stojanovska, L. and Carey, M. (1994). The effect of timing of ingestion of high glycaemic index food on muscle glycogen storage following prolonged exercise. Clinical Science, 87, 48A (suppl.).
- Fielding, R.A., Costill, D.L., Fink, W.J., King, D.S., Kovaleski, J.E. and Kirwan, J.P. (1987). Effects of pre-exercise carbohydrate feedings on muscle glycogen use during exercise in welltrained runners. *European Journal of Applied Physiology*, 56, 225-229.
- Foster, C., Costill, D. and Fink, W. (1979). Effects of preexercise feedings on endurance performance. *Medicine and Science in Sports and Exercise*, 11, 1-5.
- Gleeson, M., Greenhaff, P.L. and Maughan, R.J. (1988). Influence of a 24 h fast on high intensity cycle exercise performance in man. European Journal of Applied Physiology, 57, 653-659.
- Goforth, H.W., Hodgdon, J.A. and Hilderbrand, R.L. (1980). A double blind study of the effects of carbohydrate loading upon endurance performance. *Medicine and Science in Sports and Exercise*, 12, 108A.
- Gollnick, P. (1977). Free fatty acid turnover and the availability of substrates as a limiting factor in prolonged exercise. *Annals of the New York Academy of Sciences*, 301, 64–71.
- Gonzalez-Alonso, J., Heaps, C.L. and Coyle, E.F. (1992).Rehydration after exercise with common beverages and water.International Journal of Sports Medicine, 13, 399–406.
- Griffiths, J., Humphreys, S., Clark, M., Fielding, B. and Frayn, K. (1994a). Immediate metabolic availability of dietary fat in combination with carbohydrate. *American Journal of Clinical Nutrition*, 59, 53-59.
- Griffiths, J., Humphreys, S., Clark, M. and Frayn, K. (1994b). Forearm substrate utilisation during exercise after a meal containing both fat and carbohydrate. *Clinical Science*, 86, 165-175.
- Hatfield, F.C. (1987). Ultimate Sports Nutrition. Chicago, IL: Contemporary Books, Inc.
- Henriksson, J. and Hickner, R. (1994). Training-induced adaptations in skeletal muscle. In Oxford Textbook of Sports Medicine (edited by M. Harries, C. Williams, W. Stanish and L. Micheli), pp. 27–45. Oxford: Oxford University Press.
- Hickson, J. and Wolinsky, I. (1989). Human protein intake and metabolism in exercise and sport. In *Nutrition in Exercise and Sport* (edited by J.A.W. Hickson), pp. 5–36. Boca Raton, FL: CRC Press.
- Ivy, J.L. (1991). Muscle glycogen synthesis before and after exercise. Sport Medicine, 11, 6-19.
- Ivy, J.L., Lee, M.C., Brozinick, J.T. and Reed, M.J. (1988).
  Muscle glycogen storage after different amounts of carbohy-

- drate ingestion. Journal of Applied Physiology, 65, 2018-2023.
- Karlsson, J. and Saltin, B. (1971). Diet, muscle glycogen and endurance performance. Journal of Applied Physiology, 31, 203-206.
- Keizer, H., Kuipers, H. and van Kranenburg, G. (1987). Influence of liquid and solid meals on muscle glycogen resynthesis, plasma fuel hormone response, and maximal physical working capacity. *International Journal of Sports Medicine*, 8, 99-104.
- Klip, A. and Paquit, M. (1990). Glucose transport and glucose transporters in muscle and their metabolic regulation. *Diabetes Care*, 13, 228–243.
- Lambert, M., Speechly, D., Dennis, S. and Noakes, T. (1994a).
  Enhanced endurance in trained cyclists during moderate intensity exercise following 2 weeks adaptation to a high fat diet. European Journal of Applied Physiology, 69, 287-293.
- Lambert, M., Velloza, P., Wilson, G. and Dennis, S. (1994b). The effect of carbohydrate and branch chain supplementation on cycling performance and mental fatigue. *Clinical Science*, 87, 53 (suppl.).
- Lemon, P. (1991a). Effect of exercise on protein requirements. Journal of Sports Sciences, 9, 53-70 (suppl.).
- Lemon, P.W.R. (1991b). Protein and amino acid needs of the strength athlete. *International Journal of Sport Nutrition*, 1, 127-145.
- Lugo, M., Sherman, W., Wimer, G. and Garleb, K. (1993).
  Metabolic responses when different forms of carbohydrate energy are consumed during cycling. *International Journal of Sport Nutrition*, 3, 398–407.
- Millard-Stafford, L.M., Sparling, P.B., Rosskope, L.B. and Dicarlo, L.J. (1992). Carbohydrate-electrolyte replacement improves distance running performance in the heat. *Medicine* and Science in Sports and Exercise, 24, 934-940.
- Morris, P.G., McIntyre, D.J.O., Coxon, R., Bachelard, H., Moriarty, K.T., Greenhaff, P.L. and Macdonald, I. (1994). Nuclear magnetic resonance spectroscopy as a tool to study carbohydrate metabolism. *Proceedings of the Nutrition Society*, 53, 335-343.
- Neufer, P.D., Costill, D.L., Flynn, M.G., Kirwan, J., Mitchell, J. and Houmard, J. (1987). Improvements in exercise performance: Effects of carbohydrate feedings and diet. *Journal of Applied Physiology*, 62, 983-988.
- Nevill, M.E., Holmyard, D., Hall, G., Allsop, P., van Oosterhout, A. and Burrin, J.M. (1993a). Growth hormone responses to treadmill sprinting in sprint- and endurance-trained male athletes. *Journal of Physiology*, 473, 73P.
- Nevill, M.E., Williams, C., Roper, D., Slater, C. and Nevill, A.M. (1993b). Effect of diet on performance during recovery from intermittent sprint exercise. *Journal of Sports Sciences*, 11, 119-126.
- Newsholme, E.A., Parry-Billings, M., McAndrews, N. and Budgett, R. (1991). A biochemical mechanism to explain some characteristics of overtraining. In *Advances in Nutrition and Top Sport* (edited by F. Brouns), pp. 79–93. Basel: Karger.
- Nicholas, C., Nuttall, F., Hawkins, R., Green, P. and Williams, C. (1994). Influence of diet on recovery from intermittent

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high intensity exercise. Journal of Sports Sciences, 12, 147.

- Nieman, D.C., Carlson, K.A., Brandstater, M., Naegele, R.T. and Blankenship, J.W. (1987). Running endurance in 27-h-fasted humans. *Journal of Applied Physiology*, 63, 2502-2509.
- Nose, H., Mack, G.W., Shi, X. and Nadel, E.R. (1988). Role of osmolality and plasma volume during rehydration in humans. *Yournal of Applied Physiology*, 65, 325-331.
- Pernow, B. and Saltin, B. (1971). Availability of substrates and capacity for prolonged heavy exercise. *Journal of Applied Physiology*, 31, 416–422.
- Piehl, K., Adolfsson, S. and Nazar, K. (1974). Glycogen storage and glycogen synthetase activity in trained and untrained muscle of man. Acta Physiologica Scandinavica, 90, 779-788.
- Poortmans, J., Castell, L., Leclercq, R., Brasseur, M., Duchateau, J. and Newsholme, E.A. (1994). Influence of glutamine supplementation on blood lymphocytes and plasma substrate levels after a marathon race. *Clinical Science*, 87, 25 (suppl.).
- Reed, M., Brozinick, J., Lee, M. and Ivy, J. (1989). Muscle glycogen storage postexercise: Effect of mode of carbohydrate administration. *Journal of Applied Physiology*, 66, 720-726.
- Reeds, P., Fjeld, C. and Jahoor, F. (1994). Do differences between the amino acid composition of acute phase and muscle proteins have a bearing on nitrogen loss in traumatic states? *Journal of Nutrition*, 124, 906–910.
- Romijn, J., Coyle, E., Sidossis, L., Gastaldelli, A., Horowitz, J., Endert, E. and Wolfe, R. (1993). Regulation of endogenous fat and carbohydrate metabolism in relation to exercise intensity and duration. *American Journal of Physiology*, 265, E380-E391.
- Sanders, T. (1993). Marine oils: Metabolic effects and role in human nutrition. Proceedings of the Nutrition Society, 52, 457-472.
- Schobel, H. (1965). The Ancient Olympic Games. New York: Van Nostrand.
- Seifert, J., Paul, G., Eddy, D. and Murray, R. (1994). Glycemic and insulinemic responses to preexercise carbohydrate feedings. *International Journal of Sport Nutrition*, 4, 46-53.
- Sherman, M. (1992). Recovery from endurance exercise. *Medicine and Science in Sports and Exercise*, 24, S366-S339 (suppl.).
- Sherman, W., Costill, D., Fink, W. and Miller, J. (1981). Effect of exercise-diet manipulation on muscle glycogen and its subsequent utilisation during performance. *Inter*national Journal of Sports Medicine, 114, 114-118.
- Sherman, W., Brodowicz, G., Wright, D., Allen, W.K., Simonsen, J. and Dernbach, A. (1989). Effects of 4 h preexercise carbohydrate feedings on cycling performance. *Medicine and Science in Sports and Exercise*, 21, 598-604.
- Sherman, W., Peden, M. and Wright, D. (1991). Carbohydrate feedings 1 h before exercise improves cycling performance. American Journal of Clinical Nutrition, 54, 866-870.

Thomas, D., Brotherhood, J. and Brand, J. (1991). Carbohydrate feeding before exercise: Effects of the glycemic index. *International Journal of Sports Medicine*, 12, 180-186.

- Tsintzas, K.O., Liu, R., Williams, C., Campbell, I. and Gaitanos, G. (1993). The effect of carbohydrate ingestion on performance during a 30-km race. *International Journal of Sport Nutrition*, 3, 127-139.
- Tsintzas, K., Williams, C. and Boobis, L. (1994). Muscle glycogen in different fibre types during running with and without carbohydrate ingestion. *Clinical Science*, 87, 35A (suppl.).
- Tsintzas, K., Williams, C., Wilson, W. and Burrin, J. (1995). Influence of carbohydrate-electrolyte drinks on marathon running performance. *European Journal of Applied Physiology*, 70, 154-160.
- Turcotte, L.P., Richter, E.A. and Kiens, B. (1992). Increased plasma FFA uptake and oxidation during prolonged exercise in trained vs untrained humans. *American Journal of Physiology*, **262**, E791-799.
- van Hall, G., Raaymakers, J., Saris, W. and Wagenmakers, A. (1994). Supplementation with branched-chain amino acids (BCCA) and tryptophan has no effect on performance during prolonged exercise. *Clinical Science*, 87, 52 (suppl.).
- Vollestad, N., Vaage, O. and Hermansen, L. (1984). Muscle glycogen depletion patterns in Type I and subgroups of Type II fibres during prolonged severe exercise in man. Acta Physiologica Scandinavica, 122, 433-441.
- Wallberg-Henriksson, H., Constable, S.H., Young, D.A. and Holloszy, J.O. (1988). Glucose transport into rat skeletal muscle: Interaction between exercise and insulin. *Journal* of Applied Physiology, 65, 909-913.
- Wilber, R. and Moffatt, R. (1992). Influence of carbohydrate ingestion on blood glucose and performance in runners. *International Journal of Sport Nutrition*, 2, 317– 327.
- Williams, C., Brewer, J. and Walker, M. (1992). The effect of a high carbohydrate diet on running performance during a 30-km treadmill time trial. European Journal of Applied Physiology, 65, 18-24.
- Yan, Z., Spencer, M. and Katz, A. (1992). Effect of low glycogen on glycogen synthase in human muscle during and after exercise. *Acta Physiologica Scandinavica*, 145, 345-352.
- Zachwieja, J., Costill, D.L., Pascoe, D.D., Robergs, R.A. and Fink, W.J. (1991). Influence of muscle glycogen depletion on the rate of resynthesis. *Medicine and Science in Sports and Exercise*, 23, 44-48.
- Zachwieja, J., Costill, D. and Fink, W. (1993). Carbohydrate ingestion during exercise: Effects on muscle glycogen resynthesis after exercise. *International Journal of Sport* Nutrition, 3, 418-430.
- Zawadzki, K.M., Yaspelkis III, B.B. and Ivy, J.L. (1992). Carbohydrate-protein complex increases the rate of muscle glycogen storage after exercise. Journal of Applied Physiology, 72, 1854-1859.