Abstract
Dietary protein ingestion after exercise stimulates muscle protein synthesis, inhibits protein breakdown and, as such, stimulates net muscle protein accretion following resistance as well as endurance type exercise. Protein ingestion during and/or immediately after exercise has been suggested to facilitate the skeletal muscle adaptive response to each exercise session, resulting in more effective muscle reconditioning. A few basic guidelines can be defined with regard to the preferred type and amount of dietary protein and the timing by which protein should be ingested. Whey protein seems to be most effective to increase post-exercise muscle protein synthesis rates. This is likely attributed to its rapid digestion and absorption kinetics and specific amino acid composition. Ingestion of approximately 20 g protein during and/or immediately after exercise is sufficient to maximize post-exercise muscle protein synthesis rates. Additional ingestion of large amounts of carbohydrate does not further increase post-exercise muscle protein synthesis rates when ample protein is already ingested. Dietary protein should be ingested during and/or immediately after cessation of exercise to allow muscle protein synthesis rates to reach maximal levels. Future research should focus on the impact of the timing of protein provision throughout the day on the adaptive response to more prolonged exercise training.

Skeletal Muscle Plasticity
It has been well established that nutrition is a key factor in determining exercise performance capacity. Many recreational and professional athletes apply short-term nutritional interventions to maximize performance capacity. Specifically designed sports nutrition products have been developed and are widely used among athletes in an effort to compensate for the metabolic demands imposed
upon by competition. However, as many athletes will reach their limits with regard to training volume and intensity, proper dietary practice to support the adaptive response to more prolonged training has become of key importance. A greater adaptive response to the many training hours spent in the gym or on the field would improve training efficiency and, as such, improve performance capacity. The latter has renewed the interest among athletes, coaches, and scientists in the role of the diet and nutritional modulation in optimizing training efficiency. This chapter will provide an overview on the impact of dietary protein administration following exercise on the skeletal muscle adaptive response.

Skeletal muscle tissue easily adapts to structural changes in muscle (dis)use. This level of adaptability, often referred to as muscle tissue plasticity, becomes most evident when we compare the phenotypic response to more prolonged resistance versus endurance type exercise training. Simply compare the physique of a professional weightlifter with that of a marathon runner. The capacity of skeletal muscle tissue to adapt to changes in its use (or disuse) is a consequence of the fact that skeletal muscle tissue turns over at a rate of $\sim1$–$2\%$ per day. Throughout a normal day, muscle protein synthesis rates may vary considerably and range between 0.04 and 0.14\% per hour. The latter largely depends on food intake and habitual physical activity, the two main anabolic stimuli. Food intake, or rather protein ingestion, directly elevates muscle protein synthesis rates. Following protein digestion and absorption, the rise in plasma essential amino acid (EAA) concentrations (with leucine in particular) stimulates muscle protein synthesis rates. Such a postprandial increase in muscle protein synthesis rate will typically last for 2–3 h after meal ingestion. It is obvious that amino acids are much more than simply precursors of de novo muscle protein synthesis, as they also act as strong nutritional signaling molecules regulating multiple cellular processes.

In addition to food intake, physical activity represents another potent anabolic stimulus. A single bout of physical activity or exercise will strongly increase muscle protein synthesis rates, an effect that can persist for more than 24 h. The stimulating properties of food intake and physical activity on muscle protein synthesis throughout the day compensate for daily protein breakdown, thereby allowing skeletal muscle maintenance throughout most of our lifespan.

**Dietary Protein Ingestion following Exercise**

For any athlete in training, the main goal is to adapt to the exercise training regimen, thereby allowing structural changes to occur that will allow him or her to obtain a higher performance level. For muscle tissue reconditioning to
occur, muscle protein synthesis and breakdown rates need to be increased over a given period of time. A single session of exercise will increase skeletal muscle protein synthesis and, to a lesser extent, muscle protein breakdown rates, thereby improving muscle protein balance [1]. Of course, differences will exist in the specific sets of muscle proteins that are expressed following various types of exercise. Whereas resistance type exercise mainly stimulates the expression of myofibrillar proteins, endurance type exercise mainly increases the expression of proteins involved in oxidative metabolism, thereby allowing sport-specific muscle adaptation [2]. Though exercise will improve muscle protein balance, net balance will remain negative in the absence of food intake. Consequently, nutrition is required for proper muscle reconditioning and to allow muscle hypertrophy to occur. It is here that the synergy between exercise and nutrition becomes evident. When protein is ingested following a single bout of exercise, muscle protein synthesis rates are increased to a much higher level. Furthermore, muscle protein synthesis rates also remain elevated for an extended period of time when compared with a normal postprandial response [3]. More recent work from our laboratory shows that exercise performed prior to food intake will allow more of the ingested protein to be used for de novo muscle protein synthesis [4]. The latter clearly shows that the metabolic fate of ingested protein largely depends on the activity performed prior to food consumption. These stimulating effects of exercise on the postprandial muscle protein synthetic response seem to be long-lived, with the protein synthetic response to protein ingestion still being elevated 24 h after the last exercise session [5]. There is a big challenge ahead to investigate how we can use this information to define dietary regimens that will optimize post-exercise muscle protein reconditioning. So far, there are surprisingly little data on the impact of the various nutritional factors that can modulate the post-exercise muscle protein synthetic response. However, some data have been acquired on the amount and type of dietary protein and the desired timing of protein ingestion that will optimize post-exercise muscle protein synthesis rates.

**Amount of Dietary Protein**

Protein/amino acid administration is required to stimulate post-exercise muscle protein synthesis rates, suppress the exercise-induced increase in protein breakdown and, as such, to achieve a positive muscle protein balance [6]. Tipton et al. [7] showed that ingestion of either mixed amino acids (MAA) or EAA only effectively stimulated post-exercise muscle protein synthesis rates. Since then,
numerous other studies have shown that amino acid and/or protein administration increases muscle protein synthesis rates following resistance type exercise [7–14] as well as endurance type exercise activities [15–17]. In short, post-exercise protein ingestion is required to facilitate subsequent muscle reconditioning.

Previously, Tipton et al. [7] showed that ingestion of 40 g MAA or EAA effectively stimulated post-exercise muscle protein synthesis. Since the ingestion of 40 g MAA or 40 g EAA resulted in a similar net protein balance, it was suggested that it might not be necessary to ingest nonessential amino acids during immediate post-exercise recovery. Follow-up studies assessed the impact of ingesting merely 6 g EAA (which would translate to ~12 g protein) with and without carbohydrate, and showed that this amount was also effective in stimulating post-exercise muscle protein synthesis. However, ingestion of such a small amount of EAA after exercise resulted in a positive net protein balance for up to 2 h only, after which net protein balance became negative again [9]. The latter implies that ingestion of such a small amount of amino acids is insufficient to remain in an anabolic state. Recently, Moore et al. [18] conducted a dose-response study to investigate the relationship between the amount of dietary protein ingested and subsequent post-exercise muscle protein synthesis rates (fig. 1). The fractional mixed muscle protein synthetic rate increased with the ingestion of greater amounts of protein, reaching maximal synthesis rates fol-

Fig. 1. Dose-response relationship between the amount of protein ingested and post-exercise muscle protein synthesis rates. Values represent means ± SEM. Means with different letters are significantly different from each other. Figure redrawn from Moore et al. [18].
following ingestion of 20 g intact (egg) protein, which provides approximately 8.6 g EAA. The authors speculated that athletes should ingest such an amount of dietary protein 5–6 times daily to allow maximal stimulation of skeletal muscle protein synthesis rate throughout the day. More work is needed to assess the dose-response relationship between the amount of protein and the expression of different sets of protein during recovery from various types of exercise.

**Source of Dietary Protein**

Various dietary protein sources have been used in studies investigating the impact of post-exercise protein provision on the muscle protein synthetic response. Improvements in post-exercise protein balance and/or greater muscle protein synthesis rates have been reported following the ingestion of whey protein [8], casein protein [8], soy protein [19], casein protein hydrolysate [11, 20], egg protein [18], and whole-milk and/or fat-free milk [19, 21]. So what protein source maximizes post-exercise muscle protein synthesis rates? That question is difficult to answer as it is impossible to compare protein synthesis rates between these studies. Differences in the type, intensity, and duration of the exercise performed prior to protein ingestion, the duration of the recovery period that is being assessed, and the amount, type, and timing of the protein administered, modulate the post-exercise muscle protein synthetic rate. Only a few studies have compared differences in the post-exercise muscle protein synthetic response following the ingestion of protein sources.

Milk-derived proteins, such as whey and casein, seem to offer an anabolic advantage over soy protein [19, 22]. Casein and whey protein have distinct anabolic properties, which can be attributed to differences in digestion and absorption kinetics as well as amino acid composition [23, 24]. Whey protein is a soluble protein that is rapidly digested and absorbed following ingestion. In contrast, intact casein tends to clot in the stomach after ingestion, thereby delaying digestion and absorption, resulting in a slower release of protein-derived amino acids in the circulation [25]. The faster, more transient rise in plasma amino acid concentrations following whey ingestion generally leads to a more pronounced stimulation of muscle protein synthesis rate during the first few hours following ingestion when compared with casein ingestion [23]. The latter is likely also attributed to the higher leucine content of whey versus casein protein [22, 24]. However, these findings do not imply that additional leucine supplementation can further augment the post-exercise muscle protein synthetic response to food intake. Previously, we have reported that coingestion of crystalline leucine does not further increase post-exercise muscle protein synthesis rates when ample protein is already ingested [11, 20, 26].
More work is required to assess the impact of digestion and absorption kinetics and amino acid composition of a protein source on stimulating muscle protein reconditioning following resistance or endurance type exercise activities.

**Carbohydrate Ingestion**

Carbohydrate ingestion following exercise inhibits exercise-stimulated muscle protein breakdown, but does not affect muscle protein synthesis rates [8]. Though carbohydrate ingestion can improve muscle protein balance, net balance will remain negative without protein intake. The inhibitory effect of carbohydrate ingestion on protein breakdown has been attributed to the concomitant rise in circulating insulin. Consequently, many athletes involved in resistance type exercise training often ingest large quantities of carbohydrate with protein following cessation of exercise. Though the combined ingestion of protein with large amounts of carbohydrate is generally advocated in popular media, there is little scientific support to suggest that coingestion of carbohydrate will augment net muscle protein accretion following exercise. In an attempt to assess whether carbohydrate coingestion is required to maximize post-exercise muscle protein synthesis, we observed no benefit of the coingestion of either a small or large amount of carbohydrate on post-exercise muscle protein synthesis rates under conditions where ample protein is ingested [10]. Though carbohydrate coingestion does not seem to be required to maximize post-exercise muscle protein synthesis rates, it is likely that some carbohydrate can attenuate the post-exercise rise in muscle protein breakdown rate, thereby improving net protein balance [8]. Furthermore, as muscle glycogen content can be reduced by 30–40% following a single session of resistance type exercise [27], some carbohydrate coingestion may be preferred when these athletes wish to allow full muscle glycogen repletion to maintain exercise performance capacity.

**Timing of Dietary Protein Ingestion**

Besides the amount and type of protein, the timing of protein ingestion forms another key factor modulating post-exercise muscle anabolism. Levenhagen et al. [28] reported a more positive post-exercise net protein balance after consuming a (protein containing) supplement immediately after cessation of exercise as opposed to 3 h later. Furthermore, recent studies suggest that protein coingestion prior to and/or during exercise may further stimulate post-exercise muscle protein accretion [14, 29]. Tipton et al. [14] were the first to show that amino acid in-
Dietary protein ingestion prior to, as opposed to after, exercise augments net muscle protein accretion during subsequent post-exercise recovery. The stimulating effects of protein or amino acid supplementation prior to exercise on muscle protein synthesis after exercise have previously been attributed to a more rapid supply of amino acids during the acute stages of post-exercise recovery. In addition, we speculated that protein ingestion prior to and/or during resistance type exercise could already stimulate muscle protein synthesis during exercise conditions, allowing muscle protein synthesis rates to be elevated for an extended duration. In a recent study, we confirmed that coingestion of protein with carbohydrate before and during 2 h of intermittent resistance type exercise stimulates muscle protein synthesis during exercise [29] (fig. 2). The impact of protein coingestion on mixed muscle protein synthesis during exercise may be restricted to intermittent, resistance-type exercise activities [29]. It remains to be determined if protein ingestion before and/or during exercise can also increase muscle protein synthesis rates during continuous endurance type exercise. Preliminary findings suggest that protein coingestion stimulates muscle protein synthesis also during more prolonged endurance type exercise [30]. More work is needed to address the relevance of the potential to stimulate muscle protein synthesis during exercise, thereby creating a larger time frame for muscle protein synthesis rates to be increased.

For obvious methodological issues, post-exercise muscle reconditioning has hardly been studied during overnight sleep. Recently, we evaluated the impact of exercise performed in the evening on muscle protein synthesis during subsequent

**Fig. 2.** Dietary protein ingestion prior to and during resistance type exercise stimulates muscle protein synthesis during exercise. Fractional synthesis rate of mixed muscle protein during exercise following carbohydrate (CHO) or carbohydrate plus protein (CHO+PRO) ingestion. Values represent means ± SEM. Asterisk denotes significant difference vs. CHO. Figure redrawn from Beelen et al. [29].
overnight recovery [31]. Though an increase in muscle protein synthesis rates was observed during the first few hours of post-exercise recovery, muscle protein synthesis rates remained unexpectedly low during subsequent overnight sleep. Clearly, though post-exercise protein ingestion stimulates muscle protein synthesis during the acute stages of post-exercise recovery, these elevated muscle protein synthesis rates are not maintained during subsequent overnight recovery. It will be of interest to explore the impact of protein ingestion prior to or even during sleep on subsequent overnight muscle protein synthesis rates [32]. Overall, more work is needed to address the impact of the distribution of dietary protein throughout the day on prolonged training responses.

**Conclusion**

Protein ingestion following resistance or endurance type exercise will facilitate the skeletal muscle adaptive response to each successive exercise bout, resulting in more effective muscle reconditioning. Whey protein seems to be the most effective in stimulating acute post-exercise muscle protein synthesis. Ingestion of ~20 g protein during and/or immediately after each exercise bout is sufficient to allow maximal post-exercise muscle protein synthesis rates (table 1). Co-ingestion of large amounts of carbohydrate is not required to maximize post-exercise muscle protein accretion when ample protein is already ingested. A healthy diet with smart timing of the dietary protein ingestion after each bout of exercise will likely improve the skeletal muscle adaptive response to more prolonged exercise training.

**Disclosure Statement**

The author declares that no financial or other conflict of interest exists in relation to the content of the chapter.
References


Questions and Answers

Question 1: Are there large differences in the post-exercise muscle protein synthesis response regarding different types of proteins?

Answer: Yes. If you perform exercise, your protein synthesis will increase, and the types of protein that you are using will have an effect on the post-exercise muscle protein synthesis rates. For example, if you use animal-based proteins, generally the response seems to be greater than when you use plant-derived proteins.

Question 2: So where’s the big difference between whey protein and casein?

Answer: If you go for milk protein, which is composed of both whey as well as casein, you will see that whey protein ingestion following exercise actually leads to a greater post-exercise muscle protein synthetic response when compared with casein protein.

Question 3: What protein source do you recommend to athletes?
Answer: For post-exercise recovery, you should actually have a protein that is rapidly digested and absorbed, and subsequently also has a high leucine content. So, whey protein would be one of the best proteins for post-exercise recovery.

Question 4: Is there a specific amount of protein that should be ingested following exercise?

Answer: There are a lot of studies still lacking, and it likely depends on the athlete and the type of exercise, but basically 20 g of protein should be enough to maximize post-exercise muscle protein synthesis rates. We don’t necessarily need to ingest more than 20 g, and that’s about the amount of protein you will find in a normal meal.

Question 5: Should endurance athletes worry about protein ingestion?

Answer: Every athlete should worry about protein ingestion. For example, endurance athletes also see an increase in protein synthesis following exercise, and to allow muscle reconditioning they also have to ingest dietary protein.

Question 6: Should they take supplements or just normal food?

Answer: Not necessarily supplements, but supplements sometimes are very practical because you can ingest them immediately after an exercise bout, but if you time your meals well, you can also have your meal (containing protein) after an exercise session.

Question 7: Do you take any supplements?

Answer: Yes, sometimes when I can’t time my meals well, I take protein supplements following an exercise session.