Feeding Meals Containing Soy or Whey Protein after Exercise Stimulates Protein Synthesis and Translation Initiation in the Skeletal Muscle of Male Rats

Tracy G. Anthony,1,4* Brent J. McDaniel,4 Peter Knoll,4 Piyawan Bunpo,4 Greg L. Paul,5 and Margaret A. McNurlan6

1 Department of Biochemistry and Molecular Biology, Indiana University School of Medicine-Evansville, Evansville, IN 47712; 2 The Solae Company, St. Louis, MO 63188; and 3 Department of Surgery, State University of New York-Stony Brook, NY 11790

Abstract

The purpose of this investigation was to compare the early response of skeletal muscle protein synthesis and translation initiation following the ingestion of different protein sources after endurance exercise. Treadmill-acclimated rats were designated as either nonexercised controls (NEX) or treadmill exercised for 2 h at 26 m/min (~75% VO2max) and then fed either carbohydrate only (EC), carbohydrate plus soy protein (ES), or carbohydrate plus whey protein (EW). One hour after exercise, serum insulin concentrations in EC, ES, and EW were greater than in NEX (P < 0.05); the concentration in EW was greater than in EC, with that in ES intermediate. Serum concentrations of branched-chain amino acids in ES and EW were higher than in EC, but serum leucine and isoleucine in EW were higher than in ES (P < 0.05). Nevertheless, both ES and EW promoted the fractional rate of skeletal muscle protein synthesis significantly more than EC. Likewise, compared with EC, both ES and EW increased formation of the mRNA cap binding complex eIF4F and stimulated phosphorylation of the translational repressor, 4E-BP1, the 70kD ribosomal protein S6 kinase (S6K1), and the mammalian target of rapamycin (mTOR) kinase at serine 2448. On the other hand, phosphorylation of S6K1 and mTOR was greater in EW than in ES (P < 0.05). In conclusion, general protein synthesis and the mRNA cap binding step are promoted comparably by soy protein and whey protein in the skeletal muscle of exercised rats. Furthermore, the data suggest that mTOR signaling in skeletal muscle is acutely responsive to physiological variations in dietary amino acids. J. Nutr. 137: 357–362, 2007.

Introduction

Soy protein serves as an important source of nitrogen and essential amino acids for long-term maintenance in adult humans (1). Despite this, some are cautious to incorporate soy protein into their exercise regimen, due in part to confusion or controversy surrounding soy isoflavones in addition to lay media messages promoting animal-based proteins. In fact, the types of protein(s) that are the best for achieving muscle recovery after endurance exercise are not defined. Current opinions are based on studies focused on resistance exercise models (2) and/or studies that examine the digestibility or gastric emptying of a particular protein, categorizing it as “fast” (e.g., whey) or “slow” (e.g., casein) and extrapolating the influence of the protein digestion rate on protein anabolism (3,4). Metabolic studies conducted in humans examining whole body protein kinetics following the ingestion of soy or milk proteins report that dietary amino acids from soy proteins are directed toward deamination pathways and splanchic/liver protein synthesis, resulting in lower postprandial nitrogen retention (5,6). However, these studies compare soy protein to pure casein or cow’s milk (in which total milk protein content is ~80% casein). Compared with casein, soy protein is a relatively fast protein, with absorption kinetics closer to whey (2,7,8). Indeed, differences in nitrogen kinetics have been reported between whey and casein due to their digestion rate (9,10). To our knowledge, no study to date has directly compared soy protein with whey in terms of stimulating protein synthesis in skeletal muscle after ingestion.

Previous work demonstrates that treadmill exercise represses, and ingestion of a protein-containing meal or leucine alone immediately following exercise stimulates, skeletal muscle protein synthesis (11–13). These changes in global protein synthesis are driven at the level of mRNA translation initiation by altering the formation of eukaryotic initiation factor (eIF)4F, a complex

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2 T. G. Anthony received travel support by The Solae Company to present this work at the 6th International Symposium on the Role of Soy in Preventing and Treating Chronic Disease, held in Chicago, IL.
3 Supplemental Table 1 is available with the online posting of this paper at jn.nutrition.org.
4 To whom correspondence should be addressed. E-mail: tganthon@iupui.edu.
5 Abbreviations used: eIF, eukaryotic initiation factor; 4E-BP1, eIF4E-binding protein 1; EC, postexercise 100% carbohydrate meal; ES, postexercise carbohydrate plus soy protein; EW, postexercise carbohydrate plus whey protein; NEX, nonexercise controls; mTOR, mammalian target of rapamycin; S6K1, ribosomal protein S6 kinase 1.
of translation factors important in the selection and binding of mRNA to the small ribosomal subunit. The formation of eIF4F is regulated in part by a kinase named mammalian target of rapamycin (mTOR). The mTOR kinase is a central player in the phosphatidylinositol 3’-OH kinase signaling pathway and integrates information on the cellular supply of nutrients and cellular energy state to downstream factors that regulate mRNA translation and other processes (14,15). mTOR is involved in the regulation of muscle growth (16,17) and, through a protein named Raptor, catalyzes the phosphorylation of the translational inhibitor, eIF4E-binding protein 1 (4E-BP1) and the p70 ribosomal protein S6 kinase (S6K1) (18). Phosphorylation of 4E-BP1 facilitates eIF4F formation by reducing its affinity for the mRNA cap binding protein, eIF4E. Activation of S6K1 results in phosphorylation of the ribosomal protein S6 and also serves as a phosphorylating kinase of mTOR at serine 2448 (19,20). Postprandial activation of 4E-BP1 and S6K1 in skeletal muscle is dependent on amino acids, and in particular, leucine (21,22).

Although much is known about the impact of individual amino acids on mTOR signaling, to our knowledge, there are no published data on comparative effects of specific dietary proteins on mTOR signaling after exercise. Thus, the purpose of the present study was to compare meals containing soy vs. whey protein on the stimulation of muscle protein synthesis and translation initiation in male rats after treadmill exercise.

Experimental Design and Methods

Animals. The experimental protocol was approved by the Institutional Animal Care and Use Committee of the Indiana University School of Medicine-Evansville campus. Before each experiment, male SpragueDawley rats were maintained on a 12:12-h light-dark cycle with free access to a commercial pelleted soy-free diet (Harlan Teklad product TD 96155) and tap water. The commercial diet consisted of ~20% protein, 5.5% fat, and 3% fiber.

The day after arrival, all rats (initially weighing 140–150 g) began an 8-d treadmill acclimation schedule that gradually increased either speed or duration up to 26 m/min for 15 min [described in (12)]. Rats that refused to run during the acclimation period were eliminated from the study. All exercise sessions began at the beginning of the light cycle after the recording of body weight and were performed on a nonshocking motor-driven treadmill (custom designed and built by Keith Benedict of Bigfoot Industries). On the day of the experiment, treadmill-acclimated rats (n = 6–8 per group) remained in their cages (nonexercise controls, NEX) or were exercised and then fed 1 of the following 3 meals immediately after the experimental run: carbohydrate in the form of 50% sucrose plus 50% maltodextrin (EC); a mixed meal containing ~20% soy protein (ES); or a mixed meal containing ~20% whey protein (EW). The macronutrient and amino acid composition of the diets are listed in Tables 1 and 2. There was no added fat, vitamins, or minerals to the diets, only what remained associated with the isolated or concentrated protein naturally following commercial preparation. As expected, the carbohydrate-only and the whey protein contained no isoflavones, whereas the soy protein isolate contained 0.16 mg/g product aglycone units. A 2nd soy group, consisting of a soy protein concentrate high in naturally occurring isoflavones (0.63 mg/g protein aglycone units) was originally analyzed separately from the other 3 exercised groups to examine whether the isoflavone content of soy protein altered any metabolic or molecular responses. However, all measured variables in the 2 soy groups did not differ from one another (Supplemental Table 1) and their statistical relations to all other groups were the same; therefore, the 2 soy groups were combined in the final data presentation. The carbohydrate source was a 50:50 sucrose-maltodextrin dry mixture reconstituted in water at room temperature on the day of oral administration. Carbohydrate was chosen instead of water or saline to serve as the exercise control group in accounting for the effect of insulin on muscle protein synthesis, because insulin has been reported to stimulate protein synthesis in young pigs, and the effect of leucine on mTOR signaling is maximized by the presence of insulin (23,24). The source of whey protein was Hilmar 8010 Instantized Whey Protein Concentrate (Hilmar Cheese). All diets were provided by The Solae Company.

Food was removed from exercised rats 7 h before the experimental run to reduce fecal elimination during exercise. The experimental run consisted of 2 h of treadmill running at 26 m/min, previously shown to significantly depress muscle protein synthesis and translation initiation 1 h after exercise (12). At the end of the exercise bout, rats were administered an isocaloric dose of their designated meal by oral gavage [44 kJ in 4 mL test dose; representing ~15% of daily energy needs as previously determined (12)] and returned to their cages. Rats were allowed free access to water, but no food was available beyond the defined postexercise meals. Nonexercised rats received a “postexercise” oral gavage of 4 mL water and were freely fed beforehand. All rats were killed 60 min after gavage.

Administration of metabolic tracer and sample collection. Ten minutes before killing, a bolus dose (250 mg/kg body weight, 25 g/L) of phenylalanine labeled with deuterium ([2H5]Phe, Cambridge Isotope Laboratories) was injected via the tail vein for the in vivo measurement of skeletal muscle (gastrocnemius + plantaris) protein synthesis as previously described (25,26). One hour following meal administration, rats were decapitated and blood was collected from the neck into prechilled tubes and allowed to clot on ice for 1 h and then centrifuged at 1800 × g for 10 min (4°C) to obtain serum. The right gastrocnemius and plantaris were rapidly excised and immediately frozen in liquid nitrogen before storage in a −80°C freezer. The left hind limb muscles were weighed and homogenized in 7 volumes of buffer A [20 mM N-2-hydroxyethylpiperazine-N’-2-ethanesulfonic acid (pH 7.4), 100 mM KCl, 0.2 mM EDTA, 2 mM/L ethylene glycol-bis(β-aminoethyl ether)-N,N,N’,N’-tetraacetic acid, 1 mM/L dithiothreitol, 50 mM/L NaF, 50 mM/L β-glycerophosphate, 0.1 mM/L phenylmethylsulfonyl fluoride, 1 mM/L benzamidine, and 0.5 mM/L sodium vanadate] with a Polytron homogenizer. The homogenate was centrifuged at 10,000 × g for 10 min at 4°C and the resulting supernatant was used for determination of protein expression and activity as described below.

Serum measurements. Serum samples were stored at −20°C or sent frozen to the Indiana University School of Medicine Quantitative Amino Acid Core Facility (under the direction of Edward Liechty, M.D.) for the determination of amino acid profiles by the ninhydrin method, using standard ion exchange chromatography with a Beckman 6300 automated amino acid analyzer. Serum insulin was measured using a commercial radioimmunoassay kit for rat insulin (Linco).

Measurement of protein synthesis. The rate of protein synthesis in individual tissues was measured by the incorporation of injected [3H]phenylalanine into muscle proteins (25,26). The determination of

<table>
<thead>
<tr>
<th>TABLE 1</th>
<th>Macronutrient composition of postexercise meals</th>
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<tbody>
<tr>
<td>Product</td>
<td>CHO1</td>
</tr>
<tr>
<td>---------</td>
<td>------</td>
</tr>
<tr>
<td>Carbohydrate only</td>
<td>100.0</td>
</tr>
<tr>
<td>Soy protein meal</td>
<td>77.15</td>
</tr>
<tr>
<td>Whey protein meal</td>
<td>75.06</td>
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1 CHO, carbohydrate.

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tissue, expressed in days, and Eb and Ea are the enrichments of $^{2}$H$^{5}$Phe where $t$ is the time interval between injection and cooling of sampled Sepharose 4B (Amersham Pharmacia Biotech). Muscle extract of equal the mRNA cap binding protein in 10,000 examined by protein immunoblot analysis after affinity purification of Quantitation of eIF4E, 4E-BP1 in hydrolyzed tissue protein and in muscle free amino acids, respectively.

according to the formula: \[ \text{FSR} = \frac{(E_s - E_t)}{(E_t \times t)} \] where $t$ is the time interval between injection and cooling of sampled tissue, expressed in days, and $E_s$ and $E_t$ are the enrichments of $^{2}$H$^{5}$Phe in hydrolyzed tissue protein and in muscle free amino acids, respectively.

**Quantitation of elf4E, 4E-BP1, elf4G, and elf4G elf4E complexes.**

The association of 4E-BP1 and elf4G with elf4E in muscle extracts was examined by protein immunoblot analysis after affinity purification of the mRNA cap binding protein in 10,000 x g supernatants with m7GTP-Sepharose 4B (Amersham Pharmacia Biotech). Muscle extract of equal protein concentration was added to prewashed and pre-equilibrated m$^{7}$GTP-Sepharose 4B in buffer A. Following incubation for 1 h with mixing at 4°C, columns were washed 3 times with 1.5 mL ice-cold buffer A. The resin was then resuspended in 0.1 mL of SDS sample buffer, boiled for 3 min and centrifuged at 10,000 x g for 5 min. The resulting supernatant was loaded onto polyacrylamide gels for SDS-PAGE and subsequent electrophoresis onto PVDF membranes. Membranes were blotted using a rabbit polyclonal antibody to either elf4E (Cell Signaling Technology), elf4G (Santa Cruz Biotechnology), or 4E-BP1 (Santa Cruz Biotechnology), as described previously (27).

**Phosphorylation of 4E-BP1, 6K1, and mTOR.** Muscle supernatants were subjected to protein immunoblot analysis as described previously (27,28), using a rabbit polyclonal antibody to 4E-BP1 (Bethyl Labs) and a rabbit polyclonal 6K1 antibody (Santa Cruz Biotechnology). Phosphorylation of mTOR at Ser2448 was detected using an antiphospho Ser2448 mTOR antibody (Cell Signaling Technology) and expressed as a ratio of total mTOR expression, determined using an anti-mTOR antibody (Cell Signaling Technology).

**Statistical analysis.** All data were analyzed by the STATISTICA statistical software package for the Macintosh, volume II (StatSoft). A 1-way ANOVA was performed with treatment group as the independent variable. When a significant overall effect was detected, differences among individual means were assessed using Tukey’s Unequal Sample Size Highly Significant Difference post hoc test. The level of significance was set at $P < 0.05$ for all statistical tests. Values in the text are means ± SEM.

**Results**

In this study, we compared soy protein to whey protein in terms of the short-term recovery of muscle protein synthesis and translation initiation in skeletal muscle following endurance exercise. Whereas the 2 proteins were delivered so as to contain similar amounts of total nitrogen, the amount of each amino acid consumed varied according to the source profile. The total amount of indispensable AA in the soy products (g/100 g protein) were ~85% that of whey, with lower amounts of methionine, leucine, isoleucine, valine, lysine, tryptophan, and threonine and higher levels of arginine, histidine, and phenylalanine (Table 2).

In the EC group, serum insulin was 46% greater than in NEX (P < 0.05, Table 3). The insulin concentration in EW was

| Table 3 | Serum amino acid and insulin concentrations in male rats 1 h after feeding postexercise meals
<table>
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<tr>
<th></th>
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<tbody>
<tr>
<td>Amino acid</td>
<td>NEX</td>
<td>EC</td>
<td>ES</td>
</tr>
<tr>
<td>Alanine</td>
<td>751.7 ± 63.3</td>
<td>382.5 ± 24.3</td>
<td>608.5 ± 32.5</td>
</tr>
<tr>
<td>Arginine</td>
<td>167.9 ± 24.9</td>
<td>68.0 ± 20.6</td>
<td>84.4 ± 20.2</td>
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<tr>
<td>Aspartic acid</td>
<td>31.2 ± 4.8</td>
<td>34.4 ± 1.5</td>
<td>41.9 ± 0.9</td>
</tr>
<tr>
<td>Asparagine</td>
<td>58.7 ± 7.7</td>
<td>34.8 ± 2.9</td>
<td>68.3 ± 3.5</td>
</tr>
<tr>
<td>Glutamic acid</td>
<td>182.5 ± 30.9</td>
<td>132.2 ± 4.3</td>
<td>159.5 ± 5.3</td>
</tr>
<tr>
<td>Glutamine</td>
<td>708.3 ± 30.0</td>
<td>317.5 ± 17.6</td>
<td>421.1 ± 15.1</td>
</tr>
<tr>
<td>Glycine</td>
<td>406.7 ± 32.7</td>
<td>296.3 ± 24.8</td>
<td>372.1 ± 13.8</td>
</tr>
<tr>
<td>Histidine</td>
<td>100.4 ± 1.6</td>
<td>92.1 ± 4.3</td>
<td>122.9 ± 6.6</td>
</tr>
<tr>
<td>Isoleucine</td>
<td>81.6 ± 17.3</td>
<td>52.5 ± 6.2</td>
<td>109.2 ± 3.6</td>
</tr>
<tr>
<td>Leucine</td>
<td>170.3 ± 25.3</td>
<td>72.5 ± 9.6</td>
<td>150.0 ± 5.8</td>
</tr>
<tr>
<td>Lysine</td>
<td>1029.5 ± 140.4</td>
<td>331.0 ± 21.7</td>
<td>492.7 ± 36.7</td>
</tr>
<tr>
<td>Methionine</td>
<td>122.4 ± 12.4</td>
<td>27.2 ± 3.7</td>
<td>35.3 ± 3.0</td>
</tr>
<tr>
<td>Proline</td>
<td>237.7 ± 56.1</td>
<td>81.0 ± 5.0</td>
<td>141.1 ± 7.2</td>
</tr>
<tr>
<td>Serine</td>
<td>323.6 ± 23.3</td>
<td>242.1 ± 13.6</td>
<td>302.1 ± 11.2</td>
</tr>
<tr>
<td>Threonine</td>
<td>256.6 ± 17.8</td>
<td>269.9 ± 7.3</td>
<td>412.5 ± 17.4</td>
</tr>
<tr>
<td>Valine</td>
<td>188.9 ± 18.9</td>
<td>127.6 ± 22.5</td>
<td>233.2 ± 8.2</td>
</tr>
<tr>
<td>Insulin, pmol/L</td>
<td>304.8 ± 34.4</td>
<td>445.9 ± 46.5</td>
<td>600.9 ± 89.5</td>
</tr>
</tbody>
</table>

Values are means ± SEM, n = 4–12. Means in a row with superscripts without a common letter differ, P < 0.05.
significantly greater than in EC and that in ES was intermediate. Serum concentrations of essential amino acids were generally reduced in EC compared with NEX. On the other hand, both ES and EW had higher concentrations of threonine, lysine, leucine, isoleucine, and valine than EC, and serum concentrations of threonine, histidine, isoleucine, leucine, and valine were the same as or greater than NEX. Serum alanine, asparagine, and glutamine in ES and EW also were greater than in EC. Of note, serum leucine and isoleucine concentrations were higher in EW than in EC.

Feeding carbohydrate to EC after treadmill exercise resulted in muscle protein synthesis rates significantly less than in NEX (Fig. 1). In contrast, both ES and EW were effective at promoting general protein synthesis in skeletal muscle after treadmill exercise. Indeed, muscle FSR in ES and EW did not differ from one another and were greater than in EC.

Formation of the eIF4F complex was evaluated by determining the association of eIF4E with 4E-BP1 (Fig. 2A) vs. eIF4G (Fig. 2B). Consistent with global rates of muscle protein synthesis, EC demonstrated decreased eIF4F formation after exercise that was represented by a reduction in the eIF4G-eIF4E complex and increase in the eIF4-BP1-eIF4E complex compared with NEX. Both protein-containing meals reversed these effects; ES and EW did not differ from NEX.

To evaluate the effects of soy vs. whey on mTOR signaling, the phosphorylation of 4E-BP1 and S6K1 were analyzed. Carbohydrate ingestion by EC following prolonged treadmill running reduced 4E-BP1 phosphorylation compared with NEX (Fig. 2C). In contrast, the ES and EW groups did not differ from NEX. ES and EW had greater phosphorylation of S6K1 than EC (Fig. 2D). However, EW exhibited significant hyperphosphorylation of S6K1 relative to all other groups. Phosphorylation of mTOR at Ser2448 was greater in EW than in ES and both of these were greater than EC and NEX, which did not differ (Fig. 2E). In summary, both soy protein and whey protein promoted general muscle protein synthesis and eIF4F formation after treadmill exercise. On the other hand, phosphorylation of S6K1 and mTOR were most responsive to whey protein ingestion.

**Discussion**

To our knowledge, this study is the first to compare a vegetable-based protein to an animal-based protein in promoting the recovery of skeletal muscle protein synthesis and mRNA translation initiation factor activity after endurance exercise. We found that general protein synthesis and eIF4F formation were comparable among rats fed the different protein-containing meals after exercise. In contrast, rats fed whey protein demonstrated enhanced mTOR phosphorylation via S6K1 compared with those fed soy protein. These latter findings suggest that mTOR signaling in skeletal muscle is acutely responsive to variations in circulating insulin and AA concentrations following ingestion of intact dietary proteins.

As in our previous work, we found that high-intensity treadmill running decreased muscle protein synthesis after exercise. In support of our findings, Williamson et al. (13) found that 10–30 min of intense treadmill running in mice caused the disaggregation of polysomes into free ribosomes. In addition, 90 min of exercise on a cycle ergometer at 67% VO2 max in healthy men reportedly increased phosphorylation of eukaryotic elongation factor 2 (eEF2), indicating decreased eEF2 activity and mRNA translation (29). These results support the concept that high intensity aerobic exercise stymies muscle anabolism in the short term. This is in contrast to less intense aerobic exercise, which reportedly increases muscle and plasma protein synthesis in humans (30).

We previously found that consumption of a protein-containing meal or leucine alone stimulates muscle protein synthesis after exercise (11, 12). The current results extend our previous findings to include soy protein as an effective means to stimulate muscle protein synthesis. Also consistent with our previous work, we found that protein feeding after exercise does not stimulate muscle protein synthesis equal to that in sedentary-fed rats but, rather, recovers synthesis rates to a slightly lower level.
This lower level was previously shown to reflect nonexercised rats that were not fed for 10 h (12). Perhaps postexercise muscle protein synthesis rates are higher at an earlier point after feeding, insofar as maximal stimulation of muscle protein synthesis following leucine ingestion occurs at 30 min postingestion (23). Or, perhaps if more energy were provided, a greater stimulation might have been achieved. Additional time-course and dose-response studies are needed to fully answer these questions.

There is little information in the exercise literature, particularly with respect to aerobic exercise, on divergent responses to different protein sources. Soy and whey were the chosen comparisons because of their similar digestibility and absorption kinetics. The temporal release of amino acids into the blood from both soy protein and whey protein are relatively fast, as both are soluble at low pH. In contrast, casein clots when in contact with stomach acid, providing a much slower release of amino acids into the circulation (3,31–33). Metabolic studies in subjects at rest indicate that prandial responses to ingestion or infusion of soy protein differ greatly from responses to milk (3,7,33,34). The current study concurs that the circulating amino acid profile differs following ingestion of soy protein vs. whey, with lower circulating concentrations of the BCAA and in particular, leucine. Nevertheless, muscle protein synthesis rates were comparable in the ES and EW groups. Additional time-course studies are required to determine whether the similar responses reported here are maintained over time.

Recent studies demonstrate that physiological increases in circulating leucine stimulate mTOR signaling in muscle (21). In addition, leucine alone or as a supplement has been shown to stimulate muscle protein synthesis after exercise in both endurance and resistance exercise models (11,35). In contrast to muscle protein synthesis and eIF4F formation, phosphorylation of S6K1 is highly responsive to physiological differences in leucine concentrations. Signaling through S6K1 is involved in regulating cell size and is required for muscle hypertrophy (17,36). S6K1 is also a major effector of mTOR phosphorylation at Ser2448 in response to both mitogens and nutrients (19,20). Both amino acids (leucine) and insulin have been reported to stimulate phosphorylation of mTOR at Ser2448 (37,38). In the current study, both soy and whey meals increased circulating concentrations of insulin and leucine, with whey protein producing the highest concentrations of both. As such, it follows that phosphorylation of mTOR at Ser2448 followed this pattern. It is unknown if the differential response in mTOR signaling to soy protein and whey protein translates to differences in muscle growth or function, particularly insofar as eIF4F complex formation and global protein synthesis in skeletal muscle did not differ between the ES and EW groups. Whether mTOR signaling more directly or accurately reflects the growth status of myofibers compared with the measurement of protein synthesis and eIF4F complex formation is also unclear and requires further study.

Taken in total, the current study suggests that both soy and whey proteins are useful sources of protein for muscle support following aerobic exercise. The concept of testing mixes of different dietary proteins to achieve and/or maximally sustain an optimal BCAA profile remains to be tested. It also remains to be determined how formation of the mRNA cap binding complex and mTOR signaling change over time in relation to global rates of protein synthesis following ingestion of soy, whey, and other proteins. Finally, additional research is needed to understand which classes of proteins within skeletal muscle are directed by eIF4F complex formation vs. mTOR signaling, particularly when these measurements diverge from each other.

Acknowledgments

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Literature Cited


