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Metabolism Clinical and Experimental 54 (2005) 151–156

Metabolism
Clinical and Experimental

www.elsevier.com/locate/metabol

The effect of resistance training combined with timed ingestion of protein on muscle fiber size and muscle strength

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Received 15 January 2004; accepted 8 July 2004

Abstract

Acute muscle protein metabolism is modulated not only by resistance exercise but also by amino acids. However, less is known about the long-term hypertrophic effect of protein supplementation in combination with resistance training. The present study was designed to compare the effect of 14 weeks of resistance training combined with timed ingestion of isoenergetic protein vs carbohydrate supplementation on muscle fiber hypertrophy and mechanical muscle performance. Supplementation was administered before and immediately after each training bout and, in addition, in the morning on nontraining days. Muscle biopsy specimens were obtained from the vastus lateralis muscle and analyzed for muscle fiber cross-sectional area. Squat jump and countermovement jump were performed on a force platform to determine vertical jump height. Peak torque during slow ($30^\circ\ s^{-1}$) and fast ($240^\circ\ s^{-1}$) concentric and eccentric contractions of the knee extensor muscle was measured in an isokinetic dynamometer. After 14 weeks of resistance training, the protein group showed hypertrophy of type I (18% ± 5%; $P < .01$) and type II (26% ± 5%; $P < .01$) muscle fibers, whereas no change above baseline occurred in the carbohydrate group. Squat jump height increased only in the protein group, whereas countermovement jump height and peak torque during slow isokinetic muscle contraction increased similarly in both groups. In conclusion, a minor advantage of protein supplementation over carbohydrate supplementation during resistance training on mechanical muscle function was found. However, the present results may have relevance for individuals who are particularly interested in gaining muscle size.

1. Introduction

It is generally accepted that training and nutrition in the restitution period affects the development of skeletal muscles. Recently, focus has been on optimal nutrition and especially on the ingestion of protein to enhance hypertrophic response to resistance training. Previous research has revealed that muscle protein metabolism can be modulated not only by resistance exercise [1-4] but also by changes in circulating amino acids [2,5,6]. Administration of amino acids in combination with resistance exercise augments protein synthesis acutely [2,7], which would be expected to result in a more pronounced muscle hypertrophy over a prolonged period. In contrast, if subjects remain fasted after a bout of resistance training, muscle net protein balance remains negative and a catabolic state is induced [1,4]. It therefore seems of paramount importance to ingest sufficient amounts of dietary protein in conjunction with resistance training when muscular hypertrophy or optimal restitution is the goal. Postexercise carbohydrate supplementation may also be beneficial because of a decreased rate of muscle protein breakdown [8]. Thus, a general energy intake after each training bout may be important.

On this background, the present study aimed to compare the effect of a 14-week resistance training combined with timed ingestion of isoenergetic protein vs carbohydrate supplementation on muscle morphology (determined as muscle fiber hypertrophy) in addition to muscle functional performance (determined as maximal muscle contraction strength and vertical jump performance) of young men.

2. Materials and methods

2.1. Subjects and study design

Twenty-two young healthy men (age, 23.2 ± 0.6 years; height, 184.5 ± 2.0 cm; weight, 77.0 ± 2.6 kg; mean ± SD)

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doi:10.1016/j.metabol.2004.07.012

participated in the study. Exclusion criteria included the following: (*a*) elite athletes, (*b*) those who engaged in resistance training in the past 6 months, (*c*) vegetarians, and (*d*) those who had regular ingestion of nutritional supplements (eg, creatine, protein drink, ribose) in the past 3 months. Most subjects were physically active on a recreational basis. All enrolled subjects gave written informed consent to participate in the study, which was approved by the Ethics Committee of Copenhagen and Frederiksberg (Denmark). The subjects were ranked according to the maximal isometric torque of the knee extensor muscles, which was determined on a screening visit to the laboratory, matched accordingly in pairs, and randomly assigned to either the protein group or the carbohydrate group. Subject characteristics are outlined in Table 1. To keep the study double blinded, neither the subjects nor any of the involved researchers knew which group the subjects belonged to. The randomization code was broken after completion of the laboratory analysis.

2.2. Supplementation

On training days, the subjects received one sachet of either carbohydrate or protein supplementation dissolved in 1/2 L of water for oral ingestion immediately before training and another sachet immediately after the last set of the training session. Subjects were instructed not to ingest anything else aside from plain water 2 hours before and 2 hours after the training session. On nontraining days, subjects were instructed to self-administer one sachet mixed with water in the morning. Each sachet of protein powder supplementation contained 25 g of protein (16.6 g of whey protein; 2.8 g of casein; 2.8 g of egg white protein; and 2.8 g of L-glutamine). Each sachet of carbohydrate powder contained 25 g of maltodextrin to keep the protein and carbohydrate supplements isoenergetic. The protein and carbohydrate supplements were stored in identical opaque sachets and heavily flavored with vanilla to render identification of the respective supplements difficult.

2.3. Training

Training was performed 3 times a week for 14 weeks. The resistance training program consisted of 3 to 4 sets of obligatory leg exercises: inclined leg press, isolated knee extension, and hamstring curls (Nordic Gym, Bolinäs, Sweden). Training was done in accordance to the principle of periodization with relative loadings ranging between 4 and 15 repetition maximums. Absolute training loads were progressively increased to maintain relative loadings at the intended level. To ensure adequate training load and intensity, all training sessions were surveyed and supervised by the authors of the study.

Table 1
Subject characteristics at pretraining

	Protein group	Carbohydrate group
Age (y)	23 ± 0.6	23 ± 0.6
Weight (kg)	76.2 ± 2.5	77.8 ± 2.8
Height (cm)	184 ± 1.6	185 ± 2.3
BMI (kg/m^2)	22.6 ± 0.7	22.7 ± 0.5
Daily energy intake (kJ)	11,571 ± 890	11,756 ± 794
Daily protein intake (g)	97 ± 5.3	98 ± 6.3
SJ height (cm)	27.0 ± 1.1	28.2 ± 1.2
Isometric strength (Nm)	296 ± 15	288 ± 18
Type I fCSA (μm^2)	4698 ± 207	5770 ± 354
Type II fCSA (μm^2)	5390 ± 296	5954 ± 314

Data are mean ± SE. No significant pretraining group differences were found in any parameter.

2.4. Muscle biopsy sampling and analysis

Muscle biopsy specimens were taken at pretraining and posttraining from the right vastus lateralis muscle [9,10], midway between the patella and the greater trochanter, in an area where no major nerves and blood vessels are located. The tissue samples were immediately mounted with Tissue-Tek (Electron Microscopy Sciences, Hatfield), frozen in isopentane precooled with liquid nitrogen, and stored in a freezer at −80°C until processing. Pretraining and posttraining biopsy specimens were taken from the same region and depth of the vastus lateralis muscle and placed approximately 1 cm apart. The posttraining biopsy specimen was taken 3 days after the last training session. The biopsy specimens were blinded, and transverse serial sections (10 μm) of the embedded muscle biopsy specimen were cut in a cryostat (−22°C; Microm, Walldorf, Germany) and mounted on glass slides. Standard adenosine triphosphate analysis was performed after preincubation at pH values of 4.37, 4.60, and 10.30 [11]. A serial section of the muscle biopsy samples was also immunohistochemically stained for dystrophin (Novocastra NCL-DYS 2, Newcastle upon Tyne, UK). Dystrophin forms part of the large and complex arrays of molecules that are attached to the inside surface of the muscle cell membranes, and the staining was performed to accurately identify the mask used for the fiber cross-sectional area (fCSA) analysis. Quantitative analysis of all muscle samples for fiber-type composition and fCSA was performed using a digital image analysis program (TEMA 1.04, Scanbeam, Hadsund, Denmark). The biopsy sections were visualized on a computer screen using a Carl Zeiss light microscope (Zeiss Axiolab; Carl Zeiss GmbH, Jena, Germany), a JVC high-resolution color digital camera (TK-C1381EG, JVC), and an 8-bit Matrox Meteor Framegrabber (Matrox Electronic Systems, Quebec, Canada). Type I and II muscle fibers were differentiated, and mean fCSA was determined [12]. A median of 230 fibers (range, 139-400) was counted per muscle sample.

2.5. Food recording

Before the training period started, food records were kept for 4 consecutive days, starting on a Sunday, to determine daily food intake. It has been found that a longer period of repetitive recording may per se influence recording patterns and food intake [13,14]. Subjects received portable electronic scales (Tefal, Romilly, France) with ±1 g accuracy to weigh the food at home. Subsequent analyses of the food

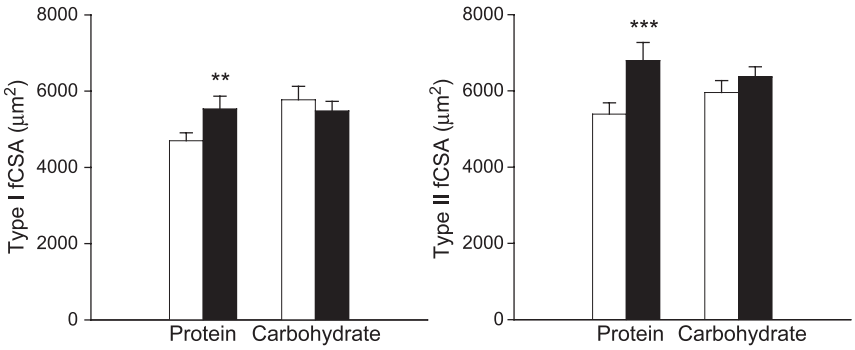

Fig. 1. Fiber cross-sectional area of type I (left) and type II (right) muscle fibers at pretraining (open bars) and posttraining (filled bars). Only the protein group increased muscle fCSA in response to resistance training. Asterisks indicate significant difference from pretraining values: $^{**}P < .01$; $^{***}P < .001$.

records were performed by dietitians at the Bispebjerg Hospital (Denmark).

2.6. Vertical jump performance

Two types of vertical jumps were performed: the squat jump (SJ) starting from a 90° knee joint angle and the countermovement jump (CMJ) starting from an upright position [15]. Warm-up consisted of 10-minute bicycling at 100 W. During each jump, the subjects kept their hands on their hips. During the SJ, attempts with a visible countermovement were discarded. After a few habituation jumps, 6 to 8 maximal jumps with a pause of 30 seconds in between were performed for each jump type. The subjects were verbally encouraged to jump as high as possible. A force platform was used to measure vertical ground reaction force. The force signal was sampled at 1000 Hz by an A/D converter (dt2801-A, Data Translation, Marlboro, Mass) and stored into a personal computer for further analysis. During subsequent off-line analysis, jump height was determined from the impulse (area under the force-time curve) during the concentric phase of the jump [16].

2.7. Isokinetic peak torque

After the vertical jump test, unilateral isokinetic knee extensor peak torque was measured in a commercial isokinetic dynamometer (Kinetics Communicator, Chattecx Corp, Chattanooga, Tenn) using a setup that has been previously described [17]. The subjects performed maximal concentric and eccentric muscle contractions at slow (30° s^{-1}) and fast (240° s^{-1}) speeds through a 10° to 90° knee joint range of motion (0° full extension). A number of contractions, typically 6 to 8, were performed in a noncyclic manner separated by approximately 60 seconds of rest until peak torque could not be improved any further. Visual feedback of the dynamometer force output was provided to the subjects on a computer screen. After undergoing the isokinetic measurements, the subjects performed 3 maximal voluntary isometric contractions at a static knee joint angle of 70°. Two weeks before testing, the subjects were familiarized with the dynamometer and jump test procedure.

2.8. Statistics

The effect of training combined with protein vs carbohydrate supplementation was investigated using 2-way analysis of variance. If a significant interaction was found, post hoc analysis (Bonferroni-corrected Student t test) was performed to locate differences. Statistical significance was set to $P \leq .05$. Values are reported as group mean ± SE.

3. Results

3.1. Pretraining

At pretraining, no statistical difference between the groups was observed with regard to muscle fCSA, vertical

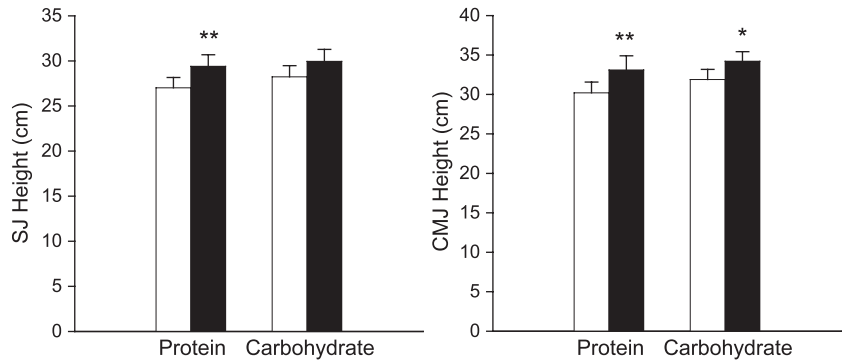

Fig. 2. Squat jump height (left) and CMJ height (right) at pretraining (open bars) and posttraining (filled bars) for the protein and carbohydrate groups. The protein group enhanced SJ height, whereas both groups enhanced CMJ height. Asterisks indicate significant difference from pretraining values: $^{*}P < .05$; $^{**}P < .01$.

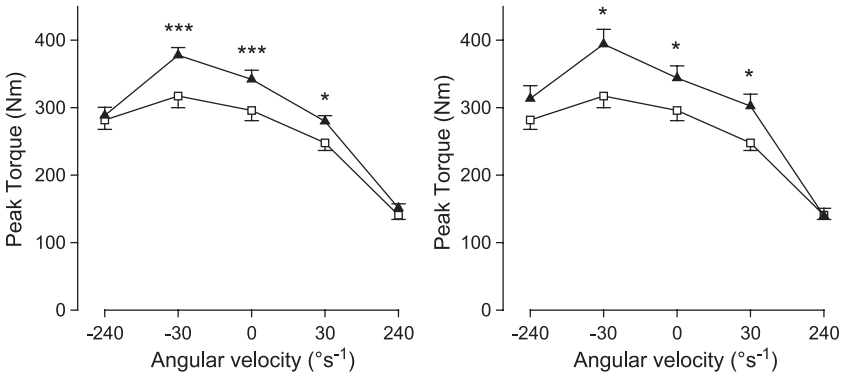

Fig. 3. Isokinetic peak torque at pretraining (open squares) and posttraining (filled triangles) for the protein group (left) and carbohydrate group (right). Both groups increased peak torque during slow isokinetic and isometric muscle contractions. Asterisks indicate significant difference from pretraining values: *$P < .05$; **$P < .01$; ***$P < .001$.

jump height, and isokinetic peak torque. In addition, no significant difference in any dietary parameter was seen between the carbohydrate and protein groups. Both groups fulfilled the recommended daily allowances of macronutrient and micronutrient intake. Furthermore, the 2 groups were similar in age, body weight, and height (Table 1).

3.2. Muscle hypertrophy

After 14 weeks of resistance training, only the protein group showed muscle fiber hypertrophy of the trained leg muscles. Type I and type II muscle fCSA of the vastus lateralis increased by 18% ± 5% ($P < .01$) and 26% ± 5% ($P < .01$), respectively, in the protein group, whereas no significant change occurred in the carbohydrate group (Fig. 1).

3.3. Vertical jump performance

The protein group gained 9% ± 2% ($P < .01$) in SJ height, whereas no significant change occurred in the carbohydrate group (Fig. 2). The protein group and carbohydrate group increased in CMJ height by 10% ± 2% ($P < .01$) and 7% ± 6% ($P < .05$), respectively, from pretraining to posttraining.

3.4. Peak torque

Isometric and isokinetic eccentric and concentric peak torque at the slow velocities increased 11% to 20% ($P < .001$-.05; Fig. 3), with no significant difference between the 2 groups. Peak torque during fast eccentric and fast concentric contractions remained unchanged in both groups.

4. Discussion

The main findings of the present study were that resistance training combined with protein vs carbohydrate supplementation induced similar gains in mechanical muscle performance, whereas only protein supplementation induced muscle hypertrophy. Thus, resistance training combined with protein supplementation resulted in 18% and 26% increased type I and type II muscle fCSA, respectively (Fig. 1). In contrast, resistance training combined with carbohydrate supplementation did not affect muscle fCSA. The underlying metabolic explanation for muscle fiber hypertrophy is that protein synthesis is stimulated to a rate that exceeds muscle protein breakdown, thus inducing a net positive protein balance. It has previously been reported that increased availability of circulating amino acids will lead to a more positive net protein balance during resting conditions [2,5,6] as well as after an exercise bout [1-4]. Clearly, resistance training has a strong stimulatory effect on muscle protein synthesis as well [18]. However, in response to resistance training, protein breakdown is also elevated. If a subject remains in a postabsorptive state, the net protein balance remains negative [4,19]. Previous studies have shown that postexercise ingestion of carbohydrate can inhibit the rate of muscle protein breakdown [8,20]. The present results indicate that resistance training combined with carbohydrate supplementation alone may not result in long-term muscle anabolism. Conversely, increased amino acid availability immediately after a training bout has been shown to improve acute net protein balance [1-4]. In a training study by our laboratory, the ingestion of protein immediately after resistance training by elderly subjects resulted in muscle hypertrophy, whereas postponed protein intake for 2 hours did not [21]. One study has further indicated that the acute effect of protein supplementation on muscle anabolism is even greater if protein is ingested before the training bout [22]. In the present training study, this current knowledge was applied in an attempt to optimize anabolism over a prolonged training period. Thus, the protein group ingested protein just before and immediately after each training session to optimize anabolism. Although protein synthesis was not determined directly in this study, the timed intake of protein may explain the marked muscle fiber hypertrophy seen in the protein group. Furthermore, the present subjects ingested supplementation in the morning on nontraining days, which may have augmented overall anabolism in the protein group [2,5,6].

It is noteworthy that the carbohydrate group did not display any significant muscle fiber hypertrophy after 14 weeks of intense resistance training. Resistance training studies of similar intensity and duration that have not reported training-associated nutrition have usually reported muscle hypertrophy [12,23-25], although not all the time [26,27]. It should be mentioned that the latter studies [26,27] used isokinetic training protocols that may differ in training intensity as compared with traditional resistance training. Based on these previous findings, habitual dietary protein intake may be sufficient and adequately timed in most cases. Thus, prohibition of protein in the carbohydrate group for 2 hours before and 2 hours after each training bout may not resemble habitual dietary habits. Ingestion of protein immediately after resistance exercise has been shown to be important in the elderly population [21]. Nevertheless, the present study is the first to suggest the long-term importance of timed protein ingestion as compared with isoenergetic carbohydrate intake on muscle fiber hypertrophy in young healthy men.

The intensity of exercise is an important factor that could influence the magnitude of muscle hypertrophy in response to resistance training. Training protocols that did not induce muscle hypertrophy may have used an insufficient intensity of exercise. Based on the training logs recorded during the present study, total training load appeared adequate and not different between groups, with both groups experiencing a 3-fold increase in training load during the 14 weeks of training. Thus, intensity and duration of the present training protocol should be sufficient to stimulate muscle protein accretion.

Furthermore, dietary analysis showed that the 2 groups had the same levels of energy and protein intake before the training intervention. However, a methodological limitation of the present study is the lack of food recording during the training period. Thus, we have no assurance that the 2 groups had the same level of energy intake during the 14 weeks of training. Theoretically, the carbohydrate group could consume less energy during the training period, and this could partially explain the lack of muscle fiber hypertrophy in that group. On the other hand, it would be uncommon that one group but not the other should make a systematic change in habitual diet.

It should also be mentioned that despite the lack of statistical difference in muscle fiber size between the 2 groups pretraining, there was a considerable numerical discrepancy, especially with regard to type I muscle fibers (Fig. 1). Thus, an alternative explanation for the present findings may be that the carbohydrate group had larger muscle fibers before training and that the 2 groups "equalized" as a result of training.

With regard to muscle functional tests, only the protein group increased SJ height in response to training. Jumping performance has previously been related to the fiber-type profile of the muscle with a more type II dominated musculature, resulting in greater SJ height [28]. In this context, note that only the protein group increased the fCSA of type II muscle fibers. Type II muscle fibers possess the ability to generate very high contractile power as compared with type I muscle fibers [29], which in turn makes them suitable for explosive dynamic movements. Thus, the marked hypertrophy of type II muscle fibers in the protein group as opposed to the carbohydrate group may explain that SJ height increased in the protein group alone. However, improvements in vertical jump height appear to be dependent on gains in maximal muscle contraction strength as well [30], which may explain that both groups increased in CMJ height.

In agreement with previous studies, the present regimen of resistance training increased isokinetic and isometric peak torque [17,23,31,32]. Similar increases in peak torque were seen in the protein group and carbohydrate group. Thus, there seems to be a discrepancy between the present gains in muscle size and muscle contraction strength (ie, muscle fiber hypertrophy in the protein group did not result in proportionately greater strength gains as compared with the carbohydrate group). Several reasons suggest that the present increase in isometric and isokinetic peak torque was mainly a result of adaptive changes in neural function rather than of muscle morphological adaptations. First, isokinetic peak torque increased only at the slow velocities tested ($0^\circ\ s^{-1}$ and $30^\circ\ s^{-1}$) and not during fast isokinetic contraction ($240^\circ\ s^{-1}$). This could reflect velocity-specific neural adaptations [27,33] because the training velocity was slow to medium (ie, raising [concentric] and lowering [eccentric] the weight stack in a controlled manner). Second, previous studies using electromyogram recording indicate that gains in maximal muscle contraction strength are accompanied by neural adaptations [17,23,34]. Third, lack of muscle fiber hypertrophy in the carbohydrate group suggests that muscle strength gains in that group were probably a result of neural factors. However, it is noteworthy that the observed muscle fiber hypertrophy in the protein group did not result in proportionately greater gains in peak torque as compared with the carbohydrate group, suggesting a complex interplay between morphological and neural adaptations yet to be explained. Speculatively, specific neural adaptation mechanisms may have overruled the effect of muscle hypertrophy on maximal muscle contraction strength in this phase of training.

In conclusion, a minor advantage of protein supplementation over carbohydrate supplementation during resistance training on mechanical muscle function was detected in the present study. Nevertheless, the present results indicate that ingestion of protein is advantageous when muscle hypertrophy is desirable, which may be relevant for bodybuilders and individuals concerned with augmenting muscle size. Lack of food recording during the training period and a large numerical discrepancy in muscle fiber size between the 2 groups were some of the methodological limitations of the present results. Future studies should address whether combined intake of protein and carbohydrate in addition to

resistance training yields greater muscle hypertrophy and strength as compared with either supplement alone.

Acknowledgments

This study was supported by Numico Research BV (Wageningen, the Netherlands), Danish Research Council (Copenhagen, Denmark) grant 22010254, and Danish National Foundation (Copenhagen, Denmark) grant 504-14. We thank Birgitte Lillethorup and Hanne Overgaard for technical assistance.

References

[1] Phillips SM, Tipton KD, Aarsland A, et al. Mixed muscle protein synthesis and breakdown after resistance exercise in humans. Am J Physiol 1997;273:E99-E107.
[2] Biolo G, Tipton KD, Klein S, et al. An abundant supply of amino acids enhances the metabolic effect of exercise on muscle protein. Am J Physiol 1997;273:E122-9.
[3] Rasmussen BB, Tipton KD, Miller SL, et al. An oral essential amino acid-carbohydrate supplement enhances muscle protein anabolism after resistance exercise. J Appl Physiol 2000;88:386-92.
[4] Biolo G, Maggi SP, Williams BD, et al. Increased rates of muscle protein turnover and amino acid transport after resistance exercise in humans. Am J Physiol 1995;268:E514-20.
[5] Bennet WM, Connacher AA, Scrimgeour CM, et al. Increase in anterior tibialis muscle protein synthesis in healthy man during mixed amino acid infusion: studies of incorporation of [1-^{13}C]leucine. Clin Sci (London) 1989;76:447-54.
[6] Smith K, Reynolds N, Downie S, et al. Effects of flooding amino acids on incorporation of labeled amino acids into human muscle protein. Am J Physiol 1998;275:E73-8.
[7] Tipton KD, Ferrando AA, Phillips SM, et al. Postexercise net protein synthesis in human muscle from orally administered amino acids. Am J Physiol 1999;276:E628-34.
[8] Roy BD, Tarnopolsky MA, MacDougall JD, et al. Effect of glucose supplement timing on protein metabolism after resistance training. J Appl Physiol 1997;82:1882-8.
[9] Bergström J. Muscle electrolytes in man. Scand J Clin Lab Invest 1962;68(Suppl.):1-110.
[10] Evans WJ, Phinney SD, Young VR. Suction applied to a muscle biopsy maximizes sample size. Med Sci Sports Exerc 1982;14:101-2.
[11] Brooke MH, Kaiser KK. Muscle fiber types: how many and what kind. Arch Neurol 1970;23:369-79.
[12] Andersen JL, Aagaard P. Myosin heavy chain IIX overshoot in human skeletal muscle. Muscle Nerve 2000;23:1095-104.
[13] Craig MR, Kristal AR, Cheney CL, et al. The prevalence and impact of 'atypical' days in 4-day food records. J Am Diet Assoc 2000;100: 421-7.
[14] Goris AH, Meijer EP, Westerterp KR. Repeated measurement of habitual food intake increases under-reporting and induces selective under-reporting. Br J Nutr 2001;85:629-34.
[15] Asmussen E, Bonde-Petersen F. Storage of elastic energy in skeletal muscles in man. Acta Physiol Scand 1974;91:385-92.
[16] Caserotti P, Aagaard P, Simonsen EB, et al. Contraction-specific differences in maximal muscle power during stretch-shortening cycle movements in elderly males and females. Eur J Appl Physiol 2001; 84:206-12.
[17] Aagaard P, Simonsen EB, Andersen JL, et al. Neural inhibition during maximal eccentric and concentric quadriceps contraction: effects of resistance training. J Appl Physiol 2000;89:2249-57.
[18] Phillips SM, Tipton KD, Ferrando AA, et al. Resistance training reduces the acute exercise-induced increase in muscle protein turnover. Am J Physiol 1999;276:E118-24.
[19] Pitkanen HT, Nykanen T, Knuutinen J, et al. Free amino acid pool and muscle protein balance after resistance exercise. Med Sci Sports Exerc 2003;35:784-92.
[20] Biolo G, Williams BD, Fleming RY, et al. Insulin action on muscle protein kinetics and amino acid transport during recovery after resistance exercise. Diabetes 1999;48:949-57.
[21] Esmarck B, Andersen JL, Olsen S, et al. Timing of postexercise protein intake is important for muscle hypertrophy with resistance training in elderly humans. J Physiol 2001;535:301-11.
[22] Tipton KD, Rasmussen BB, Miller SL, et al. Timing of amino acid-carbohydrate ingestion alters anabolic response of muscle to resistance exercise. Am J Physiol Endocrinol Metab 2001;281:E197-E206.
[23] Hakkinen K, Alen M, Komi PV. Changes in isometric force- and relaxation-time, electromyographic and muscle fibre characteristics of human skeletal muscle during strength training and detraining. Acta Physiol Scand 1985;125:573-85.
[24] Narici MV, Roi GS, Landoni L, et al. Changes in force, cross-sectional area and neural activation during strength training and detraining of the human quadriceps. Eur J Appl Physiol Occup Physiol 1989;59:310-9.
[25] Sale DG, Martin JE, Moroz DE. Hypertrophy without increased isometric strength after weight training. Eur J Appl Physiol Occup Physiol 1992;64:51-5.
[26] Cote C, Simoneau JA, Lagasse P, et al. Isokinetic strength training protocols: do they induce skeletal muscle fiber hypertrophy? Arch Phys Med Rehabil 1988;69:281-5.
[27] Seger JY, Arvidsson B, Thorstensson A. Specific effects of eccentric and concentric training on muscle strength and morphology in humans. Eur J Appl Physiol Occup Physiol 1998;79:49-57.
[28] Mero A, Jaakkola L, Komi PV. Relationships between muscle fibre characteristics and physical performance capacity in trained athletic boys. J Sports Sci 1991;9:161-71.
[29] Bottinelli R, Canepari M, Peregrino MA, et al. Force-velocity properties of human skeletal muscle fibres: myosin heavy chain isoform and temperature dependence. J Physiol 1996;495(Pt. 2):573-86.
[30] Saliba L, Hrysomallis C. Isokinetic strength related to jumping but not kicking performance of Australian footballers. J Sci Med Sport 2001;4:336-47.
[31] Colliander EB, Tesch PA. Effects of eccentric and concentric muscle actions in resistance training. Acta Physiol Scand 1990;140:31-9.
[32] Aagaard P, Simonsen EB, Trolle M, et al. Specificity of training velocity and training load on gains in isokinetic knee joint strength. Acta Physiol Scand 1996;156:123-9.
[33] Paddon-Jones D, Leveritt M, Lonergan A, et al. Adaptation to chronic eccentric exercise in humans: the influence of contraction velocity. Eur J Appl Physiol 2001;85:466-71.
[34] Aagaard P, Simonsen EB, Andersen JL, et al. Increased rate of force development and neural drive of human skeletal muscle following resistance training. J Appl Physiol 2002;93:1318-26.