A High Protein Diet Does Not Improve Protein Synthesis in the Nonweight-Bearing Rat Tibialis Anterior Muscle\textsuperscript{1,2}

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ABSTRACT We recently demonstrated that a high protein intake partially prevented the decrease in protein synthesis in the atrophied dark soleus muscle of rats that were hindlimb suspended (HS) for 21 d. To study the possible role of protein intake in a muscle more representative of the whole musculature, we measured the effect of a high protein (HP) (30\%) and a medium protein (MP) (15\%) diet on protein synthesis in the pale fast-twitch tibialis anterior muscle of HS rats. The HS animals were suspended by the tail for 21 d so that only their front legs were able to rest on the floor. The fractional rate of protein synthesis ($K_p$) was determined in vivo using a flooding dose method. A significantly lower $K_p$ (24–25\%) was found in both HS-HP and HS-MP rats compared with their pair-fed control groups. Reduced $K_p$ in HS-MP rats relative to their pair-fed controls resulted from a decrease in the translational efficiency (KRNA, 23\%, $P < 0.01$), while the ratio of RNA to protein (Cr) was unaffected. In contrast, the decrease in KRNA was prevented in the HS-HP animals compared with their pair-fed controls ($P < 0.05$). Hindlimb suspension did not alter fiber type distribution in the tibialis anterior muscle. However, a higher proportion of intermediate and Type I fibers with a concomitant decrease in Type II fibers was observed in both CT and HS animals fed the HP diet compared with those fed the MP diet ($P < 0.05$). These data clearly establish that depressed protein synthesis contributes to altered protein accretion in fast-twitch muscles during long-term hindlimb suspension. Although the HP diet prevented the decrease in translational efficiency in muscles from HS rats, it neither sustained protein synthesis nor prevented the reduction in muscle growth. Thus, it seems very unlikely that a high protein diet had any beneficial effect on the overall musculature during weightlessness in rats. J. Nutr. 126: 266–272, 1996.

INDEXING KEY WORDS:
• protein intake  • skeletal muscle
• protein synthesis  • simulated weightlessness
• rats

Both postural and phasic muscles undergo atrophy during real or simulated weightlessness experiments (Desplanches et al. 1990, Martin et al. 1988, Musacchia et al. 1992, Thomason et al. 1989) because of reduced activity, energy deficit and stress. Rapid muscle wasting occurs in postural (that is, antigravity) muscles such as the soleus, and many studies performed in hindlimb suspended (HS)\textsuperscript{a} rats have contributed to the identification of mechanisms responsible for protein loss in that particular muscle (see Thomason and Booth 1990 for a review). However, the musculature mainly comprises phasic muscles such as the extensor digitorum longus (EDL), tibialis anterior or plantaris muscle. Although their mass is less responsive to hindlimb suspension than antigravity muscles (Desplanches et al. 1987, Elder and McComas 1987, Goldspink et al. 1986, Thomason et al. 1989), there are important alterations in their physiological and metabolic properties. For example, changes in enzyme activities and in the fiber cross-sectional areas have been described in the HS tibialis anterior muscle (Chi et al. 1992, Goldspink et al. 1986, Jiang et al. 1992, Thomason et al. 1987). The mechanisms responsible for these alterations are poorly documented. In short-term studies no significant variation in protein synthesis was ob-

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Abbreviations used: ASR, absolute synthesis rate; Ce, RNA to protein ratio; CT, control; EDL, extensor digitorum longus; HP, high protein diet; HS, hindlimb suspended; KRNA, translational efficiency; Kr, fractional protein synthesis rate; MP, medium protein diet; $S_h$, specific radioactivity of homogenates; $S_p$, specific radioactivity of plasma; $S_v$, protein-bound valine specific radioactivity; TCA, trichloroacetic acid; T3, triiodothyronine.

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served within 5 d in the phasic EDL and tibialis anterior muscles [Goldspink et al. 1986]. In another study, Loughna et al. [1986] even reported an increased rate of protein synthesis in the EDL within 3 d of treatment. Such observations may have resulted from the limited alterations that would likely have occurred in these muscles over such a short time period. Therefore, the first goal of the study was to determine whether altered protein synthesis can explain a loss of protein in phasic muscles during long-term hindlimb suspension.

Protein intake modulates both muscle protein synthesis and breakdown in healthy growing animals [Jepson et al. 1988b; McNurlan and Garlick 1989, Waterlow et al. 1978] and humans [Garlick et al. 1991, McNurlan and Garlick 1989, Waterlow et al. 1978]. We recently reported that a 300 g/kg protein (HP) diet partially prevented the decrease in protein synthesis and the fiber type alterations that normally occur in the HS soleus muscle (Taillandier et al. 1993). There is no information in the literature addressing such effects of protein intake in phasic muscles. We previously found that hindlimb suspension induced a reduction in food intake [Taillandier et al. 1993]. Therefore changes in protein metabolism that were observed during hindlimb suspension may partly be explained by a decrease in food intake. Thus, using pair-fed controls, the second aim of this study was to investigate whether a HP diet had any beneficial effect on protein synthesis, translational efficiency, total RNA content, fiber type distribution and cross-sectional areas in the tibialis anterior muscle during 21 d of hindlimb suspension compared with a 150 g/kg (MP) protein diet.

MATERIALS AND METHODS

Animals. Forty male Wistar rats [Iffa-Credo, L’Arbresle, France] with an average body weight of 150 g were randomly assigned to a control (CT) or a hindlimb suspended (HS) group. Twenty animals were used for either protein synthesis experiments or for histochemical analysis. All animals were maintained in a temperature-controlled room (22 ± 1°C) with a 12:12-h light:dark cycle. The experiments were conducted in accordance with the National Research Council Guide for the Care and Use of Laboratory Animals.

Diets. Two isonenergetic (18.81 kJ/g dry matter) semiliquid fish-based diets containing a balanced pattern of essential amino acids (Balage et al. 1986) and providing either 150 [MP] or 300 [HP] grams of protein per kg of dry matter were used [Taillandier et al. 1993]. Diet composition and animal feeding were as previously described [Balage et al. 1986]. The HP diet was isonenergetic with respect to MP diet by reducing the proportion of nonessential lipids.

Experimental design. The HS rats were suspended by the tail as previously described [Taillandier et al. 1993], so that only their front legs were able to rest on the floor. The system permits the animal free access to all parts of the cage and can be adjusted daily without manipulation of the animal. Animals were divided into four groups: CT-MP, HS-MP, CT-HP and HS-HP. We recently showed that HS rats have a reduced food intake [Taillandier et al. 1993]. Therefore, CT animals were given the average amount of food consumed by their corresponding [MP or HP] HS groups. Dry matter intake was measured daily in HS rats and pair-fed CT. Animals has free access to water and were adapted to the diets for 1 wk before initiation of the studies.

Protein synthesis. After 21 d of treatment, the fractional rate of protein synthesis was determined in the tibialis anterior muscle by a large dose method, using a subcutaneous injection of 2.5 mL [2-3-4-3H]-valine [CEA, Saclay, France] and L-valine [Merck, Darmstadt, Germany] [330 mmol/L, 24 GBq/L] [Taillandier et al. 1993]. In each group, one rat was killed by cervical dislocation 10, 15, 20, 25 and 30 min after injection. Blood collected at that time by exsanguination was immediately centrifuged at +4°C, and plasma was frozen in liquid nitrogen. Tibialis anterior muscles were rapidly excised, weighed and frozen in liquid nitrogen. All samples were stored at −20°C until analyzed.

Plasma and tissue analysis. Plasma and tibialis anterior muscles were homogenized in 100 g/L trichloroacetic acid (TCA) as previously described [Taillandier et al. 1993]. Free amino acids and TCA-insoluble pellets were separated by centrifugation. Free valine specific radioactivity of plasma [S_p] or muscle homogenates [S_m] was obtained with an automatic amino acid analyzer connected to a liquid scintillation counter [Flo-One DR, Radiomatic Instrument and Chemical, Tampa, FL] [Taillandier et al. 1993]. An aliquot of the pellet solubilized in 1.0 mol/L NaOH was assayed for protein using bicinchoninic acid [Pierce Chemical, Rockford, IL] [Smith et al. 1985]. Another aliquot was reacidified and the acid-soluble fraction assayed for RNA by the method of Munro and Fleck (1978). The protein-bound valine specific radioactivity [S_v] was determined as previously described [Taillandier et al. 1993]. Valine contents were measured using an automatic amino acid analyzer [Liquimat III, Kontron Instruments, Montigny le Bretonneux, France]. The radioactivity associated with valine was measured on valine peaks collected after chromatography [Gisson 201, Gilson Medical Electronics, Middleton, WI] using liquid scintillation counting [Packard 460 CD, Packard, Downers Grove, IL].

Fractional rate of protein synthesis. The fractional rate of protein synthesis [\( K_s \)] was calculated at each time point [Attaix et al. 1988] from the equation given by McNurlan et al. [1979]:
where all parameters are as described. Translational efficiency (KR\(\text{RNA}\)) was estimated by multiplying the fractional synthesis rate by the ratio of RNA to protein (Cs) to yield milligram of protein synthesized per milligram of total RNA per day.

**Histochemical analysis.** Fiber type determination and distribution, and cross-sectional areas in tibialis anterior muscle were determined as previously described [Desplanches et al. 1987]. Measurements were made on 500 fibers in each section.

**Statistics.** All results are expressed as means ± SE. The effects of treatments were evaluated by two-way ANOVA except the variation in food intake throughout the study, which was evaluated by repeated measures ANOVA with the Statistical Analysis System 1988 [SAS Institute, Cary, NC]. A difference occurring with \(P < 0.05\) was considered significant. Individual t-tests were used when an interaction between diet and suspension was detected \(P < 0.10\).

## RESULTS

During the adaptation period, body weights and animal growth rates were similar in all groups. Suspension induced an early sharp depression in food intake during the first 2 d of treatment (Table 1). During that period, growth rate was impaired in both HS and CT rats \((-3.21 ± 0.80\) and \(0.92 ± 0.78\) g/d, respectively). Thereafter, both food intake (Table 1) and growth rate increased in HS rats. However, weight gain remained significantly lower in HS animals than in pair-fed CT rats \((5.0\) vs. \(8.1\) g/d, \(P < 0.01\)) with both MP and HP diets.

Twenty-one days of hindlimb suspension significantly decreased \((P < 0.0001)\) the tibialis anterior muscle mass by an average of 17% in MP and HP groups (Table 2). Total protein content of tibialis anterior was similarly decreased. Diet had no effect on muscle mass, muscle weight per whole body weight and total protein content. It should be noted that hindlimb suspension induced a reduced muscle growth rate and not an atrophy, because we determined in related experiments that the average tibialis anterior mass and protein content in both CT-MP and CT-HP groups was \(407 ± 11\) and \(75 ± 4\) mg at d zero.

Hindlimb suspension significantly reduced \((P < 0.01)\) total RNA content by 12 and 55% in MP and HP animals, respectively (Table 2). For total RNA and Cs, there was a tendency \((P < 0.09)\) for a diet × HS interaction; therefore, we also performed individual t-tests. In CT rats, HP protein diet enhanced total RNA content by 25% \((P < 0.01)\), whereas in HS animals HP diet reduced total RNA content by 35% \((P < 0.01)\).

We previously reported that suitable conditions for measuring protein synthesis in the soleus muscle of CT and HS animals were achieved following a subcutaneous injection of a flooding dose of \[^{3}H\]valine [Taillardier et al. 1993]. The free valine specific radioactivity was not significantly different between the plasma and muscle homogenates, and the plot of valine incorporation into protein was linear with respect to time and went through time 0 (Fig. 1). Therefore, the conditions of utilization of this technique have been satisfied. Further, the degree of flooding was not altered by the nature of the diet, the free valine specific radioactivities being very close to the injected specific radioactivity, even with the HP diet (Fig. 1).

Twenty-one days of hindlimb suspension reduced \(K_s\) by approximately 25% \((P < 0.001)\) in the tibialis anterior muscles from both MP and HP rats (Table 2). In MP-fed animals, individual t-tests showed that this effect was primarily due to a decrease in protein synthesis efficiency (KR\(\text{RNA}\)) while ribosomal capacity (Cs) remained unchanged (Table 2). In contrast, the decrease in KR\(\text{RNA}\) was prevented in HP rats, whereas Cs

### TABLE 1

**Food intake in hindlimb suspended (HS) rats and their corresponding pair-fed controls (CT) fed a medium (150 g/kg, MP) or a high (300 g/kg, HP) protein diet**

<table>
<thead>
<tr>
<th></th>
<th>Food intake</th>
<th>Before suspension</th>
<th>D 1</th>
<th>D 5</th>
<th>D 9</th>
<th>D 15</th>
<th>D 21</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>g dry matter/day</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CT-MP</td>
<td>20.16 ± 1.21</td>
<td>13.70 ± 1.04(a)</td>
<td>15.26 ± 0.94(a)</td>
<td>18.03 ± 0.92</td>
<td>17.87 ± 0.87</td>
<td>17.20 ± 0.68</td>
<td></td>
</tr>
<tr>
<td>HS-MP</td>
<td>19.77 ± 0.95</td>
<td>12.37 ± 2.94(a)</td>
<td>14.99 ± 1.40(a)</td>
<td>16.21 ± 1.65</td>
<td>15.79 ± 1.11</td>
<td>17.80 ± 0.74</td>
<td></td>
</tr>
<tr>
<td>CT-HP</td>
<td>18.61 ± 0.54</td>
<td>13.24 ± 0.38(a)</td>
<td>14.53 ± 0.23(a)</td>
<td>17.26 ± 0.44</td>
<td>16.54 ± 0.65</td>
<td>17.15 ± 0.54</td>
<td></td>
</tr>
<tr>
<td>HS-HP</td>
<td>18.71 ± 0.21</td>
<td>12.52 ± 0.92(a)</td>
<td>15.22 ± 0.31(a)</td>
<td>15.87 ± 2.38</td>
<td>16.37 ± 0.87</td>
<td>16.50 ± 0.48(b)</td>
<td></td>
</tr>
</tbody>
</table>

\(1\) Values are means ± s.e for 10 rats, except in HS-MP group, in which 1 rat became unhooked and was excluded from analysis. Food intake of rats fed the MP and HP diets was never significantly different between HS and CT rats. Significantly different from presuspension period, \(aP < 0.01\), \(bP < 0.05\).
tended to be lower \( P < 0.09, \) Table 2). The absolute synthesis rate (ASR) was depressed by 32–40\% \( P < 0.001 \) in HS rats.

Diet had significant effects on fiber type distribution (Table 3). The HP diet induced a decrease in the proportion of Type II fibers with a concomitant increase in intermediate and Type I fibers, as previously reported in the soleus muscle (Taillandier et al. 1993).

**DISCUSSION**

Muscles containing a high proportion of fast-twitch fibers (plantaris, medial gastrocnemius, extensor digitorum longus and tibialis anterior) are less sensitive to hindlimb suspension than slow-twitch muscles (soleus, adductor longus) especially during short-term treatments (< 14 d) (Desplanches et al. 1987, Elder and McComas 1987, Goldspink et al. 1986, Loughna et al. 1986, Thomason et al. 1989). However, our data clearly show that the tibialis anterior muscle mass, protein and RNA content were significantly affected by long-term hindlimb suspension compared with pair-fed age-matched animals (Table 2), although it should be noted that reduced muscular growth and not atrophy likely was involved.

The present experiments firmly establish that 21 d of hindlimb suspension resulted in a reduction in protein synthesis (25\%) in the tibialis anterior muscle mass of rats fed the MP diet. The fact that Goldspink et al. (1986) found no variation in \( K_s \) during the first 5 d of hindlimb suspension likely resulted from the time at which the experiment was done. This impairment in protein synthesis in MP-fed rats was due to a reduced efficiency of translation that was totally attributable to lack of use in our experimental design, and not to a reduction in food intake. When compared with age-matched controls, the reductions in muscle mass, \( K_s \) and \( K_r \) seen are similar to those reported in the rat EDL muscle after 7 d of immobilization of the ankle in a flexed position (Goldspink 1977). Such adaptations probably reflect a sparing energy mechanism in unused muscles.

Protein intake markedly influences protein turnover in humans and other mammals (McNurlan and Garlick

### TABLE 2

<table>
<thead>
<tr>
<th></th>
<th>CT (g)</th>
<th>HS (g)</th>
<th>CT (g)</th>
<th>HS (g)</th>
<th>Statistical significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Muscle mass, mg</td>
<td>563</td>
<td>459</td>
<td>563</td>
<td>478</td>
<td>0.0001</td>
</tr>
<tr>
<td>Muscle wt per whole body wt, mg/100 g</td>
<td>189</td>
<td>174</td>
<td>192</td>
<td>177</td>
<td>0.01</td>
</tr>
<tr>
<td>Total protein content, mg</td>
<td>95</td>
<td>95</td>
<td>110</td>
<td>88</td>
<td>0.01</td>
</tr>
<tr>
<td>Total RNA, ( \mu ) g</td>
<td>183</td>
<td>162</td>
<td>234</td>
<td>105</td>
<td>0.05</td>
</tr>
<tr>
<td>( C_s ), ( \mu ) RNA/mg protein</td>
<td>1.76</td>
<td>1.71</td>
<td>2.13</td>
<td>1.20</td>
<td>0.089</td>
</tr>
<tr>
<td>( K_r ), %/d</td>
<td>7.05</td>
<td>5.27</td>
<td>5.73</td>
<td>4.34</td>
<td>0.054</td>
</tr>
<tr>
<td>ASR, mg protein/d</td>
<td>7.37</td>
<td>4.99</td>
<td>6.36</td>
<td>3.79</td>
<td>0.054</td>
</tr>
<tr>
<td>( K_r ), mg protein ( \cdot ) mg RNA^{-1} ( \cdot ) d^{-1,4}</td>
<td>40.1</td>
<td>30.8</td>
<td>26.9</td>
<td>36.2</td>
<td>0.014</td>
</tr>
</tbody>
</table>

1. \( C_s \), ribosomal capacity; \( K_r \), fractional rate of protein synthesis; ASR, absolute synthesis rate; \( K_r \), translational efficiency.
2. Probability under the null difference hypothesis.
3. Pooled \( S_e \) calculated from the error mean squares for means of five rats, except in the HS-MP group in which one rat became unhooked and was excluded from analysis.
4. Student t-test analysis. Significantly different from CT \( *P < 0.01 \); or from comparably treated MP animals \( ^{bp} P < 0.01, ^{cp} P < 0.05 \).
has recently been reported to inhibit RNA degradation in cultured rat hepatocytes (Balavoine et al. 1993), which could explain Cs preservation in both the tibialis anterior (Table 2) and the soleus muscle (D. Taillandier, unpublished data) of rats fed the HP diet. Further studies are needed to clarify our observations, since the flooding dose technique used in this experiment resulted in perturbations of amino acid levels. For example, skeletal muscle glutamine and alanine concentrations are sharply enhanced (D. Attaix, unpublished data) after a flooding dose of [3H]valine.

The HP diet did not improve K, in phasic muscles from HS rats in contrast with our previous study in the soleus muscle (Taillandier et al. 1993). In addition, the lower protein content of the tibialis anterior muscle from HS rats was not reversed by a HP diet. In contrast, the HP diet resulted in an elevation in Krna (18%, <0.05) in the HS group, that is, the reverse pattern observed in CT rats (Table 2). A similar effect was also found in the soleus muscle in HS animals (82%, <0.01) (D. Taillandier, unpublished data). In HS rats, HP diet tended to decrease Cs in both tibialis anterior (30%, <0.09) and soleus muscles (39%, <0.10), D. Taillandier, unpublished data. Thus, the variation in Krna [and possibly in Cs] in skeletal muscle seemed to be influenced by the metabolic status of rats adapted to high protein diets. Although the reasons for these different responses are not clear, these alterations in Krna and Cs may involve changes in hormonal status and responsiveness (Thomason and Booth 1990), as well as in amino acid metabolism (Jaspers et al. 1986 and 1989) that could partly explain the differential effects of the HP diet on CT and HS rat muscle.

A higher proportion of intermediate and Type I fibers (and decrease in Type II) was observed in animals fed the HP diet. We recently reported that a higher percentage of Type I fibers was maintained in the soleus muscle of HS-HP rats, and we hypothesized that this could reflect the decrease in plasma free triiodothyronine (T3) concentration observed in these rats.

1 Probability under the null difference hypothesis.
2 Pooled st calculated from the error mean squares for means of five rats.

1989, Millward et al. 1976, Waterlow et al. 1978], a strong positive correlation exists between skeletal muscle K, and protein intake in rats fed free access [Jepson et al. 1988b]. However, when protein is fed above that required for optimal growth, the opposite appears to be true. In our study, the HP diet resulted in a reduction in muscle K, of CT animals (19%, <0.02), in accordance with previous data from Laurent et al. (1984) in rats fed a 40% protein diet. The mechanisms explaining reduced in vivo protein synthesis in muscle of rats fed HP diets are presently unknown. We showed here that this impairment in protein synthesis resulted from a reduction in the translational efficiency in the tibialis anterior muscle in CT animals (33%, <0.01, Table 2). A similar observation also prevailed in the soleus muscle where KRNA was 28.4 ± 3.1 and 18.4 ± 3.5 mg of protein synthesized·mg RNA·d·1 in CT pair-housed animals fed the MP and HP diets, respectively (P < 0.01) (D. Taillandier, unpublished data). The reduction in protein synthesis may also be related to depressed amino acid concentrations. Moundras et al. [1993] recently reported in rats adapted to high protein diets (that is, 30 and 60%) that threonine, serine, glycine and glutamine concentrations in skeletal muscle were depressed. Enhanced glutamine concentrations, in both physiological and pharmacological ranges, markedly stimulated protein synthesis in perfused rat (MacLennan et al. 1987) and isolated chick (Wu and Thompson 1990) skeletal muscle, and a reduced glutamine concentration paralleled the fall in K, and KRNA in rat skeletal muscle (Jepson et al. 1988a). The reduced intramuscular glutamine concentration observed in rats fed a 30% protein diet (Moundras et al. 1993) may therefore contribute to explain the reduction in protein synthesis in CT rats. Depressed concentrations of other amino acids may also affect the initiation process (and consequently reduce KRNA), as shown in isolated rat hepatocytes (Everson et al. 1989). High protein diets are also known to elevate branched-chain amino acids concentrations (Moundras et al. 1993); leucine

<table>
<thead>
<tr>
<th>Table 3</th>
<th>Tibialis anterior muscle fiber type composition in control (CT) and hindlimb suspended (HS) rats fed a medium (150 g/kg, MP) or a high (300 g/kg, HP) protein diet</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>CT</td>
</tr>
<tr>
<td>Type I fibers, %</td>
<td>3.6</td>
</tr>
<tr>
<td>Intermediate fibers, %</td>
<td>0.5</td>
</tr>
<tr>
<td>Type II fibers, %</td>
<td>95.6</td>
</tr>
<tr>
<td>Type I fiber areas, μm²</td>
<td>989</td>
</tr>
<tr>
<td>Type II fiber areas, μm²</td>
<td>1929</td>
</tr>
</tbody>
</table>

1 Probability under the null difference hypothesis.
2 Pooled st calculated from the error mean squares for means of five rats.
(Taillandier et al. 1993). Thyroid hormones can potentially mediate a response to dietary protein in muscle (Jepson et al. 1988b) and are known to play an important role in muscle fiber type distribution (Nwoye et al. 1982). Thus, the shift from glycolytic to more oxidative fibers in the tibialis anterior of CT and HS rats fed the 30% protein (HP) diet could also result from the decrease in free T3 observed in these animals (Taillandier et al. 1993).

In conclusion, our data clearly demonstrate that a reduction in protein synthesis and translational efficiency was observed in phasic muscles following long-term hindlimb suspension. A high protein intake depressed KRNA in CT rats but restored the translational efficiency in the tibialis anterior muscles of suspended animals. However, the HP diet neither sustained protein synthesis nor prevented the reduction in muscle growth in HS phasic muscle, but even further decreased total RNA content. Thus, it seems very unlikely that a high protein diet had any beneficial effect on overall musculature during weightlessness in rats.

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LITERATURE CITED


