The effect of branched chain amino acids on proteosynthesis in skeletal muscles of Japanese quail during ontogenesis

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ABSTRACT: We studied the influence of branched chain amino acids on the muscle proteosynthesis of Japanese quail during ontogenesis. We used *in vitro* incubation of these muscles: *musculus extensor metacarpalis radialis* (EMR) – wing muscle, *musculus ambiens* (MA) – leg muscle. The incorporation of ^{14}C-tyrosine into the individual protein fractions was evaluated. Influences of valine, leucine and isoleucine on proteosynthesis on day 14, 28 and 53 of life of Japanese quails were compared. Different patterns of individual protein fractions were detected. During ontogenesis, in the MA the number of fractions remained unchanged while in the EMR it differed. Four fractions with molecular weight 200–1 000 kDa present on day 14 and 28 were absent on day 53. A new fraction over 200 kDa was detected on day 53. The ^{14}C-tyrosine incorporation after leucine treatment was enhanced only in the MA of 28 days old quails. The protein content in the EMR decreased (50%) in several fractions. The addition of valine had no effect in the MA while in the EMR the protein content decreased in 14 and 28 days old quails. The incorporation of ^{14}C-tyrosine was decreased by the influence of isoleucine in the EMR of 28 and 53 days old quails, in the MA only in 28 days old birds. We assume that the effect of regulatory amino acids on proteosynthesis depends both on muscle type and on the age of Japanese quail.

Keywords: proteosynthesis; isolated muscles; ^{14}C-tyrosine incorporation; individual protein fraction

Protein balance of the whole body and of individual tissues is a dictate by the relative rates of protein synthesis and degradation. The regulation of protein metabolism depends on food intake and quality of diet. Since the muscle tissue is very sensitive to internal and external influences, it is a very good indicator of nutritional changes. The role of branched chain amino acids (BCAA) in the regulation of muscle protein turnover is still unclear. Studies on protein turnover in mammals have shown promoting effect of the branched chain amino acids on protein synthesis and inhibiting effect on degradation. Particularly leucine has an anabolic effect on the isolated rat diaphragm in which stimulation of proteosynthesis (Buse and Reid, 1975) and inhibition of protein degradation was found (Buse and Wieghand, 1977; Tischler *et al.*, 1982). Hong and Layman (1984) reported enhanced protein synthesis without any effect on protein degradation. The reports on effects of valine and isoleucine treatment also differ (Fulks *et al.*, 1975; Hong and Layman, 1984).

Unfortunately, little information is available about the protein turnover in avian species (Klasing and Jarrel, 1985; Pinchasov and Nir, 1988; Baracos *et al.*, 1989). In a preliminary experiment we evaluated the influence of BCAA on the fractional rate of protein synthesis (FSR) in two skeletal muscles of Japanese quails (Antalíková *et al.*, 1999). The addition of valine, leucine and isoleucine significantly decreased the value of the fractional synthetic rate in a wing muscle (*musculus extensor metacarpalis radialis* – EMR). In a leg muscle (*musculus ambiens* – MA) only the application of leucine increased the

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FSR significantly, while valine and isoleucine had no effect. This controversy could result from the fact that only whole muscles – the proteins mixture – were analysed. We presumed that analysing of individual protein fractions of muscles would help to clarify these contradictions. The *in vitro* preparation of incubated muscles was used in order to eliminate the effect of other organs and endocrine glands. The effects of valine, leucine and isoleucine on the incorporation of ^{14}C-tyrosine into proteins as well as on the protein content of individual protein fractions were compared. *Musculus extensor metacarpalis radialis* and *musculus ambiens* of 14, 28 and 53 days old Japanese quails were used.

MATERIAL AND METHODS

All commercially available chemicals were of the highest purity. ^{14}C-tyrosine was purchased from ÚVVR Prague, acrylamide, bisacrylamide, phenylmethylsulphonyl fluoride (PMSF), CBB-G250, and L-amino acids from Serva and chloramphenicol from Calbiochem. Molecular weight standard kits were from Boehringer.

Birds and experimental design. 14, 28 and 53 days old cockerels of Japanese quail (six birds in each group) were used. Quails were fed with commercial diet *ad libitum* which was withdrawn 48 hours prior to processing. The EMR and MA were removed, weighed and used for subsequent examination according to Li *et al*. (1973). Muscles were preincubated in a medium consisting of 3 ml of Krebs-Ringer buffer with 10 mM glucose, 0.3 μg/ml chloramphenicol. Trichloroacetic acid-soluble fraction of the plasma from birds fasted for 48 hours was added and bubbled with CO_2/O_2 (1 : 19) mixture. The muscles were incubated for 60 min at 41°C (body temperature of birds) and then replaced into a fresh incubation medium of the same composition, containing 0.21 μCi/ml ^{14}C-tyrosine. In experimental groups the medium was supplemented with 0.5 mM leucine or isoleucine or valine. After the 90 min incubation at 41°C the muscles were washed with Krebs-Ringer buffer, frozen in liquid nitrogen and pulverised.

Electrophoresis. Pulverised muscles were extracted by 10 volumes of 0.1 M K-phosphate buffer pH 7.4 with addition of 4 M urea and 50 mM PMSF at 4°C for 16 hours. Centrifuged supernatants were mixed at a 1 : 1 ratio with the sample buffer containing 0.1% SDS, 1% mercaptoethanol, 5 mM EDTA, 5 M Tris-HCl pH 8.0, 10% glycerol and bromphenol blue and heated at 100°C for 2 minutes. The 2% polyacrylamide gel strengthened with agarose (Tatsumi and Hattori, 1995) with Fairbanks' gel buffer (Fairbanks *et al*., 1971) was used. Electrophoresis was performed on 20 mA/plate for 30 minutes and 30 mA/plate for 4 hours on the apparatus Protean II BIORAD. After the run the gel was stained with CBB G-250 (Neuhoff *et al*., 1985).

Analysis of individual protein fractions from the gel. After scanning gels images using Adobe Photoshop changes in the intensity and size of the spots of individual protein fractions were mutually compared. The individual fractions were cut from the gel. In the aliquots solubilised by $H_2O_2 : NH_3$ (99 : 1) at 50°C for 3 hours radioactivity was assessed by liquid scintillation counting (Beckman LS 6000 SE). In the aliquots hydrolysed by 6 M HCl at 125°C for 2.5 hours free tyrosine was determined by fluorometry (Udenfried and Cooper, 1952).

Statistical analysis. Differences between experimental groups were evaluated using paired Student's *t*-test.

RESULTS

Musculus extensor metacarpalis radialis and musculus ambiens differed substantially in protein fraction patterns. The number of individual protein fractions in the EMR differs also with the age of quail (Figure 1). There are four fractions in the range of 200–1 000 kDa present on the 14th and 28th day that are absent on the 53rd day of life. On the 53rd day another fraction with the molecular weight over 200 kDa was detected. In the AM the number of fractions was unchanged during ontogenesis (Figure 2). We observed quite different effects of leucine in two muscles of quail, mainly on the 28th day of life. In the MA leucine stimulated the incorporation of ^{14}C-tyrosine in four protein fractions without changes in the protein content while in the EMR it had no influence on the incorporation of ^{14}C-tyrosine and the protein content fell approximately by 50% in many protein fractions (Table 1). On day 14 and 53 of life of quails the incorporation of ^{14}C-tyrosine decreased without changes in the protein content in both muscles. The addition of valine to the medium in the EMR of 14 and 28 days old birds influenced the protein content (fall in 6 fractions) without changes in the incorporation of ^{14}C-tyrosine. Valine had no effect

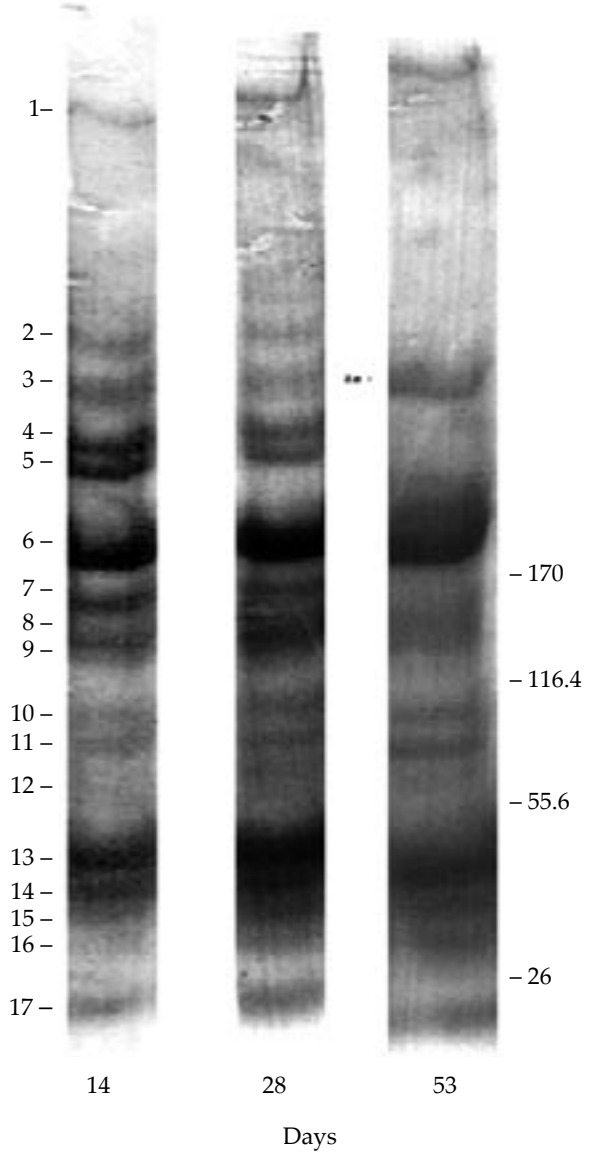

Figure 1. The pattern of protein fractions during ontogenesis of *musculus extensor metacarpalis radialis*: left – the number of protein fractions, right – the molecular weight of standard

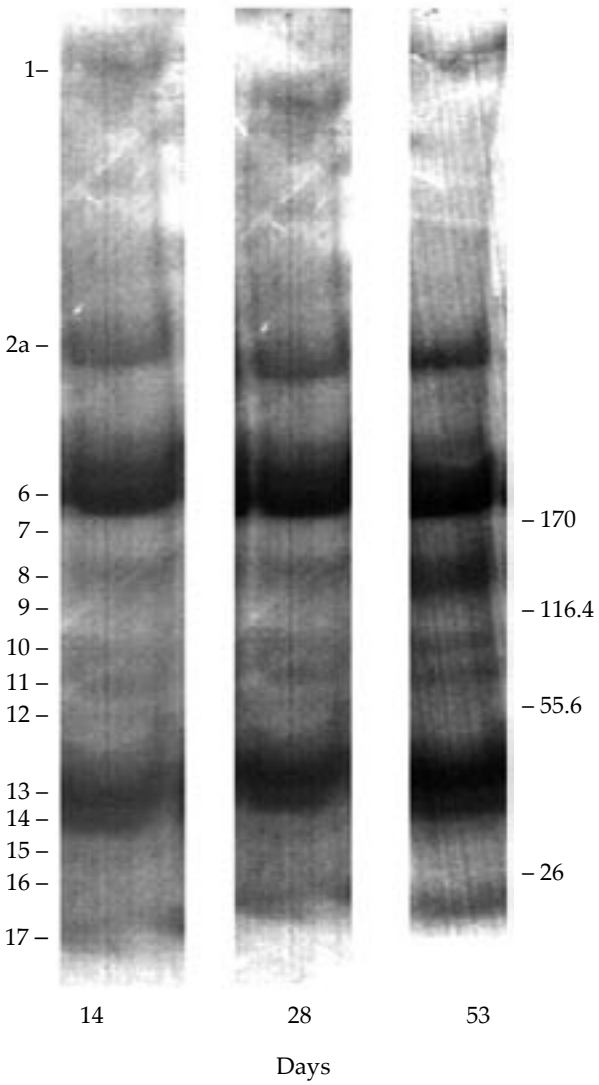

Figure 2. The pattern of protein fractions during ontogenesis of *musculus ambiens*: left – the number of protein fractions, right – the molecular weight of standard

in the MA. The effect of isoleucine treatment was significant predominantly in the EMR of the 14 and 53 days old quails. On day 14 we observed a 50% decrease of the protein content in many fractions without changes in the incorporation of ^{14}C-tyrosine. On day 53 isoleucine caused the decrease in the incorporation of tyrosine (Table 2). In the AM valine decreased the incorporation of tyrosine while the protein content increased only in a few fractions.

DISCUSSION

The effects of BCAA treatment in two muscles of Japanese quail differed significantly predominantly on the 28th day of life. Leucine in the MA stimulated the incorporation of ^{14}C-tyrosine without changes in the protein content while in the EMR the incorporation of ^{14}C-tyrosine was not affected and the protein content fell approximately by 50%. It corresponded with our previous research of the fractional

Table 1. Incorporation of ^{14}C-tyrosine and protein content in fractions of *m. extensor metacarpalis radialis* and *m. ambiens* of 28 days old quails in control group and in experimental groups with addition of 0.5 mM leucine to the incubation medium

Fractions	*Musculus extensor metacarpalis radialis*				*Musculus ambiens*			
	Control		Leucine		Control		Leucine	
	Tyrosine[b]	Proteins[a]	Tyrosine[b]	Proteins[a]	Tyrosine[b]	Proteins[a]	Tyrosine[b]	Proteins[a]
6	16.69 ± 3.04	6.34 ± 2.61	19.45 ± 3.40	4.31 ± 1.35	23.66 ± 13.97	7.04 ± 2,59	16.81 ± 4.25	4.85 ± 0.90
7	16.39 ± 2.31	6.68 ± 2.43	25.13 ± 6.48	3.28 ± 0.77*	14.25 ± 11.16	7.86 ± 3,03	12.24 ± 6.12	5.15 ± 0.82
8	68.5 ± 10.47	6.03 ± 2.31	33.45 ± 5.42*	3.21 ± 0,52	19.18 ± 9.53	5.31 ± 1,39	37.43 ± 6.16*	3.79 ± 0.55
9	29.69 ± 9.38	5.56 ± 1.76	35.92 ± 6.60	2.94 ± 0.32*	30.98 ± 7.55	4.99 ± 1,24	38.25 ± 5.02	3.69 ± 0.59
10	48.12 ± 22.35	5.14 ± 1.56	28.91 ± 6.84	3.06 ± 0.24*	26.00 ± 4.85	5.01 ± 1,21	39.80 ± 17.01	3.88 ± 0.79
11	47.65 ± 17.08	5.37 ± 1.60	54.68 ± 33.10	3.24 ± 0.44*	24.62 ± 3.57	5.23 ± 1,40	38.51 ± 9.95	3.98 ± 0.70
14	35.86 ± 17.73	6.54 ± 2.04	38.45 ± 22.85	3.87 ± 0.84*	12.19 ± 2.55	7.27 ± 2,77	22.53 ± 3.22*	5.16 ± 0.76
15	46.42 ± 21.62	5.86 ± 1.88	48.25 ± 18.5	3.29 ± 0.36*	34.64 ± 2.05	5.52 ± 1,95	44.73 ± 6.89	4.27 ± 0.89
16	53.88 ± 5.53	50.8 ± 1.56	51.99 ± 27.84	2.88 ± 0.33*	33.29 ± 3.55	4.36 ± 1.4	44.68 ± 15.41	2.69 ± 1.57

[a]protein content is in relative numbers (derived from the intensity of the colour of spots on th e gel), [b] ^{14}C-tyrosine incorporated in protein (dpm/ng/h)× 10^{-3}
*means ± SD were significantly different ($P < 0.05$)

Table 2. Incorporation of ^{14}C-tyrosine and protein content in fractions of *m. extensor metacarpalis radialis* of 14 and 53 days old quails in control group and in experimental groups with addition of 0.5 mM isoleucine to the incubation medium

Fractions	14 days old quails				53 days old quails			
	Control		Isoleucine		Control		Isoleucine	
	Tyrosine[b]	Proteins[a]	Tyrosine[b]	Proteins[a]	Tyrosine[b]	Proteins[a]	Tyrosine[b]	Proteins[a]
6	14.73 ± 4.62	5.82 ± 2.06	16.84 ± 4.29	2.78 ± 0.63*	12.16 ± 3.34	7.84 ± 1.80	6.21 ± 2.78*	7.56 ± 1.33
8	35.83 ± 15.64	5.22 ± 2.60	54.12 ± 13.11	2.20 ± 0.52*	39.49 ± 20.36	5.68 ± 1.21	11.82 ± 3.05*	6.71 ±0.77
9	108.8 ± 63.56	4.04 ± 1.70	151.8 ± 13.98	1.62 ± 0.48*	34.55 ± 14.82	5.38 ± 1.30	10.90 ± 3.25*	6.50 ± 0.76
10	77.8 ± 22.30	3.58 ± 1.5	87.14 ± 26.13	1.90 ± 0.46*	25.12 ± 6.61	5.81 ± 1.62	9.80 ± 2.48*	6.37 ± 0.84
11	47.57 ± 25.62	3.96 ± 1.49	91.06 ± 32.81	2.05 ± 0.50*	30.18 ± 11.01	5.95 ± 1.66	10.56 ± 3.36*	6.48 ± 0.95
14	33.68 ± 11.62	3.36 ± 2.55	66.02 ± 21.83	2.65 ± 0.56*	16.13 ± 3.14	8.12 ± 1.93	7.74 ± 3.04*	7.91 ± 1.16
15	70.79 ± 41.84	4.86 ± 1.83	53.55 ± 4.32	2.32 ± 0.53*	37.72 ± 26.11	6.72 ± 1.68	12.50 ± 4.03*	7.05 ± 1.16
16	68.71 ± 46.43	3.04 ± 1.20	93.15 ± 8.58	1.80 ± 0.43*	40.78 ± 20.78	5.02 ± 1.93	12.87 ± 1.1*	6.35 ± 1.14

[a]protein content is in relative numbers (derived from the intensity of the colour of spots on the gel), [b]^{14}C-tyrosine incorporated in protein (dpm/ng/h) × 10^{-3}
*means ± SD were significantly different ($P < 0.05$)

synthetic rate (FSR) of the whole muscle. In the EMR leucine caused the 50% fall of the FSR while in the AM this value increased 1.5 times (Antalíková *et al.*, 1999). We assume that in the AM leucine stimulates proteosynthesis while in the EMR it is without effect, at least in observed protein fractions. Since there were some changes in the protein content of these fractions we suppose some effects of leucine on the level of degradation. Since the protein content in the whole muscles was unchanged (Antalíková *et al.*, 1999) we suppose the effect of leucine only in a part of protein fractions. This assumption is supported by the report of Reeds *et al.* (1993) about the different nutritional regulation of myofibrillar and sarcoplasmatic protein degradation. In our experiment predominantly the myofibrillar proteins were analysed while in the previous report the total protein pool was evaluated. On the 14th and 53rd days of life of quails the incorporation of ^{14}C-tyrosine decreased without changes in the protein content in both muscles. We assume an inhibitory effect of leucine on protein degradation.

Concerning the treatment of valine and isoleucine in the MA our results are in accordance with the report of Buse and Reid (1975) about no effect of these amino acids on proteosynthesis and degradation in the rat diaphragm. In the EMR the application of valine influenced only the protein content. It suggests the importance of the degradation process in the nutritional regulation of the protein turnover. The total resistance of both muscles to the effect of valine in the 53 days old birds complies with the report of Reeds *et al.* (1993) that the sensitivity of the degradation rate of myofibrillar proteins in rats decreased with the age of animals. We also assume isoleucine to influence the degradation of proteins in both muscles predominantly in the 14 days old quails as the protein content decreased by 50% without changes in the incorporation of ^{14}C-tyrosine. The effect of this amino acid on the 28th day in the MA is controversial. Despite the inhibiting effect of isoleucine on the ^{14}C-tyrosine incorporation the protein content increased. We assume the depression of the degradation process. On day 53 the protein content was unchanged while the incorporation of ^{14}C-tyrosine decreased. This observation also suggests some changes in the process of protein degradation.

Our assumption of the probable inhibitory effect of BCAA in the EMR on protein degradation corresponds with observations of Chua *et al.* (1979) that high levels of the decarboxylated products of leucine, valine and isoleucine decreased protein degradation in perfused rat hearts. However, Tischler *et al.* (1982) found that proteolysis was inhibited only by leucine alone in the diaphragm but not in *m. soleus* and *m. digitorum longus*. Since BCAA share common transamination and decarboxylation pathways (Odessey and Goldberg, 1979; Smith *et al.*, 1983) and products of BCAA catabolism reduced protein degradation in perfused hearts (Chua *et al.*, 1980), it is unclear why proteolysis is suppressed in the hemidiaphragm with leucine but not with valine or isoleucine (Buse and Reid, 1975; Fulks *et al.*, 1975; Tischler *et al.*, 1982). Differences in the metabolism of BCAA in cardiac muscle and in diaphragm and other types of skeletal muscles (Veerkamp and Wagenmakers, 1981) might account for this (Mitch and Clark, 1984). There were also reports of a different metabolism of BCAA in the organism of Japanese quail compared to mammals or chicken. The leucine-induced antagonism of BCAA reported in rats (May *et al.*, 1991; Torres *et al.*, 1993) and even in chickens (Boorman and Buttery, 1972; Smith and Austic, 1978) was not found in Japanese quail (Mason *et al.*, 1981).

Apparently the effect of BCAA on the protein turnover depends on the age of Japanese quail. During ontogenesis the rate of protein synthesis or degradation depends on the importance of these processes for the regulation of protein turnover. It is assumed that the effect of BCAA is specific, at least in the myofibrillar and sarcoplasmatic pools of proteins. Our results indicate the influence of BCAA on proteosynthesis but their effect on degradation is probably more significant (especially in young quails). This assumption corresponds with observations that in contrast with mammals, the nutritional effects on skeletal muscles of young, growing birds result predominantly in a change of the rate of degradation without change in the proteosynthetic rate (Nieto *et al.*, 1994).

Our results also indicate that the EMR and AM differ in the level of myogenesis probably in response to the muscle function. The number of individual fractions in the EMR varies during ontogenetic development while in the AM it is unchanged. It is in accordance with reports of Maltin *et al.* (1989) that various muscles develop in a different manner. The sensitivity of proteosynthesis (or degradation) of individual protein fractions to the effect of BCAA depends probably on the level of myogenesis. To confirm this assumption it is necessary to evaluate the degradation rate of the same protein fractions in both muscles.

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ABSTRAKT

Vplyv rozvetvených aminokyselín na syntézu svalových bielkovín japonskej prepelice počas ontogenézy

Cieľom tejto práce bolo sledovať vplyv rozvetvených aminokyselín na syntézu bielkovín vo svaloch japonskej prepelice počas ontogenézy na úrovni jednotlivých bielkovinových frakcií. Využili sme *in vitro* inkubáciu izolovaného svalu *musculus extensor metacarpalis radialis* (EMR) – krídelný sval, *musculus ambiens* (MA) – stehenný sval. Ako marker proteosyntézy sme použili ^{14}C-tyrozín. Analyzovali sme individuálne frakcie bielkovín, v ktorých sme stanovili množstvo ^{14}C-tyrozínu inkorporovaného do jednotkového množstva bielkoviny za jednotku času. Tento parameter sme sledovali po pridaní valínu, leucínu a izoleucínu do inkubačného média u prepelíc vo veku 14, 28 a 53 dní. Spektrum bielkovín v MA a EMR nie je rovnaké. Zatiaľ čo v MA ostáva počas ontogenézy nezmenené, v EMR sme u 14- a 28-dňových prepelíc detegovali štyri bielkovinové frakcie s Mr 200–1 000 kDa, ktoré už neboli viditeľné v 53. dni. U prepelíc v tomto veku sme zistili prítomnosť inej frakcie. Pôsobenie leucínu bolo rozdielne vo svaloch 28-dňových prepelíc. V MA inkorporácia tyrozínu stúpla, v EMR nebola ovplyvnená, ale klesol obsah bielkovín (50 %) vo vysokom počte frakcií. Valín v MA neovplyvnil žiaden zo sledovaných parametrov, kým v EMR spôsobil pokles obsahu bielkovín v 14. a 28. dni v polovici z celkového počtu sledovaných frakcií. Pôsobením izoleucínu v EMR klesla inkorporácia tyrozínu u 28- a 53-dňových, v AM len u 28-dňových prepelíc. Regulačný vplyv rozvetvených aminokyselín na syntézu bielkovín závisí teda pravdepodobne nielen od svalu, ale aj od veku prepelice.

Kľúčové slová: proteosyntéza; izolované svaly; inkorporácia ^{14}C- tyrozínu; individuálne bielkovinové frakcie

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