Changes in the mRNA Expressions of Insulin-like Growth Factors, Their Receptors, and Binding Proteins during the Postnatal Development of Rat Masseter Muscle

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Source: Zoological Science, 20(4) : 441-447

Published By: Zoological Society of Japan

URL: https://doi.org/10.2108/zsj.20.441

ZOOLOGICAL SCIENCE **20**: 441–447 (2003)

Changes in the mRNA Expressions of Insulin-like Growth Factors, Their Receptors, and Binding Proteins during the Postnatal Development of Rat Masseter Muscle

Takashi Saito[1], Satonari Akutsu[2], Toki Urushiyama[3], Katsunori Ishibashi[1], Yoichi Nakagawa[1], Charles F. Shuler[4], Akira Yamane[5*]

[1]*Second Department of Oral and Maxillofacial Surgery,*
[2]*High Technology Research Center,* [5]*Department of Pharmacology, Tsurumi University School of Dental Medicine, Yokohama, Japan*
[3]*Master's Program in Biosystem Studies, University of Tsukuba, Tsukuba, Japan*
[4]*Center for Craniofacial Molecular Biology, University of Southern California, Los Angels, USA*

ABSTRACT—Morphological, biochemical, and functional changes in rat masseter muscle reportedly occur during the shift of rat feeding behavior from suckling to chewing. To determine whether insulin-like growth factors (IGFs), their receptors (IGFRs), and binding proteins (IGFBPs) are involved in the changes in rat masseter muscle during the shift of rat feeding behavior, we analyzed the expressions of IGF-I, IGF-II, IGFR1, IGFR2, and IGFBP1~6 mRNAs in rat masseter muscle between 0 and 70 days after birth using the competitive, reverse transcriptase-polymerase chain reaction (RT-PCR) method. Between 14 and 19 days of age, sharp falls in the quantities of IGF-I, IGF-II, IGFR1, IGFR2, IGFBP3, IGFBP5, and IGFBP6 mRNAs were observed, whereas the quantity of IGFBP4 mRNA rose sharply during the same period. IGFBP1 and 2 mRNAs were not detectable during the postnatal development. In the present study, the shift of rat feeding behavior from suckling to chewing occurred between 14 and 19 days of age, since the pups took residues of a pellet diet which had been dropped in a cage after 14 days of age, and we removed the pups from the dams and fed them on a pellet diet at 19 days of age. Thus, the drastic changes in the quantities of IGF, IGFR, and IGFBP mRNAs in the rat masseter muscle between 14 and 19 days of age seem to be involved in the shift of rat feeding behavior.

Key words: masseter muscle, insulin-like growth factor, competitive RT-PCR, rat, feeding behavior

INTRODUCTION

The feeding behavior of the rat changes from suckling to chewing between 14 and 28 days after birth (Maeda *et al*., 1981a). During this postnatal period, morphological, biochemical, and functional changes in the masseter muscle reportedly occur. In this process, the masseter myofibers grow rapidly and markedly (Maeda *et al*., 1981b; Miyata *et al*., 1996); expression profiles of myosin heavy chains markedly change (Saito *et al*., 2002a); the diameters of motoneurons innervating the masseter muscle increase and the pattern of electromyography changes markedly (Kubota *et al*., 1988; Miyata *et al*., 1996); and the transition of nicotinic acetylcholine receptors (nAChRs) from embryonic to adult types and the elimination of nAChRs are completed. (Saito *et al*., 2002b).

It is well known that the insulin-like growth factors (IGF)-I and IGF-II are essential for the embryonic development of skeletal muscle, including its proliferation, differentiation, and synaptogenesis (Ishii, 1989; Florini *et al*., 1996; Yamane *et al*., 2000a). IGFs are also reported to play important roles in the postnatal growth of skeletal muscle (Beck *et al*., 1988; Alexandrides *et al*., 1989) and the change in the mass and phenotype of adult skeletal muscle (Yang *et al*., 1997; Lalani *et al*., 2000; Olson and Williams, 2000). These signals of IGFs are mediated via IGF receptor 1 (IGFR1) (Ewton *et al*., 1987; Quinn *et al*., 1994; Navarro *et al*., 1997), while IGF receptor 2 (IGFR2) serves as a factor for the turnover IGF-II protein in skeletal muscle (Kiess *et al*., 1987; Wang *et al*., 1994; Ludwig *et al*., 1996). The IGF actions are

* Corresponding author: Tel. +81-45-580-8452;
FAX. +81-45-573-9599.
E-mail: GAH03667@nifty.ne.jp

regulated and modified by a family of six high-affinity IGF binding proteins (IGFBP), designated as IGFBP1 to IGFBP6 (Jones Clemmons, 1995). These findings suggest that the IGFs, IGFRs, and IGFBPs are closely related to the morphological, biochemical, and functional changes in masseter muscle in association with the shift of feeding behavior from suckling to biting, and that their expressions change markedly during the postnatal development of masseter muscle.

However, there are, to date and to the best of our knowledge, no published data on the expressions of IGFs, IGFRs, and IGFBPs during the postnatal development of rat masseter muscle. We analyzed the expressions of IGF, IGFR, and IGFBP mRNAs in rat masseter muscle between 0 and 70 days after birth using the competitive, reverse transcriptase-polymerase chain reaction (RT-PCR) method. We then related our findings with changes in the rat masseter muscle during postnatal development.

MATERIALS AND METHODS

Experimental animals

Ten pregnant Wistar rats with similar birth windows were purchased (Nippon Clea, Tokyo, Japan) and then housed in individual cages. After birth, pups (each litter containing 10–12 pups) were randomly selected for study at 1, 7, 14, and 19 days of age (n=6 each). At 19 days of age, only male pups were removed from their dams, and fed a pellet diet (CE-2, CLEA Inc., Tokyo, Japan) until they reached 70 days of age. They were then randomly selected for study at 28, 49, and 70 days of age (n=6 each). All animals were weighed and killed by exsanguination under anesthesia with pentobarbital sodium (Nembutal; Abbott Laboratories, Chicago, IL, USA) at a fetal overdose of 50 mg/kg. The body weight of the animals increased gradually with development (Fig. 1). The central portion of the superficial masseter muscles was immediately dissected, rapidly frozen in liquid nitrogen, and stored at –85°C until subsequent analyses. The protocols used in the present study were approved by the Institutional Animal Care Committee of Tsurumi University School of Dental Medicine.

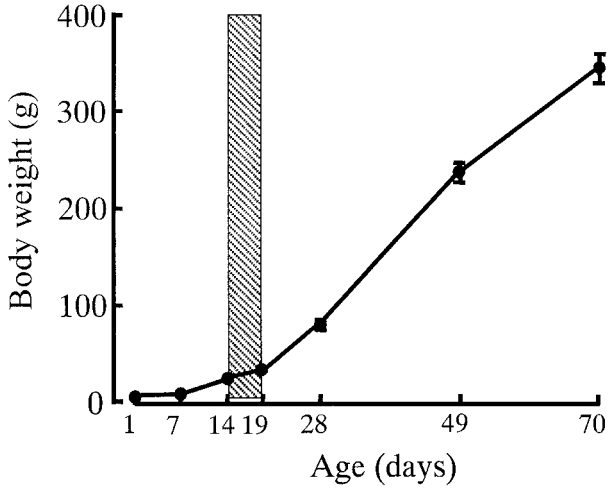

Fig. 1. Changes in rat body weight. Each point and its vertical bar represent the mean ± SD of six rats. The diagonal rectangle shows the period for the shift of rat feeding behavior from suckling to chewing.

RNA extraction, reverse transcription, and competitive polymerase chain reaction (competitive RT - PCR) amplification.

Total RNA extraction, reverse transcription, and competitive PCR amplification were performed as described previously (Ohnuki *et al.,* 2000; Yamane *et al*., 1998; Yamane *et al*., 2000b). Briefly, total RNA was isolated from individual masseter samples (30–50 mg in wet weight) using FastRNA^{TM} Kit-GREEN according to the manufacturer's specifications (BIO 101, Vista, CA, USA). The RNA was treated with 2 unit of ribonuclease-free deoxyribonuclease I (Life Technologies, Inc., Rockville, MD, USA), and was then reverse-transcribed to cDNA with 200 unit of reverse-transcriptase (SuperScript II; Life Technologies).

Table 1 shows the primer sequences and product sizes for IGFs, IGFRs, and IGFBPs; those for the house keeping gene S16 (ribosomal protein) were previously reported (Ohnuki *et al*., 2000). In the competitive PCR, target cDNA (reverse-transcribed target mRNA) existing in the total cDNA (reverse-transcribed total RNA) was coamplified together with the externally added DNA fragment (competitor), which had identical primer-annealing sites to those of the target cDNA. The competitor was constructed by using a PCR MIMIC construction kit (Clontech Laboratory, Inc., Palo Alto, CA, USA) or Competitive DNA Construction Kit (TaKaRa Biochemicals, Shiga, Japan). The PCR products were separated by electrophoresis in a 3% agarose gel containing ethidium bromide to visualize the PCR products as bands (Fig. 2). The fluorescent intensity of each band was measured with an image analyzer (FLA-3000, Fujifilm, Tokyo, Japan). To normalize the variations in the yield of total RNA and efficiency of reverse transcription, we performed PCR amplification for S16 together with its competitor, and also obtained the S16 standard curve. Then, the quantity of endogenous S16 mRNA was quantified to normalize the quantity of target mRNA relative to the quantity of S16 mRNA, as in our previous study (Ohnuki *et al.,* 2000). Here, the quantity of target mRNA was represented by the ratio of the target mRNA to S16 mRNA quantities (target mRNA/S16 mRNA).

Statistical analysis

Data were expressed as mean ± SD. Sheffe's method was used to compare the mean values between each age groups. Differences were considered significant at $p< 0.05$.

RESULTS

Figs. 3A and 3B show the data for IGF-I and IGF-II mRNA expressions, respectively. The quantity of IGF-I mRNA drastically decreased between 1 and 19 days of age and reached 31% ($p<0.0001$) of the 1 day value at 19 days. The rate of decrease (8% per a day) between 14 and 19 days was approximately 4-times greater than that (2.1% per a day) between 1 and 14 days. After 19 days, the quantity of IGF-I mRNA increased and recovered to 52% ($p<0.05$) of the 1 day value at 28 days, then decreased again gradually up to 70 days of age. The quantity of IGF-II mRNA, though transient, increased to 246% ($p<0.0001$) of the 1 day value between 1 and 14 days. After that, the quantity sharply fell and became only 66% ($p<0.0001$) of the 1 day value at 19 days. Thereafter, the level of IGF-II mRNA expression was quite constant up to 70 days.

Figs. 4A and 4B show the data for IGFR1 and IGFR2 mRNA expressions, respectively. IGFR1 mRNA was highly expressed between 1 and 14 days, then drastically fell by 19 days to 46% of the value at 1 day ($p<0.0001$). After that, the

Table 1. Sequences of target gene-specific PCR primers and, target and competitor sizes

Target genes	Sequences	References
IGF-I		
Forward	5'-GCT CTT CAG TTC GTG TGT GG-3'	Hannon *et al*., 1992
Reverse	5'-TTG GGC ATG TCA GTG TGG -3'	
Target size	221 bp	
Competitor size	338 bp	
IGF-II		
Forward	5'-CGT GGA AGA GTG CTG CTT CC-3'	Hannon *et al*., 1992
Reverse	5'-GAC ATC TCC GAA GAG GCT CC-3'	
Target size	329 bp	
Competitor size	440 bp	
IGFR1		
Forward	5'-TCT TGG ATG CGG TGT CCA ATA AC-3'	Wada *et al*., 1993
Reverse	5'-GCA GCA CTC ATT GTT CTC GTT GC-3	
Target size	215 bp	
Competitor size	370 bp	
IGFR2		
Forward	5'-TGC ACA CTC TTC TTC TCC TGG CA-3'	Yamane *et al*., 2000b
Reverse	5'-GCA GAT GTT GAT ATA GAA GTC AGG-3'	
Target size	186 bp	
Competitor size	247 bp	
IGFBP1		
Forward	5'-CCA GGG ACT CAG CTG CCG TGC G-3'	Schuller *et al*., 1994
Reverse	5'-GGC GTT CCA CAG GAT GGG CTG-3'	
Target size	259 bp	
Competitor size	343 bp	
IGFBP2		
Forward	5'-CAA CTG TGA CAA GCA TGG CCG-3'	Schuller *et al*., 1994
Reverse	5'-CAC CAG TCT CCT GCT GCT CGT-3'	
Target size	176 bp	
Competitor size	242 bp	
IGFBP3		
Forward	5'-GAC ACC CAG AAC TTC TCC TCC-3'	Schuller *et al*., 1994
Reverse	5'-CAT ACT TGT CCA CAC ACC AGC-3'	
Target size	220 bp	
Competitor size	292 bp	
IGFBP4		
Forward	5'-CGT CCT GTG CCC CAG GGT TCC T-3'	Schuller *et al*., 1994
Reverse	5'-GAA GCT TCA CCC CTG TCT TCC G-3'	
Target size	214 bp	
Competitor size	294 bp	
IGFBP5		
Forward	5'-GTT TGC CTC AAC GAA AAG AGC T-3'	Yamane *et al*., 2002
Reverse	5'-CTG CTT TCT CTT GTA GAA TCC TT-3'	
Target size	393 bp	
Competitor size	245 bp	
IGFBP6		
Forward	5'-CCC CGA GAG AAC GAA GAG ACG-3'	Schuller *et al*., 1994
Reverse	5'-CTG CGA GGA ACG ACA CTG CTG-3'	
Target size	351 bp	
Competitor size	441 bp	

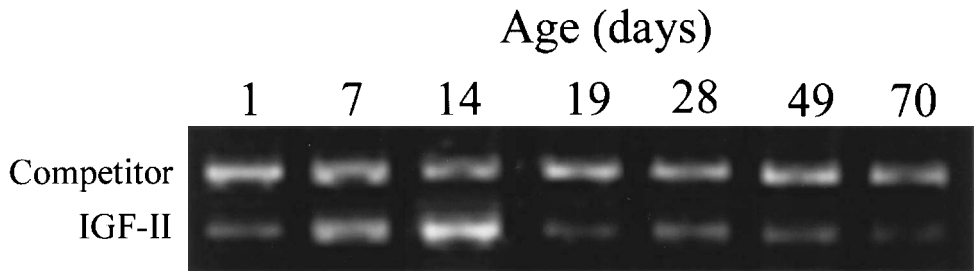

Fig. 2. Typical example of a gel electrophoretic pattern for IGF-II competitive PCR products of rat masseter muscle at 1, 7, 14, 19, 28, 49, and 70 days of age.

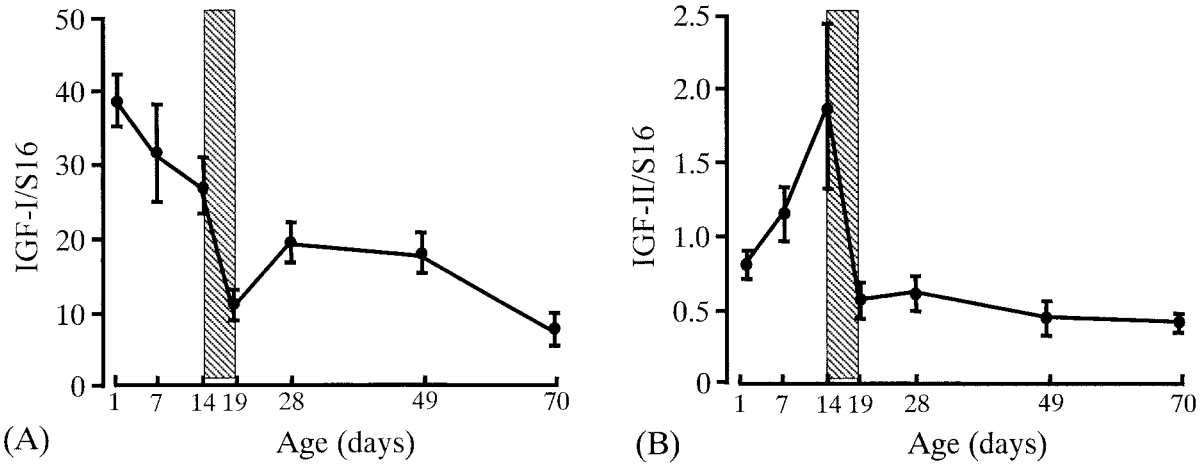

Fig. 3. Relative changes in the quantities of IGF-I (A) and IGF-II (B) mRNAs in the rat masseter muscle at 1, 7, 14, 19, 28, 49, and 70 days of age assessed by using competitive RT-PCR. Each point with its vertical bar represents the mean ± SD of six samples. The vertical axis is expressed as a ratio of the target mRNA to S16 mRNA quantities. The diagonal rectangle shows the period for the shift of rat feeding behavior from suckling to chewing.

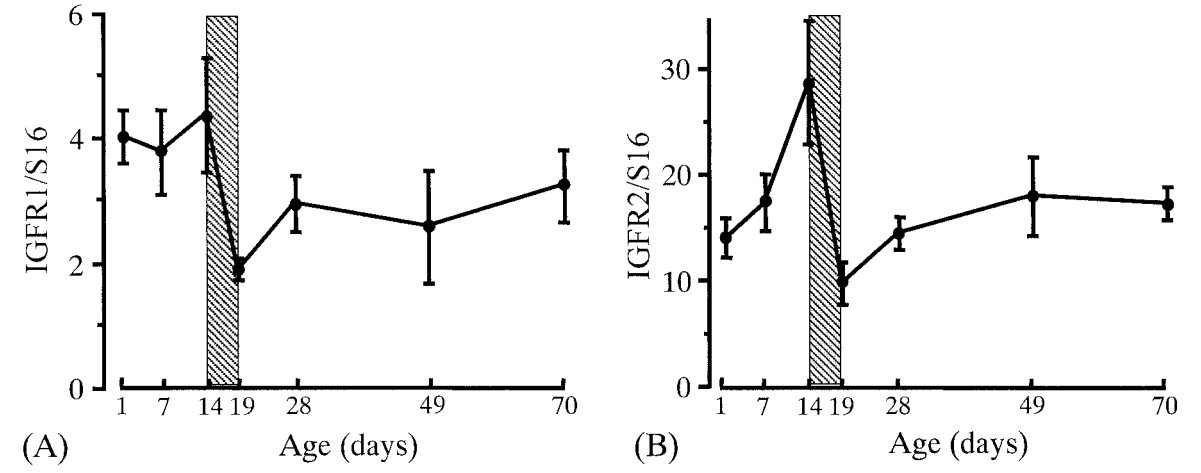

Fig. 4. Relative changes in the quantities of IGFR1 (A) and IGFR2 (B) mRNAs in the rat masseter muscle at 1, 7, 14, 19, 28, 49, and 70 days of age assessed by using competitive RT-PCR. Each point with its vertical bar represents the mean ± SD of six samples. The vertical axis is expressed as a ratio of the target mRNA to S16 mRNA quantities. The diagonal rectangle shows the period for the shift of rat feeding behavior from suckling to chewing.

quantity of IGFR1 mRNA did not change significantly. The quantity of IGFR2 mRNA markedly and transiently increased to 204% of the 1 day value between 1 and 14 days ($p<0.0001$). After that, the quantity sharply fell and became only 69% ($p<0.0001$) of the 1 day value at 19 days. After 19 days, the quantity of IGFR2 mRNA increased and reached 128% ($p<0.01$) of the 1 day value at 49 days. Thereafter, the quantity did not change significantly up to 70 days.

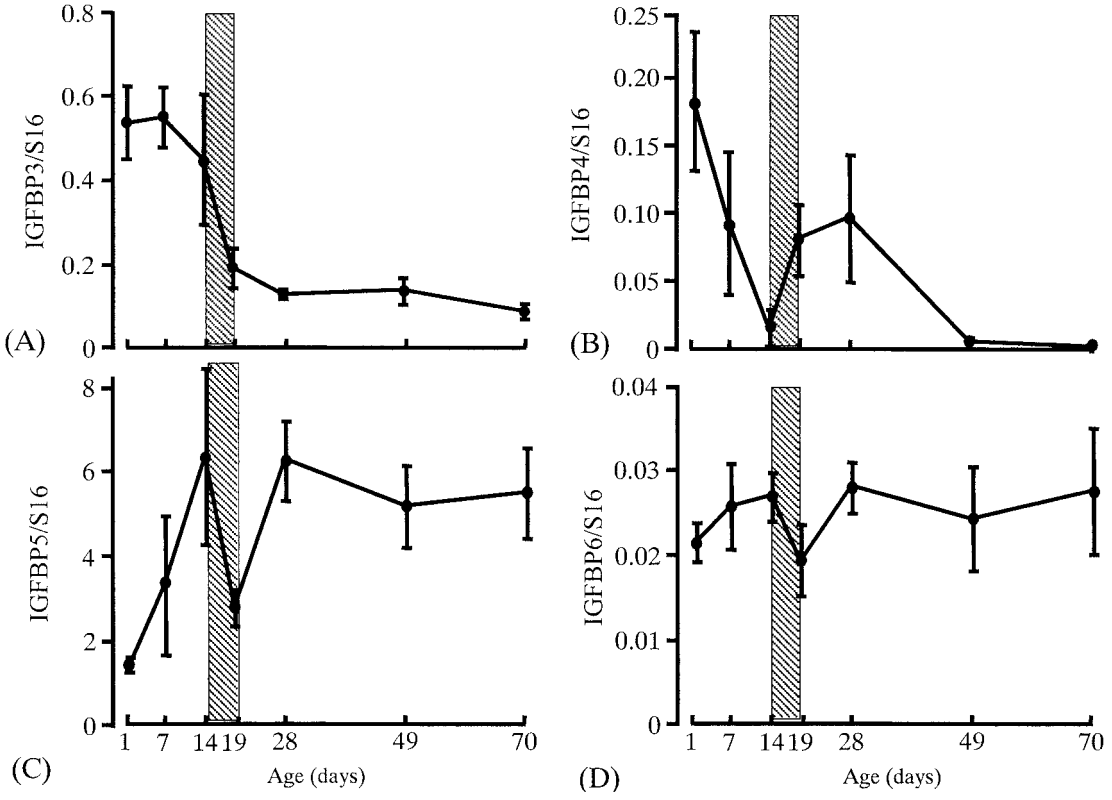

Fig. 5. Relative changes in the quantities of IGFBP3 (A), IGFBP4 (B), IGFBP5(C), and IGFBP6 (D) mRNAs in the rat masseter muscle at 1, 7, 14, 19, 28, 49, and 70 days of age assessed by using competitive RT-PCR. Each point with its vertical bar represents the mean ± SD of six samples. The vertical axis is expressed as a ratio of the target mRNA to S16 mRNA quantities. The diagonal rectangle shows the period for the shift of rat feeding behavior from suckling to chewing.

Figs. 5A, 5B, 5C, and 5D show the data for IGFBP3, IGFBP4, IGFBP5, and IGFBP6 mRNA expressions, respectively. No expression of IGFBP1 and IGFBP2 mRNAs was detected throughout the experimental period according to this PCR approach. IGFBP3 mRNA was highly expressed between 1 and 7 days of age, then began to decrease in the quantity at 14 days. The quantity sharply fell between 14 and 19 days, and became only 35% ($p<0.001$) of the 1 day value at 19 days. After that, the quantity gradually decreased up to 70 days. The quantity of IGFBP4 mRNA linearly decreased between 1 and 14 days, and became only 7.5% of the 1 day value ($p<0.0001$) at 14 days. However, the quantity increased transiently between 14 and 28 days and recovered to 53% of the 1 day value ($p<0.05$) at 28 days. After that, the quantity decreased again and reached a negligible level at 49 days of age. IGFBP5 mRNA expression increased to 414% ($p<0.0001$) of the 1 day value between 1 and 14 days, decreased to 184% ($p<0.01$) of the 1 day value at 19 days, then increased again to 409% ($p<0.01$) of 1 day value at 28 days. After that, the high expression level of IGFBP5 mRNA continued up to 70 days. IGFBP6 mRNA was expressed quite constantly throughout the experimental period, except for during a transient reduction and recovery between 14 and 28 days.

DISCUSSION

In the present study, the shift of rat feeding behavior from suckling to chewing occurred between 14 and 19 days of age, since we observed that the pups took residues of a pellet diet which had been dropped in a cage after 14 days of age, and since pups were removed from the dam and fed on a pellet diet at 19 days of age. During this period, we observed sharp falls in the quantity of all gene mRNAs, which were examined and measurable, except for IGFBP4, although the quantity of IGFBP4 mRNA rose sharply during the same period. Since proteins, not mRNA, are responsible for biological functions of these molecules, it seems to be necessary to analyze the level of protein expression in order to understand the biological meaning of these drastic changes in the quantities of IGF, IGFR, and IGFBP mRNAs in this period. However, since the period for these drastic changes appears to be consistent with the period for the shift of rat feeding behavior from suckling to chewing (14 ~ 19 days of age), these changes may be involved in the shift of rat feeding behavior.

The roles of both IGF-I and IGF-II in the embryonic development of skeletal muscle have been studied extensively, but no marked difference in the roles has been found between IGF-I and IGF-II except that the effect of exogenous IGF-II on the differentiation of cultured myoblasts is

more potent than that of exogenous IGF-I (Ewton *et al*., 1994; Florini *et al*., 1996). In the present study, we observed much higher expression level of IGF-I mRNA than that of IGF-II mRNA and the different expression profiles of IGF-I and IGF-II mRNAs except for the sharp fall between 14 and 19 days during the postnatal development of rat masseter muscle (Fig. 3). These suggest that IGF-I plays a main role distinct from that of IGF-II in the postnatal development of rat masseter muscle.

IGFR2 is reported to be involved in the breakdown of IGF-II protein (Kiess *et al*., 1987; Wang *et al*., 1994; Ludwig *et al*., 1996). In the present study, the quantities of IGF-II and IGFR2 mRNAs rose sharply and then fell between 1 and 19 days of age, suggesting that very active synthesis and breakdown of IGF-II occur during this period. This active metabolism of IGF-II may be involved in the suckling movement of masseter muscle and the shift of rat feeding behavior.

It is reported that all six IGFBPs are expressed in skeletal muscles and that IGFBP4, 5, and 6 play important roles in the embryonic development of skeletal muscle cells such as proliferation and differentiation (Ferguson *et al*., 1992; Florini *et al*., 1996). IGFBP4, 5, and 6 inhibit the proliferation and differentiation of cultured myogenic cell lines such as C2 and L6, although IGFBP5 has the additional capability of stimulating differentiation of these cell lines under the proper conditions (James *et al*., 1993; Ewton and Florini, 1995; Rotwein *et al*., 1995; Silverman *et al*., 1995; Ewton *et al*., 1998). However, the roles of these IGFBPs in the postnatal development of skeletal muscle are unclear. In the present study, we observed that the expression level of IGFBP5 mRNA was highest in all 4 IGFBPs during the whole period of postnatal development and that the high level of expression continued until 70 days of age (Fig. 5). These results suggest that IGFBP5 may play a major role in the postnatal development of rat masseter muscle.

ACKNOWLEDGEMENTS

We would like to thank Professor M. Chiba, Tsurumi University School of Dental Medicine, for his support and encouragement throughout the present study. A part of the present study was supported by grants-in-aid for funding scientific research (No. 13671955), the Bio-ventures and High-Technology Research Center of the Ministry of Education, Culture, Sports, Science, and Technology of Japan.

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(Received November 13, 2002 / Accepted February 13, 2003)