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Effects of first exogenous nutrients on the mRNA levels of atrogin-1/MAFbx and GLUT1 in the skeletal muscles of newly hatched chicks

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ABSTRACT

The aim of this study was to examine the effects of first exogenous nutrients on the mRNA levels of muscle atrophy F-box (atrogin-1/MAFbx) and glucose transporters (GLUTs) in the skeletal muscles of newly hatched chicks with no feed experience. In experiment 1, newly hatched chicks had free access to feed or were fasted for the first 24 h. The chicks having free access to feed for the first 24 h increased their body weight and had decreased atrogin-1/MAFbx mRNA levels in their sartorius and pectoralis major muscles compared with the fasted chicks. In experiment 2, newly hatched chicks received a single feed via intubation into the crop. Three hours after intubation, levels of atrogin-1/MAFbx mRNA in the sartorius muscle were decreased whereas the plasma insulin concentration and phosphorylated AKT levels in the sartorius muscle were increased. In addition, the mRNA levels of GLUT1 and GLUT8 were increased in the sartorius muscle after the intubation. However, in the pectoralis major muscle, AKT phosphorylation and levels of atrogin-1/MAFbx, GLUT1 and GLUT8 mRNA were not affected 3 h after intubation. The first exogenous nutrients increased the level of phosphorylated AKT in the sartorius muscle of newly hatched chicks, possibly because of the decrease in atrogin-1/MAFbx mRNA levels. Furthermore, the sartorius muscle in newly hatched chicks appeared to be more susceptible to the first feed compared with the pectoralis major muscle.

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1. Introduction

After birth, the first exogenous nutrients are essential for the subsequent growth of animals. In pig and rat neonates, the first nutrition an animal receives is considered to induce the expression of many genes and to cause numerous metabolic changes (Davis and Fiorotto, 2009). In chicken, the first exogenous nutrients stimulate the expression of the genes encoding malic enzymes and fatty acid synthase in the liver of newly hatched chicks (Morris et al., 1984). In addition, in the skeletal muscle of newly hatched chicks, exogenous nutrients enhance the levels of insulin-like growth factor-1 (IGF-1) mRNA, which is a positive regulator of skeletal muscle growth (Guernec et al., 2004).

Skeletal muscle growth is controlled by the delicate balance between protein synthesis and protein degradation (Russell, 2010). In birds, changes in the rate of muscle protein degradation may contribute to normal muscle growth (Hayashi et al., 1985). During the embryonic growth of chickens, a remarkable reduction in the rate of protein degradation occurs throughout the body between days 12 and 19 of incubation (Muramatsu et al., 1987). However, little information is available on the rate of muscle protein degradation or the effects of the first exogenous nutrients on muscle protein degradation during the neonatal period.

The rate of protein degradation is regulated through the ubiquitin (Ub)-proteasome system (Jagoe and Goldberg, 2001; Lecker et al., 2004, 2006). Proteins destined for degradation are covalently linked to a chain of Ub molecules, which marks them for breakdown by the 26S proteasome (Ciechanover, 1998; Hershko and Ciechanover, 1998). The mRNA levels of Ub ligases clearly correlate with polyubiquitination (Sacheck et al., 2004), indicating that they play an important, rate-limiting role in controlling polyubiquitination in the Ub–proteasome system (Ciechanover, 1998).

In skeletal muscles, muscle atrophy F-box (atrogin-1/MAFbx) is considered to function as a muscle-specific Ub ligase (Bodine et al., 2001). The level of atrogin-1/MAFbx mRNA correlates linearly and positively with the overall rate of protein degradation (Sacheck et al., 2004; Ohtsuka et al., 2011). In mammals, the IGF-1/AKT pathway suppresses

Abbreviations: GLUT, glucose transporter; MAFbx, muscle atrophy F-box; Ub, ubiquitin; MeHis, 3-methylhistidine.

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the levels of atrogin-1/MAFbx mRNA by inhibiting FOXO transcription factors (Sandri et al., 2004). FOXO transcription factors are phosphorylated by AKT, which results in their exclusion from the nucleus and hence suppression of their transcriptional activity (Daitoku et al., 2011). However, it is not known whether the first exogenous nutrients affect the mRNA levels of atrogin-1/MAFbx in the skeletal muscle.

Glucose is an essential metabolic substrate for birds, including chickens, and it is established that plasma glucose levels of birds are comparable with those of reptiles but high compared with those of mammals (Umminger, 1977). In mammalian skeletal muscle, the mechanism for glucose uptake by glucose transporters (GLUTs) has been well described (Watson and Pessin, 2001). Among the 12 GLUT isoforms that have been identified in mammals (Wood and Trayhurn, 2003), GLUT4 plays a major role in insulin-stimulated glucose uptake into skeletal muscle (Watson and Pessin, 2001). However, chickens lack a homologous GLUT4 gene (Seki et al., 2003) and both GLUT1 and GLUT12 play a significant role in insulin-stimulated glucose uptake in chicken skeletal muscle (Kono et al., 2006; Zhao et al., 2012; Coudert et al., 2015). However, few studies have reported on the GLUT isoforms that are responsible for glucose uptake into the skeletal muscle of newly hatched chicks.

Thus, the aim of this study was to examine the effects of the first exogenous nutrition on the mRNA levels of atrogin-1/MAFbx and GLUT isoforms in skeletal muscles of newly hatched chicks.

2. Materials and methods

2.1. Experimental diet

The diet used in experiments 1 and 2 was designed to satisfy the requirements detailed in "The Japanese Feeding Standard for Chickens" (Agriculture, Forestry and Fisheries Research Council Secretariat, Ministry of Agriculture, Forestry and Fisheries of Japan, Tokyo, Japan). The ingredients and nutrient composition of the diet are shown in Table 1.

2.2. Animals

Newly hatched ROSS308 broiler male chicks (*Gallus gallus domesticus*) with no feed experience were supplied by a commercial hatchery (Kumiai Hina Center, Kagoshima, Japan) within 24 h of hatching. All experimental protocols and procedures were reviewed and approved by the Animal Care and Use Committee of Kagoshima University (Kagoshima, Japan).

Table 1
Composition of experimental diets.

Ingredients (g/100 g)	
Corn meal	48.50
Soybean meal	42.00
Corn oil	5.73
$CaCO_3$	0.66
$CaHPO_4$	2.00
NaCl	0.50
DL-Methionine	0.11
Mineral and vitamin premix[a]	0.50
Calculated analysis	
Crude protein (%)	22.5
Metabolizable energy (MJ/kg)	13.0

[a] Content per kg of the vitamin and mineral premix: vitamin A 90 mg, vitamin D3 1 mg, DL-alpha-tocopherol acetate 2000 mg, vitamin K3 229 mg, thiamin nitrate 444 mg, riboflavin 720 mg, calcium D-pantothenate 2174 mg, nicotinamide 7000 mg, pyridoxine hydrochloride 700 mg, biotin 30 mg, folic acid 110 mg, cyanocobalamine 2 mg, calcium iodinate 108 mg, MgO 198,991 mg, $MnSO_4$ 32,985 mg, $ZnSO_4$ 19,753 mg, $FeSO_4$ 43,523 mg, $CuSO_4$ 4019 mg and choline chloride 299,608 mg.

2.3. Experiment 1

Eighteen newly hatched chicks were randomly divided into three groups. The first group, which served as chicks at hatching, was killed immediately after assignment by cervical dislocation using carbon dioxide anesthesia. The second group was fed with the experimental diet ad libitum, and the third group of chicks was fasted for 24 h. All chicks had free access to drinking water and were housed in an electrically heated battery brooder at 35 °C. After 24 h, the second and third groups were killed by cervical dislocation using carbon dioxide anesthesia. After dissection, the weights of the pectoralis major muscle, leg muscles (thigh and drumstick), liver, and heart were measured. Blood samples were collected in heparinized test tubes, immediately centrifuged (5900 × *g*, 10 min, 4 °C) to separate the plasma, and stored at −30 °C until analysis.

2.4. Experiment 2

The aim of the experiment 2 was to examine the effects of the first exogenous nutrients on atogin-1/MAFbx mRNA levels in skeletal muscles of newly hatched chicks with no feed experience. Twenty-four newly hatched chicks were randomly divided into four groups. The chicks were housed in an electrically heated battery brooder at 35 °C. Three of the four groups were fed with the experimental diet as a diet-water mixture (0.3:1, *w*/*v*) by intubation into the crop and were killed by cervical dislocation using carbon dioxide anesthesia 1, 3, and 6 h after feeding. The amount of intubated diet (0.3 g) was the same as that eaten by the newly hatched chicks in the first 3 h of feeding in experiment 1. Chicks in the remaining group, which served as a control, were intubated with 1 mL of water and were killed by cervical dislocation using carbon dioxide anesthesia 1 h after intubation. Blood samples were collected in heparinized test tubes, immediately centrifuged (5900 × *g*, 10 min, 4 °C) to separate the plasma, and stored at −30 °C until analysis. The pectoralis major and sartorius muscles were dissected, immediately frozen in liquid nitrogen and stored at −80 °C until use.

2.5. Biochemical blood testing and 3-methylhistidine (MeHis) analysis

Plasma glucose concentration was measured with the Fuji DRI-CHEM 3500 analyzer system (Fujifilm, Tokyo, Japan), according to the manufacturer's instructions. Plasma insulin concentration was measured with the porcine insulin ELISA kit (AKRIN-013T), according to the manufacturer's instructions. Plasma MeHis concentration was determined by HPLC as previously described Hayashi et al. (1987). In brief, 500 μL of plasma was mixed with 170 μL of 20% sulfosalicylic acid and centrifuged. The supernatant was collected, and MeHis was roughly separated from acidic and neutral amino acids by ion-exchange chromatography.

2.6. RNA extraction and quantitative real-time PCR

The pectoral and sartorius muscles were homogenized in ISOGEN II (Nippon Gene, Tokyo, Japan) according to the manufacturer's instructions. Real-time PCR was performed as described previously (Shimamoto et al., 2016). In brief, cDNA was synthesized from 40 ng of RNA per 10 μL of reaction solution using the PrimeScript RT Reagent Kit (RR036A; Takara, Shiga, Japan). Samples were incubated at 37 °C for 15 min, 85 °C for 5 s, and 4 °C for 5 min. Gene expression was measured by real-time PCR using the 7300 Real-Time PCR system (Applied Biosystems, Foster City, CA, USA) with SYBR Select Master Mix (Applied Biosystems). Thermal cycling conditions were as follows: an initial hold at 50 °C for 2 min, 95 °C for 2 min, and then 40 cycles at 95 °C for 15 s, 55 °C for 15 s, and 72 °C for 1 min. The level of 18S ribosomal RNA was used as an internal standard. In this study, the following primers were used: atrogin-1/MAFbx (5′-CCAACAACCCA GAGACCTGT-3′ and 5′-GGAGCTTCACACGAACATGA-3′), GLUT1 (5′-

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