

The Effect of Sulfur Amino Acid Content of the Diet upon Plasma Taurine Concentration and Hepatic Cysteinesulfinate Decarboxylase Activity of the Early Weaned Pigs

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ABSTRACT

Eighteen crossbred pigs were weaned at 4 days of age and fed up to 28 days of age to examine the effect of sulfur amino acid content of three diets upon plasma taurine concentration and hepatic cysteinesulfinate decarboxylase activity. The experimental diets consisted of either whey protein (W) or partially hydrolyzed soy protein (S) as the source of protein. 0.25% methionine was added to the S diet for the third dietary regimen (SM). Sulfur amino acid content (methionine plus cystine) of the three diets was 1.53%, 1.34% and 1.09% for the W, SM and S diet, respectively. Plasma taurine concentration from the pigs fed the three experimental diets reflected the total sulfur amino acid content of the diet. The S diet resulted in a significantly lower plasma taurine level than the W and SM diets throughout the experiment. After three weeks, pigs fed the W diet had significantly higher plasma taurine concentration than those fed SM diet. Therefore it appears that taurine requirement of the pig depends on the sulfur amino acid contents of the diets and the conversion of sulfur amino acid to taurine seemed not to be limited by any factor when sulfur amino acid was below 1.53% of the diet. There was no significant differences between three dietary groups in hepatic cysteinesulfinate decarboxylase activity and this suggests that the reduced cysteinesulfinate decarboxylase activity due to high sulfur amino acid in the diet may not occur in the pig liver. (*Korean J Nutrition* 29(3) : 260~266, 1996)

KEY WORDS : cysteinesulfinate decarboxylase · taurine · pig liver · dietary sulfur amino acid.

Introduction

The dietary requirement of taurine is well established in the cat the most. The taurine depleted cats show retinal degeneration and visual dysfunction¹⁾ ²⁾³⁾, various neurological abnormalities⁴⁾⁵⁾ and many adverse effects on reproductive⁵⁾ and immunological functions⁶⁾⁷⁾. Now, it is generally accepted that taurine is a "conditionally essential nutrient" to human infants and children, especially those born prematurely or under long-term parenteral nutrition, and possibly also for adults⁸⁾⁹⁾¹⁰⁾. Now, almost all the preparations

of infant formula manufactured in the developed countries contain added taurine in concentrations that are roughly equal to those found in human milk.

Although the predominant route of taurine biosynthesis varies among species and depends on the type of tissue, the major pathway is considered to be the formation and decarboxylation of cysteinesulfinic acid by cysteine dioxygenase and cysteinesulfinate decarboxylase (CSAD : EC 4.1.1.29)¹¹⁾. CSAD has been thought to have a rate limiting role in the taurine synthetic route and it is generally agreed that the activity of this enzyme reflects the synthetic capacity of different tissues and species¹²⁾¹³⁾. In most species, CSAD activity is highest in liver and several investigators

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have suggested that the differences in hepatic CSAD activity among species account for the observed differences in taurine synthetic rates¹⁴⁾¹⁵⁾. For example, rat, mouse and dog livers have high levels of CSAD activity and these species synthesize taurine rapidly compared to the cat, monkey or man that have lower CSAD level and appear to synthesize taurine slowly.

However, there have been several reports in the literature that CSAD activity and taurine concentration in rat liver are not correlated¹⁶⁾¹⁷⁾ and these suggest that hepatic CSAD may not play the rate limiting role in taurine biosynthetic pathway. Rat liver and urinary taurine concentration increased when hepatic CSAD activity was reduced due to a high protein diet¹⁷⁾¹⁸⁾. Later, the activity of this enzyme was also found to decrease after feeding rats methionine¹⁹⁾- or cysteine²⁰⁾-supplemented diets and Jerkins and Steele²¹⁾ suggested that the depression of hepatic CSAD activity in response to high-protein feeding is specially regulated by sulfur amino acids metabolized by S-adenosyl methionine-dependent pathway of methionine metabolism.

Depression of hepatic CSAD activity by a high protein diet or sulfur amino acid supplementation has never been studied in any other animal but the rat. Neonatal pigs have been used extensively to evaluate the nutritional requirements of human infants due to anatomical and physiological similarities between two species²²⁾²³⁾²⁴⁾. Therefore, in the present study, plasma taurine concentration and hepatic CSAD activity were investigated using the early weaned piglet to examine how they are related in the pig body fed the different level of sulfur amino acid and whether the depression

of this enzyme due to high dietary sulfur amino acid also occur in the other animal except the rat.

Experimental procedure

1. Animals and Diets

Eighteen crossbred pigs were weaned at 4 days of age and divided into three groups of six which were matched for sex, age and weight. The pigs were placed in a 5'x6' pen with a plastic coated, woven-wire floor.

At 7 days of age the pigs were assigned to experimental diets(Table 1). The experimental diets consisted of either whey protein(W) or partially hydrolyzed soy protein(S) as the protein source. Supplemental methionine was added to S diet for the third dietary regimen(SM) to bring the total methionine content to 0.74%, which is similar to the methionine content of the W diet. Table 2 shows the amino acid content of the three experimental diets determined by high performance liquid chromatography after acid hydrolysis. The three experimental diets were isocaloric and isonitrogenous. The pigs were fed according to the formula, 12.5ml per hour per(kg body weight)^{0.75} by the automatic feeder.

2. Blood Preparation and Plasma Amino Acid Concentration

Blood was collected from the jugular vein using the heparinized syringe. Plasma stored at -20°C was deproteinized by mixing with 1/4 part of 15% 5-sulfosalicylic acid and supernatant was stored at -20°C. The frozen supernatant was thawed at room temperature and filtered through a 0.45µm filter and stored at -20°C. Pico-Tag Derivatization Procedures des-

Table 1. Composition of the experimental diets

Ingredients	Diets(g/10kg)		
	W	SM	S
Fat 4/80 ¹⁾	2000	2000	2000
WPC ²⁾	6630	0	0
SY35F3 ³⁾	0	6630	6630
Stardry 24R ⁴⁾	1120	1095.4	1120
L-Methionine	0	24.6	0
Syloid ⁵⁾	100	100	100
Dicalcium phosphate	90	90	90
Vit/Min ⁶⁾	60	60	60

- 1) Merrick Foods, 4% whey protein : 80% fat
- 2) Whey protein concentrate, 35% protein
- 3) Liquid whey and liquified soy diet supplied by Del-town Chemurgic, 35% protein
- 4) Hydrolyzed Starch(DE=24)
- 5) Silicon drying agent
- 6) Vitamin/mineral package rom Carl Akey, Inc. Present at NRC recommendations.

Table 2. Amino acid composition of the experimental diets¹⁾

Amino Acid	Diet		
	W	SM	S
Phenylalanine	1.18	1.51	1.51
Valine	1.56	1.72	1.72
Threonine	1.06	1.37	1.37
Isoleucine	0.78	1.79	1.79
Methionine	0.68	0.74	0.49
Histidine	0.73	0.72	0.72
Arginine	0.83	2.10	2.10
Leucine	2.39	2.57	2.57
Lysine	1.95	2.07	2.07
Cystine	0.85	0.60	0.60
Methionine+Cystine	1.53	1.34	1.09

- 1) Expressed as % of the diet : µg/100g diet.

cribed by Cohen et al²⁵). was used to determine plasma amino acid concentration by high performance liquid chromatography. Ten microliters of the deproteinized mixture was dried under vacuum, dried again after suspending in redrying agent (methanol : 1.0M sodium acetate : rithylamine=2 : 2 : 1), derivatized with phenylisothiocyanate, and then dried as before. The dried and derivatized samples were stored at -20°C and suspended in 5 mM phosphate buffer, pH 7.4, shortly before injection to C-18 pico-tag reverse column maintained at 35°C. A linear gradient from eluent A to eluent B was used at the flow rate of 1 ml/min in 24 minutes. The starting buffer A consisted of sodium acetate buffer pH 6.4 containing 6% (V/V) acetonitrile. Buffer B was a 60/40 mixture of water/acetonitrile.

3. Determination of CSAD activity

By the jugular injection of 2.0 ml of T-61 Euthanasia, the pigs were killed after three weeks of experimental period. The fresh liver was disrupted in an Omnimixer with a 3 fold volume (V/W) of 20mM potassium phosphate buffer, pH 7.1, containing 1.0mM 2-mercaptoethanol, 0.1mM EDTA and 0.1mM pyridoxal phosphate. After the suspension was filtered through four layers of cheesecloth, the filtrate was homogenized in a Dounce tissue homogenizer. The homogenate was centrifuged at 10,800xg for 40minutes in a refrigerated centrifuge and the supernatant was used to determine the CSAD activity.

Standard assay conditions were those modified from the method described by Daniels and Stipanuk²⁰. The incubation was carried out in a total volume of 1.5ml in a 25ml Erlenmeyer flask. The reaction mixture contained 12mM L-[1-¹⁴C]-cysteinesulfonic acid, 8 nCi, 0.5mM dithiothreitol, 250mM potassium phosphate buffer, pH 7.1 and homogenate supernatant. All components of the reaction mixture were added to the flask in an ice bath. A plastic center well was inserted, and the flask was sealed with septum rubber stopper. The center well contained 0.3 ml of a 1 : 2 mixture of 2-ethanolamine and ethylene glycol monomethyl ether and a folded piece of Whatman No. 1 filter paper. The reaction was initiated by transferring the flasks to a 37°C shaking water bath and allowed to proceed for 30 minutes. Each reaction was stopped by injecting 1 ml of 10% trichloroacetic acid through the septum rubber stopper into the reaction mixture. The flask was left in the 37°C shaking water bath for an additional 60minutes to allow complete trapping of

evolved carbon dioxide. The center well and its contents were placed in a scintillation vial, 5 ml of Intragel was added and the radioactivity was determined by a Packard Tricarb Scintillation Spectrometer. One unit of enzyme activity represents the amount of enzyme that produces 1 nmole of carbon dioxide per minute at 37°C. The method of Lowry et al., as modified by Zak and Cohen²⁶) was used to determine the concentration of the protein using bovine serum albumin as a standard.

4. Statistical Analysis

The significances of the effect of dietary sulfur amino acids on the plasma sulfur amino acids and hepatic CSAD activity were tested by Duncan's multiple range test after analysis of variance²⁷.

Results

Table 3 shows that the plasma taurine concentration of the three dietary groups of pigs parallels that of the total sulfur amino acid content of the diets while plasma methionine and cystine patterns seem to reflect that of dietary methionine content. The S group had significantly lower plasma methionine concentrations than the other two groups throughout the three week experimental period. Plasma methionine concentrations of the SM group was the same as those of W group in the first 2 week. By the end of 3-week experimental period, pigs fed the SM diet had significantly higher plasma methionine concentration than those fed the W diet.

Plasma cystine concentration of the S group was significantly lower than that of the W and SM diets after consuming the experimental diet for 1 week, and lower than those fed the SM diet after consuming the experimental diet for 2 week. Added methionine to the S diet resulted in plasma cystine concentrations similar to those obtained from W diet.

Throughout the experimental period, the pigs fed the S diet had significantly lower plasma taurine concentrations than those fed the W and SM diets. Pigs fed the SM diet had plasma taurine concentrations about the same as those of the W diet-fed pigs for the first 2 weeks but by the end of 3 week experimental period, plasma taurine concentration of the SM group was significantly lower than that of the W group.

Supplementation of 0.25% methionine to a partially hydrolyzed soy protein-based diet resulted in significantly higher plasma taurine concentrations. The

Table 3. Plasma sulfur amino acid levels¹ and hepatic cysteinesulfinate decarboxylase activities² of the pigs fed diets differing in sulfur amino acid content

Age and Group	Methionine	Cystine	Taurine	Cysteinesulfinate Decarboxylase
<u>14 days</u>				
W(4) ³	215.5 ± 29.2 ^{4,a}	28.0 ± 2.5 ^a	265.8 ± 4.7 ^a	
SM(4)	211.0 ± 10.45 ^a	37.6 ± 3.5 ^a	249.1 ± 32.45 ^a	
S(3)	84.6 ± 10.91 ^b	10.1 ± 4.27 ^b	103.0 ± 4.56 ^b	
<u>21 days</u>				
W(3)	179.3 ± 23.04 ^a	36.6 ± 12.64 ^{ab}	192.0 ± 42.72 ^a	
SM(4)	179.1 ± 19.4 ^a	47.4 ± 4.5 ^a	129.7 ± 8.5 ^a	
S(4)	60.2 ± 5.7 ^b	19.1 ± 3.4 ^b	66.1 ± 14.5 ^b	
<u>28 days</u>				
W(6)	126.8 ± 8.94 ^a	30.8 ± 7.84 ^a	268.9 ± 14.94 ^a	0.80 ± 0.033 ^a
SM(6)	206.8 ± 17.31 ^b	41.2 ± 7.02 ^a	148.3 ± 23.03 ^b	0.90 ± 0.082 ^a
S(6)	35.3 ± 2.08 ^c	31.1 ± 2.69 ^a	55.2 ± 10.49 ^c	0.94 ± 0.065 ^a

1) Expressed as umoles/L.

2) Expressed as nmoles CO₂/min/mg soluble protein.

3) Numbers in parentheses are numbers of samples.

4) Values are means ± S.E.

a, b, and c : At each day, within a column, values followed by the same superscript letter are not significantly different ($p < 0.05$).

significant difference between the plasma taurine concentrations of the two dietary groups (S vs SM) due to methionine-supplementation occurred from the end of the first experimental week and extended to the last of the experimental period. The pigs fed whey protein-based diet had plasma taurine concentrations essentially same at the first bleeding, higher but not significantly at the second bleeding, and finally significantly higher at the end of three weeks compared to those fed the partially hydrolyzed soy protein-based diet with methionine supplementation. Thus, the differences in plasma taurine concentrations between the groups due to the different total sulfur amino acid content of the three experimental diets appeared to increase as the pigs consumed more experimental diet.

Hepatic CSAD activity of the three dietary groups is shown in Table 3. The pigs fed the S diet tended to have a higher hepatic CSAD activity than the SM diet-fed pigs, which in turn tended to have a higher enzyme activity than those fed the W diet. However, the differences in the enzyme activity among the three dietary groups were not significant ($p < 0.05$).

Discussion

A significantly higher plasma methionine concentration of the pigs fed SM diet than that of the pigs fed W diet for three weeks is difficult to be explained. It is thought to be complicated to compare

data from S and SM groups only according to the different sulfur amino acid content with those from W group since the W diet was based on the different protein source from the other two experimental diets. It has been well established that the relative importance of taurine decreases in many mammalian tissues with the development and this may provide the possible explanation that the plasma taurine concentration of SM group is significantly lower than W group despite the same or higher methionine and cystine levels of SM group compared to W group at 28 days of age. Although table 3 does not demonstrate statistical analysis for the significance of day effect, there are significant changes in plasma taurine and methionine concentrations according to the development of the pigs while the changes in plasma cystine level with age are not significant during the period of the present experiment. Namely, plasma methionine and taurine concentrations decrease from 21 and 14 days of age, respectively. Many researchers have attempted to relate the nutritional importance of taurine specially in the developing organ to the higher taurine concentration in that organ than the mature one. For example, the observation of unusually high taurine levels in the immature mammalian brain and the decrease in taurine concentration during development provided the basis to the hypothesis that taurine may have a special role in brain ontogeny in addition to its role in mature brain^{15,32}. Also, all the mammals in-

cluding the human have the highest taurine concentration in colostrum and taurine level decreases during the lactation. While the nutritional importance of taurine decreases with the development, the need to keep plasma cysteine concentration may not reduced (for instance, in order to synthesize glutathione) throughout the period of 14 to 28 days of age. The increasing relative importance of plasma cysteine concentration compared to plasma taurine level with time can be the possible explanation why the plasma cysteine level of S group increased to those of the other two groups at the end of the 28 days of age, although the plasma taurine concentration of S group was significantly lower than the other two groups.

The effect of supplemental methionine on plasma taurine has been studied in growing rats by Lombardini and Medina²⁸. They observed that DL-methionine, when added to the basal diet increased taurine concentrations in all tissues but the plasma. In a similar study with the cat²⁹, plasma taurine was found to be sensitive to the total sulfur amino acid content of the diet independent of total protein when methionine plus cystine was below 1.55% of the diet. Plasma taurine concentration did not increase further when 2.40% and 2.92% sulfur amino acids of the diet were fed and it was not influenced by the source of fat. In the present study, it appears that taurine requirement of the pig depends on the sulfur amino acid contents of the diets and the conversion of sulfur amino acid to taurine seems not to be limited by any factor below the level of 1.53% sulfur amino acid. Whether plasma taurine concentration increases further if more sulfur amino acid is fed has not determined. In this moment, it has not observed whether low plasma taurine concentration in pigs fed low sulfur amino acid diet is associated with any adverse effect. Although it has not established that low plasma taurine concentration represents taurine deficiency, this study suggests that 1.09% and 1.34% sulfur amino acid is not sufficient to saturate plasma taurine pool.

The lack of the significance in the differences among the CSAD activities of the three dietary groups may result from the species difference. The rat has been the only animal model for the study concerning the effect of dietary modulation on this enzyme and there is a big difference in the enzyme activity and dependence on dietary taurine between species. In this experiment, which is considered to be the only study reporting the hepatic CSAD activity in

the pig so far, the activity of this enzyme was determined to be 52.8 and 55.2 nmoles CO₂/hr/mg soluble protein in 28 day-old and adult pig liver, respectively. In contrast, the activity of this enzyme in 28-day old and adult rat liver has been reported to be 276 and 468 nmoles CO₂/hr/mg soluble protein, respectively¹⁶. Therefore, the rat is considered to be able to synthesize taurine 5-8 times faster than the pig. It is clear that taurine is essential to the nutrition of cats and totally nonessential to that of rodent while the nutritional significance is still debatable in human nutrition from the massive body of investigation. Essentially nothing has been reported about taurine in the pig, which shares many anatomical and physiological similarities with humans, except that reported by Stephen et al.³⁰. They examined the suitability of the piglet as an animal model with respect to taurine metabolism and suggested that the pig provided a useful model for the human infant.

The amount of amino acid and protein added to basal diet may affect the degree of decrease in hepatic CSAD activity due to high protein diet or sulfur amino acid supplementation. To see the decreased hepatic CSAD activity, some researchers supplemented the basal diet with a much higher amount of sulfur amino acid than we did in the present study, namely 1.4% methionine¹⁹ and 2.6% cystine²⁰ whereas Jerkins and Steele²¹ could observe the significant 23% decrease of the enzyme activity by supplementing methionine by 0.25%, which is the same amount added to the S diet in the present study. They also suggested that decrease in hepatic CSAD activity by feeding graded levels of dietary casein¹⁸ and methionine²¹ was in a dose dependent manner.

The observations that the dietary manipulations increasing plasma taurine concentration decrease CSAD activity in rat liver has challenged the rate limiting role of this enzyme in taurine biosynthetic pathway and more recent work³¹ suggested that the reaction catalyzed by cysteine dioxygenase rather than CSAD plays the major role in determining the extent of cysteine conversion to taurine in rat hepatocytes. In hepatocytes isolated from rats fed the 30% casein diet, cysteine dioxygenase activity was 10 times as great and CSAD activity was only 0.2 times as much and these were consistent with increased taurine production from cysteine and decreased taurine production from cysteinesulfinic acid in the hepatocytes from rats fed 30% casein diet³¹.

While reduced CSAD activity due to high sulfur amino acid of the diet in the pig liver was not observed in the present study, at least it was shown that the increased plasma taurine concentration of the pigs fed the high sulfur amino acid diet was not due to the increased hepatic CSAD activity. More study is needed to determine whether the reduced CSAD activity due to high sulfur amino acid in the diet also occur in the pig liver, using more dramatic difference in the sulfur amino acid content in the diet or using more proper experimental design, namely, the supplementation of the graded levels of sulfur amino acid to the basal diet.

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=국 문 초 록=

초기 이유된 돼지에 있어서 식이내 함황 아미노산 함량이 혈장 타우린 농도와 간의 Cysteinesulfinate decarboxylase 활성에 미치는 영향

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식이중 함황 아미노산 함량이 혈장 타우린 농도와 간의 cysteinesulfinate decarboxylase 활성에 미치는 영향을 생후 4일에 이유된 잡종 돼지를 이용하여 연구하였다. 실험식이의 단백질 급원은 유장 단백질 (W)이나 부분적 가수분해된 콩단백질 (S)이었으며, SM 식이는 S 식이에 methionine을 0.25% 첨가하여 W 식이와 비슷한 methionine 함량을 갖게 하였다. W, SM, S 식이의 함황 아미노산의 함량은 차례로 1.53%, 1.34%, 1.09% 이었다. 각 실험군의 혈장 타우린 농도는 실험식이의 함황 아미노산 총량을 반영하여, S 식이를 먹은 돼지들은 다른 두 식이군의 돼지들 보다 혈중 타우린 농도가 전 실험기간 동안 유의적으로 낮았고, SM 식이를 3주간 먹은 돼지들은 W 식이를 같은 기간 먹은 돼지들에 비해 혈중 타우린 농도가 유의적으로 낮았다. 따라서 총 함황 아미노산의 식이중 함량이 1.53% 이하일 때는, 함황 아미노산의 타우린으로의 전환이 어떤 제한을 받지 않는 것으로 보여진다. 돼지 간의 Cysteinesulfinate decarboxylase의 활성은 세 식이군 간에 유의적인 차이가 없었으므로, 쥐의 간에서 보여졌던 함황 아미노산의 식이내 첨가로 인한 cysteinesulfinate decarboxylase의 활성 감소 효과가 돼지의 경우에는 없을 수도 있음을 시사한다.