

◀ Review ▶

## Association Between Arachidonic Acid and Chicken Meat and Egg Flavor, and Their Genetic Regulation

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In Japan, the majority of chicken meat is obtained from fast-growing broiler chickens. Because most Japanese chicken breeds have a low meat yield and egg production, many of these breeds are endangered. Recently, the palatability of meat and eggs of native chickens has been reevaluated in the Japanese market. Jidori, which means chicken from the local, is an indigenous local chicken that is more delicious, firmer in texture, and more expensive than the broiler chickens. Most Japanese consumers recognize that the meat of Jidori chicken is richer in flavor than that of the broiler chicken. However, the reason for this rich flavor of the meat of Jidori chicken has not been elucidated. Recently, we found that arachidonic acid (AA) (C20:4n-6), a polyunsaturated fatty acid, is associated with the rich flavor of the meat and eggs of Jidori chicken. The present paper summarizes the discovery of the involvement of AA in the flavor characteristic of the meat and eggs of chicken, and also the genetic regulation of the AA content in the meat and eggs of Jidori chicken.

**Key words:** arachidonic acid, chicken, egg, flavor, genetics, meat

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### Introduction

Globally, the majority of chicken meat is obtained from a limited number of fast-growing broiler strains supplied by commercial breeding companies that employ intensive fattening strategies to ensure high meat yield. However, some consumers are willing to pay a higher price for a better quality of chicken meat, especially for the meat of Jidori chicken. Most Jidori chickens were initially bred by crossing the native Japanese breeds with selected lines having rapid growth rate. For example, Hinai-jidori chicken, a cross between Hinai-dori (a chicken breed native to Akita prefecture, Japan) sires and Rhode Island Red dams, is a popular variety of Jidori chicken (Rikimaru and Takahashi, 2007). As Jidori chickens require a relatively long growing period with a considerably high cost of production, their selling price can be 2-5 times more than that of the broilers.

Most Japanese consumers recognize that the meat of Jidori chicken has a richer flavor than that of the broiler chickens. However, the underlying reason for this rich flavor has not been elucidated. Meat texture is an important factor, and most Japanese consumers believe that Jidori meat is characteristically tough (Ito *et al.*, 1996; Matsuishi *et al.*, 2005).

Other key factors include the presence of free amino acids (FAA), including glutamic acid (Glu) and purine compounds, such as inosine 5'-monophosphate (IMP). Because Glu and IMP are well known active components of *umami* taste (the taste of L-glutamate), their salts have been widely used as flavor enhancers of food (Yamaguchi and Ninomiya, 2000). Studies conducted in the 1980s and 1990s have compared the contents of FAA, including Glu and IMP, in the meat of Jidori and broiler chickens. Karasawa *et al.* (1989) reported that the contents of Glu and total FAA in the leg muscle (gastrocnemius muscle) of three types of Jidori chicken was significantly higher than those in the leg muscle of the broilers. However, subsequent studies have reported no significant difference in the content of FAA between Jidori and broiler chickens (Fujimura *et al.*, 1994, 1996; Ito *et al.*, 1996). Fujimura *et al.* (1996) reported that the content of IMP in the meat of Hinai-jidori chicken is significantly higher than that in the meat of the broiler chicken. Other studies have not shown a significant difference in the IMP content in the meat of Jidori and broiler chickens (Fukunaga *et al.*, 1989; Karasawa *et al.*, 1989; Ito *et al.*, 1996). Most Japanese consumers recognize that the meat of Jidori chicken is more delicious than that of the broilers; however, it has not been verified if the difference in the contents of FAA, Glu, and IMP is actually correlated with the flavor of Jidori chicken. Based on earlier studies, we conclude that to determine the flavor of chicken meat, it is necessary to characterize the active substances related to the flavor of broiler and Jidori

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chicken meat.

### Arachidonic Acid Effectively Improves the Flavor of Chicken Meat

To identify the substances influencing the flavor of chicken meat, we quantitatively analyzed the general biochemical components, such as the FAAs, including Glu, IMP, and fatty acids, in thigh meat of Hinai-jidori and broiler chickens (Rikimaru and Takahashi, 2010). Since nearly 100% of Hinai-jidori chickens, sold commercially, are female, we compared the females belonging to the two strains. Female chicks, which hatched on the same day, were reared under identical environmental conditions for the same duration. The results showed that relatively high contents of AA and docosahexaenoic acid (DHA, C22: 6) is a characteristic feature of Hinai-jidori chicken (Table 1). As described elsewhere (Rikimaru and Takahashi, 2010), the total FAA content, in 8-wk-old broiler, was significantly higher than those in 22-wk-old broiler and 22-wk-old Hinai-jidori chicken. The content of Glu was the highest in the 8-wk-old broiler and lowest in the 22-wk-old broiler. The content of IMP in the 22-wk-old Hinai-jidori chicken was significantly higher than that in the 8-wk-old broiler, whereas there was no significant difference in the IMP content between the 22-wk-old broiler and 22-wk-old Hinai-jidori chicken. These data suggest that 1) FAA content decreases with age, 2) IMP content increases with age, and 3) difference in the FAA and

IMP contents, observed in the broiler and Hinai-jidori chickens, reflects their age at the time of slaughter.

To elucidate the relationship between the content of AA and flavor of Hinai-jidori chicken, we examined the effects of a diet supplemented with palm oil (PO), corn oil (CO), or AA-enriched oil (AAO) (SUNTGA40S; Nippon Suisan Co., Tokyo, Japan) on the fatty acid content and sensory perception of thigh meat (Kiyohara *et al.*, 2011). The oils were individually mixed with silicate at a ratio of 7:3, and 5% of fresh matter was added to finisher diet. Hinai-jidori chickens were fed these diets for 2 wk before slaughter. The AA content in the thigh meat of the AAO group was over 2-times higher than that of the PO and CO groups. The contents of other fatty acids were not significantly different among the groups. Sensory evaluation using chicken soup that included fat and steamed minced meat revealed that the total intensity of taste, *umami*, *kokumi* (continuity, mouthfullness, and thickness [Yamamoto *et al.*, 2009]), and aftertaste of the AAO group were significantly improved when compared with those of the PO and CO groups (Table 2). These data suggest that the flavor of chicken meat can be improved by dietary supplementation of arachidonic acid.

To elucidate the relationship between the AA content and flavor of broiler meat, we evaluated the effects of AAO supplement on the fatty acid content and sensory perception of thigh meat (Takahashi *et al.*, 2012). We formulated four types of oil: CO; a 1:1 mixture of AAO and PO (1/2 AAO); a

Table 1. Arachidonic acid and docosahexaenoic acid contents (percent of total analyzed fatty acids) in the thigh meat of the broiler and Hinai-jidori chickens (mean  $\pm$  SD)

	Broiler, female	Broiler, female	Hinai-jidori, female
Age (wk)	8	22	22
N	5	5	5
AA	1.42 $\pm$ 0.27 <sup>b</sup>	1.26 $\pm$ 0.33 <sup>b</sup>	1.92 $\pm$ 0.04 <sup>a</sup>
DHA	0.20 $\pm$ 0.07 <sup>b</sup>	0.24 $\pm$ 0.11 <sup>ab</sup>	0.38 $\pm$ 0.04 <sup>a</sup>

<sup>a,b</sup> Means within a row without a common superscript are significantly different ( $P < 0.05$ ). AA, arachidonic acid; DHA, docosahexaenoic acid.

Table 2. Sensory evaluation of steamed minced meat from Hinai-jidori chicken fed experimental diets

Characteristic	Chicken soup		Steamed minced meat	
	PO-AAO <sup>1</sup>	CO-AAO <sup>2</sup>	PO-AAO <sup>1</sup>	CO-AAO <sup>2</sup>
Total taste intensity	0.86**	0.75**	0.72**	0.56**
Sweetness	0.27*	0.27*	-0.03	0.34*
Sourness	0.55**	0.11	0.34*	0.03
<i>Umami</i>	0.68**	0.64**	0.59**	0.50*
<i>Kokumi</i>	0.73**	0.77**	0.66**	0.75**
Aftertaste	0.86**	0.61**	0.69**	0.50*

AAO, AA-enriched oil; CO, corn oil; PO, palm oil.

<sup>1</sup> Average AAO score of each subject when PO score was 0.

<sup>2</sup> Average AAO score of each subject when CO score was 0.

\* statistically significant at  $P = 0.05$ ; \*\* statistically significant at  $P = 0.01$ .

1:3 mixture of AAO and PO (1/4 AAO); and a 1:7 mixture of AAO and PO (1/8 AAO). Each type of oil was mixed with silicate at a ratio of 7:3, and 5% of fresh matter was added. Broiler chickens were fed these diets for 1 wk before slaughter. The AA content in the thigh meat of the groups 1/2 AAO and 1/4 AAO was significantly higher than that in the thigh meat of the CO group. Further, the AA content in the thigh meat ( $y$ , mg/g) increased linearly with the increasing content of dietary AAO ( $x$ , g/100 g of diet) according to the equation  $y=0.5674+0.4596x$  ( $R^2=0.8454$ ). The content of other fatty acids was not significantly different among the four diet groups. The sensory evaluation revealed that the flavor intensity, *umami*, *kokumi*, and aftertaste, of the groups 1/2 AAO and 1/4 AAO were significantly improved when compared with those of the CO group. Furthermore, there were significant positive correlations between the AA content of the thigh meat and flavor intensity, total taste intensity (*umami*), and aftertaste. These data suggest that the flavor of the broiler and Hinai-jidori chickens can be improved by increased supplementation of dietary AA.

In our previous studies (Kiyohara *et al.*, 2011; Takahashi *et al.*, 2012), we measured the Glu and IMP contents of the chicken samples and calculated the *umami* intensity of each experimental group. The value was expressed as the content of monosodium glutamate (MSG; mg/100 mL) with respect to the synergistic effect between Glu and IMP according to Yamaguchi (1967). Earlier studies reported that the difference in the intensity of *umami* among the experimental groups was less than 1%. This suggests that the difference in the intensity of *umami* between the experimental groups cannot be attributed to the contents of Glu and IMP. Because Yamaguchi (1967) reported that the differential threshold of *umami* between samples was 21%. Therefore, we conclude that the difference in chicken flavor, observed in our previous studies, was caused by AA and not by water-soluble *umami* substances, such as Glu and IMP.

### Genetic Regulation of Arachidonic Acid Content in Chicken Meat

In the thigh meat of Hinai-jidori chicken, we observed a strong correlation between the contents of AA and DHA (Fig. 1) suggesting that this was due to common molecular pathways. Arachidonic acid originates from dietary sources by the elongation-desaturation process of its precursor, linoleic acid (LA, C18:2n-6). The key enzymes delta ( $\delta$ )-5 desaturase (D5D) and  $\delta$ -6 desaturase (D6D) mediate this pathway (Fig. 2) (Malerba *et al.*, 2008). The enzyme D6D catalyzes the conversion of LA to  $\gamma$ -linolenic acid (C18:3n-6), which is then elongated to dihomo- $\gamma$ -linolenic acid (C20:3n-6) by elongase 5 (EL5). Further, C20:3n-6 is desaturated to AA by D5D. The enzymes EL5, D5D, and D6D are also involved in the n-3 fatty acid pathway (Fig. 2), which favors the conversion of  $\alpha$ -linolenic acid (ALA) into DHA. The enzymes D5D and D6D are encoded by the genes fatty acid desaturase 1 (*FADS1*) and 2 (*FADS2*), respectively. Furthermore, the *FADS1* and *FADS2* genes are clustered in a back-to-back configuration on chromosome 5 of chicken (Ensembl

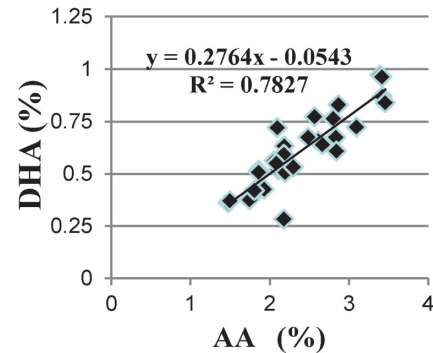


Fig. 1. Correlation between arachidonic acid (AA) and docosahexaenoic acid (DHA) contents (percent of total analyzed fatty acids) in the thigh meat of Hinai-jidori chicken.

Genomes, 2017; UCSC Genome Browser Gateway, 2017). Therefore, we speculated that the genes *FADS1* and *FADS2* control the contents of AA and DHA in chicken meat.

We genotyped the polymorphism of the genes *FADS1* and *FADS2* and investigated their association with the fatty acid profile of the meat of Hinai-jidori (Rikimaru *et al.*, 2016). The 5'-flanking regions, all exons, and 3'-untranslated regions of the genes *FADS1* and *FADS2* in three chicken breeds (Hinai-dori, Rhode Island Red, and White Plymouth Rock) were amplified by PCR. Subsequently, their nucleotides were sequenced and single nucleotide polymorphisms (SNPs) were identified. Of the 71 and 46 SNPs found in *FADS1* and *FADS2* genes, respectively, two SNPs (rs 733003230 (adenine (A)>guanine (G)) and LC060926 (g.25 A>G)) were chosen from each gene. Hinai-jidori female chickens, which hatched on the same day and reared under identical environmental conditions for the same duration, were used for all analyses. In each SNP of the genes *FADS1* and *FADS2*, the compositions of AA and DHA were significantly high in allele G than allele A (Table 3). We also examined the association of the *FADS1* and *FADS2* haplotypes with the contents of fatty acids. The contents of AA and DHA of the G-G-haplotype were significantly higher than that of the A-A-haplotype (Table 4). Thus, we conclude that the SNPs in the *FADS1* and *FADS2* gene cluster increase the contents of AA and DHA. Furthermore, this result might help develop strategies for improving the flavor of Hinai-jidori chicken.

In the present study, we will discuss the effects of sex, and the genes *FADS1* and *FADS2* on the fatty acid profile of chicken meat. Sirri *et al.* (2011) compared the fatty acid profile of breast and thigh meat of fast- (Cobb 700), medium- (Naked Neck Kabir), and slow- (Brown Classic Lohman) growing chicken strains slaughtered at the age of 81 d. The contents of stearic acid (SA, C18:0), AA, and DHA in the slow-growing strain were significantly higher than those of the fast- and medium-growing strains. However, the contents of myristic (C14:0), palmitoleic (C16:1), and oleic (C18:1) acids in the slow-growing strain were significantly

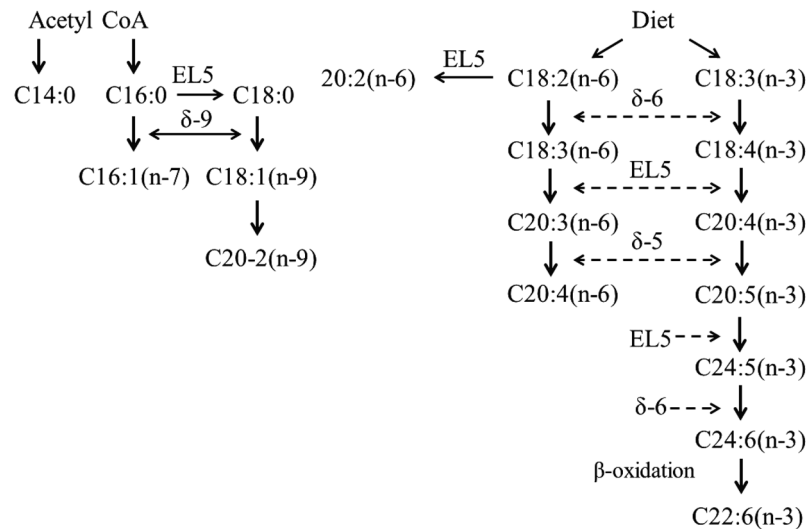


Fig. 2. **Metabolic pathway of fatty acid synthesis.**  $\delta$ -5, delta-5 desaturase;  $\delta$ -6, delta-6 desaturase;  $\delta$ -9, delta-9 desaturase; EL5: elongase 5.

Table 3. **Effects of single nucleotide polymorphism (SNP) of the genes fatty acid desaturase 1 (*FADS1*) and 2 (*FADS2*) on the fatty acid profile of Hinai-jidori thigh meat (mean  $\pm$  SE)**

Gene	<i>FADS1</i>		<i>FADS2</i>	
	rs733003230 (A>G)		LC060926 (g.25 A>G)	
Locus	rs733003230 (A>G)		LC060926 (g.25 A>G)	
SNP type	A	G	A	G
SNP Frequency	0.453	0.547	0.813	0.188
Fatty acid % of total analyzed fatty acids				
AA	1.01 $\pm$ 0.15	1.33 $\pm$ 0.07*	1.10 $\pm$ 0.07	1.55 $\pm$ 0.19*
DHA	0.25 $\pm$ 0.04	0.35 $\pm$ 0.02*	0.28 $\pm$ 0.02	0.40 $\pm$ 0.06*

\* statistically significant at  $P=0.05$ ; \*\* statistically significant at  $P=0.01$ .

AA, arachidonic acid; DHA, docosahexaenoic acid; A, adenine; G, guanine.

Table 4. **Effects of haplotype of the genes fatty acid desaturase 1 (*FADS1*) and 2 (*FADS2*) on the fatty acid profile of Hinai-jidori thigh meat (mean  $\pm$  SE)**

Combined haplotypes of <i>FADS1</i> and <i>FADS2</i>	A-A	G-A	G-G
Frequencies of plausible haplotypes under linkage equilibrium	0.453	0.359	0.188
Fatty acid % of total analyzed fatty acids			
AA	0.99 $\pm$ 0.12 <sup>b</sup>	1.24 $\pm$ 0.15 <sup>ab</sup>	1.56 $\pm$ 0.24 <sup>a</sup>
DHA	0.25 $\pm$ 0.04 <sup>b</sup>	0.32 $\pm$ 0.04 <sup>ab</sup>	0.40 $\pm$ 0.07 <sup>a</sup>

<sup>a,b</sup> Means within a row without a common superscript letter are significantly different ( $P<0.05$ ).

AA, arachidonic acid; DHA, docosahexaenoic acid; A, adenine; G, guanine.

lower than those of the fast- and medium-growing strains. Jayasena *et al.* (2014) reported that 100-d-old Korean native chickens exhibited significantly higher contents of LA, AA, and DHA than those of the 32-d-old broilers. Boschetti *et al.* (2016) reported that the medium-growing (Kabir Red) and in particular slow-growing (Hyline W36) strains showed higher expression of the genes *FADS1* and *FADS2* in the hepatic tissue than that in the fast-growing line (Cobb 500) at the age

of 81 days. However, in the present study, we did not assess the association between the polymorphism of the genes *FADS1* and *FADS2* and fatty acid profile of the meat. These reports suggest that there is a significant difference in the fatty acid profile of the meat between strains. However, these studies did not verify if the differences in the samples were caused by the difference in the sex of the examined chickens. Rikimaru and Takahashi (2010) used Hinai-jidori

**Table 5. Effects of single nucleotide polymorphism (SNP) of the enzyme fatty acid desaturase 1 (*FADS1*) on the fatty acid profile of yolk in Suruga-shamo chicken eggs (mean  $\pm$  SE)**

SNP type	G	A
SNP Frequency	0.802	0.198
Fatty acid % of total analyzed fatty acids		
AA	0.977 $\pm$ 0.010	0.913 $\pm$ 0.031*
n-6/n-3 PUFA	3.698 $\pm$ 0.069	4.093 $\pm$ 0.193*

\* statistically significant at  $P=0.05$ .

AA, arachidonic acid; PUFA, polyunsaturated fatty acids; G, guanine; A, adenine.

females, while Sirri *et al.* (2011), Jayasena *et al.* (2014), and Boschetti *et al.* (2015) used males. Furthermore, Sirri *et al.* (2009) reported that the contents of AA, DHA, and docosapentaenoic acid (C22:5n-3) in the breast and thigh meat of cocks were significantly higher than those in 180-d-old capons. Further, the difference between the cocks and capons was attributed to the testosterone affecting the activity of D6D. Clejan *et al.* (1982) demonstrated that the decreased contents of AA and DHA in castrated rats was due to the lack of testosterone, and the administration of testosterone elevated the content of AA to normal level. Testosterone exists in plasma before the onset of puberty in cockerels (Sharp *et al.*, 1977; Tanabe *et al.*, 1981; Rikimaru *et al.*, 2009). The differences in the fatty acid profile observed among 81-d-old Cobb 700, Naked Neck Kabir, and Brown Classic Lohman (Sirri *et al.*, 2011), and between 100-d-old Korean native chicken and 32-d-old broiler (Jayasena *et al.*, 2014) might reflect the concentration of plasma testosterone of each strain at the age of slaughter. In our previous study (Rikimaru *et al.*, 2016) we assessed the effects of the genes *FADS1* and *FADS2* on the fatty acid profile of chicken meat. The effects of testosterone and environmental factors on fatty acid profile were negligible, because we used female chickens that hatched on the same day and were reared under identical environmental conditions for the same duration.

### Genetic Regulation of Fatty Acid Profile and Flavor of Eggs

Most Japanese consumers recognize that the eggs of Jidori chickens have a rich *kokumi* flavor. We speculated that: 1) AA might be the substance related to the flavor of the eggs of Jidori chicken, and 2) *FADS1* and *FADS2* are the key genes that control the AA content in the eggs. We verified if the polymorphism of the genes *FADS1* and *FADS2* affected the fatty acid profile of the eggs of Suruga-shamo—a Japanese chicken breed (Matsui and Takahashi, 2017). An SNP in the *FADS1* gene was significantly associated with the AA content. The n-6/n-3 polyunsaturated fatty acid ratio in yolk showed that the SNP allele, which was associated with high AA content, had a low n-6/n-3 ratio (Table 5). Further, we found that adding trace amounts of AA corresponding to the difference in the SNP genotype enhanced the flavor intensity and continuity of the eggs (Table 6). We concluded that the SNP of the *FADS1* gene can be used to develop strategies to

**Table 6. Sensory evaluation of yolk seasoned with soy sauce**

Characteristic	Score <sup>1</sup>
Egg odor	0.263
Egg flavor intensity	0.842**
Egg flavor continuity	0.579*

<sup>1</sup> Average score of yolk with arachidonic acid-enriched oil (AAO) when the yolk without the AAO score was 0.

\* statistically significant at  $P=0.05$ ; \*\* statistically significant at  $P=0.01$ .

improve egg flavor and decrease the n-6/n-3 ratio in the yolk.

Because consumers, worldwide, are growing more health conscious, the reduction in the n-6/n-3 ratio is a special concern for the poultry and egg industry. Feed additives, such as flaxseed and fish oil, are used for this purpose (Fraeye *et al.*, 2012). However, the increased amount of n-3 polyunsaturated fatty acids (PUFA) in the egg yolk is proportional to the decreased amount of n-6 PUFAs, in particular AA (Bean and Leeson, 2003; Hayat *et al.*, 2009). The organoleptic quality of n-3 PUFA-enriched eggs is similar to that of the regular eggs; however, occasionally, off-flavored eggs can be detected (Elswyk *et al.*, 1992; Caston *et al.*, 1994). In contrast, we found that in the *FADS1* gene, the allele exhibiting a high AA also has a low n-6/n-3 ratio. A synonymous observation in the *FADS2* gene with respect to the n-6/n-3 ratio has been reported in Japanese quail by Khang *et al.* (2007). These data suggest that the n-6/n-3 ratio in the eggs is genetically changeable by manipulating the gene polymorphism of the enzymes mediating the LA—AA pathway. This approach might render the use of feed additives unnecessary.

### A Proposed Mechanism to Explain the Effect of Arachidonic Acid on the Enhancement of Food Flavor

The addition of AAO to cooked foods improves its flavor; this is widely recognized in Japan. For instance, when food, such as vegetable soup, croquettes, and fried rice, are cooked in vegetable oil containing AAO, their palatability index increases (Kiyohara *et al.*, 2009). Arachidonic acid-enriched cooking and frying oils, Bimi-Tokutoku, are commercially available from J-OIL MILLS, Inc. (Yokohama, Japan) in the

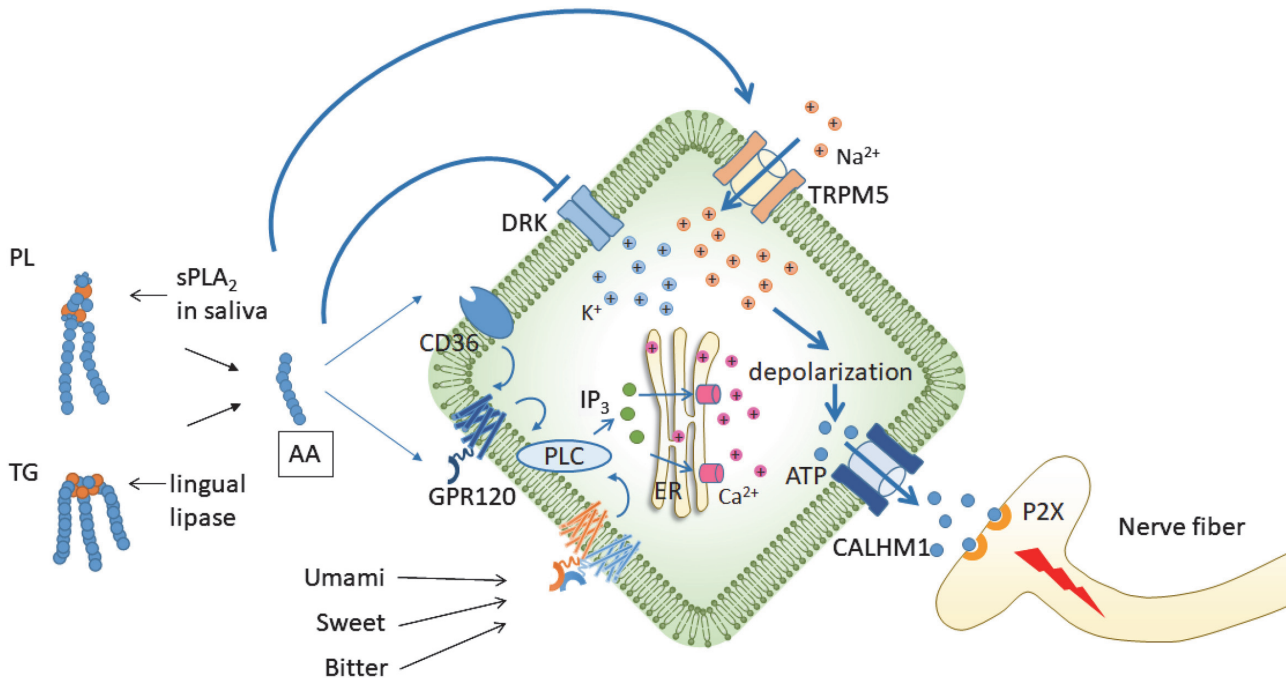


Fig. 3. **Proposed signaling pathway in type II receptor cells.** AA inhibits the DRK channel and activates the TRPM5 channel. Intracellular  $K^+$  ions and influx of  $Na^+$  ions, through the TRPM5 channel, cause depolarization of the cells and firing of action potentials. AA, arachidonic acid;  $Ca^{2+}$ , calcium ion; CALHM1, calcium homeostasis modulator 1; CD36, cluster of differentiation 36; DRK, delayed rectifying  $K^+$  channel; ER, endoplasmic reticulum; GPR120, G-protein coupled receptor 120;  $IP_3$ , type 3 isoform of inositol 1,4,5-trisphosphate;  $K^+$ , potassium ion;  $Na^+$ , sodium ion; P2X, purinergic receptors; PL, phospholipids; PLC, phospholipase C; sPLA<sub>2</sub>, secreted phospholipase A<sub>2</sub>; TG, triglycerides.

Japanese market. However, the mechanism through which AA enhances food flavor has not been clearly elucidated.

Dietary fats, including AAO, are predominantly in the form of triglycerides, which are not effective at stimulating taste. Kawai and Fushiki (2003) propose that lingual lipase produces FFA from triglycerides rapidly enough to enable detection by a fat sensor on the surface of the tongue. Recently, cluster of differentiation 36 (CD36) and G-protein coupled receptors (GPR), such as GPR120 and GPR40, have been identified as putative FFA taste receptors (Cartoni *et al.*, 2010; Laugerette *et al.*, 2005). Because CD36 is expressed in some type II (sweet, bitter, and *umami*) receptor cells in mouse taste buds (Laugerette *et al.*, 2005) and GPR120 and GPR40 are mainly expressed in type II and type I (salty) receptor cells, respectively (Cartoni *et al.*, 2010), FFA might affect the taste perception of sweet, bitter, *umami*, and salty flavors based on the distribution of taste receptors. However, the presence of GPR40 has not been confirmed in the gustatory papillae of humans (Galindo *et al.*, 2012). Gilbertson *et al.* (1997) reported that PUFAs, especially LA, AA, DHA, and eicosapentaenoic acid, might inhibit the delayed rectifying  $K^+$  (DRK) channels. Because  $K^+$  is a major intra-

cellular monovalent cation, the inhibition of DRK channels might elicit a rapid cell depolarization response caused by the transient accumulation of positive charges in taste bud cells. Oike *et al.* (2006) reported that AA activates transient receptor potential cation channel subfamily M member 5 (TRPM5) channel, which is a component of the sweet, bitter, and *umami* taste pathways in the type II receptor cells. Additionally, TRPM5-null mice showed no licking response to a sweet tastant, a diminished preference ratio for sweet and *umami* tastants, and a reduced response to bitter taste (Damak *et al.*, 2006). These data suggest that by modulating the DRK and TRPM5 channels, AA might serve as a flavor enhancer for the type II receptor cells. A model of fatty acid signal transduction in the type II receptor cells has been proposed in our previous report (Figure 2; Matsui and Takahashi, 2017).

Apart from cholesterol, triglycerides and phospholipids constitute approximately 2/3 and 1/3 of the total lipid content in egg yolk, respectively (Awad *et al.*, 1997). In the yolk, AA is present almost entirely in the second carbon group of glycerol of phospholipids (Gładkowski *et al.*, 2011). Therefore, phospholipase A<sub>2</sub> (sPLA<sub>2</sub>), secreted in saliva, is re-

quired to release AA from the second carbon group of glycerol in phospholipids. The activity of sPLA<sub>2</sub> has been documented in acinar cells and a fraction of apical plasma membrane acquired from the salivary gland of rat (Mizuno-Kamiya *et al.*, 2001; Takuma and Ichida, 1997). Komiyama *et al.* (2009) reported that type V sPLA<sub>2</sub> (sPLA<sub>2</sub>-V) is expressed in the human parotid and submandibular glands under disease-free conditions. We hypothesize that the yolk phospholipids are digested by the salivary sPLA<sub>2</sub>-V, releasing free AA, which affects the taste perception of the yolk. We conclude that the free AA, generated in the oral cavity, is one of the keys that enhance the flavor of the egg.

### Other Chemical Substances Affect the *Umami* Characteristic of Chicken Meat

As mentioned earlier, Glu and IMP are the typical active taste components of *umami*. Based on recent reports, comparing the quality of meat between broiler and Jidori chickens, it appears that the broiler has a higher Glu content than that of Jidori chicken, when the comparison was made at the marketable age of each strain (Goda, 2003; Matsuishi *et al.*, 2005; Rikimaru and Takahashi, 2010; Yamada and Yamada, 2013). Because the content of Glu decreases with age in broiler chicken (Chow and Jacobson, 1968; Rikimaru and Takahashi, 2010; Chae *et al.*, 2012), the difference in the content of Glu between broiler and Jidori chicken might be a reflection of their marketing age. Further, Wattanachant *et al.* (2004) reported that Thai indigenous chicken had higher Glu content than the broilers. Jayasena *et al.* (2014) reported that there was no difference in Glu content between Korean native and broiler chickens. These data suggest that the Glu content varies among different genotypes of chicken. Furthermore, the FAA content in the chicken meat increased with postmortem aging, and is responsible for improving the taste of the meat (Nishimura *et al.*, 1988). Watanabe *et al.* (2017) reported that a reduction in dietary lysine increases the content of free Glu in the broiler meat and improves its taste. An elevation in dietary lysine also increases the content of free Glu in the broiler meat, thus improving its taste (Watanabe *et al.*, 2015).

Jidori chicken exhibited a higher IMP content than that of the broiler when their meat was compared at the marketing age of each strain (Goda, 2003; Rikimaru and Takahashi, 2010). Similar results were obtained when the meat of the broiler chicken was compared with three Chinese native breeds (Tang *et al.*, 2009). Because there was no significant difference in the IMP content between 22-wk-old broiler and 22-wk-old Hinai-jidori chicken (Rikimaru and Takahashi, 2010), the difference in the IMP content between broiler and Jidori chicken might reflect their marketing age. Furthermore, the IMP content can be increased by dietary supplementation of IMP (Zhang *et al.*, 2008), purine nucleotides, betaine, soybean isoflavones, and combinations thereof (Wang *et al.*, 2014). Terasaki *et al.* (1965) reported that the IMP content of broiler breast meat reached maximal level at 8 h after slaughter, and then decreased gradually when the meat was stored at 4°C. Further, the flavor of the chicken

was more pleasant at 8 h after slaughter than that of the chicken immediately after slaughter. Postmortem aging might increase the content of IMP more effectively than that by the slaughter age and feed additives.

In conclusion, we have shown that the content of AA in chicken meat can be manipulated by dietary supplementation of AA and by genetic selection exploiting the polymorphism of the genes of *FADS1* and *FADS2* as selection markers. These approaches improve the flavor of chicken meat. Furthermore, we have shown the possibility of using the *FADS1* gene polymorphism as a selection marker to improve the fatty acid profile, in particular the content of AA and n-6/n-3 ratio, thereby improving the flavor of chicken eggs. We will be conducting studies on improving the flavor of Jidori meat and eggs, using molecular breeding and marker-assisted selection techniques in the near future.

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