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Flavor of Poultry Meat: A New Look at an Old Issue

Hideaki Takahashi

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Abstract

In Japan, fast-growing broiler occupies over 90% of poultry meat production. Meanwhile, many of Japanese native breeds of chickens are on the verge of annihilation, because most of them have low meat yield and egg production. Recently, meat flavor produced from native chickens has been reevaluated in the Japanese market. Most high-quality chickens, “Jidori” in Japanese, were initially bred by crossing native Japanese breeds with highly selected lines with rapid growth rate or relatively high egg production. Japanese consumers recognize that the meat from Jidori chickens is more palatable than that from broiler chickens; however, the reason behind this rich flavor of Jidori meat has not been elucidated. We found that (1) the high arachidonic acid (ARA, C20:4n-6) content is a characteristic feature of Hinai-jidori meat, (2) chicken meat containing higher levels of ARA is more palatable than that containing low ARA content, and (3) single-nucleotide polymorphisms in the fatty acid desaturase 1 and 2 gene cluster are associated with ARA content in meat. Our findings predict the beginning of a new era that the flavor of commercial chicken meat can be designed according to a commercial breeding program.

Keywords: chicken, meat, flavor, arachidonic acid, genetics

1. Introduction

Globally, chicken meat is obtained from a few fast-growing broiler strains. Meanwhile, countries, especially in Asia, have been keeping native breeds of chickens. Since most native chicken breeds have low meat yield and egg production, many of these breeds have been in danger of disappearing in many countries. Meanwhile, in Japan, some consumers are willing to pay a high retail price for a palatable meat known as “Jidori” chicken. Jidori, that is translated as an indigenous chicken in a local, is far more delicious, firm in texture, and expensive than the affordable broiler chicken. Most Jidori chickens were bred by crossing native Japanese breeds...
with highly selected lines with rapid growth. For example, the Hinai-jidori chicken, a popular brand in the Japanese market, is produced by crossing of Hinai-dori (a breed native to Akita prefecture, Japan) cocks and Rhode Island Red hens.

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, because most Japanese consumers believe that Jidori meat is characteristically tough. Other key factors are the presence of free amino acids (FAA) including glutamic acid (Glu) and purine compounds such as inosine 5'-monophosphate (IMP). As is well known, Glu and IMP salts are widely used as food additives for the purpose of enhancing the flavor of general foods. So, in the past three decades, studies have compared the content of FAAs such as Glu and IMP in broiler and Jidori meat in Japan.

For example, Karasawa et al. [1] reported that the Glu and total FAA content, in the gastrocnemius muscle from three types of Jidori chickens (Satsuma breed, Satsuma × broiler F₁ cross, and Kukin × broiler F₁ cross), is significantly higher than that in the muscle from broiler chickens, while subsequent studies have reported no significant differences between the FAA contents of Jidori and broiler chickens [2, 3]. Matsuishi et al. [4] reported that soup prepared from broiler meat has a significantly higher FAA and Glu content than that prepared from a Jidori (Nagoya breed) meat and the broiler soup is pleasanter than the Jidori soup. In other words, Matsuishi et al. [4] pointed out for the first time that the intensity of umami that are felt by Japanese consumers and the Glu content of Jidori meat are not necessarily proportional. Meanwhile, Fujimura et al. [2] reported that the IMP content in the meat from Hinai-jidori chicken was significantly higher than that of the meat from broilers, while other studies have not shown a significant difference in the IMP content between Jidori and broiler meat [1, 5]. Therefore, 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.

Reflecting on past studies, we concluded that to determine the flavor of chicken meat, it is necessary to define candidate substances related to characteristic differences between broiler and Jidori chicken meat.

2. Association of arachidonic acid content and flavor in chicken meat

To identify the candidate substances influencing chicken meat palatability, quantitative analyses were performed on general biochemical components, such as FAAs including Glu, IMP, and fatty acids in the thigh meat of Hinai-jidori and broiler chickens. Female chicks hatched on the same day were reared under identical environmental conditions for the same duration. The results showed that higher arachidonic acid (ARA, 20:4n-6) and docosahexaenoic acid (DHA, C22:6) content was a characteristic feature of Hinai-jidori chicken (Table 1) [6].

Actually, Fujimura et al. [3] compared fatty acid profiles of Hinai-jidori and broiler chicken meat; however, they did not detect the phenomenon. Causes of the discrepancy may be that
ARA is a polyunsaturated fatty acid (PUFA) which exists in animal fat. ARA serve as an intracellular second messenger in many cells, as well as a precursor for biologically active molecules, such as eicosanoids (molecules of oxygenated ARA metabolites that act as second messengers and/or local mediators) and anandamide (an endogenous cannabinoid) [7]. When we found that a high ARA content is a characteristic feature of Hinai-jidori chicken [6], we noticed that a report patented in the 1960s [8] documented that autoxidized ARA has a flavor like cooked chicken meat. In addition, Yamaguchi et al. [9, 10] reported the relationships between the levels of PUFA including ARA, and food palatability. For example, the addition of trace amounts of ARA to vegetable oil used for cooking enhance umami (L-glutamate taste), kokumi (continuity, mouthfulness, and thickness), aftertaste, and total taste intensity of such foods as fried potatoes, Chinese noodle soup, and Hamburg steak cooked with the oil. Therefore, we assumed that ARA is associated with chicken flavor.

To elucidate the relationship between the ARA content and the flavor of Hinai-jidori meat, Hinai-jidori chickens were administered diets containing 3 oils (palm oil (PO), corn oil (CO), and ARA-enriched oil (AO, SUNTGA40S, Nippon Suisan Co., Tokyo, Japan)) during rearing; meat was subsequently evaluated by biochemical and sensory analyses [11]. Each oil was mixed in a weight ratio of 7:3 with silicate (TIXOSIL38A, Rhodia Silica Korea Co., Seoul, South Korea) and three types of oil supplements were prepared. Five percent of the supplements (3.5% equivalent of each oil) was added to the finisher diet and Hinai-jidori chickens were fed the test diets for 2 weeks before slaughter. As a result, in thigh meat, the ARA content of the AO group was twice higher than those of the PO and CO groups. Contents of other fatty acid components excluding ARA were not significantly different among the three groups. Sensory evaluation of steamed minced meat revealed that umami, kokumi, aftertaste, and total taste intensity of the AO group were significantly higher than those of PO and CO groups (Table 2). These data suggest that the flavor of chicken meat might be improved by dietary ARA supplementation.

To elucidate the relationship between the ARA content and the flavor of broiler meat, we evaluated the effects of AO supplements on the fatty acid content and sensory perceptions of thigh meat [12]. We prepared four types of oil: CO; a 1:1 mixture of AO and PO (1/2 AO); a 1:3 mixture of AO and PO (1/4 AO); and a 1:7 mixture of AO and PO (1/8 AO). Each type of oil was then mixed with silicate in a weight ratio of 7:3 and added to the finisher diet at a

<table>
<thead>
<tr>
<th>Item</th>
<th>Broiler, female (8 weeks of age)</th>
<th>Broiler, female (22 weeks of age)</th>
<th>Hinai-jidori, female (22 weeks of age)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ARA</td>
<td>1.42 ± 0.27a</td>
<td>1.26 ± 0.33a</td>
<td>1.92 ± 0.04a</td>
</tr>
<tr>
<td>DHA</td>
<td>0.20 ± 0.07a</td>
<td>0.24 ± 0.11a</td>
<td>0.38 ± 0.04a</td>
</tr>
</tbody>
</table>

Table 1. ARA and DHA content (% of total analyzed fatty acids) in broiler and Hinai-jidori thigh meat (mean value ± SD).

Within a row, means without a common superscript are significantly different (P < 0.05).

[3] analyzed a limited number of samples per chicken strain and Hinai-jidori chickens in the 1990s and 2010s are different.

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In this experiment, broiler chickens were fed the four diets for 1 week before slaughter. As a result, the ARA content in the thigh meat (y, mg/g) increased linearly with the increasing content of dietary AO. The ARA content in the thigh meat of the 1/2 AO and 1/4 AO groups was significantly higher than that in the thigh meat of the CO group. Contents of other fatty acid components excluding ARA were not significantly different among the four diet groups. Sensory evaluation showed that the flavor intensity, umami, kokumi, and aftertaste, of the 1/2 AO and 1/4 AO groups, were significantly improved compared with those of the CO group (Table 3). Additionally, there were significant positive correlations between the ARA content of the thigh meat and flavor intensity, total taste intensity, umami, and aftertaste. These data suggest that the flavor of broiler chickens can be improved by increased supplementation of dietary ARA as well shown in Hinai-jidori chickens.

In our previous reports [11, 12], we measured the Glu and IMP contents of the 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 [13]. In these reports [11, 12], the differences in the intensity of umami among the experimental groups were less than 1%. These data suggest that the differences, in the intensity of umami between the groups, cannot be attributed to the contents of Glu and IMP, because Yamaguchi [13] reported that the differential threshold of umami between samples was 21%. Thus, we conclude that the differences in chicken flavor, observed in our reports, were caused by ARA and not by water-soluble substances, such as Glu and IMP.

After our sequential reports [6, 11, 12] were published, we found a report showing that Korean native chickens (KNC) had a higher content of ARA than broiler chickens; however, the sensory acceptance was not significantly different between KNC and broilers [14]. It is clear that [14] reported only a tendency of ARA content in KNC, but the authors failed to find an association between the ARA content and meat flavor.

<table>
<thead>
<tr>
<th>Comparisons</th>
<th>PO vs. AO(^1)</th>
<th>CO vs. AO(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sourness</td>
<td>0.34*</td>
<td>0.03</td>
</tr>
<tr>
<td>Sweetness</td>
<td>-0.03</td>
<td>0.34*</td>
</tr>
<tr>
<td>Umami</td>
<td>0.59**</td>
<td>0.50*</td>
</tr>
<tr>
<td>Kokumi</td>
<td>0.66*</td>
<td>0.75**</td>
</tr>
<tr>
<td>Aftertaste</td>
<td>0.69**</td>
<td>0.50*</td>
</tr>
<tr>
<td>Total taste intensity</td>
<td>0.72**</td>
<td>0.56**</td>
</tr>
</tbody>
</table>

\(^1\) An average of the AO score of each subject when PO score is 0.
\(^2\) An average of the AO score of each subject when CO score is 0.
*Statistically significant at P = 0.05 level.
**Statistically significant at P = 0.01 level.

Table 2. Sensory evaluation of steamed minced meat of Hinai-jidori chickens fed experimental diets.
3. Flavor: a new breeding target of chickens

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. The comparison was made at the marketable age of each strain \[4, 6, 15, 16\]. Because the content of Glu decreases with the age in broiler chicken \[6, 17, 18\], the difference in the content of Glu between broiler and Jidori chicken might be a reflection of their marketing age. Further, Wattanachant et al. \[19\] reported that Thai indigenous chicken had higher Glu content than the broilers. Jayasena et al. \[20\] 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 \[21\]. Watanabe et al. \[22\] 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 \[23\].

Jidori chicken exhibited a higher IMP content than that of the broiler when their meat was compared at the marketing age of each strain \[6, 15\]. Similar results were obtained when the meat of the broiler chicken was compared with three Chinese native breeds \[24\]. Because there was no significant difference in the IMP content between 22-weeks-old broiler and 22-weeks-old Hinai-jidori chicken \[6\], the difference in the IMP content between broiler and Jidori chicken might be a reflection of their marketing age. Further, Wattanachant et al. \[19\] reported that Thai indigenous chicken had higher IMP content than the broilers. Jayasena et al. \[20\] reported that there was no difference in IMP content between Korean native and broiler chickens. These data suggest that the IMP content varies among different genotypes of chicken.

Table 3. Sensory evaluation of steamed minced meat of broiler chickens fed experimental diets.

<table>
<thead>
<tr>
<th>Item</th>
<th>CO vs. 1/2 AO</th>
<th>CO vs. 1/4 AO</th>
<th>CO vs. 1/8 AO</th>
<th>1/8AO vs. 1/2 AO</th>
<th>1/4AO vs. 1/2 AO</th>
<th>1/8AO vs. 1/4 AO</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flavor intensity</td>
<td>0.88*</td>
<td>0.63*</td>
<td>0.63</td>
<td>0.13</td>
<td>0.25</td>
<td>0.25</td>
</tr>
<tr>
<td>Umami(^1)</td>
<td>0.88*</td>
<td>0.63*</td>
<td>0.50</td>
<td>0.25</td>
<td>0.13</td>
<td>0.00</td>
</tr>
<tr>
<td>Kokumi(^2)</td>
<td>0.50*</td>
<td>0.75*</td>
<td>0.63</td>
<td>0.25</td>
<td>0.38</td>
<td>0.38</td>
</tr>
<tr>
<td>Aftertaste</td>
<td>0.75*</td>
<td>0.75*</td>
<td>0.50</td>
<td>0.13</td>
<td>0.25</td>
<td>0.50</td>
</tr>
<tr>
<td>Total taste intensity</td>
<td>1.00*</td>
<td>0.63</td>
<td>0.25</td>
<td>0.38</td>
<td>0.50*</td>
<td>0.00</td>
</tr>
</tbody>
</table>

\(^1\)Umami = L-glutamate taste.
\(^2\)Kokumi = continuity, mouthfulness, and thickness.
\(^3\)CO = Corn oil; 1/2, 1/4, and 1/8 AO = 1/2, 1/4, and 1/8 arachidonic acid-enriched oil.
\(^4\)An average of the 1/2 AO score of each subject when CO score is 0.
\(^5\)An average of the 1/4 AO score of each subject when CO score is 0.
\(^6\)An average of the 1/8 AO score of each subject when CO score is 0.
\(^7\)An average of the 1/2 AO score of each subject when 1/8 AO score is 0.
\(^8\)An average of the 1/4 AO score of each subject when 1/4 AO score is 0.
\(^9\)An average of the 1/4 AO score of each subject when 1/8 AO score is 0.
\(^*\)Statistically significant at P = 0.05 level.
\(^**\)Statistically significant at P = 0.01 level.

Table 3. Sensory evaluation of steamed minced meat of broiler chickens fed experimental diets.
chicken might reflect their marketing age. Furthermore, the IMP content can be increased by dietary supplementation of IMP [25], purine nucleotides, betaine, soybean isoflavones, and combinations thereof [26].

Terasaki et al. [27] 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. Thus, postmortem aging may increase the content of IMP more effectively than that by the slaughter age and feed additives.

As mentioned previously, we experimentally proved that the ARA content in chicken meat is changeable by adding AO to the feed; however, AO is so expensive that it is not suitable for the daily use. Therefore, we examined the possibility of genetic regulation of arachidonic acid content in chicken meat.

As shown in Figure 1 [28], ARA originates from both dietary sources and the elongation desaturation process of linoleic acid (LA, C18:2n-6) in animals. D6D exerts a catalysis on a change in γ-linolenic acid (GLA, C18:3n-6), which is elongated to dihomo-γ-linolenic acid (DGLA, C20:3n-6) by elongases.
Then, GLA is desaturated to ARA by D5D. As well as in the n-6 pathway, these enzymes are involved in the n-3 fatty acid pathway from α-linolenic acid (ALA, C18:3n-3) to DHA (Figure 1). D5D and D6D are known as encodes for fatty acid desaturase 1 and 2 genes (FADS1 and FADS2), respectively. FADS1/2 cluster is located at chicken chromosome 5 [29, 30]. Therefore, we supposed that FADS1, FADS2, and FADS1/2 clusters are the keys that regulate ARA and DHA content in chicken meat.

We genotyped the polymorphisms of FADS1 and FADS2 and investigated their association with the fatty acid profile in the Hinai-jidori meat [31]. We found 71 and 46 SNPs in FADS1 and FADS2, respectively. Of the SNPs, rs733003240 (A > G) and LC060926 (g.25 A > G) were chosen in FADS1 and FADS2, respectively. Then, the Hinai-jidori female chickens, hatched on the same day and reared under identical environmental conditions over the same duration, were used for all analyses. In each SNP of FADS1 and FADS2, the compositions of AA and DHA were significantly higher in the G, rather than in the A, allele, respectively (Table 4).

We also examined the association of the FADS1 and FADS2 haplotypes with the content of fatty acids. The AA and DHA content of the G-G-haplotype was significantly higher than that of the A-A-haplotype (Table 5).

Thus, we conclude that the SNPs, in the FADS1 and FADS2 gene cluster, increase the content of fatty acids. The AA and DHA content of the G-G-haplotype was significantly higher than that of the A-A-haplotype (Table 5).

### Table 4. SNP effects of chicken fatty acid desaturase 1 and 2 genes (FADS1 and FADS2) on ARA and DHA content (% of total analyzed fatty acids) in Hinai-jidori thigh meat (mean value ± SE).

<table>
<thead>
<tr>
<th>Gene</th>
<th>Fatty acid desaturase 1 (FADS1)</th>
<th>Fatty acid desaturase 2 (FADS2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Locus</td>
<td>rs733003240 (A &gt; G)</td>
<td>LC060926 (g.25 A &gt; G)</td>
</tr>
<tr>
<td>SNP allele</td>
<td>A</td>
<td>G</td>
</tr>
<tr>
<td>Allele frequency</td>
<td>0.453</td>
<td>0.547</td>
</tr>
<tr>
<td>ARA</td>
<td>1.01 ± 0.15</td>
<td>1.33 ± 0.07*</td>
</tr>
<tr>
<td>DHA</td>
<td>0.25 ± 0.04</td>
<td>0.35 ± 0.02*</td>
</tr>
</tbody>
</table>

*Statistically significant at P = 0.05 level.

### Table 5. Haplotype effects of chicken fatty acid desaturase 1 and 2 genes (FADS1 and FADS2) on ARA and DHA content (% of total analyzed fatty acids) in Hinai-jidori thigh meat (mean value ± SE).

<table>
<thead>
<tr>
<th>Combined haplotype of FADS1 and FADS2</th>
<th>A-A</th>
<th>G-A</th>
<th>G-G</th>
</tr>
</thead>
<tbody>
<tr>
<td>Frequencies of plausible haplotype under linkage equilibrium</td>
<td>0.453</td>
<td>0.359</td>
<td>0.188</td>
</tr>
<tr>
<td>ARA</td>
<td>0.99 ± 0.12*</td>
<td>1.24 ± 0.15*</td>
<td>1.56 ± 0.24*</td>
</tr>
<tr>
<td>DHA</td>
<td>0.25 ± 0.04*</td>
<td>0.32 ± 0.04*</td>
<td>0.40 ± 0.07*</td>
</tr>
</tbody>
</table>

*Means within a row with different superscript letters are significantly different at P = 0.05 level.
chicken meat can be designed according to a plan. Thus, we are testing whether the flavor of Jidori meat can be improved by using molecular breeding and marker-assisted selection techniques.

4. A proposed mechanism to explain the effect of ARA on the enhancement of chicken flavor

The fact that the addition of AO to cooked foods improves the taste is widely recognized in Japan. To date, J-OIL MILLS, Inc. (Tokyo, Japan) sells AO-supplemented cooking and frying oils in the Japanese market. However, a mechanism to explain the effect of ARA regarding the enhancement of food taste has not been yet satisfactorily elucidated.

Alimentary fat is mainly in the form of triglycerides, which are not effective taste stimuli; however, on the tongue surface, free fatty acids (FFA) might be generated from triglycerides by lingual lipase and resultant FFA might be detected by FFA sensors [32].

To date, the CD36, GPR120, and GPR40 have been reported as putative FFA taste receptors [33, 34]. Because CD36 is expressed in some type II (sweet, bitter, and umami) receptor cells

![Figure 2. Proposed mechanism why ARA enhances taste perception in type II receptor cells [39]. DRK, delayed rectifying K+ channel; ER, endoplasmic reticulum; IP3, type 3 isoform of inositol 1,4,5-trisphosphate; PLC, phospholipase C.](image-url)
in mouse taste buds [34] and GPR120 and GPR40 are mainly expressed in type II and type I (salty) receptor cells [33]. FFA might affect taste perception of sweet, bitter, umami, and salty based on taste receptor distribution, although the presence of GPR40 has not been confirmed in the gustatory papillae of humans [35]. PUFAs, especially LA, ARA, DHA, and eicosapentaenoic acid (EPA), might inhibit the delayed rectifying K+ (DRK) channel in taste receptor cells [36]. Resultantly, DRK channel inhibition might elicit a fast cell depolarization due to transient accumulation of positive charges in taste bud cells, since K+ is the major intracellular monovalent cation in taste receptor cells. Oike et al. [37] reported that ARA activates the TRPM5 cation channel, which is an essential component of the sweet, bitter, and umami taste pathways of type II receptor cells. As a supporting evidence of TRPM5 function, it has been reported that 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 [38]. Together, these data suggest that ARA may serve as a taste enhancer for type II receptor cells by modulating the TRPM5 channel and blocking the DRK channel (Figure 2). Details of the proposed mechanism were described by Matsui and Takahashi [39].

Meanwhile, the Matsui-Takahashi model [39] lacks aspect of the effect of volatile odor generated from ARA, AO, and cooked chicken meat. Therefore, further studies are needed to characterize volatile odor components of ARA and to define whether the components affect sensory evaluation.

5. Conclusions

We have shown that the content of AA in chicken meat can be manipulated by dietary ARA supplements and by genetic selection, using FADS1 and FADS2 gene polymorphisms as selection markers; these approaches improve the flavor of chicken meat. 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.

Acknowledgements

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Conflict of interest

The author declares that there is no conflict of interest that could be perceived as prejudicing the impartiality of the research reported.
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