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Canine Taste Responses to Elements of Food Deliciousness Closely Resemble Those of Human Responses, While Rodent Responses are Very Different from Canine Responses

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Abstract

In the studies of taste receptor mechanism, rodents (rats and mouse) have been usually used. However, taste responses of rodents are quite different from ones of humans.

In a mixture that has the taste of crab meat, sodium chloride is an essential ingredient in addition to three amino acids and umami substances. Withdrawing the sodium chloride from the mixture results in a very weak taste because sodium chloride has the ability to enhance the other taste stimuli. However, in the rodent taste system, sodium chloride has no enhancing effect on the other stimuli. In the canine taste system, sodium chloride greatly enhances the responses to amino acids, sugars, and umami substances as it does in humans.

Withdrawal of umami substances from the mixture with the taste of crab meat leads to a taste that is quite different taste from the crab meat taste. Umami substances are contained in many foods such as seaweed, bonito, sardine, tomato, mushroom, cheese, cured ham, and mother's milk. Furthermore, various soup stocks contain height content of umami substances.

It is difficult to achieve good flavors without umami substances. There are three umami substances (glutamate, 5'-inosinate, and 5'-guanylate). There is synergism between glutamate and 5'-inosinate and between glutamate and 5'-guanylate. The response to umami substances alone is rather small, but the response elicited by this synergism is very large. In humans, the response elicited by the synergism is the main umami response. In rodents, the umami response elicited by the synergism is very small, but it is very large in dogs, as with the response in humans.

The reason that the canine taste system resembles that of humans is that dogs have been eating the same foods as humans in the past 15,000 years, and the canine taste system has assimilated to the human taste system.

Keywords: Deliciousness; NaCl enhancement; Umami; Amino acid; Umami receptor; Dog; Human; Rat

Introduction

We shake sodium chloride to fishes and meats in cooking. In soaps and sauces, rather high concentration of sodium chloride is contained. In addition, natural foods contain a certain amount of sodium chloride. Thus, sodium chloride is essential for deliciousness for foods.

Fuke and Konosu [1] clarified that the essential components of the taste of crab meat are three amino acids, umami substances, and sodium chloride. Withdrawal of the sodium chloride from the mixture leads to a very weak taste Psychophysical data showed that the tastes of the amino acids are greatly enhanced by sodium chloride and that withdrawal of the sodium chloride greatly weakens the tastes of the amino acids. Furthermore, the tastes of sugars and umami substances are also enhanced by sodium chloride.

In electrophysiological studies on the taste system, rodents (rats and mice) have mainly been used. However, the taste responses of rodents to these stimuli are not enhanced by sodium chloride. On the other hand, the taste responses of dogs to sugars, amino acids, and umami substances are greatly enhanced by sodium chloride, much like those of humans.

There are three umami substances (glutamate, 5-'inosinate, and 5'-guanylate). A high level of synergism occurs between glutamate and 5'-inosinate and between glutamate and 5'-guanylate. The tastes of umami substances alone are rather weak, but the tastes induced by this synergism are extremely strong. The main response to umami substances is due to the response induced by the synergism. In rodents, the synergism is very small, but the synergism in the canine taste system is very large, much like it is in humans.

Thus, the canine taste system closely resembles the human system. This is because dogs have been eating the same foods as humans in the past 15,000 years. The dog taste system has evolved to resemble the human system. For studies on food elements that taste good to humans, such as sugars, amino acids,

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and umami substances, the dog taste system is a good model for the human taste system.

There are several elements of food acceptability, which we review below.

Elements of Food Acceptability

As shown in (Figure 1), there are several elements of food acceptability.

Odor: When people compare the tastes of bottled apple and grapefruit juices while holding their noses, many cannot differentiate between them. The difference in the taste of these juices is mainly due to the difference in their odors. The is true of many foods, so that the odor of a dish greatly contributes to its taste. When one catches a cold, a lot of foods lose their taste and become unpleasant. This is not due to the loss of tongue function but rather to the loss of olfactory function.

The liking and disliking of specific tastes are intrinsic, as described above. For example, many animals like sugars. On the other hand, the liking and disliking of odors are learned behaviors, and so the likes and dislikes that both animals and humans have for various odors do not show consistent similarities. Some people like foods with strong odors such as garlic, coriander, and fresh cheese, but others do not like these foods.

Texture: Japanese noodles are made from wheat flour. The shape of the noodle is similar to that of macaroni. The noodles come in many types, and among the most popular are *inaniwa udon* in Akita, *kishimen* in Nagoya, and *sanuki udon* in Kagawa. Each noodle has a characteristic texture, although all of these noodles are made from wheat flour. People think that each noodle has a different taste. Thus, the texture is a very important factor in food acceptability.

Vision: People in different cultures have different associations with specific foods. For example, squid and octopus are referred to as "devil fish" in America and England, as the features of the fish evoke bad associations in these countries. In India, the cow is a sacred animal, and Islam prohibits the eating of pork.

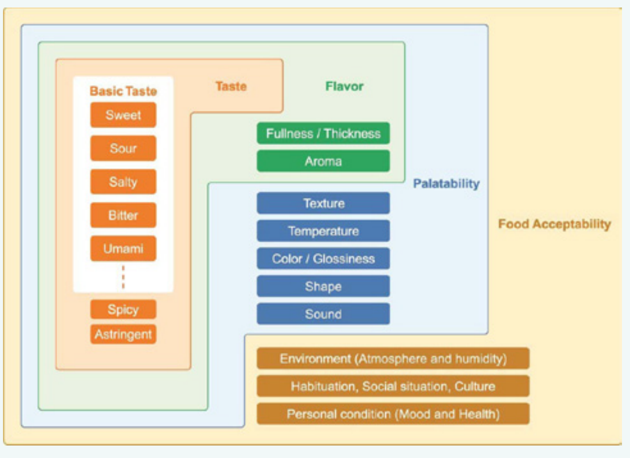

Figure 1 Acceptability of elements of foods (Umami Information Center).

Many Japanese people do not have favorable images of locusts and bee larvae, but some people eat them for pleasure. Sea cucumbers are not eaten in America or Europe, but they are popular in Japan and China. The salted and fermented internal organs of the sea cucumber are very delicious, although they are expensive in Japan.

Usually people eat a food only after having identified the food. Even when one cannot identify the food, one determines the category of the food such as fish, meat, or vegetable. One eats foods after recalling memories of eating the food in the past.

Animals are cautious when eating a food for the first time. This is called neophobia. When a rat is given apple juice for the first time, the rat drinks only about 2 ml of the juice. The second time the rat is given the juice, it drinks about 5 ml. After the juice is offered repeatedly, the rat willingly drinks the juice. This is because the rat has learned that the juice is delicious and safe.

Memories of foods: The memories of foods eaten in childhood can be very strong. The taste of home cooking from one's childhood is remembered as a good taste even in adulthood. The tastes of foods are memorized along with the circumstances under which they are eaten. Foods eaten in comfortable circumstance are remembered as good foods, but foods eaten in bad circumstances such as unhappy family situations are not remembered as good foods. People who develop symptoms of poisoning caused by eating oysters often come to dislike oysters for a long time. In prior research, rats were fed a food, and soon after lithium chloride, which induces poisoning, was injected. The rats associated the food with the poisoning and did not eat that food again for a long time.

A gourmet is a person who eats many delicious foods and has a highly cultivated sense of taste. This is not because his or her tongue is more sensitive to the tastes of foods, but because he or she has accumulated abundant memories of foods. A gourmet's brain can differentiate slight differences in taste.

Food likes and dislikes vary greatly from country to country. This is due to differences in eating habits formed from childhood. Foods that one has been eating for a long time tend to taste delicious. Furthermore, the metabolic system of the body is well suited to such familiar foods.

Taste: The most important element of food acceptability is taste. There are five basic tastes: sweet, salty, umami, bitter, and sour. Each basic taste has its own physiological role. Typical sweet substances are sugars, which supply energy. Hence, a sweet taste is a sign that a food contains energy. Salts are essential elements for health, and a salty taste is a sign of minerals. Glutamate, which is the main umami substance, is most abundantly contained in proteins. Glutamate is a precursor of a protein and a component of protein hydrolysate. Umami taste is a sign of protein. Sugars, salts, and proteins are important for nutrition, and hence humans like to consume foods having these tastes.

Poisonous substances have a bitter taste in general, and hence bitterness is a sign of poison. Putrid matter has a sour taste. In addition, unripe fruits have a sour taste. The seeds of mature fruits are spread through the droppings of animals. The seeds of unripe fruits cannot be germinated. Unripe fruits have a sour taste to prevent them from being eaten by animals. For animals, the sour taste is a signal to protect them from eating putrid foods and unripe fruits. Since bitter and sour substances are bad for our health, babies and animals do not eat foods having these tastes. Babies show a satisfied expression in response to sweet and umami tastes and a threatening expression in response to sour and bitter tastes.

As adults, humans learn that not all bitter and sour substances are harmful. For example, coffee and green tea has bitter tastes, but adults like these drinks. Adults also like some sour foods such as lemons and sour cream. It is instinctive for babies and animals not to like bitter and sour tastes, while it is a learned behavior for adults to like some bitter and sour foods.

Hot pepper has a hot taste. The active component of hot pepper is capsaicin, which stimulates a sense of pain and does not stimulate the taste cells. Immature persimmon has an astringent taste. The active component of immature persimmon is tannin. Tannin has an ability to denature protein and hence has been used for tanning leather. Tannin does not stimulate the taste cells but stimulates a kind of pain by denaturing proteins on the tongue. Thus, hot and astringent tastes are not tastes in the strict sense, but the sensations induced by these stimuli are transmitted to the brain and conjugated with signals induced by taste stimuli. Thus, we can call these hot and astringent sensations “tastes” in a broad sense. Hot and astringent tastes contribute to the flavor palates of many cuisines.

Essential Elements of Deliciousness of Foods

Fuke and Konosu [1] determined the essential components of the taste of snow crab meat by the omission test. First, the chemical composition of boiled crab meat was analyzed. A mixture of the pure chemicals that make up the crab meat components tastes like crab meat. The omission of some components still elicits a crab meat taste, but when other components are omitted, the mixture does not elicit the crab meat taste anymore. Thus, the essential components of the crab meat taste were determined. As shown in (Table 1) [1], three amino acids (glycine, alanine, and arginine), two umami substances (glutamate and 5’-inosinate), and two salts (NaCl and K_2HPO_4) are essential components of the crab meat taste. According to our experience, K_2HPO_4 is not always necessary.

Amino acids

The essential components of many other foods are also amino acids, umami substances, and salts. (Table 2) shows the tastes of various amino acids. In the table, the tastes of many amino acids are classified as bitter, but the bitterness of each amino acid is not identical to the others. In the crab meat taste, arginine is essential. The taste of arginine is bitter and not very good, but it is needed to produce the crab meat taste.

Scallops are sweet shellfish because they contain very high glycine content (1,925mg/100 g), which is a sweet amino acid, together with alanine and arginine. Sea urchin eggs have a unique taste that is due to methionine. Thus, the types and amounts of amino acids contribute to the characteristic tastes of different foods.

Table 1: Composition of the mixture with crab meat taste.

Component	Concentration (mg/100ml)	Role of component
Glycine	600	Characterization of taste of crab meat
Alanine	200	
Arginine	6000	
Glutamate	30	Addition of umami
5’-Inosinate	20	
NaCl	500	Enhancement of tastes of amino acids and umami substances
K_2HPO_4	400	

Table 2: Tastes of amino acids.

Sweet	Bitter	Umami
Glycine	Methionine	Glutamate
Alanine	Histidine	Aspartate (week)
Threonine (week)	Leucine	
Proline (week)	Isoleucine	
Serine (week)	Valine	
Glutamine (week)	Leucine	
	Phenylalanine (week)	
	Arginine (week)	
	Tyrosine (week)	

Enhancement by sodium chloride

Elimination of NaCl from the components making up the crab meat taste results in a very weak taste. That is, NaCl enhances the tastes of the other components. In order to clarify the enhancing effect of NaCl, the effect of NaCl on the sweet taste of glycine was examined psychophysically [2]. The results show that the sweet taste of glycine is greatly enhanced by the presence of NaCl. To confirm the enhancement of NaCl more quantitatively, recording of the rat corda tympani nerve was carried out, but NaCl did not bring any enhancement of amino acids (unpublished data). Next recording of the canine chorda tympani nerve was carried out [3]. (Figure 2) shows that the response to glycine is greatly enhanced by adding NaCl. The maximum enhancing effect is seen at 100 mM (0.6%) NaCl. One hundred mM NaCl has only weak saltiness. A further increase of the NaCl concentration decreases the enhancement. The enhancement by NaCl was also seen with the other amino acids.

Some fruits have a sweet taste. It is known that NaCl enhances the sweet taste in foods in humans. For example, we add NaCl to watermelon to increase its sweetness. However, NaCl does not enhance the response to sugars in the rat chorda tympani. In the canine chorda tympani, NaCl greatly enhanced the response to sugar (sucrose) as shown in Figure 3 [4]. The maximum enhancing effect is seen at 100 mM NaCl, as with glutamate. As mentioned above, tastes of amino acids were very small without addition of NaCl. On the other hand, taste of sucrose is relatively large without NaCl and addition of NaCl enhances sucrose taste

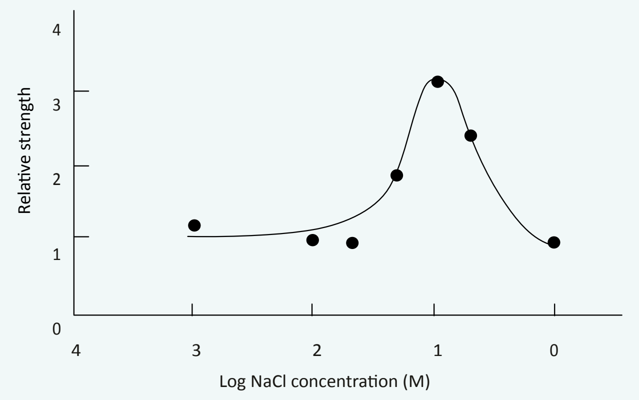

Figure 2 Relative strength of canine taste nerve response to 100 mM glycine as a function of logarithmic NaCl concentration.

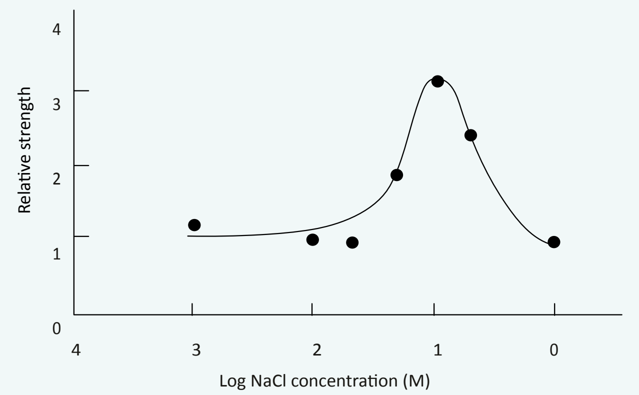

Figure 3 Relative strength of canine taste nerve response to 0.5 M sucrose as a function of logarithmic NaCl concentration.

both in humans and dogs. It is surprising that canine taste system so closely looks like human system.

Umami Substances

The responses to umami substances such as glutamate, 5'-inosinate, and 5'-guanylate were also enhanced by NaCl [5]. (Figure 4) shows the enhancing effect of NaCl on the response to glutamate. The maximum enhancing effect is also seen at 100 mM NaCl. Thus, NaCl at a rather low concentration enhances the tastes of various foods. (Table 3) summarizes the effects of NaCl on tastes of glycine, sucrose and glutamate in humans, dogs and rats. It is clearly understandable that taste system of dogs closely resembles that of humans, while that of rats is quite different from humans and dogs.

The first function of umami substances is to provide the umami taste itself. As mentioned before, *kombu dashi* (glutamate) is a pure umami solution. *Kombu dashi* and the *dashi* made from dried bonito (5'-inosinate) both have a pure umami taste. The second function of umami substances is to make foods more delicious. For example, elimination of the umami substances from the essential components of the crab meat taste made the crab meat flavor less delicious.

Discovery of umami substances [6]

The seaweed *kombu* has been used as a material to make *dashi* (soup stock) in Japan for a long time. In 1908, Ikeda found that the active principle is glutamic acid [7]. At neutral pH, glutamic acid exists in salt form, mainly as sodium glutamate.

Dried bonito has been used to make *dashi* in Japan for a long time. In 1913, Kodama, who was the best pupil of Ikeda, found that the active principle of dried bonito is 5'-inosinate (salt of 5'-inosinic acid) [8]. 5'-Inosinic acid is a nucleotide and has a phosphate residue. At neutral pH, 5'-inosinate is an anion. Like glutamate, the anion form of 5'-inosinic acid has an umami taste.

In 1957, Kuninaka found that 5'-guanylate has an umami taste [9]. 5'-Guanylate is also a nucleotide which has a phosphate residue. At neutral pH, 5'-guanylate is an anion. Later, it was found that 5'-guanylate is an umami component in *shiitake* mushrooms.

Content of umami substances in various foodstuffs

As described above, there are three umami substances: glutamate, 5'-inosinate, and 5'-guanylate. The contents of these substances in various foodstuffs have been measured. The contents vary with the state of preservation and aging and with the measurement method. The data shown in (Table 3) are the most reliable ones at present [10].

Glutamate is contained universally in both plant and animal foodstuffs. *Kombu* and seaweed *nori* have very high glutamate content (Table 3). Among vegetables, tomatoes have the highest glutamate content (Table 4). Animal foodstuffs also contain glutamate, but the content is relatively lower than in plant foodstuffs.

Fermented foods have a high glutamate content brought about by the hydrolysis of proteins during fermentation. Cheese and cured ham also have high glutamate content. (Figure 5) shows that the glutamate content in cured ham is greatly increased during aging. This implies that glutamate is produced from protein in the ham during fermentation.

There is a wide variety of soup stocks used throughout the world. The best *dashi* (soup stock) in Japan is *kombu dashi*. To

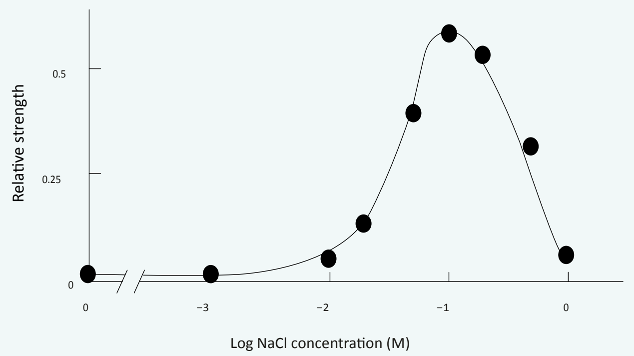

Figure 4 Relative strength of canine nerve response to 100 mM glutamate as a function of logarithmic NaCl concentration.

Table 3: Effect of NaCl on taste responses to amino acid, sugar and glutamate in human, dog and rat.

	100 mM Glycine		500 mM Sucrose		100 mM Glutamate	
	No NaCl	100 mM NaCl	No NaCl	100 mM NaCl	No NaCl	100 mM NaCl
Human	Weak taste	Large enhancement	Moderate taste	Large enhancement	Weak taste	Large enhancement
Dog	Weak taste	Large enhancement	Moderate taste	Large enhancement	Weak taste	Large enhancement
Rat	Weak taste	No enhancement	Moderate taste	No enhancement	Weak taste	No enhancement

make it, *kombu* is soaked in water at 60◦C for one hour. (Figure 6) shows the amino acid composition of the *kombu dashi* that is obtained. Surprisingly, the *kombu dashi* contains only glutamate and aspartate (Figure 6). Aspartate is also an umami substance, although its umami taste is much weaker than that of glutamate. To obtain the best dashi, dried bonito containing 5'-inosinate is added to obtain synergism between glutamate and 5'-inosinate.

Mother's milk has a high glutamate content (Figure 6) [11]. The concentration of glutamate is similar to that in *kombu dashi.* Furthermore, mother's milk contains 5'-inosinate.

In Japan and China, soy source is very popular. In China, shantung is also a typical soup stock. In France and Italy, bouillon is the most popular soup stock. Soy source, shantung, and bouillon all contain high concentrations of glutamate. Thus, the main taste in soup stock is umami.

5'-Inosinate is contained only in animal foodstuffs. Particularly, dried foodstuffs such as dried sardines and bonito have a high 5'-inosinate content.

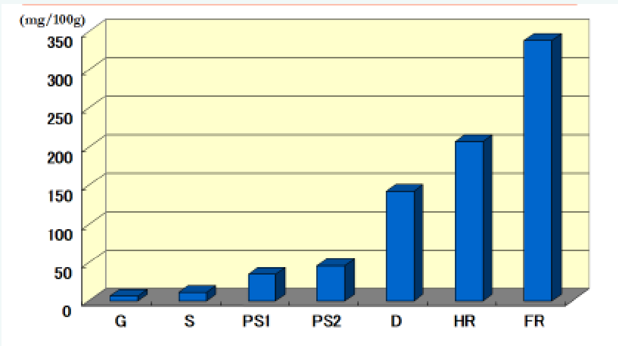

Figure 5 Changes of glutamate content during ageing.

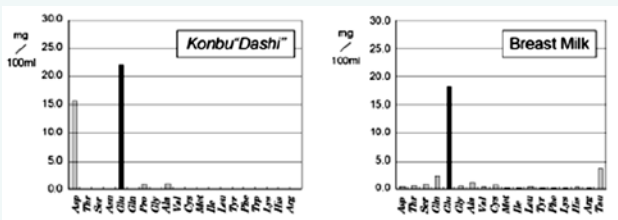

Figure 6 Amino acid composition of kombu dashi and breast milk.

5'-Guanylate is contained mainly in mushrooms.

Production of umami substances

Glutamate: Free glutamate exists in various foodstuffs as shown in Table 3. Proteins are composed of 20 different amino acids. Most proteins have a high glutamate content. For example, the glutamate contents of casein in milk, gluten in wheat, glycinin in soybean, and myosin in muscle range from 21–35%. Although free glutamate has an umami taste, glutamate in proteins has no taste. Proteolysis during fermentation produces high free glutamate content. Free glutamate is not easily broken by heating, after which it is rather stable.

5'-Inosinate: 5'-Inosinate is produced by the decomposition of adenosine triphosphate (ATP). ATP is decomposed into AMP, which is further decomposed into 5'-inosinate. The production of 5'-inosinate begins when an animal is dead and proceeds slowly. In the case of yellowtail, the decomposition of ATP and the production of 5'-inosinate begin at death, and the concentration of 5'-inosinate reaches a maximum level about10 hours after death. This means that the fish does not have a good taste just after death but the taste becomes good about 10 hours after death.

ATP → AMP → 5'-Inosinate

5'-Inosinate is not easily broken by heating.

5'-Guanylate: 5'-Guanylate is produced by the decomposition of ribonucleic acid. In living cells, ribonucleic acid does not contact with ribonuclease, and the decomposition does not occur. When cells are dead, they break, and ribonuclease makes contact with ribonucleic acid. Then 5'-guanylate is produced. The optimum temperature of the enzyme is 60~70°C. 5'-Guanylate is decomposed into guanosine by nucleotidase. The optimum temperature of this enzyme is 45~50°C.

Ribonucleic acid 5'- Guanylate Guanosine ribonucleasenucleotidase

5'-Guanylate as an umami substance was first found in dried *shiitake* mushrooms. The content of 5'-guanylate in raw mushrooms is rather low, but it is very high in dried mushrooms. In the process of drying, mushroom cells are broken, and 5'-guanylate is produced by the decomposition of ribonucleic acid by ribonuclease. Before cooking, dried mushrooms are soaked in water. The water should be cold because 5'-guanylate is decomposed into guanosine by nucleotidase at room temperature. When cooking, the temperature of the water

Table 4: Contents of umami substances.					
Glutamate (mg/100g)					
Plant		**Animal**		**Traditional foods**	
Kombu	1200-3400	Scallop	140	Anchovies	630-1440
Non (seaweed)	1380	Kuruma shrimp	120	cheese	300-1680
Tamarillo*	470-1200	Sea urchin	100	Fish sauce	620-1380
Tomato	150-250	Shen necked clam	90	Soy sauce	410-1260
Macambo**	220	Crab	20-80	Green tea	220-670
Garlic	110	EFS Yolk	50	Aged cured ham	340
Potato	30-100				
Chinese cabbage	40-90				
Carrot	4040				
On	20-50				
		5 4nounate (mg11004)		5 -Guanylate (mg/100 g)	
		Dried bonito	470-800	Dried thurakt	150
		Dried sardine	350-800	Knell (cooked)	50
		Yellowtail	410-470	Dried morel	40
		Sardine	420	Dried porcini	10
		Sea bream	180-400		
		Tana	250-360		
		Chicken	230		
		Pork	230		
		Beef	80		
*Relative to cacao plant					
**Relative to tomato					

containing 5'-guanylate from the mushroom should be quickly increased to 60~70∘C to produce more 5'-guanylate.

Synergism between glutamate and the nucleotides

Synergism between glutamate and 5'-nucleotides (5'-inosinate and 5'-guanylate) was found by Kuninaka [9]. Kuninaka first tasted 5'-inosinate and felt that the umami taste of 5'-inosinate was rather weak, and then he tasted glutamate. He felt that the umami taste of glutamate is much stronger than that of 5'-inosinate. To confirm this fact, he tasted 5'-inosinate again without rinsing his mouth. Surprisingly, he sensed a very strong umami taste. This was because 5`-inosinate was mixed with the glutamate remaining on the tongue. Such synergism also occurs between glutamate and 5'-guanylate. Empirically, the synergism has been used in cooking since before Kuninaka's finding.

Figure 7 plots the strength of the umami taste against the ratio of glutamate and 5'-inosinate in humans [12]. The strength of the umami taste of glutamate alone is rather weak (left end of the graph). Increasing the ratio of 5'-inosinate brings about a very strong umami taste. The strength of the umami taste of 5'-inosinate alone (right end of the graph) is rather weak. Thus, the umami taste induced by the synergism is extremely strong, and so the synergism is crucially important.

In rats, the synergism occurs between 5'-inosinate and various amino acids including glutamate. The response of the chorda tympani nerve to glutamate and 5'-inosinate is enhanced by about 1.7 times [13]. Thus, the extent of the synergism in rats is much smaller than that in humans.

Although the synergism between glutamate and the

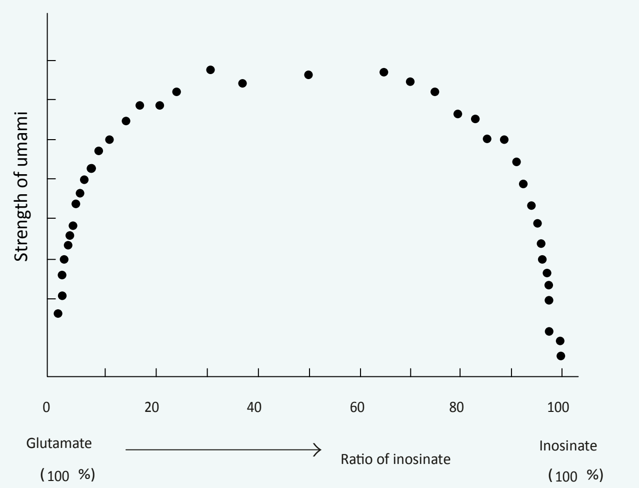

Figure 7 Effects of addition of 5'-inosinate to glutamate on strength of umami in humans.

nucleotide was rather small in rats, the synergism was very large in dogs [14]. As shown in (Figure 8), guanylate monophosphate (GMP) (0.5 mM) alone and a low concentration of monosodium glutamate (MSG) alone do not elicit the response. But an increase in the MSG concentration induces a large response even at concentrations at which MSG alone does not elicit the response. This large synergism is like that in humans.

Receptor of umami

The identification of olfactory receptors has affected studies of taste receptors. Buck and Axel [15] looked for G-protein-coupled receptors (GPRs) from the olfactory epithelium since cyclic AMP was established to be a second messenger in the olfactory system. GPRs have a seven-spanning transmembrane region (Figure 9).

Similarly, attempts have been made to identify GPRs from the tong epithelium. The heterodimeric complex T1R1 T1R2

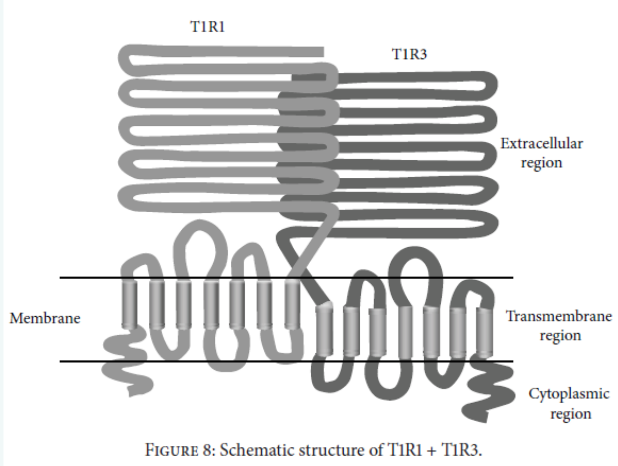

Figure 10 Schematic structure of T1R1 + T1R3 [17].

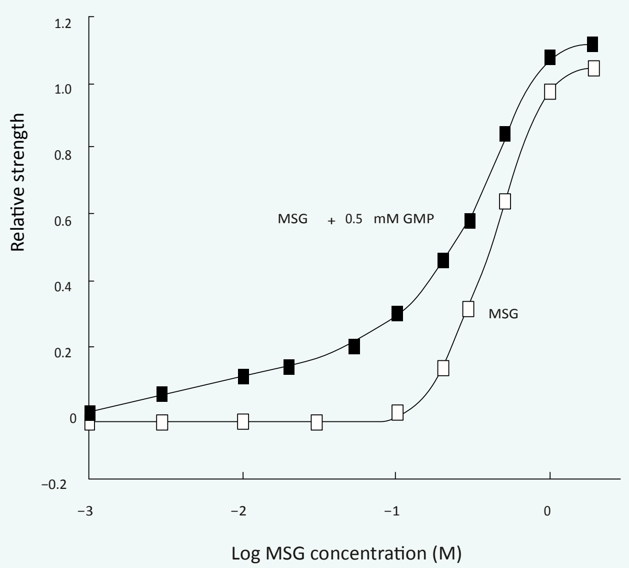

Figure 8 Canine taste nerve response to monosodium glutamate (MSG) in the absence and presence of 0.5 mM 5'-guanylate (GMP).

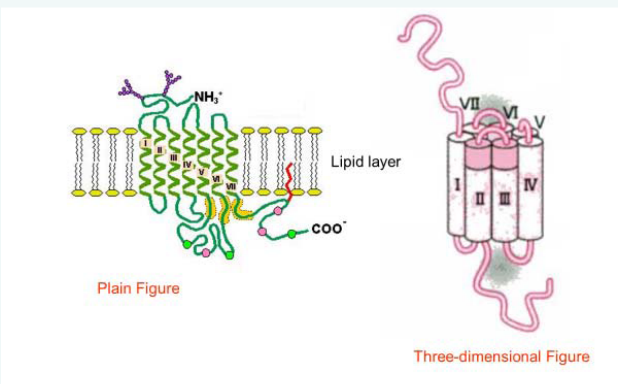

Figure 9 G-protein coupled receptor.

was identified to be a receptor for sweet stimuli. Later T1R1 + T1R3 (Figure 10) was identified as an amino acid receptor [16]. This receptor identified in mice showed synergism between 5'-inosinate and not only glutamate but also many other amino acids. This is consistent with the recording of taste nerve responses in rats [13], although in humans, the synergism is seen only between 5'-inosinate and glutamate. Human T1R1 + T1R3 were produced, and this receptor showed the synergism only between 5'-inosinate and glutamate [17]. The behavior of this receptor is consistent with the psychophysical data in humans, and so T1R1 + T1R3 were established to be an umami receptor in humans.

By site-directed mutagenesis and molecular modeling, binding sites for glutamate and 5'-inosinate in human umami receptors were clarified to exist in the T1R1 subunit (Figure 11) [18-20]. Here glutamate binds close to the binding site for 5'-inosinate, which leads to stabilization of the active conformation. This leads to further stabilization of the active conformation. The structure of T1r1 is in dynamic equilibrium, where the ratio between the closed (active) and open (inactive) conformations is modulated by the presence/absence of ligands. Thus, the synergism is produced by an allosteric regulation.

Glutamate is a neurotransmitter in brain. mGluR4 which is a member of metabotropic receptors in brain was expressed in taste buds. It was proposed that mGluR4 is a receptor of umami [21]. However, the synergism between glutamate and the 5'-nucleotides is not seen in taste-mGluR4. It works in rodent taste system. But, probably it does not work in human taste system because umami response induced by the synergism is main umami response.

Umami was recognized as the fifth basic taste

All umami substances were found by Japanese scientists, and hence the umami taste has been well accepted by Japanese. However, in Europe and America, umami taste has not been accepted for a long time. Glutamate itself has been considered to have no taste, but to have the ability to enhance food flavors. Thus,

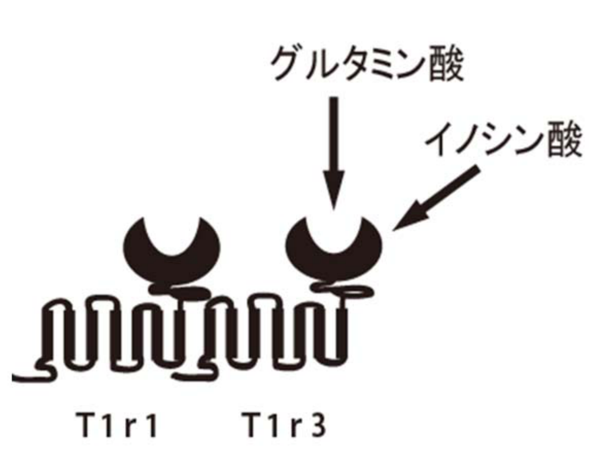

Figure 11 Binding sites of glutamate and inosinate in T1R1 subunit.

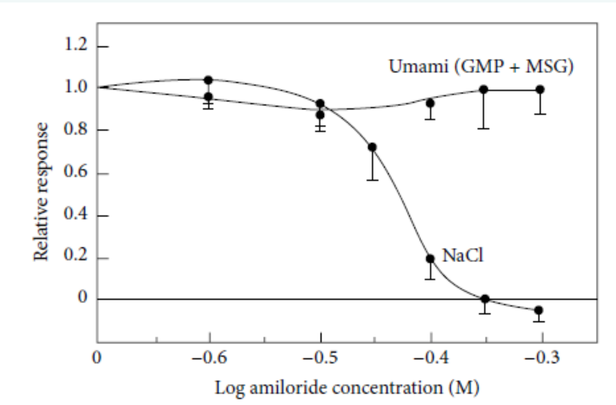

Figure 12 Canine taste nerve response to a mixture of 100 monosodium glutamate (MSG) and 0.5 mM 5'-guanylate (GMP) and 100 mM NaCl as a function of logarithmic amiloride concentration.

glutamate has been called a "flavor enhancer." While "Ajinomoto" sold in Japan contained 5'-inosinate in addition to glutamate, "Ajinomoto" sold in America and Europe was pure glutamate. As mentioned before, pure glutamate has a very weak umami flavor, and so people in America and Europe felt that glutamate had no taste.

In these times, no original paper on umami taste was accepted in any journal published in America or Europe. In 1982, Japanese scientists who studied umami established the "Umami Research Organization." This organization held international umami symposiums in Hawaii [22], Sicily [23], Bergamo [24], and Tokyo [25].

Glutamic acid exists in a salt form (MSG). Hence, in the first symposium, it was insisted that the response to MSG is due to Na^+. Hence, we applied amiloride, which is a suppresser of the salt response, whether the large response elicited by the synergism was suppressed or not. As shown in (Figure 12), amiloride did not suppress the response [26]. It is evident that the response to umami substances is not due to Na^+, but to umami.

Furthermore, Ninomiya and Funakoshi [27] found that there are single fibers which do not respond to NaCl but do respond to glutamate. Rolls [28] measured the responses of single nerve fibers in the macaque taste cortex and found the single fibers that responded best to glutamate.

1. Since the first umami symposium, data indicating that umami taste is a basic taste have been accumulated. The criteria for a basic taste are as follows: A basic taste should not be produced by any combination of other basic tastes.
2. That a basic taste is independent of other basic tastes should be proved by psychophysical and electrophysiological studies.
3. Specific receptor for a basic taste should exist.
4. A basic taste should be found universally in many foods. Umami meets these requirements and was admitted internationally as the fifth basic taste.

Why the Dog Taste System Closely Resembles the Human System

Shima described the history of the dog as follows [29]. A group of wolves approached humans. The wolves were able to eat the humans' food leftovers on a daily basis. Wolves have the ability to notice outside dangers, and so the wolves and humans began fighting together to defend against wild animals. Then humans accepted this group of wolves, which became domesticated as dogs. This was 15000 years ago. Since then, dogs have eaten the same foods as humans. Dogs willingly eat sweet fruits such as bananas, while wolves do not eat bananas. Such findings suggest that the dog taste system evolved to resemble the human system.

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