Umami and Food Palatability[1]

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ABSTRACT Umami is the term that identifies the taste of substances such as L-glutamate salts, which were discovered by Ikeda in 1908. Umami is an important taste element in natural foods; it is the main taste in the Japanese stock "dashi," and in bouillon and other stocks in the West. The umami taste has characteristic qualities that differentiate it from other tastes, including a taste-enhancing synergism between two umami compounds, L-glutamate and 5′-ribonulceotides, and a prolonged aftertaste. The key qualitative and quantitative features of umami are reviewed in this paper. The continued study of the umami taste will help to further our general understanding of the taste process and improve our knowledge of how the taste properties of foods contribute to appropriate food selection and good nutrition. J. Nutr. 130: 921S–926S, 2000.

KEY WORDS: • *umami* • *glutamic acid* • *nucleotides* • *taste* • *food* • *food palatability*

Palatability promotes the selection, intake, absorption and digestion of foods. All five senses are involved in determining food palatability, with taste playing a major role. Umami is a characteristic taste imparted by glutamate and 5′-ribonucleotides such as inosinate and guanylate. Glutamate and nucleotides are present in many foods and play important roles in the taste, palatability and acceptability of foods. This distinctive taste was first discovered in 1908 by K. Ikeda, who coined the term "umami" to identify it. There is no English word synonymous with umami. However, the closest related terms are savory, meaty and broth-like. Because umami was originally a Japanese term, it is often thought to describe a unique, oriental taste familiar only to the Japanese and other Asians. However, many researchers in Japan and in the West have now studied the unique taste quality of umami, and together have established it as a fifth basic taste (in addition to sweet, sour, salty and bitter). Although the acceptance and classification of umami as a basic taste is a relatively recent development, foods and ingredients rich in umami substances have been used throughout history.

Discovery of umami

The traditional Western diet derives many of its pleasant sensory qualities from animal fat, whereas traditional Japanese cuisine contains less fat and relies more on "dashi" or Japanese stock to enhance palatability. In the West, Brillat-Savarin in his classic 1825 treatise "The Physiology of Taste" proposed the name "osmasome" to identify the essence of meaty taste, but was not able to isolate the key substance. The discovery of umami in Japan may have been in part due to the simplicity of "dashi," which is prepared simply by dipping dried kelp (konbu) into boiling water. At the beginning of the 20th century, Ikeda noticed that an unidentified taste quality, distinct from the four basic tastes (sweet, salty, sour and bitter), was present in palatable foods. He detected this taste most clearly in soups and in "dashi" prepared from kelp (konbu) or dried skipjack (katsuobushi), both of which have been used traditionally in Japanese cooking. Subsequently, he investigated the constituents of the dried konbu and discovered the taste to be contributed by the glutamate it contained. He named this taste "umami" (Ikeda 1908).

In 1913, Kodama examined the constituents of katsuobushi, and reported that inosinate also had umami taste characteristics (Kodama 1913). Many years later, during a study of ribonucleotide production through biochemical degradation of yeast RNA, Kuninaka identified guanylate to be another important umami substance (Kuninaka 1960 and 1964, Sakaguchi et al. 1958). Subsequently, guanylate was found to occur naturally in dried shiitake mushrooms, which are used widely in Japanese and Chinese cooking (Nakajima et al. 1961). Soon thereafter, Kuninaka described the taste synergism between glutamate and nucleotides (Kuninaka 1960 and 1964, Sakaguchi et al. 1958), i.e., when glutamate and 5′-ribonucleotides are mixed together, the intensity of the umami taste is markedly enhanced.

Even before the formal identification of umami as a separate taste, it is interesting to note that glutamate-rich foods and ingredients were used in many civilizations. The use of fer-

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TABLE 1

Free glutamic acid in foods

Food category item	Free glutamic acid
	mg/100 g
Meat and poultry	
Beef	10
Pork	9
Chicken	22
Seafood	
Scallop	140
Snow crab	19
Blue crab	43
Alaska king crab	72
White shrimp	20
Seaweed	
Dried lever	1378
Kelp	1608
Wakame (*Undaria pinnetifida*)	9
Vegetable	
Cabbage	50
Spinach	48
Tomato	246
Green asparagus	49
Corn	106
Green peas	106
Onion	51
Potato	10
Mushroom	42
Shiitake mushroom (fresh)	71
Fruits	
Avocado	18
Apple	4
Grape (*V. labrusca*)	5
Kiwi	5
Cheese	
Emmenthaler	308
Parmegiano reggiano	1680
Cheddar cheese	182
Milk	
Cow	1
Goat	4
Human breast milk	19
Fish sauce	
China	828
Japan	1383
Indonesia	727
Malaysia	621
Myanmar	948
Philippine	988
Thailand	950
Vietnam	1370
Soy sauce	
China	926
Japan	782
Korea	1264
Philippine	412
Fermented beans	
Natto/Soy beans (Japan)	136
Daw dawa/Soy beans (West Africa)	965
Soumbara/Locust beans (West Africa)	1700
Douchi/Soy beans (China)	476

mented fish sauce in ancient Greece and Rome is well documented (Curtis 1991). From the recorded methods of production, it is thought to be similar to fish sauces currently produced in Southeast Asia, which have high glutamate contents. Soy sauce is also rich in glutamate (**Table 1**) (Yoshida 1998). Further, the long tradition of using combinations of foods to make soups and stocks might conceivably have been to achieve a combination of glutamate and 5′-ribonucleotides, which would have greatly enhanced the umami taste. Thus, it is common knowledge in Japan that seaweed and bonito make tastier soups, in France that meat (or fish) and vegetables make more flavorful stocks, and in Italy that cheese or tomato cooked with seafood produces a tastier dish. The combination of these food ingredients would certainly have brought glutamate and 5′-ribonucleotides together in sufficient amounts to impart a greatly enhanced umami taste to the foods prepared from them.

Natural occurrence

Glutamic acid is a major constituent of food proteins (plant and animal). In addition, free glutamic acid is present naturally in most foods, such as meat, poultry, seafood and vegetables (Table 1) (Ninomiya 1998). Two ribonucleotides that contribute most to the umami taste, 5′-inosinate and 5′-guanylate, are also present in many foods. Inosinate is found primarily in meats, whereas guanylate is more abundant in plants. Another ribonucleotide, 5′-adenylate, is abundant in fish and shellfish (**Table 2**).

Ripening or maturation. The ripening of vegetables generally makes them more flavorful. For example, flavor maturation in ripening tomatoes has been related to the increase in their natural contents of free amino acids (e.g., glutamate), sugars and organic acids (Inaba et al. 1980, Kader et al. 1977, Stevens et al. 1977a and 1977b). Okumura et al. (1968) prepared synthetic extracts of tomato containing citric acid, glucose, potassium hydrogen phosphate, magnesium sulfate, calcium chloride, glutamate and aspartate. The taste of the synthetic extract was affected greatly by the ratio of glutamate to aspartate. The ratio and the coexistence of both amino acids were the most important factors in reproducing tomato taste. When no glutamate was added to the extract, the taste was similar to green tomato or citrus. It is difficult to perceive a clear umami taste in tomatoes, but it is one of the most important taste components.

During the ripening of cheese, proteins are broken down progressively into smaller polypeptides and individual amino

TABLE 2

5′-Ribonucleotides in foods[1]

Food item	IMP	GMP	AMP
		mg/100 g	
Beef	70	4	8
Pork	200	2	9
Chicken	201	5	13
Squid	ND	ND	184
Tuna	286	ND	6
Snow crab	5	4	32
Scallop	ND	ND	172
Tomato	ND	ND	21
Green peas	ND	ND	2
Shiitake mushroom (fresh)	ND	ND	
Shiitake mushroom (dried)	ND	150	
Fungi portini (dried)	ND	10	
Oyster mushroom (dried)	ND	10	
Morel (dried)	ND	40	

[1] ND, not detected; blank, not analyzed; IMP, inosine 5′-monophosphate.

TABLE 3

Detection thresholds of the five basic taste substances [% (wt/v)][1]

Solvent	Sucrose	NaCl	Tartaric acid	Quinine sulfate	MSG
Water	0.086	0.0037	0.00094	0.000049	0.012
0.094% (5 *mmol/L*) MSG solution	0.086	0.0037	0.0019	0.000049	—
0.25% (5 *mmol/L*) IMP solution	0.086	0.0037	0.03	0.0002	0.00019

[1] MSG, monosodium glutamate; IMP, inosine 5′-monophosphate.

acids. In particular, significant increases in leucine, glutamate, valine, lysine, phenylalanine and valine are noted (Weaver and Kroger 1978). Increases in these amino acids are generally recognized to be a reliable indicator of cheese ripening (Puchades et al. 1989, Weaver and Kroger 1978), and contribute to the taste and texture of the cheese (Ramos et al. 1987). Large increases in free amino acid content also occur during the curing of ham; glutamate is the most abundant free amino acid found in the final product (Cordoba et al. 1994).

Breast milk. Of the 20 free amino acids in human breast milk, glutamic acid is the most abundant, accounting for >50% of the total free amino acid content (Rassin et al. 1978). Its presence may influence the taste acceptability to nursing infants; Steiner conducted a series of studies on facial expressions of neonates in response to stimulation with different tastes (Steiner 1987 and 1993). Neonatal human infants responded with a quiet and relaxed face when ingesting distilled or tap water. Liquids with a sour taste always triggered nose-wrinkling, lip pursing and some gaping, whereas bitter-tasting solutions induced head-shaking, frowning, tight closure of the eyes, depressed mouth-corners, wide mouth opening and tongue protrusion, leading to wide gaping and sometimes spitting and drooling. In contrast, sweet-flavored water always induced eager sucking/smacking and licking movements; although an unseasoned vegetable-broth precipitated facial displays similar to those induced by sour tasting liquids, a monosodium glutamate (MSG)-seasoned vegetable broth triggered facial expressions very similar to those induced by the sweet taste. These results suggest that glutamate is a palatable taste stimulus for humans infants; by virtue of its presence in breast milk, it might conceivably contribute to the taste acceptability of this liquid.

Basic properties of umami substances

Although Ikeda coined the term "umami" in 1908, it took >75 years for it to become accepted internationally as a basic taste. During this interval, its flavor quality was variously described by such terms as "amplitude" (Cairncross and Sjöstrom 1950, Caul 1951), "mouth fullness" and "bloom," and MSG was generally regarded as a flavor enhancing agent, not a basic taste. One of the impediments to the recognition of umami as a basic taste may have been the lack of traditional words to describe it in Western languages. Yamaguchi profiled the effects of MSG on a variety of foods using semantic differentials (Yamaguchi 1979). When Japanese subjects familiar with the umami taste were asked to express the changes in the flavor profile of foods after MSG addition *without using the word "umami,"* they reported that the overall taste intensity of the foods was increased by the addition of MSG. The most notable descriptions of the changes were major increases of the flavor characteristics, continuity, mouth fullness, impact, mildness and thickness. These descriptors are all similar to the term "amplitude" used previously in Western cultures to describe the taste effect of MSG.

A second impediment may have been the belief by many researchers that umami could be duplicated by appropriate combinations of the four basic tastes (sweet, sour, salty and bitter). The recent development of multidimensional scaling has made it possible to study the composition of taste qualities in greater detail; this approach has now shown that umami is positioned *outside* the taste tetrahedron formed by the four basic tastes (Yamaguchi 1987). This result indicated that umami cannot be a composite of the other four basic tastes. The independence of umami as a basic taste has also been demonstrated in recent years by the use of behavioral and electrophysiological paradigms in animals (Baylis and Rolls 1991, Kumazawa et al. 1991, Ninomiya and Funakoshi 1987 and 1989, Yamamoto et al. 1988). The discovery of possible glutamate receptors on taste buds further indicates that there is a separate taste reception mechanism for glutamate (Chaudhari et al. 1996, 2000).

Synergistic effects. The detection thresholds for five representative taste substances are shown in **Table 3** (Yamaguchi and Kimizuka 1979). The threshold for MSG is low enough to be used as a seasoning, but not as low as that for tartaric acid or quinine sulfate. It should be noted, however, that the detection threshold of MSG is markedly lowered in the presence of inosine 5′-monophosphate (IMP). This is due to a synergistic taste effect between MSG and IMP. It is known that such synergistic effects can occur between sweet substances (Cameron 1947, Yamaguchi et al. 1970). But the most remarkable synergistic actions have been found with umami substances. The relationship between the proportion of IMP in a mixture of MSG and IMP, and the taste intensity of the mixture are shown in **Figure 1**. The synergistic effect between MSG and IMP can be expressed by the following formula: $y = u + \gamma v$, where u and v are the respective concentrations (g/dL) of MSG and IMP in the mixture, γ is a constant, 1218, and y is the concentration (g/dL) of MSG alone that would create the same intensity umami taste as the mixture. Although the taste intensity of IMP by itself is weak, a strong umami taste is induced in the presence of MSG. In this regard, it is of interest that because human saliva normally contains a small amount of glutamate (1.5 ppm MSG equivalents), the apparent umami taste attributed to IMP *alone* may actually result from the interaction of IMP with this small concentration of glutamate present in saliva (i.e., the IMP itself may not have intrinsic umami taste, but simply enhance the umami taste of the glutamate normally present in the mouth) (Yamaguchi and Kobori 1991).

Effect of umami substances on the taste of foods. Umami makes a variety of foods palatable, although umami by itself is not particularly palatable. For example, a solution of MSG is not very palatable, but MSG added to soup greatly enhances its palatability (Yamaguchi and Kimizuka 1979). The effect of

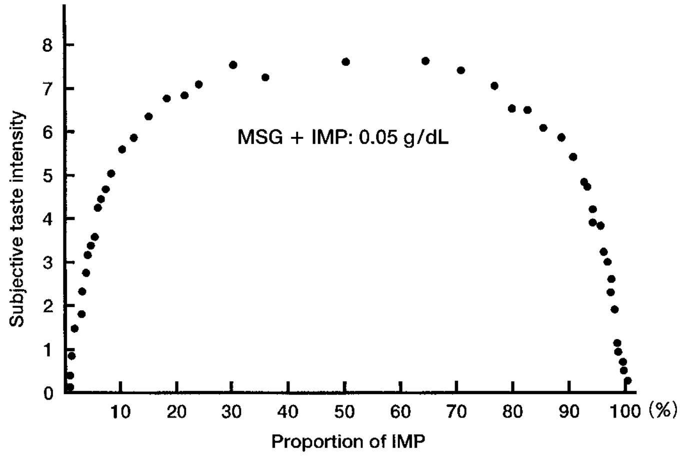

FIGURE 1 Relationship between the mixing ratio of monosodium glutamate (MSG) and inosine 5′-monophosphate (IMP) and taste intensity.

adding MSG to various foods has been investigated by a number of researchers. In the 1950s, an exhaustive series of studies of MSG was conducted at the Quartermaster Food Container Institute in Chicago (Girardot and Peryam 1954). These studies were designed to test the usefulness of MSG in recipes of the Army's master menu. The study continued for 18 mo and involved ~2150 individuals in preference tests of 50 foods and recipes. The results indicated that 25 foods/recipes were clearly improved by MSG addition, whereas 3 showed a trend toward improvement. The palatability of 18 was not changed by MSG, and 4 were worsened. Meat dishes, fish and canned vegetables were most often improved, whereas cereals, milk products and sweet-flavored recipes were not.

Interaction of umami and saltiness on palatability. Because contemporary medical evidence indicates that reducing sodium intake improves certain disease states (e.g., hypertension), it is important to find solutions to the problem that foods often become less palatable when their salt content is reduced (and thus compliance with low salt diets becomes an issue in disease management). In this regard, it is recognized that umami substances in combination with salt (sodium chloride) improve the acceptance of many foods. Umami substances might thus be of value in maintaining the palatability of foods in which the salt content must be reduced. As an illustration of this concept, Yamaguchi and Takahashi (1984a), using a Japanese clear soup model, reported that palatability could be maintained when reducing NaCl content by the addition of MSG. Similar results were obtained using chicken broth (Chi and Chen 1992). In a series of studies involving different menus, Yamaguchi (1987) showed that a 30% reduction in added sodium with no addition of umami substances lowered all scores of saltiness, umami and palatability. The addition of umami substances significantly increased taste quality and decreased the desire for saltiness (Yamaguchi 1987). However, it should be noted that added in excess, MSG and other umami substances will diminish the palatability of foods. MSG intake is thus self limiting (Yamaguchi and Takahashi 1984b).

Taste sensitivities on the tongue. Foods are masticated in the mouth and mixed with saliva during eating. Various taste substances dissolved in water or saliva stimulate thousand of taste buds distributed on the tongue and on other parts of the oral cavity (e.g., roof of the mouth or throat). The sensitivity to each of the basic tastes (including umami) has been tested on all such sites using a filter-paper method (Maruyama and Yamaguchi 1994) in which a small piece of filter paper containing the taste substance is applied directly to the area of

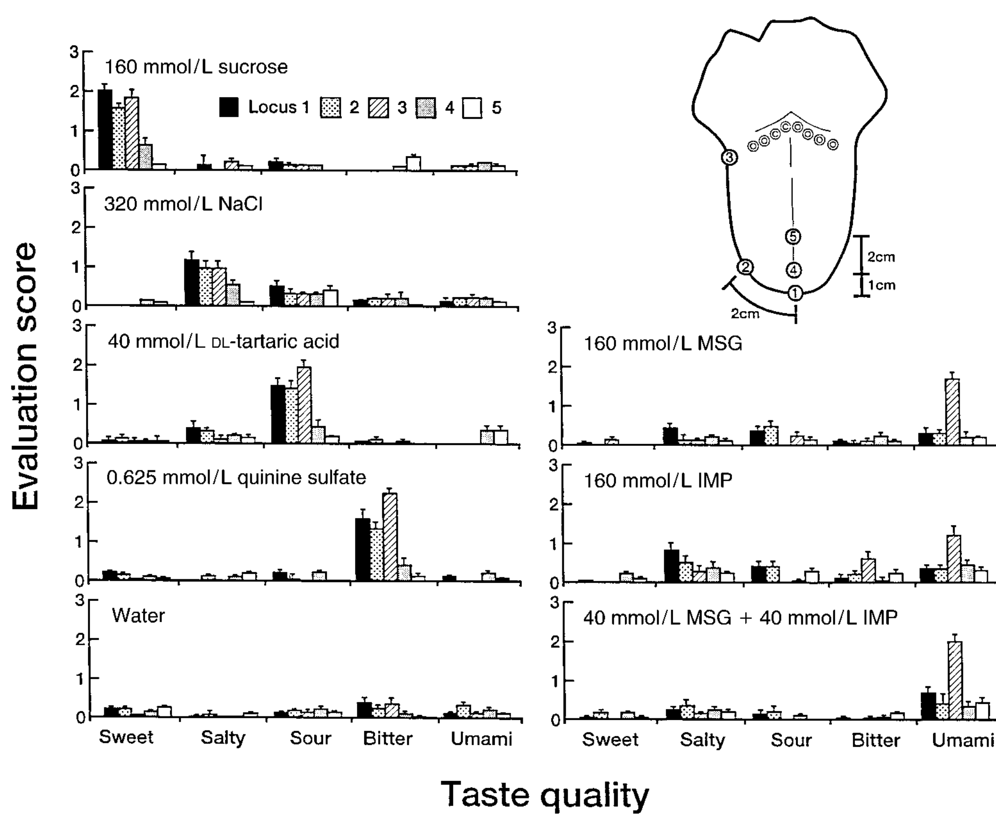

FIGURE 2 Evaluation score (± SEM) as mean certainty ratings (0 = none or uncertain, 1 = likely, 2 = fairly, 3 = absolutely) for each taste quality perceived for each taste stimuli at five loci of the tongue stimulated with the taste solutions by a filter-paper disc method (n = 30). Location of area of the tongue: 1, tip; 2, side area 2 cm posterior to the tip; 3, root area of the foliate papillae; and 4 and 5, the septum linguae 1 and 3 cm posterior to the tip, respectively.

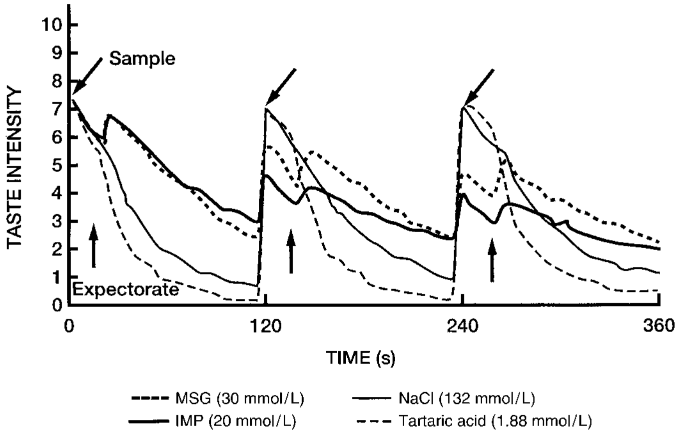

FIGURE 3 Successive time-intensity curves in response to the umami of monosodium glutamate (MSG) and inosine 5′-monophosphate (IMP), the saltiness of NaCl, and the sourness of tartaric acid (n = 30).

interest. As shown in **Figure 2**, the sensitivities to umami of MSG, IMP and their mixture were specifically high on the root area of the tongue. The tip, side and root areas of the tongue were sensitive to sucrose, NaCl, tartaric acid and quinine sulfate. The middle portion of the tongue was found to be insensitive to taste, presumably because no taste buds are found in this area. However, the outcome was different when subjects were asked to lick a small volume of a test solution placed on a spoon and indicate on which part of the tongue they perceived its taste. In this more natural tasting paradigm, subjects sensed umami over a much wider area of the tongue than simply the root, and also reported perceiving it in the middle of the tongue (Maruyama and Yamaguchi 1994 and 1996). They also reported perceiving other basic tastes on the center of the tongue. Thus the reported areas of taste perception did not always match the known locations of true taste sensors. This disparity between the true taste loci and the perceived sensitive areas could be explained in part by illusion or touch (Bartoshuk 1993). Taste perceptions are localized not only to the sites of taste buds, but also to areas touched in the mouth (Todrank and Bartoshuk 1991). These types of taste sensations might conceivably explain some reports of the spatial effects of the umami taste such as "broad development," "mouth fullness" and "mildness."

Temporal properties. Taste perception has a time dimension. Time-intensity tracking of a specific taste can thus reveal unique qualities about a tastant (O'Mahony and Wong 1989, Uchida et al. 1988). **Figure 3** presents the results of our study on time-intensity tracking of MSG, IMP, NaCl and tartaric acid (Yamaguchi and Kobori 1993). In this experiment, subjects were asked to put 10 mL of a taste solution in their mouths for 20 s, then expectorate the solution. Taste intensity was evaluated up to 100 s thereafter. The sour taste of tartaric acid decreased rapidly after expectoration, as did its residual aftertaste. The saltiness of NaCl left a somewhat stronger aftertaste than the sourness of tartaric acid. In contrast, the taste intensities of the umami substances MSG and IMP *increased* after expectoration. Moreover, the aftertaste of umami was stronger than that of the other tastes. Similar results were obtained when subjects swallowed the solutions. Considerable qualitative differences have been reported for the immediate taste and aftertaste after expectoration (at threshold levels) of MSG, IMP and GMP (Horio and Kawamura 1990). The descriptions of the immediate taste quality of solutions of these umami substances varied greatly among the subjects, but were uniform with respect to aftertaste (Kawamura 1993). An agreeable aftertaste is an important determinant of the overall pleasantness of a meal. Because of their unique time-taste characteristics, umami substances may play an unusually important role in generating the aftertaste to a meal and thus in determining its overall enjoyment.

SUMMARY

In this review, we provided a historical perspective on the discovery of umami taste and presented data on the natural occurrence of umami substances. We also outlined the evidence supporting umami as a basic taste and touched upon some qualitative and quantitative aspects of umami taste and palatability. As opined by Brillat-Savarin, "the discovery of a new dish does more for the happiness of mankind than the discovery of a star," and the discovery of umami has contributed to the enjoyment of food at dining tables around the world. In the next decade, a better understanding of the molecular mechanisms underlying umami taste perception should be forthcoming. This information will aid in the better use of umami substances to improve the palatability of foods even further.

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LITERATURE CITED

Bartoshuk, L. M. (1993) The biological bases of food perception and acceptance. Food Qual. Pref. 4: 21–32.
Baylis, L. L. & Rolls, E. T. (1991) Responses of neurons in the primate taste cortex to glutamate. Physiol. Behav. 49: 973–979.
Caincross, S. E. & Sjöstrom, L. B. (1950) Flavor profiles—a new approach to flavor problems. Food Technol. 4: 308–311.
Cameron, A. T. (1947) Sci. Rpt. No. 9: Sugar Research Foundation, Inc., New York, NY.
Caul, J. E. (1951) A flavor panel study of monosodium glutamate. Adv. Food Res. 7: 1.
Chaudhari, N., Yang, H., Lamp, C., Delay, E., Cartford, C., Than, T. & Roper, S. (1996) The taste of monosodium glutamate: membrane receptors in taste buds. J. Neurosci. 16: 3817–3826.
Chaudhari, N., Landin, A. M. & Roper, S. D. (2000) A metabotropic glutamate receptor variant functions as a taste receptor. Nature Neuroscience 3: 113–119.
Chi, S. P. & Chen, T. C. (1992) Predicting optimum monosodium glutamate and sodium chloride concentrations in chicken broth as affected by spice addition. J. Food Process. Preserv. 16: 313–326.
Córdoba, J. J., Rojas, T. A., González, C. G. & Barroso, J. V. (1994) Evolution of free amino acids and amines during ripening of Iberian cured ham. J. Agric. Food Chem. 42: 2296–2301.
Curtis, R. I. (1991) Garum and Salsamenta, Production and Commerce in Material Medica, Studies in Ancient Medicine. E. J. Brill Academic Publisher, Leiden, The Netherlands.
Girardot, N. F. & Peryam, D. R. (1954) MSG's power to perk up foods. Food Eng. 26: 71–72, 182, 185.
Horio, T. & Kawamura, Y. (1990) Studies on after-taste of various stimuli in humans. Chem. Senses 15: 271–280.
Ikeda, K. (1908) Japanese patent 4805.
Inaba, A., Yamamoto T., Ito, T. & Nakamura, R. (1980) Changes in the concentration of free amino acids and soluble nucleotides in attached and detached tomato fruits during ripening. J. Jpn. Soc. Hortic. Sci. 49: 435–441.
Kader, A. A., Stevens, M. A., Albright, M. & Morris, L. L. (1977) Amino acid composition and flavor of fresh market tomatoes as influenced by fruit ripeness when harvested. J. Am. Soc. Hortic. Sci. 103: 541–544.
Kawamura, Y. (1993) Significance and history of research on umami (in Japanese). In: Umami (Kawamura, Y., Omura, Y., Kimura, S. & Konosu, S. eds.), pp. 1–16. Kyoritsu Shuppan, Tokyo, Japan.
Kodama, S. (1913) On a procedure for separating inosinic acid, J. Tokyo Chem. Soc. 34: 751.
Kumazawa, T., Nakmura, M. & Kurihara, K. (1991) Canine taste nerve responses to umami substances. Physiol. Behav. 49: 875–881.

Kuninaka, A. (1960) Studies on taste of ribonucleic acid derivatives. J. Agric. Chem. Soc. Jpn. 34: 487–492.
Kuninaka, A. (1964) The Nucleotides, a Rationale of Research on Flavor Potentiation. Symposium on Flavor Potentiation, pp. 4–9. Arthur D. Little, Cambridge, MA.
Maruyama, I. & Yamaguchi, S. (1994) Proceedings of the 24th Symposium on Sensory Evaluation, p. 181. Japanese Union of Scientists and Engineers, Tokyo, Japan.
Maruyama, I. & Yamaguchi, S. (1996) Proceedings of the 30th Japanese Symposium on Taste and Smell. Jpn. J. Taste Smell Res. 3: 632–635.
Nakajima, N., Ichikawa, K., Kamada, K. & Fujita, E. (1961) Food chemical studies on 5′-ribonucleotides. Part I. On the 5′-ribonucleotides in foods (1) Determination of the 5′-ribonucleotides in various stocks by ion exchange chromatography. J. Agric. Chem. Soc. Jpn. 35: 797–803.
Ninomiya, K. (1998) Natural occurrence. Food Rev. Int. 14: 177–212.
Ninomiya, Y. & Funakoshi, M. (1987) Qualitative discrimination among "umami" and the four basic taste substances in mice. In: Umami: A Basic Taste (Kawamura, Y. & Kare, M. R., eds.), pp. 365–385. Marcel Dekker, New York, NY.
Ninomiya, Y. & Funakoshi, M. (1989) Peripheral neural basis for behavioral discrimination between glutamate and the four basic taste substances in mice. Comp. Biochem. Physiol. 92A: 371–376.
Okumura, S., Eguchi, S., Ogawa, W. & Suzuki, K. (1968) Methods for preparation of foods, beverages and seasoning having tomato flavor. Japanese Patent, Publication (kokoku) No. 43–11731.
O'Mahony, M. & Wong, S. Y. (1989) Time-intensity scaling with judges trained to use a calibrated scale: adaptation, salty and umami tastes. J. Sens. Stud. 3: 217–235.
Puchades, R., Lemieux, L. & Simard, R. E. (1989) Evolution of free amino acids during the ripening of cheddar cheese containing added lactobacilli strains. J. Food Sci. 54: 885–887, 945.
Ramos, M., Caceres, I., Polo, C., Alonso, L. & Juarez, M. (1987) Effect of freezing on soluble nitrogen fraction of Cabrales Cheese. Food Chemistry 24: 271–278.
Rassin, D. K., Sturman, J. A. & Gaull, G. E. (1978) Taurine and other amino acids in milk and other mammals. Early Hum. Dev. 2: 1–13.
Sakaguchi, K., Kibi, M. & Kuninaka, A. (1958) Japanese patent application SN 11586, and U.S. patent application SN 756,541.
Steiner, J. E. (1987) What the neonate can tell us about umami. In: Umami: A Basic Taste (Kawamura, Y. & Kare, M. R., eds.), pp. 97–123. Marcel Dekker, New York, NY.
Steiner, J. E. (1993) Behavioral responses to tastes and odors in man and animals. In: Proceedings of the Umami International Symposium, July 1993, Society for Research on Umami Taste, Tokyo, Japan, pp. 30–43.
Stevens, M. A., Kader, A. A. & Albright-Holton, M. (1977a) Intercultivar variation in composition of locular and pericarp portions of fresh tomatoes. J. Am. Soc. Hort. Sci. 102: 680–689.
Stevens, M.A., Kader, A. A. & Albright-Holton, M. (1997b) Intercultivar variation in composition of locular and pericarp portions of fresh tomatoes. J. Am. Soc. Hort. Sci. 102: 689–691.
Todrank, J. & Bartoshuk, L. M. (1991) A taste illusion: taste sensation localized by touch. Physiol. Behav. 50: 1027–1031.
Uchida, C., Muroya, S. & Takeshita, S. (1988) Classification of various taste substances by T-I patterns. (In Japanese) In: Proceedings of the 22nd Japanese Symposium on Taste and Smell, (Morita, H., ed.), pp. 81–84. Japanese Association for the Study of Taste and Smell.
Weaver, J. C. & Kroger, M. (1978) Free amino acid and rheological measurements on hydrolyzed lactose cheddar cheese during ripening. J. Food Sci. 43: 579–583.
Yamaguchi, S. (1970) The synergistic taste effect of monosodium glutamate and disodium 5′-inosinate. J. Food Sci. 32: 473–478.
Yamaguchi, S. (1979) The Umami Taste. In: Food Taste Chemistry (Boudreau, J. C. ed.), pp. 33–51. American Chemical Society, Washington, DC.
Yamaguchi, S. (1987) Fundamental properties of umami in human taste sensation. In: Umami: A Basic Taste (Kawamura, Y. & Kare M. R., eds.), pp. 41–73. Marcel Dekker, New York, NY.
Yamaguchi, S. & Kimizuka A. (1979) Psychometric studies on the taste of monosodium glutamate. In: Glutamic Acid: Advances in Biochemistry and Physiology (Filer, L. J., Jr., Garattini, S., Kare, M. R., Reynolds, W. A. & Wurtman, R. J., eds.), pp. 35–54. Raven Press, New York, NY.
Yamaguchi, S. & Kobori, I. (1991) Nucleotides: as umami substances or umami enhancers. Proceedings of the 25th Japanese Symposium on Taste and Smell, pp. 269–272.
Yamaguchi, S. & Kobori, I. (1993) Humans and appreciation of the umami taste. In: Olfaction and Taste XI (Kurihara, K., Suzuki, H. & Ogawa, H. eds.), pp. 353–356. Springer-Verlag, Tokyo, Japan.
Yamaguchi, S. & Takahashi, C. (1984a) Interactions of monosodium glutamate and sodium chloride on saltiness and palatability of a clear soup. J. Food Sci. 49: 82–85.
Yamaguchi, S. & Takahashi, C. (1984b) Hedonic function of monosodium glutamate and four basic taste substances used at various concentration levels in simple and complex systems. Agric. Biol. Chem. 48: 1077–1081.
Yamamoto, T., Matsuo, R., Kiyomitsu, Y. & Kitamura, R. (1988) Taste effects of 'umami' substances in hamsters as studied by electrophysiological and conditioned taste aversion techniques. Brain Res. 451: 147–162.
Yoshida, Y. (1998) Umami taste and traditional seasonings. Food Rev. Int. 14: 213–246.