Sensory and receptor responses to umami: an overview of pioneering work†–3

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ABSTRACT
This article provides a selective overview of the early studies of umami taste and outlines significant questions for further research. Umami compounds such as the amino acid glutamate [often in the form of the sodium salt monosodium glutamate (MSG)] and the nucleotide monophosphates 5′-inosinate and 5′-guanylate occur naturally in, and provide flavor for, many foods and cuisines around the world. Early researchers in the United States found that the flavor of pure MSG was difficult to describe. But they all agreed that, although humans found umami compounds, when tasted alone, to be unpalatable, subjects reported that these compounds improved the taste of foods. This taste “dichotomy” may be partly unlearned because it is also observed in very young infants. The uniqueness of umami perception is based on several lines of evidence. First, numerous perceptual studies have shown that the sensation aroused by MSG is distinct from that of the other 4 taste qualities. Second, biochemical studies that show the synergy of the binding of MSG and 5′-guanylate to tongue taste tissue mirror this hallmark perceptual effect. Third, several specific receptors that may mediate umami taste have recently been identified. There remain, however, a number of puzzles surrounding the umami concept, including the molecular basis for an apparent tactile component to umami perception, the reason for the unpalatability of pure umami, and the functional significance for human health and nutrition of umami detection. Future work aimed at understanding these and other open issues will profitably engage scientists in umami research well into the next century. Am J Clin Nutr 2009;90(suppl):723S–7S.

INTRODUCTION
The taste properties of the sodium salt of the amino acid l-glutamate were first described by Kikunae Ikeda, who isolated it from seaweed in 1908 (1). He suggested that the taste was different from any of the consensus basic tastes (sweet, sour, salty, bitter) and thus that it was a fifth basic taste. He further argued that it served to allow organisms to detect and recognize sources of protein in a manner analogous to that for sweet taste, which may signal carbohydrate calorie sources.

In the 100 y that followed this discovery, a large body of research has appeared that deals with the flavor (umami) of monosodium glutamate (MSG) and the synergizing ribonucleotides, inosine and guanosine monophosphates [5′-inosinate (IMP) and 5′-guanylate (GMP)]. Although we now have a much greater appreciation of the sensory properties of these substances, their usefulness in the flavoring of foods, and their mechanism of action, many questions remain. Below I provide a selective overview of some of the work on umami taste that has been conducted since Ikeda’s discovery, with special attention given to the work conducted outside of Japan and work that focuses on sensory and hedonic properties. I also touch on mechanistic studies and their potential functional significance. Finally, several questions are proposed that require additional investigation.

PERCEPTION
One of the early scientific articles in English on MSG, published in 1929, described glutamic acid as a rare chemical that imparted a meatlike taste, although at very low concentrations it evoked a sweet taste (2). Subsequently, as the use of MSG in foods in the United States became more common, a number of articles appeared that discussed the sensory properties of MSG, sometimes substantially disagreeing on the basic qualitative properties. Indeed, there were suggestions that MSG itself had no taste but functioned instead to enhance the other flavors in foods.

Two important early compendia on glutamate taste, published as the proceedings of 2 symposia on MSG flavor and acceptability in 1948 and 1955, were held under the auspices of the US Army Quartermaster Food and Container Institute. The military was interested in improving the quality of the food prepared for the troops. These symposia brought together scientists and manufacturers to discuss and debate, among other issues, the sensory properties of MSG. As is often the case with earlier literature, many of the individual presentations were short on data and long on speculation. But they did have one virtue often missing from more recent, formalistic presentations: they encouraged exploration of the phenomenology of the sensory experience of MSG, alone and in food.

It is useful to quote some of the descriptions of the taste of pure MSG by sensory specialists from the 1948 symposium:

“A desirable meat-like taste” (3)

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Its taste has all 4 components: sweetness, sourness, saltiness and bitterness. In addition, glutamate has the capacity of stimulating the feeling nerves of mouth and throat to produce the sensation known as ‘satisfaction’.” (4)

“In any event it is proper to consider glutamate as a stimulator of the sense of feeling as well as that of taste, and the indications are that it is unique in this capacity.” (4)

“It seems that glutamate is successful not because it adds taste, but because it adds feeling.” (4)

“The principal effect on food flavor was a balancing, blending and rounding out of total flavor.” (5)

“It is a sort of overall taste, flavor and feel.”(6)

“Glutamate creates a persistent, lingering flavor reaction.” (7)

A fundamental disagreement among these early investigators, and one that still reverberates today, concerned whether the taste properties of MSG (ie, the perception of umami) were unique, as Ikeda had suggested, or whether they could be mimicked by an appropriate combination of the other 4 basic taste qualities (eg, reference 8), as Von Skramlik (9) might have proposed. The results of such a metameric matching study (see references 10 and 11) necessary to test this hypothesis have never been published. Moreover, a failure to find the appropriate combinations of salt, sour, sweet, and bitter stimuli to duplicate exactly the taste of MSG would be uninformative because one cannot prove the negative.

As an alternative to metameric matching (and its difficulties) for testing for unique sensory properties of umami, investigators have resorted to using similarity scaling methods to determine whether MSG taste differs from the other basic tastes. In an influential study, Yamaguchi (12) used multidimensional scaling techniques to compare the perceived flavor similarities of MSG with sucrose, NaCl, tartaric acid, and quinine sulfate, as well as dyads, triads, and combinations of all 4 and all 5 compounds. She also used multiple concentrations. Very simply, she found that within the 3-dimensional space mathematically generated from the perceptual similarity data, MSG stood outside the space that encompassed the 4 other taste qualities. She concluded from this result that umami is not composed of the 4 basic tastes. Parallel studies using similar techniques have been conducted by using data from neural recordings (eg, reference 13) and have produced similar results.

One problem in interpreting these data are that they assume that MSG has only taste properties. Yet if we go back to the discussions of the overall sensory properties of MSG in earlier publications (summarized in the 2 Quartermaster symposia reports), it is evident that, in addition to having a classic taste, many investigators report that MSG also has an apparent tactile or feeling component often described as “fullness.” This obviously could complicate interpretation of conclusions derived from multidimensional scaling. Could the uniqueness of the taste properties of MSG be due to the fact that, unlike other taste substances at the concentrations used, it alone has prominent tactile properties? Although this is unlikely, it cannot be rejected without further testing.

One of the most interesting characteristics of umami taste is the synergism between MSG and the 5'-ribonucleotides IMP and GMP. It remains controversial whether IMP and GMP themselves have an umami taste. When one of these substances is placed in the mouth, a very clear umami taste can be recognized. But it has been argued that the taste of GMP and IMP results from synergism with the very small concentrations of free glutamate present in saliva (12). This hypothesis is hard to test critically, and unfortunately, recent molecular receptor studies in vitro cannot resolve the issue.

In summary, early work in the United States confirmed Ikeda’s report that MSG had a specific, perhaps unique, taste. Yet there remained (and still remains) a curious difficulty in actually defining what that taste, or more broadly, what that flavor actually is. It would seem that if, as much subsequent molecular work supports, umami is a distinct taste property, it is unlike the more widely accepted 4 basic taste qualities in that it is less distinct and more subtle.

### HEDONICS

There is universal agreement that MSG, when added to many (but not all) foods, enhances the palatability of those foods. As early as 1948 it was recognized that this enhanced palatability was particularly evident in soups, but was also present in a wide variety of other nonsweet foods. It was further reported that MSG did not enhance the acceptability of fruits, fruit juices, or some dairy products (eg, reference 5). Palatability studies in different cultures and across age groups have confirmed that umami substances added to many foods increase liking (eg, reference 14).

What was not clear was the underlying mechanism by which MSG enhanced palatability. One curious finding is that the taste of pure MSG is generally not judged to be pleasant (eg, reference 15) unlike the taste of sugar and, in some cases, salt. This finding in humans contrasts with work in rodents: these animals show a clear preference for MSG and nucleotide monophosphates at appropriate concentrations (16). This species dichotomy is another way in which umami seems to differ from the other basic tastes; we do not understand why this is the case.

A fundamental question is the extent to which the palatability-enhancing properties of umami are learned. Human milk is quite high in free glutamate, in contrast with cow milk, and it is thus possible that exposure to glutamate during nursing could influence later acceptance and liking (17). Steiner (18) addressed this question by testing newborn human infants. He gave the infants MSG either alone or in a soup broth and then evaluated their facial expressions in response to brief oral exposures. MSG alone did not elicit positive facial expressions (relative to water), although MSG in soup elicited more positive facial expressions than soup without MSG. Steiner concluded from his results that there is an innate component to umami liking.

We conducted studies in Mexican infants who were either well nourished or protein-calorie malnourished to test the hypothesis that nutritional state would feed back on taste preferences. In particular, we wondered whether malnourished infants would exhibit heightened preferences for MSG and/or hydrolyzed casein (which contains free glutamate). Testing consisted of giving infants brief (1 min) access to flavor substances in baby bottles and monitoring the amount that they consumed, a technique that has been used successfully in many studies of infant flavor perception and preference. In pilot work (Vazquez, Pearson, and Beauchamp, unpublished results, 1979), we also found that water solutions of both MSG and casein hydrolysate were not preferred by infants; indeed, they were rejected relative to the...
MECHANISM

The idea that umami taste in foods signals the presence of protein found the reverse: protein-deficient rats avoid umami substances. This was demonstrated in a study where rats preferred soup containing no MSG (19, 20). This finding thus fails to support the proposition that MSG signals the presence of protein.

Our data are consistent with Steiner’s suggestion that, added to certain foods, MSG enhances palatability even in very young infants (the youngest in our studies were 2 mo of age). They are also consistent with the adult judgment that MSG alone is not palatable. But it is interesting to speculate from our results that the sensory properties of glutamate may not actually signal the presence of protein, as Ikeda suggested, unless they are accompanied by other nutrients (other amino acids) and/or flavors that reinforce the message that nutrients are present. Indeed, many of the natural foods high in free glutamate (eg, seaweed, tomatoes) are not rich sources of protein. Moreover, there is very little human evidence that protein deficiency enhances the intake of umami-tasting foods. Our study of malnourished infants supports this view and is one of the few human studies to date that have examined this idea. One of the other studies (21) reported that both elderly individuals and individuals of lower nutritional status had a preference for higher concentrations of MSG in soup than did individuals of higher nutritional status (as would be predicted by this hypothesis). However, this effect could be the result of sensory loss rather than hedonic judgment. Moreover, in a large series of studies with protein-restricted rats, Torri et al (22) found the reverse: protein-deficient rats avoid umami substances.

The idea that umami taste in foods signals the presence of protein thus requires much more supporting evidence before it can be accepted.

FUNCTION

As noted above, Ikeda’s teleological suggestion that umami taste provides the organism with a means to detect amino acids and protein is difficult to test and has some logical difficulties. Nevertheless, this has remained the major hypothetical reason for the existence of umami as a basic taste.

In 1987 Fujita (25) published a thought-provoking article noting the anatomical similarity of endocrine cells in the gut and taste cells in the mouth. He suggested that there might be commonality of function. The more recent discovery of so-called taste receptor molecular elements in gut tissue has spurred an interest in the functional significance of this suggestion (26, 27). Umami receptors in the mouth may be just the first step in the pathway through the alimentary tract along which nutrients such as amino acids are “recognized.” Future work in this area promises to be very exciting.

OUTSTANDING QUESTIONS

Many unknowns, as indicated in the foregoing discussion, remain in our understanding of the mechanisms and functions of umami taste. A partial list of currently unanswered questions includes the following:

1) How does glutamate provide an apparent tactile component to foods? Does it actually stimulate tactile as well as taste receptors, as Crocker (4) originally suggested? Could these 2 actions be separated?

2) How is it that glutamate requires other food components to be “appreciated”? Is this a cognitive effect (responses of newborn infants in Steiner’s studies would argue against this idea) or does it have a physiologic basis?

3) Multiple taste receptors have now been identified for umami taste (23). This surfeit requires explanation: Why are multiple receptors needed? Also a puzzle are studies demonstrating umami “blindness,” ie, individuals who apparently cannot detect umami taste except at very high concentrations (28). How could this occur if, as suggested above, glutamate stimulates multiple taste receptors and perhaps tactile receptors?

4) What are the physiologic roles of umami receptors throughout the entire digestive system?

5) Although not discussed here, several recent studies have suggested that the intake of glutamate may have a role in obesity that is either protective or stimulatory (29, 30). Is there anything special about umami taste or umami substances in obesity? Also, what roles might umami substances play in the nutritive care of the sick and the elderly?
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