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## Development and Genetics of Glutamate Taste Preference<sup>a</sup>

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### Abstract

The sodium salt of glutamic acid, monosodium glutamate (MSG), and certain other amino acids and ribonucleotides impart a unique taste sensation often called ‘umami.’ We have been studying preference for umami substances in two systems: inbred mice and human infants. In 48-hr tests, C57BL/6J (C57) mice exhibit a lower preference threshold for MSG than do 129/J mice. Moreover, C57 mice show a greater preference across a wide range of concentrations and, at high (*e.g.*, 300–600 mM) concentrations, consume greater amounts of MSG. To examine whether the strain difference in MSG preference might be related to a similar strain difference in preference for sucrose and other sweeteners, as might be suggested from studies with rats, preferences for MSG and sucrose in the second (F<sub>2</sub>) generation were examined. Preferences for sucrose and for MSG were not positively correlated in the F<sub>2</sub> indicating that these strain differences depend on different genes. For human adults, unlike mice, the taste of aqueous MSG is not palatable. Our studies of human infants also indicate that MSG alone is not preferred to plain water, but, when it is added to soup, the soup plus MSG is preferred to soup alone. Ongoing studies are designed to determine whether simple mixtures of MSG with other tastants, in particular NaCl, are preferred to water alone, NaCl alone, and MSG alone.

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Our research interests in the taste of monosodium glutamate (MSG) focus on understanding the factors (experiential; genetic) that impact on its hedonic properties both as a tastant and as a flavor modulator. Two strategies have been pursued in this regard: human developmental studies and animal model studies. They will be discussed in turn.

### GLUTAMATE (UMAMI) TASTE IN INFANTS

For adults, aqueous MSG solutions are not palatable; yet MSG increases palatability when added to many foods.<sup>1</sup> Thus, the taste of glutamate increases the palatability of food, but itself is not palatable. Preferences for sweet and salty substances are likely innate,<sup>2</sup> and the reason they are typically consumed in the context of other flavors (foods) is probably because that is what adults have learned to like. Supporting this interpretation is the observation that infants prefer pure sucrose solutions and, by about 4 months of age, salt solutions to an aqueous diluent (see Ref. 2 for review and references). If, as has been suggested,<sup>3</sup> glutamate is a basic, hedonically positive taste substance similar to sweet and salty substances, one would predict that for very young infants, aqueous glutamate solutions would be hedonically positive and preferred to water.

Contradicting this hypothesis are several reports<sup>4–6</sup> that aqueous MSG solutions are not palatable to infants, nor are they preferred to water. However, as with adults, soup with

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added MSG is preferred to soup alone by these same infants. Thus, in infants *and* adults, pure umami taste seems to be unpalatable; it is only when added to foods that it becomes palatable or increases the palatability of these foods. That is, unlike sweet and salty tastes, the taste of umami substances must be experienced in the context of other chemosensory stimuli to be deemed pleasant or preferred by both infants and adults. One often-stated hypothesis to explain this is that MSG ‘potentiates’ other tastes or flavors, thereby making them more palatable. The term flavor potentiator is a fuzzy one.<sup>7</sup> If ‘potentiates’ is defined as ‘increases’ or ‘strengthens’ intensity of other flavors, there is no evidence that MSG acts in this way and substantial evidence against it. Instead, MSG as a flavorant increases the palatability of flavors with which it is mixed. We<sup>7</sup> have termed this effect flavor enhancement.

How can MSG act as a flavor enhancer? One possible mechanism is by differentially suppressing food flavors thereby allowing the more positive ones in a mixture to appear more salient.<sup>8</sup> However, in simple food systems such as chicken broth, where addition of MSG strongly enhances palatability, this seems an unlikely mechanism.

If the differential suppression hypothesis is incorrect, we are left with the possibility that, for reasons yet to be determined, umami taste must be combined with some other flavor components for the umami component itself to be palatable. That is, the umami taste itself inherently requires other tastes/flavors for it to be perceived as attractive. A biological reason for this is obscure but could be related to the fact that unlike salt and sweeteners, glutamate would never be found pure in nature.

One way to experimentally approach an investigation of this issue is to ‘deconstruct’ soup and to determine the minimal substances necessary for *an infant* to prefer glutamate + flavor over flavor alone. Early descriptive studies<sup>9</sup> identified salt (NaCl) and salty foods as having a particular affinity for MSG. We therefore hypothesized that salt-MSG mixtures should be highly palatable to infants. To test this we studied young (2- and 7-month-old) infants’ responses to MSG alone, salt alone and MSG plus salt. In this way, we tested the hypothesis that the simplest ‘soup’ is made up of the sensations of umami and saltiness and that umami becomes palatable only when tasted in the context of sufficient saltiness.

Subjects (15 2-month-old; 12 7-month-old), recruited via newspaper advertisements, came to Monell on 4 days within a 2-week period. On each day, infants were presented with one of four brief-presentation choice tests: salt (0.11 M) vs water; MSG (0.01 M) vs water; salt + MSG vs water; salt + MSG vs salt. Test order was counterbalanced. Test procedures were as previously described.<sup>10</sup>

As indicated in Figure 1, 2-month-old infants rejected MSG relative to the water diluent as previously reported.<sup>5</sup> The 2-month-old infants neither preferred nor avoided salt vs water (also as previously reported<sup>10</sup>), salt + MSG vs water, and salt + MSG vs salt. The data from the 7-month-old infants revealed that overall, older infants were indifferent to MSG alone, whereas they showed a preference for the salt over plain water (again consistent with prior studies<sup>10</sup>) and although not significant, the salt + MSG was preferred to water. Failing to support our hypothesis, we found no difference between salt + MSG vs salt alone.

Thus, based on these studies, we are still unable to understand why MSG itself is unpalatable, whereas MSG increases the palatability of a rather simple food, soup, even in human infants. Further research, perhaps with concentrations varied, is necessary to elucidate mechanisms behind this most interesting and puzzling phenomenon.

## ANIMAL MODEL STUDIES

Unlike humans, several strains and species of mammals do prefer MSG solutions to water.<sup>3</sup> One powerful approach to understanding factors underlying such preferences (which, in long-term taste tests, may or may not be mediated by sensory differences) is to study inbred mouse strains that differ in acceptance of MSG. To this end, we have conducted studies on salt,<sup>11,12</sup> sweet<sup>13</sup> and umami taste in two inbred strains of mice: C57BL/6 (C57) and 129/J (129). These strains were chosen because they showed large differences in preferences and intakes of several concentrations of salt (129 high; C57 low), sucrose (C57 high; 129 low) and MSG (C57 high; 129 low).

To analyze the inheritance of this strain difference in acceptance of MSG, we bred the second (F<sub>2</sub>) generation and tested over 400 individual male and female mice as well as, in parallel, a smaller number of each inbred strain of mice for their 96-hour intake of MSG (300 mM) for which the biggest strain difference was observed (the methods have been described in detail in Ref. 12).

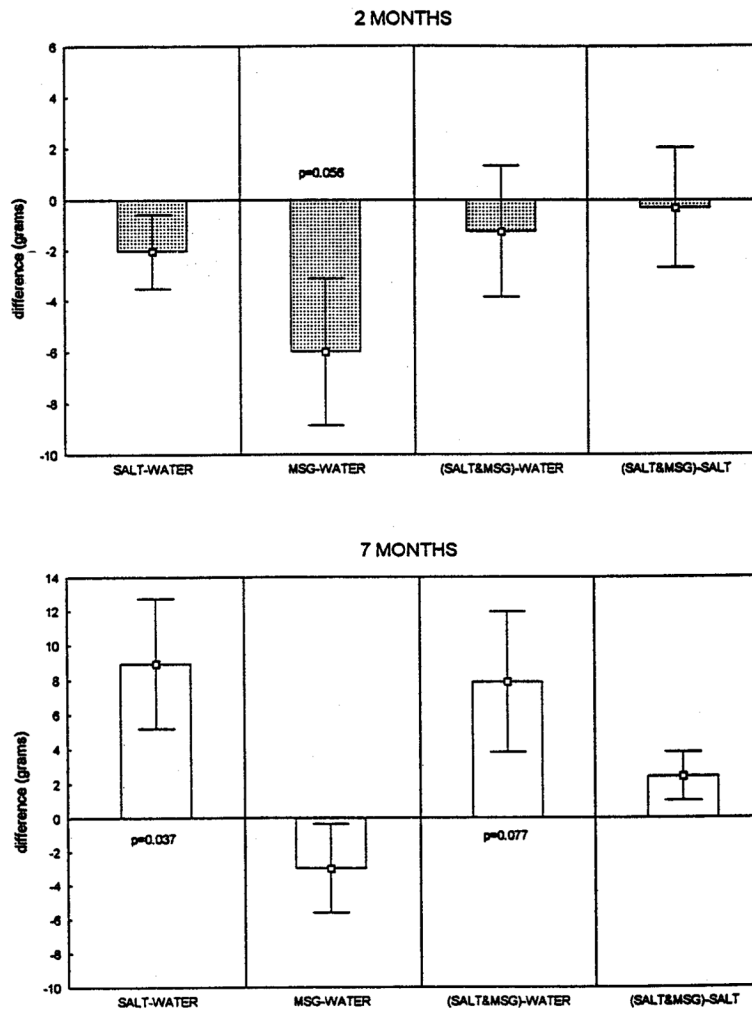
The following conclusions can be drawn from initial analyses of these data. First, there was a tendency for females of both strains and from the F<sub>2</sub> generation to ingest more MSG/30g body weight than males. Second, during testing of 300 mM MSG for 4 days there was a tendency for intake to increase among C57 animals and decrease among 129 animals, suggesting strain differences in the physiological consequences of consuming a very high concentration of MSG. Third, the 129 (lower preference) phenotype was dominant. Fourth, based on data from F<sub>2</sub> animals, a single gene explanation for the strain difference was rejected; instead, the data were most consistent with effects of a few major genes. Finally, there were no significant correlations between sweetener preference and MSG preference in the F<sub>2</sub> generation indicating that the strain differences in sweet and glutamate preferences (both higher in C57 relative to 129 mice) are controlled by different genes.

Since DNA samples of each of these F<sub>2</sub> mice have been collected, we expect to be able to localize the gene(s) underlying the strain differences in MSG consumption using a standard genome screen approach. It will then be interesting to evaluate candidate genes (some of which could be glutamate receptor genes and/or genes regulating glutamate metabolism) that have already been identified and mapped to specific regions on the mouse chromosomes. In this way, it may be possible to quickly identify genes which specifically modulate MSG preference and intake.

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**FIGURE 1.** Mean ( $\pm$  SEM) difference in consumption of taste solutions into two groups of children, ages 2 months (*top*) and 7 months (*bottom*). See text for details.