Hormones, Age, Genes and Pathology: How do we assess variation in sensation and preference?

Linda M. Bartoshuk
Ph.D., Professor,
Yale University School of Medicine, USA

Valerie B. Duffy
Ph. D., R.D., Associate Professor, University of Connecticut
Visiting Lecturer, Yale University School of Medicine

Katharine Fast
Research Associate, Yale University School of Medicine

Barry G. Green
Ph.D., Fellow, John B. Pierce Foundation Laboratory
Professor, Yale University School of Medicine

Derek J. Snyder
Research Associate, Yale University School of Medicine

Send correspondence to: Linda M. Bartoshuk
Yale University School of Medicine - 333 Cedar St., Surgery - New Haven, CT 06520-8041
Linda.Bartoshuk@Yale.edu - Phone: 203-785-2587 - Fax: 203-785-3290

Hormones, Age, Genes and Pathology: How do we assess variation in sensation and preference?

Linda Bartoshuk

Abstract

We live in different taste worlds. Some (nontasters) are taste blind to a family of bitter compounds, (e.g., 6-n-propylthiouracil, PROP). Modern psychophysical techniques have revealed that nontasters perceive the weakest tastes from most substances; a subgroup of tasters who perceive the strongest tastes are called supertasters. Anatomical links (peripheral and central) between taste and oral somatosensation mean that supertasters perceive heightened oral burn (e.g., from chilis) and oral touch (e.g., from fats and thickeners in foods). Of special importance, the incidence of supertasting varies with sex and race (higher for females and Asians). Hormonal variation alters taste (particularly bitter) in human females. Perceived intensity of bitterness varies with the menstrual cycle, rises to a maximum early in pregnancy and declines after menopause. This pattern would contribute to healthy pregnancies by enhancing the bitterness (and thus avoidance) of toxins at a critical stage in pregnancy. Interestingly, although bitterness is stable in females until menopause, bitterness declines steadily with age in males. This may be linked to pathology. The neurons mediating bitterness are the smallest and most vulnerable to injury. For example, viral infection and head trauma, common causes of taste loss, take the greatest toll on bitterness. Incidentally, taste loss is associated with burning mouth syndrome (BMS), a severe pain disorder that afflicts primarily postmenopausal women. BMS results because taste normally inhibits oral pain. Loss of taste in supertasters releases that inhibition leading to centrally-generated oral pain. This is treated with low doses of the antiepileptic clonazepam. To study variation in sensation and preference we must have methods that provide valid comparisons across groups of interest. Adjective-labeled (e.g., "weak," "strong") scales may be invalid for such comparisons, because the adjectives do not always reflect the same sensations or preferences to all groups. Magnitude matching and a modification of Green's Labeled Magnitude Scale have proved successful in revealing taste differences.

Measurement Issues

Aging, hormonal changes, genetics and interactions with the environment affect oral sensations and thus food/beverage preferences. Variation in sensory or hedonic experience is relatively easy to measure within individuals but is extremely difficult to measure across individuals. Comparisons across individuals are valid *only* if ratings are made relative to a standard that is equally intense to all. How do we find such a standard? We must make judicious assumptions. It is very difficult to make such assumptions concerning individuals; however, it is somewhat easier to make assumptions concerning groups.

Historically, there have been two types of standards: intensity adjectives (e.g., weak, moderate, very strong) and actual stimuli. We will provide a brief history of these as well as examples of valid comparisons of sensory experiences across individuals.

Adjective-Labeled Rating Scales

The adjective-labeled self-rating scales (Likert, category, visual analogue) have a variety of historical origins too lengthy to review here. However, it is important to note that most of the pioneers who developed those scales were aware of their limitations; the early usage was generally confined to within-subject comparisons or across-group comparisons in which subjects were assigned randomly to groups. Later, investigators began to use those scales to make across-group comparisons. These would be valid if the adjectives meant the same perceived intensity to all. But intensity adjectives (e.g., "weak," "medium," "strong") have no absolute meaning until they are applied to a specific domain. S.S. Stevens (1) made this point more than forty years ago: "Mice may be called large or small, and so may elephants, and it is quite understandable when someone says it was a large mouse that ran up the trunk of the small elephant."

If individuals in two groups live in different sensory worlds, members of each group will stretch or compress their adjective-labeled scales to fit their worlds; the absolute intensities reflected by the adjectives will be different.

Research on genetic variation in the ability to taste provides insights into the magnitude of the relative meanings of adjectives. Fox (2) discovered that individuals can be classified as nontasters or tasters based on whether or not they can taste certain bitter compounds (including 6-*n*-propylthiouracil or PROP). We discovered that tasters can be further divided into two groups (medium tasters and supertasters) based on how bitter PROP tastes (3). Nontasters, medium tasters and supertasters live in different taste worlds: nontasters experience the weakest tastes and supertasters, the most intense.

REVERSAL ARTIFACT
(shown by dashed lined)

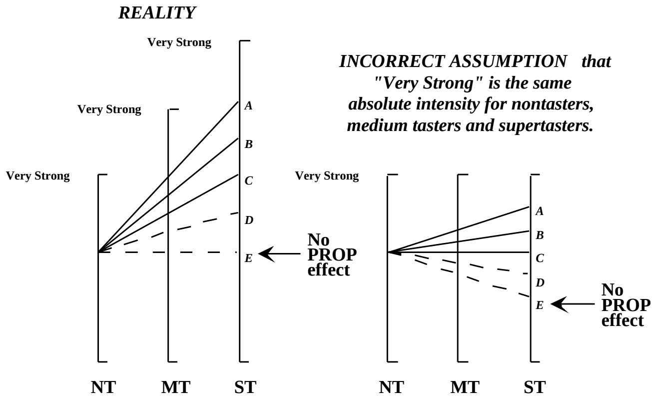

Figure 1 - The left side illustrates the actual differences across the taste worlds of nontasters (NTs), medium tasters (MTs) and supertasters (STs). The right side illustrates the consequences of assuming incorrectly that all three groups live in the same taste world.

Figure 1 illustrates reality (left side) versus the incorrect assumption that all live in the same taste world (right side). The consequences of the incorrect assumption depend on the degree to which a given stimulus varies with PROP status. On the left, *A* represents a stimulus that shows a large PROP effect; supertasters perceive the most intense tastes, medium tasters less and nontasters the least intense tastes. *B* through *D* represent stimuli showing progressively smaller PROP effects. *E* represents a stimulus that shows no PROP effect at all. The incorrect assumption that "very strong" is equal to all distorts the PROP effects. On the right, *A* and *B* still show PROP effects, albeit smaller than they actually are. *C* erroneously shows no PROP effect at all. For *D* and *E* we see a reversal artifact; stimuli actually appear to be the most intense to nontasters. This explains the occasional reversals seen in PROP studies; these are cases in which nontasters appear to experience more intense tastes than do tasters (e.g., (4), Fig. 3; (5), Fig. 5; (6), Fig. 3; (7), Fig. 4). It also explains why some studies fail to find sweet effects (compare *C* on the left and right sides of Figure 1) (e.g., (6, 7)).

S.S. Stevens and the Development of the "New Psychophysics"

The psychophysics of the nineteenth century was focused on the threshold. Fechner (8) tried to use the concept of the "just noticeable difference (jnd)" (the amount a stimulus had to be increased in order for the subject to perceive a change) to create a scale for perceived intensity. The jnd was the scale unit and the perceived intensity of a stimulus was the number of jnds necessary to get from threshold to that stimulus. But S.S. Stevens put a dramatic end to this by noting that if the jnd were an appropriate unit of sensory intensity, then the jnd scale would have ratio properties; it did not. For example, a tone 20 jnds above threshold is much more than twice as loud as a tone 10 jnds above threshold (9).

Stevens generated the "New Psychophysics" by developing methods that did have ratio properties. The most popular of these is magnitude estimation (e.g., see (10) for his work on taste); subjects assign numbers to sensations such that one sensation twice as intense as another is assigned a number twice as large. This produces a ratio scale of sensory experience within subjects. However, magnitude estimates cannot be compared across subjects. This was not a problem for Stevens, because he was interested in comparing sensory modalities; individuals were simply replicates to him.

Others were interested in across-subject comparisons. Borg (11) and Teghtsoonian (12) devised the "range theory." This theory asserted that the subjective range from zero to maximum perceived intensity is the same for each modality and each individual. If this were so, then it should be easy to compare across individuals/groups by asking subjects to rate stimuli on a scale from zero to maximal. Borg explored spacing adjectives on his zero-to-maximal scale in the hope that this would provide "absolute" comparisons across individuals. There is, however, reason to doubt these assumptions about subjective range.

Nonetheless, the idea of gaining the advantages of combining adjective labels and ratio scaling appealed to subsequent investigators. Moskowitz (13) added adjective labels to magnitude estimation for sensory evaluation of foods by simply asking subjects how they would rate "strong", etc., after they had provided ratings for stimuli. We followed Moskowitz's example for oral burn (14); Gracely (15) provided adjective labels for pain; and Green and his colleagues (16) used semantic scaling to create a new, adjective-based scale (the Labeled Magnitude Scale or LMS) intended to measure oral sensations. Schutz and Cardello used the methods of Green *et al.* to produce a scale to measure food liking/disliking (17). The addition of adjectives to ratio scales is an important development but does not solve the relativity of adjectives.

Magnitude Matching: A New Approach

J.C. Stevens and his colleagues showed that individuals are able to match sensations from different modalities for perceived intensity (18, 19). This cross-modality matching gave us a way to select a standard for PROP studies. Early investigations attributed genetic variability to the N-C=S group on molecules. Since NaCl does not contain that group, we reasoned as follows. The perceived saltiness of NaCl is not likely to be the same to all (e.g., pathology could alter saltiness to some) but there is no reason to believe that the ability to taste NaCl is systematically related to the ability to taste PROP. Thus, on average, the saltiness of NaCl will be equal to groups that vary genetically in their ability to taste PROP. Studies based on this logic led to the discovery of supertasters (3).

L.E. Marks and J.C. Stevens's work (20, 21) led to the use of loudness as a standard for taste studies (22). This showed that NaCl was a poor standard, because supertasters perceived NaCl to be saltier than did medium and nontasters (23). Using NaCl as a standard made the genetic differences look smaller than they really are.

Modification of the Labeled Magnitude Scale: A step closer to a universal sensory ruler?

The intensity adjectives that are relatively evenly spaced across typical category scales are not evenly spaced on ratio scales. For example, the relative positions of the adjectives on Green's LMS are: "barely detectable"=1.4%, "weak"=6.0%, "moderate"=17%, "strong"=34.7%, "very strong"=52.5% and "strongest imaginable"=100%. Note that the spacing among adjectives approximates a logarithmic progression. Similar spacings occurred in each of the studies in which adjectives were embedded in a ratio scaling task (11, 13–17). This is not surprising because, even though the adjectives do not have absolute meaning (e.g., "large mice" and "small elephants"), the relative distances among the adjectives remain roughly the same. Thus we can imagine a family of adjective-labeled scales appropriate to a variety of perceptual modalities and contexts as if the scales were elastic. For example, we could rate the perceived intensities of the scents of a variety of roses easily identifying a "weak" rose odor, a "very strong" rose odor or even the "strongest imaginable" rose odor. Similarly we can rate the oral burn of chili peppers. In this case the "strongest imaginable" oral burn would likely be considerably more intense than the "strongest imaginable" rose odor. Green and his colleagues addressed this issue for oral stimuli by having subjects rate sensations within the broader context of the "strongest imaginable oral sensation" (16), and for odor stimuli by asking for ratings relative to the "strongest imaginable odor of any kind" (24). We can apply this logic to create an even more general version of the LMS by labeling the top "strongest imaginable sensation of any kind" (25). Use of such a scale would not be confined to a specific sensory modality or to a specific perceptual context, such as the mouth or nose.

Although there are clearly differences across subjects for specific sensations (e.g., the genetic differences we have discussed), by instructing subjects to judge sensations in the broadest possible context we have a better chance of measuring these differences accurately. Thus, while there is good reason to believe the perceptual scale of *oral* sensations has been "stretched" by the intense taste experiences of supertasters, there is less reason to believe their scale of *all* sensations is any different from that of nontasters.

We asked subjects (N=100) to rate PROP concentrations on the general LMS ("strongest imaginable sensation of any kind" at the top) and with magnitude matching (using tones as the standards). The order of the two sessions was counterbalanced. The separation of nontasters, medium tasters and supertasters was similar for the two methods (26). This supports the assumptions underlying both scales: tones are reasonable standards for PROP studies and the general LMS bounded by "strongest imaginable sensation of any kind" provides accurate comparisons of perceived intensities across groups.

We used the general LMS to see how nontasters, medium and supertasters describe their taste worlds. Attendees at lectures (N=245) who had not previously tasted PROP were asked to rate the intensities of remembered experiences including the brightest light ever seen and the strongest salty, sweet, sour and bitter tastes ever experienced. After making these ratings, subjects tasted PROP paper (3 cm diameter pieces of filter paper impregnated with 1.6 mg PROP) and rated its bitterness. PROP bitterness did not correlate significantly with the brightest light seen but did correlate significantly with the strongest bitter, sour and salty tastes ever experienced (27).

Variation in Oral Sensation: Using Our New Psychophysical Tools

There are many questions concerning sensory or hedonic perception that require absolute comparisons across groups. As the methods for making valid across-group comparisons have evolved, we have been able to begin to answer some of those questions. Examples of our findings follow below.

Genetic Variation in Taste: Supertasters

As noted above, we are not all born into the same "taste worlds" (2, 28). Family studies show that nontasters carry two recessive alleles (29). Using magnitude estimation with NaCl as the standard, we discovered that genetic taste variation was not restricted to bitter compounds containing the N-C=S group (30, 31). As more compounds were studied, we found that supertasters perceived not only the most intense tastes but also the most intense oral burn from irritants and the most intense tactile sensations from fats in foods (see (32) for a review).

The development of video microscopy revealed an association between PROP tasting and tongue anatomy (33); supertasters tended to have the most fungiform papillae (the structures housing taste buds) (34). This explains why supertasters perceive more intense sensations from irritants and viscous compounds. Fungiform papillae are innervated by the trigeminal nerve, which mediates pain, temperature and touch (35).

The association between PROP tasting and anatomy is far from perfect. First, the areas assessed for fungiform papillae density have been relatively small. Assessments from larger (or different) areas might improve the association but are unlikely to counter it. Second, hormonal variation and pathology affect taste but do not alter the density of fungiform papillae in humans. Third, the nature of the association may be relevant to the genetics of supertasting. If the gene for PROP tasting were independent of that (or those) for tongue anatomy, then supertasters might be PROP tasters who have also inherited a lot of fungiform papillae. Presumably, nontasters lack a binding site for PROP; thus no matter how many fungiform papillae they have, this will not turn them into tasters. Tasters have the binding site for PROP and so the more fungiform papillae (and thus taste buds) they have, the more bitter PROP will taste. Complete independence of the PROP and anatomy genes seems unlikely, since individuals with a low density of fungiform papillae tend to be nontasters (36).

We know the rough location of the PROP gene (37). When the exact location is identified, we will be able to determine directly whether or not individuals with two dominant alleles are the most responsive to PROP. Kalmus addressed this issue indirectly with a very clever threshold study (38). He reasoned that if there were a phenotypical difference between individuals with a single dominant allele and those with both dominant alleles, the average PROP threshold from those with only taster siblings would be lower. They are.

Hormonal Variation and Age

Since bitter is believed to be a cue for poison, there would be survival value in a system that intensified bitter tastes early in pregnancy when a fetus would be most vulnerable to poisons. The data collected on the menstrual cycle, pregnancy and menopause are consistent with the existence of such a system. Early anecdotes compiled by Hoyme (39) linked genetic variation and hormonal effects of taste. Hoyme noted that two nontaster women became tasters with their first pregnancies; one was still a taster a year later, "becoming a 'non-taster' a day or so before her menstrual periods." Hoyme further noted that PTC (phenylthiocarbamide, a chemical relative of PROP that shows similar variation in bitterness across non-tasters, medium tasters and supertasters) tasted less intense during menstrual periods to six women, more intense to two, and showed no change for six.

Menstrual cycle. Studies following Hoyme focussed on the phase of the cycle during which taste sensitivity would be maximal (see (32) for a review) and came to no agreement. We suspect that this focus was misplaced. A hormonal change may trigger a taste change that is not immediate; the time taken for the taste change to appear might vary across women. Etter (32) tested subjects (20 females, 2 males) daily for approximately 100 days. Only cycling females (verified by thermal cycling) showed cycling of taste. Averaging across cycling women showed peak taste perception during the luteal phase; however, periodogram analyses showed that not all subjects fit that average.

Pregnancy. Hoyme's anecdotal observation that PROP sensitivity rises with pregnancy was supported by Fisher and Kaplan's observations on two sets of identical twins, one of whom was pregnant; the pregnant twin was the more sensitive in each case. Bhatia and Puri (40) classified subjects as nontasters or tasters in each trimester of pregnancy; more fell into the taster class in the first trimester. Romanus

(41) found more tasters among women who had children, suggesting that an increase in PROP tasting may even outlast pregnancy.

During the first trimester of pregnancy, we found an increase in perceived bitterness of quinine (32, 42). Interestingly, the variance was reduced during the first trimester. This is consistent with the idea that in cycling women perceived bitterness varies; pregnancy causes bitter taste to hit its maximum and this both raises the mean bitterness and reduces the variance.

This study was done prior to our current work on adjective-labeled scales. The scale we used, a horizontal line labeled "zero" at the left end and "extremely" two thirds of the way to the right (22), is subject to the very criticisms of adjective-labeled scales we have presented. Were we to redo the pregnancy study we would use a different method now (magnitude matching or the general LMS). However, since the study was longitudinal, the changes observed could be assessed by within-subject comparisons. Nonetheless, this raises an interesting question: will the taste changes that occur during pregnancy alter a woman's taste scale? We do not know how quickly we adjust our adjectival scales as our sensory worlds change.

Menopause. There is general agreement that age is associated with a reduction in the ability to taste bitter (43). We asked attendees at lectures to rate the bitterness of PROP paper using the general LMS (32, 44). In females, perceived bitterness was stable until menopause when it began to decline.

Pathology

Taste pathology offers another area in which across-group comparisons are important. Recently, we studied a sample of patients with burning mouth syndrome (45). This disorder is characterized by intense oral pain in the absence of visible oral tissue pathology. Patients rated the peak oral pain experienced with this syndrome using the general LMS ("strongest imaginable sensation of any kind" at the top). The correlation between this pain and the density of fungiform papillae was 0.8 (45, 46); the most intense oral burn was experienced by the supertasters. Patients showed taste loss (particularly for bitter) on the anterior tongue, the area innervated by the chorda tympani branch of CN VII, the facial nerve. This suggests that burning mouth syndrome is a sensory phantom that can arise when tonic inhibition processes in the central nervous system are disrupted. There is evidence that taste normally inhibits oral pain (47). Damage to taste may therefore release this inhibition, causing the patient to experience oral pain in the absence of visible tissue pathology. For many individuals that phantom pain can be relieved by low doses (0.25 mg per day) of clonazepam, an antiepileptic drug (48).

Preferences

We began our studies of the effects of PROP tasting on food/beverage preferences using the Marks scale (22) to measure the degree of liking/disliking (49). PROP tasting was negatively correlated with preference for sweet and high-fat foods in females and tended to be positively correlated in males. However, the Marks scale assumes that the adjective "extremely" means the same to all. Our concerns about this led us to use the general LMS to assess liking/disliking. We have confirmed the earlier results for sweet (50) and high-fat foods (51, 52). In addition, we have found an increase in preferences for high fat foods with age, especially for women (53), that is consistent with nutrition surveillance data (NHANES III) on intake (54).

Conclusion

We do not all experience the same sensory intensities from foods and beverages. A full understanding of the impact of variation in oral sensation on dietary behaviors will require measures of perceived intensity and degree of liking/disliking that permit valid comparisons across subjects. In this paper we have reviewed serious limitations associated with use of adjective-labeled scales in studies of genetic variation in taste. We must be prepared to look for similar examples in other fields.

References

1. Stevens SS. Adaptation-level vs the relativity of judgment. Am J Psychol 1958;4:633-646.
2. Fox AL. Six in ten "tasteblind" to bitter chemical. Science News Letter 1931;9:249.
3. Bartoshuk LM. The biological basis of food perception and acceptance. Food Qual Pref 1993;4:21-32.
4. Schifferstein HNJ, Frijters JER. The perception of the taste of KCl, NaCl, and quinineHCl is not related to PROP-sensitivity. Chem Senses 1991;16:303-317.
5. Drewnowski A, Henderson SA, Barratt-Fornell A. Genetic sensitivity to 6-n-propylthiouracil and sensory responses to sugar and fat mixtures. Physiol Behav 1998;63:771-777.
6. Drewnowski A, Henderson SA, Shore AB, Barratt-Fornell A. Nontasters, tasters, and supertasters of 6-n-propylthiouracil (PROP) and hedonic response to sweet. Physiol Behav 1997;62:649-655.
7. Smagghe K, Louis-Sylvestre J. Influence of PROP-sensitivity on taste perceptions and hedonics in French women. A study performed without retronasal olfaction. Appetite 1998;30:325-339.
8. Fechner GT. Elemente der Psychophysik. Leipzig: Breitkopf and Härterl; 1860.
9. Stevens SS. Mathematics, measurement, and psychophysics. In: Stevens SS, editor. Handbook of Experimental Psychology. New York: John Wiley & Sons, Inc.; 1951. p. 1-49.
10. Stevens SS. Sensory scales of taste intensity. Percept Psychophys 1969;6:302-308.
11. Borg G. A category scale with ratio properties for intermodal and interindividual comparisons. In: Geissler HG, Petzold P, editors. Psychophysical Judgment and the Process of Perception. Berlin: VEB Deutscher Verlag der Wissenschaften; 1982. p. 25-34.
12. Teghtsoonian R. Range effects in psychophysical scaling and a revision of Stevens' law. Am J Psychol 1973;86:3-27.
13. Moskowitz HR. Magnitude estimation: Notes on what, how, when, and why to use it. J Food Qual 1977;1:195-228.
14. Karrer T, Bartoshuk L. Capsaicin desensitization and recovery on the human tongue. Physiol Behav 1991;49:757-764.
15. Gracely RH, McGrath P, Dubner R. Validity and sensitivity of ratio scales of sensory and affective verbal pain descriptors: Manipulation of affect by diazepam. Pain 1978;5:19-29.
16. Green BG, Shaffer GS, Gilmore MM. A semantically-labeled magnitude scale of oral sensation with apparent ratio properties. Chem Senses 1993;18:683-702.
17. Schutz HG, Cardello AV. Development of a labeled affective magnitude (LAM) scale for assessing food liking/disliking. J Sen Stud 2000, in press.
18. Stevens JC. Cross-modality validation of subjective scales for loudness, vibration, and electric shock. J Exp Psychol 1959;57:201-209.
19. Stevens JC, Marks LE. Cross-modality matching of brightness and loudness. Proc Natl Acad Sci 1965;54:407-411.
20. Stevens JC, Marks LE. Cross-modality matching functions generated by magnitude estimation. Percept Psychophys 1980;27:379-389.

21. Marks LE, Rifkin B, Bartoshuk LM, Stevens JC. Individual differences in taste intensity of 6-n-propylthiouracil determined by magnitude matching. In: Association for Chemoreception Sciences; 1980; Sarasota, FL; 1980.

22. Marks LE, Stevens JC, Bartoshuk LM, Gent JG, Rifkin B, Stone VK. Magnitude matching: The measurement of taste and smell. Chem Senses 1988;13:63-87.

23. Bartoshuk LM, Duffy VB, Lucchina LA, Prutkin J, Fast K. PROP (6-n-propylthiouracil) supertasters and the saltiness of NaCl. In: Murphy C, editor. Olfaction and Taste XII. New York: New York Academy of Sciences; 1998. p. 793-796.

24. Green BG, Dalton P, Cowart B, Rankin K, Higgins J. Evaluating the labeled magnitude scale for measuring sensations of taste and smell. Chem Senses 1996;21:323-334.

25. Bartoshuk LM. Comparing sensory experiences across individuals: Recent psychophysical advances illuminate genetic variation in taste perception. Chem Senses 2000;25:447-460.

26. Bartoshuk LM, Green BG, Snyder DJ, Lucchina LA, Hoffman HJ, Weiffenbach JM, et al. Valid across-group comparisons: Supertasters perceive the most intense taste sensations by magnitude matching or the LMS scale. Chem Senses 2000;25:639.

27. Fast K, Green BG, Snyder DJ, Bartoshuk LM. Remembered intensities of taste and oral burn correlate with PROP bitterness. Chem Senses 2001, submitted.

28. Blakeslee AF, Fox AL. Our different taste worlds. Journal of Heredity 1932;23:97-107.

29. Snyder LH. Studies in human inheritance. IX. The inheritance of taste deficiency in man. Ohio J Sci 1932;32:436-440.

30. Hall MJ, Bartoshuk LM, Cain WS, Stevens JC. PTC taste blindness and the taste of caffeine. Nature 1975;253:442-443.

31. Bartoshuk LM. Bitter taste of saccharin: Related to the genetic ability to taste the bitter substance 6-n-propylthiouracil (PROP). Science 1979;205:934-935.

32. Prutkin J, Duffy VB, Etter L, Fast K, Gardner E, Lucchina LA, et al. Genetic variation and inferences about perceived taste intensity in mice and men. Physiol Behav 2000;69:161-173.

33. Miller IJ, Reedy FE. Variations in human taste bud density and taste intensity perception. Physiol Behav 1990;47:1213-1219.

34. Bartoshuk LM, Duffy VB, Miller IJ. PTC/PROP tasting: Anatomy, psychophysics, and sex effects. Physiol Behav 1994;56:1165-1171.

35. Silver WL, Finger TE. The trigeminal system. In: Getchell TV, Doty RL, Bartoshuk LM, Snow JB, editors. Smell and Taste in Health and Disease. New York: Raven Press; 1991. p. 97-108.

36. Bartoshuk LM, Duffy VB, Fast K, Kveton JF, Lucchina LA, Phillips MN, et al. What makes a supertaster? Chem Senses 2001, submitted.

37. Reed DR, Nanthakumar, E., North, M., Bell, C., Bartoshuk, L.M., and Price, R.A. Localization of a gene for bitter taste perception to human chromosome 5p15. Am J Hum Genet 1999;64:1478-1480.

38. Kalmus H. Improvements in the classification of the taster genotypes. Ann Hum Genet 1958;22:222-230.

39. Hoyme LE. Genetics, physiology and phenylthiocarbamide. J Hered 1955;46:167-175.

40. Bhatia S, Puri R. Taste sensitivity in pregnancy. Indian J Physiol and Pharmacol 1991;35:121-124.

41. Romanus T. The ability to taste PTC among Swedish men and women (Nulliparae and others). Acta Genet Med Gemellol 1965;14:417-420.

42. Duffy VB, Bartoshuk LM, Striegel-Moore R, Rodin J. Taste changes across pregnancy. In: Murphy C, editor. International Symposium on Olfaction and Taste XIX. New York: New York Academy of Sciences; 1998. p. 805-809.

43. Bartoshuk LM, Duffy VB. Taste and smell. In: Masoro EJ, editor. Handbook of Physiology, Section 11: Aging. New York: Oxford University Press; 1995. p. 363-375.

44. Weiffenbach JM, Duffy VB, Fast K, Cohen ZD, Bartoshuk LM. Bitter-sweet age, sex and PROP (6-n-propylthiouracil) effects: A role for menopause? Chem Senses 2000, in press.

45. Grushka M, Bartoshuk LM. Burning mouth syndrome and oral dysesthesias. Can J Diag 2000;17:99-109.

46. Bartoshuk LM, Grushka M, Duffy VB, Fast K, Lucchina L, Prutkin J, et al. Burning Mouth Syndrome: Damage to CN VII and Pain Phantoms in CN V. Chem Senses 1999;24:609.

47. Tie K, Fast K, Kveton J, Cohen Z, Duffy V, Green B, et al. Anesthesia of chorda tympani nerve and effect on oral pain. Chem Senses 1999;24:609.

48. Grushka M, Epstein J, Mott A. An open-label, dose escalation pilot study of the effect of clonazepam in burning mouth syndrome. Oral Surg Oral Med Oral Pathol Oral Radiol Endod 1998;86:557-561.

49. Duffy VB, Bartoshuk LM. Food acceptance and genetic variation in taste. J Am Diet Assoc 2000;100:647-655.

50. Peterson JM, Duffy VB. Genetic variation in taste: Associations with sweetness intensity, sweet liking and sweet food acceptance. Chem Senses 2000;25:638-639.

51. Duffy VB, Fast K, Cohen Z, Chodos E, Bartoshuk LM. Genetic taste status associates with fat food acceptance and body mass index in adults. Chem Senses 1999;24:545-546.

52. Fast K, Duffy VB, Bartoshuk LM. New psychophysical insights in evaluating genetic variation in taste. In: Rouby C, Schaal B, Dubois D, Gervais R, Holley A, editors. Olfaction, Taste and Cognition; 2001, in press.

53. Snyder DJ, Duffy VB, Fast K, Hoffman HJ, Ko CW, Weiffenbach JM, et al. Food preferences vary with age and sex: A new analysis using the general Labeled Magnitude Scale. Chem Senses 2001, submitted.

54. Kant AK. Consumption of energy-dense, nutrient poor foods by adult Americans: nutritional and health implications. The third National Health and Nutrition Examination Survey, 1988-1994. Am Journal Clin Nutr 2000;72:929-936.

Biography

Linda Bartoshuk

Linda M. Bartoshuk is a Professor in Surgery (Otolaryngology) at the Yale University School of Medicine (secondary appointment, Psychology). She works on the psychophysics of taste and is especially interested in psychophysical methods that can produce valid comparisons across individuals/ groups. Her lab studies focus on taste phantoms (chronic tastes similar to phantom limbs) as well as genetic variation in the ability to taste (some individuals are super-tasters with unusually large numbers of taste buds). The genetic work has led into some strange by-ways because taste buds are innervated by the trigeminal nerve which carries touch and pain. This means that supertasters also have unusual abilities to perceive fat in foods (via the sense of touch) and burn/pain on the tongue. This genetic sensory variation has clinical implications for nutrition (and the health problems associated with diet) as well as oral pain management. Pain studies focus on oral pain produced by lesions (this can be treated by desensitizing with capsaicin, the compound that makes chili peppers burn) and oral pain (eg, burning mouth syndrome) that is generated centrally when damage to taste interrupts normal central inhibition of oral pain.

Her professional activities include membership in the American Academy of Arts and Sciences, Society of Experimental Psychologists, American Psychological Association (past president of Division 6, Behavioral Neuroscience and Comparative Psychology; incoming president of Division 1, Society for General Psychology), American Psychological Society (Board of Directors), Eastern Psychological Society (past president), and Association for Chemoreception Sciences (past president).