

Chapter 2

Physiological and Psychological Foundations of Sensory Function

Abstract This chapter reviews background material underpinning sensory science and sensory evaluation methodologies. Basic and historical psychophysical methods are reviewed as well as the anatomy, physiology, and function of the chemical senses. The chapter concludes with a discussion of multi-modal sensory interactions.

There is no conception in man's mind which hath not at first, totally or in parts, been begotten upon by the organs of sense.

—Thomas Hobbes, *Leviathan* (1651)

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2.1 Introduction

In order to design effective sensory tests and provide insightful interpretation of the results, a sensory professional must understand the functional properties of the sensory systems that are responsible for the data. By a functional property, we mean a phenomenon like mixture interactions such as masking or suppression. Another example is sensory adaptation, a commonly observed decrease in responsiveness to conditions of more or less constant stimulation. In addition, it is useful to understand the anatomy and physiology of the senses involved as well as their functional limitations. A good example of a functional limitation is the threshold or minimal amount of a stimulus needed for perception. Knowing about the anatomy of the senses

can help us understand how consumers and panelists interact with the products to stimulate their senses and by what routes. Different routes of smelling, for example, are the orthonasal or sniffing route, when odor molecules enter the nose from the front (nostrils), versus retronasal smell, when odor molecules pass into the nose from the mouth or from breathing out, and thus have a reversed airflow pathway from that of external sniffing.

Another basic area that the sensory professional should have as background knowledge involves the sensory testing methods and human measurement procedures that are the historical antecedents to the tests we do today. This is part of the science of psychophysics, the quantification and measurement of sensory experiences. Psychophysics is a very old discipline that formed the basis for the early studies in experimental psychology. Parallels exist between psychophysics and sensory evaluation. For example, the difference test using paired comparisons is a version of the method used for measuring difference thresholds called the method of constant stimuli. In descriptive analysis with trained panels, we work very hard to insure that panelists use singular uni-dimensional scales. These numerical systems usually refer to a single sensory continuum like sweetness or odor strength and are thus based on changes in perceived intensity. They do not consider multiple attributes and fold them into a single score like the old-quality grading methods. Thus there is a clear psychophysical basis for the attribute scales used in descriptive analysis.

This chapter is designed to provide the reader some background in the sensory methods of psychophysics. A second objective is to give an overview of the structure and function of the chemical senses of taste, smell, and the chemesthetic sense. Chemesthesis refers to chemically induced sensations that seem to be at least partly tactile in nature, such as pepper heat, astringency, and chemical cooling. These three senses together comprise what we loosely call flavor and are the critical senses for appreciating foods, along with the tactile, force, and motion-related experiences that are part of food texture and mouthfeel. Texture is dealt with in [Chapter 11](#) and color and appearance evaluations in [Chapter 12](#). The auditory sense is not a large part of food perception, although many sounds can be perceived when we eat or manipulate foods. These provide another sense modality to accompany and reinforce our texture perceptions, as in the case of crisp

or crunchy foods, or the audible hissing sound we get from carbonated beverages (Vickers, 1991).

One growing area of interest in the senses concerns our human biodiversity, differences among people in sensory function. These differences can be due to genetic, dietary/nutritional, physiological (e.g., aging), or environmental factors. The research into the genetics of the chemical senses, for example, has experienced a period of enormous expansion since the first edition of this book. The topic is too large and too rapidly changing to receive a comprehensive treatment here. We will limit our discussion of individual differences and genetic factors to those areas that are well understood, such as bitter sensitivity, smell blindness, and color vision anomalies. The sensory practitioner should be mindful that people exist in somewhat different sensory worlds. These differences contribute to the diversity of consumer preferences. They also limit the degree to which a trained panel can be “calibrated” into uniform ways of responding. Individual differences can impact sensory evaluations in many ways.

2.2 Classical Sensory Testing and Psychophysical Methods

2.2.1 Early Psychophysics

The oldest branch of experimental psychology is that of psychophysics, the study of relationships between physical stimuli and sensory experience. The first true psychophysical theorist was the nineteenth century German physiologist, E. H. Weber. Building on earlier observations by Bernoulli and others, Weber noted that the amount that a physical stimulus needed to be increased to be just perceptibly different was a constant ratio. Thus 14.5 and 15 ounces could be told apart, but with great difficulty, and the same could be said of 29 and 30 ounces or 14.5 and 15 drams (Boring, 1942). This led to the formulation of Weber’s law, generally written nowadays as

$$\Delta I/I = k \quad (2.1)$$

where ΔI is the increase in the physical stimulus that was required to be just discriminably different from some starting level, I . The fraction, $\Delta I/I$, is sometimes called the “Weber fraction” and is an index of

how well the sensory system detects changes. This relationship proved generally useful and provided the first quantitative operating characteristic of a sensory system. Methods for determining the difference threshold or just-noticeable-difference (j.n.d.) values became the stock in trade of early psychological researchers.

These methods were codified by G. T. Fechner in a book called *Elemente der Psychophysik (Elements of Psychophysics)* in 1860. Fechner was a philosopher as well as a scientist and developed an interest in Eastern religions, in the nature of the soul, and in the Cartesian mind–body dichotomy. Fechner’s broader philosophical interests have been largely overlooked, but his little book on sensory methods was to become a classic text for the psychology laboratory. Fechner also had a valuable insight. He realized that the j.n.d. might be used as a unit of measurement and that by adding up j.n.d.s one could construct a psychophysical relationship between physical stimulus intensity and sensory intensity. This relationship approximated a log function, since the integral of $1/x \, dx$ is proportional to the natural log of x . So a logarithmic relationship appeared useful as a general psychophysical “law:”

$$S = k \log I \quad (2.2)$$

where S is sensation intensity and I is once again the physical stimulus intensity. This relationship known as Fechner’s law was to prove a useful rule of thumb for nearly 75 years, until it was questioned by acoustical researchers who supplanted it with a power law (see Section 2.2.3).

2.2.2 The Classical Psychophysical Methods

Fechner’s enduring contribution was to assemble and publish the details of sensory test methods and how several important operating characteristics of sensory systems could be measured. Three important methods were the method of limits, the method of constant stimuli (called the method of right and wrong cases in those days), and the method of adjustment or average error (Boring, 1942). The methods are still used today in some research situations and variations on these methods form part of the toolbox of applied sensory evaluation. Each of the three methods was associated

with a particular type of measured response of sensory systems. The method of limits was well suited to determine absolute or detection thresholds. The method of constant stimuli could be used to determine difference thresholds and the method of adjustment to establish sensory equivalence.

In the method of limits the physical stimulus is changed by successive discrete steps until a change in response is noted. For example, when the stimulus is increasing in intensity, the response will change from “no sensation” to “I detect something.” When the stimulus is decreasing in intensity, at some step the response will change back to “no sensation.” Over many trials, the average point of change can be taken as the person’s absolute threshold (see Fig. 2.1). This is the minimum intensity required for detection of the stimulus. Modern variations on this method often use only an ascending series and force the participants to choose a target sample among alternative “blank” samples at each step. Each concentration must be discriminated from a background level such as plain water in the case of taste thresholds. Forced-choice methods for determining thresholds are discussed in detail in Chapter 6.

In the method of constant stimuli, the test stimulus is always compared against a constant reference level (a standard), usually the middle point on a series of physical intensity levels. The subject’s job is to respond to each test item as “greater than” or “less

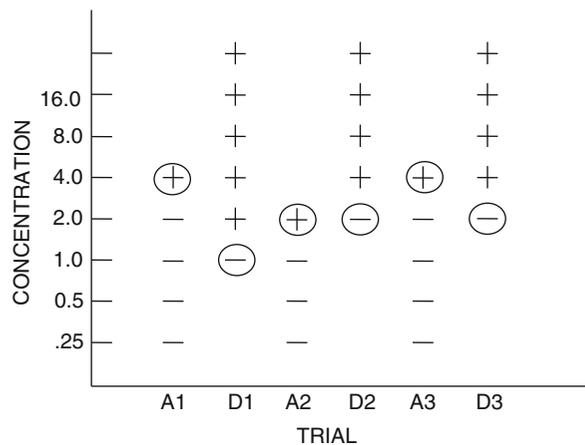


Fig. 2.1 An example of the method of limits. The circled reversal points would be averaged to obtain the person’s threshold. A: ascending series. D: descending series. In taste and smell, only ascending series are commonly used to prevent fatigue, adaptation or carry-over of persistent sensations.

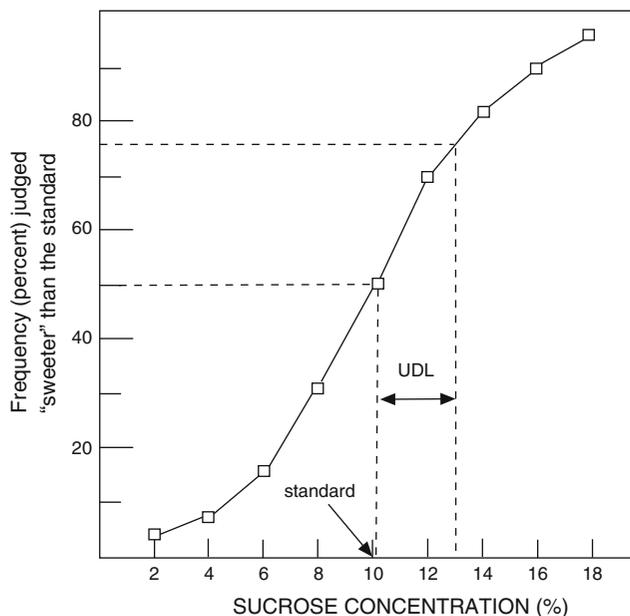


Fig. 2.2 A psychometric function derived from the Method of Constant Stimuli, a repeated series of paired comparisons against a constant (standard) stimulus, in this case 10% sucrose. Frequency of judgments in which the comparison stimulus is

judged sweeter than the standard are plotted against concentration. The difference threshold is determined by the concentration difference between the standard and the interpolated 75% (or 25%) point. UDL: Upper difference limen (threshold).

than” the standard. Many replications of each intensity level are presented. The percentage of times the response is “greater than” can be plotted as in Fig. 2.2. This S-shaped curve is called a psychometric function (Boring, 1942). The difference threshold was taken as the difference between the 50 and 75% points interpolated on the function. The method of constant stimuli bears a strong resemblance to current techniques of paired comparison, with two exceptions. One point of difference is that the method was geared toward interval estimation, rather than testing for statistically significant differences. That is, the technique estimated points on the psychometric function (25, 50, and 75%) and researchers were not concerned with statistical significance of difference tests. Also, a range of comparison stimuli were tested against the standard and not just a single paired comparison of products.

The third major method in classical psychophysics was the method of adjustment or average error. The subject was given control over a variable stimulus like a light or a tone and asked to match a standard in brightness or loudness. The method could be used to determine difference thresholds based on the variability of the subject over many attempts at matching, for example, using the standard deviation as a measure

of difference threshold. A modern application is in measuring sensory tradeoff relationships. In this type of experiment the duration of a very brief tone could be balanced against a varying sound pressure level to yield a constant perception of loudness. Similarly, the duration of a flash of light could be traded off against its photometric intensity to create a constant perceived brightness. For very brief tones or brief flashes, there is summation of the intensity over time in the nervous system, so that increasing duration can be balanced against decreasing physical intensity to create a constant perception. These methods have proven useful in understanding the physiological response of different senses to the temporal properties of stimuli, for example, how the auditory and visual systems integrate energy over time.

Adjustment methods have not proven so useful for assessing sensory equivalence in applied food testing, although adjustment is one way of trying to optimize an ingredient level (Hernandez and Lawless, 1999; Mattes and Lawless, 1985). Pangborn and co-workers employed an adjustment method to study individual preferences (Pangborn, 1988; Pangborn and Braddock, 1989). Adding flavors or ingredients “to taste” at the benchtop is a common way of initially formulating

products. It is also fairly common to make formula changes to produce approximate sensory matches to some target, either a standard formula or perhaps some competitor's successful product. However, the method as applied in the psychophysics laboratory is an unwieldy technique for the senses of taste and smell where elaborate equipment is needed to provide adjustable stimulus control. So methods of equivalency adjustment are somewhat rare with food testing.

2.2.3 Scaling and Magnitude Estimation

A very useful technique for sensory measurement has been the direct application of rating scales to measure the intensity of sensations. Historically known as the "method of single stimuli," the procedure is highly cost efficient since one stimulus presentation yields one data point. This is in contrast to a procedure like the method of constant stimuli, where the presentation of many pairs is necessary to give a frequency count of the number of times each level is judged stronger than a standard. Rating scales have many uses. One of the most common is to specify a psychophysical function, a quantitative relationship between the perceived intensity of a sensation and the physical intensity of the stimulus. This is another way of describing a dose–response curve or in other words, capturing the input–output function of a sensory system over its dynamic range.

The technique of magnitude estimation grew out of earlier procedures in which subjects would be asked to fractionate an adjustable stimulus. For example, a subject would be asked to adjust a light or tone until it seemed half as bright as a comparison stimulus. The technique was modified so that the experimenter controlled the stimulus and the subject responded using (unrestricted) numbers to indicate the proportions or ratios of the perceived intensities. Thus if the test stimulus was twice as bright as the standard, it would be assigned a number twice as large as the rating for the standard and if one-third as bright, a number one-third as large. An important observation in S. S. Stevens' laboratory at Harvard was that the loudness of sounds was not exactly proportional to the decibel scale. If Fechner's log relationship was correct, rated loudness should grow in a linear fashion with decibels, since

they are a log scale of sound pressure relative to a reference ($\text{db} = 20 \log (P/P_0)$ where P is the sound pressure and P_0 is the reference sound pressure, usually a value for absolute threshold). However, discrepancies were observed between decibels and loudness proportions.

Instead, Stevens found with the direct magnitude estimation procedure that loudness was a power function of stimulus intensity, with an exponent of about 0.6. Scaling of other sensory continua also gave power functions, each with its characteristic exponent (Stevens, 1957, 1962). Thus the following relationship held:

$$S = kI^n \text{ or } \log S = n \log I + \log k \quad (2.3)$$

where n was the characteristic exponent and k was a proportionality constant determined by the units of measurement. In other words, the function formed a straight line in a log–log plot with the exponent equal to the slope of the linear function. This was in contrast to the Fechnerian log function which was a straight line in a semilog plot (response versus log physical intensity).

One of the more important characteristics of a power function is that it can accommodate relationships that are expanding or positively accelerated while the log function does not. The power function with an exponent less than one fits a law of diminishing returns, i.e., larger and larger physical increases are required to maintain a constant proportional increase in the sensation level. Other continua such as response to electric shocks and some tastes were found to have a power function exponent greater than one (Meiselman, 1971; Moskowitz, 1971; Stevens, 1957). A comparison of power functions with different exponents is shown in Fig. 2.3.

Many sensory systems show an exponent less than one. This shows a compressive energy relationship that may have adaptive value for an organism responding to a wide range of energy in the environment. The range from the loudest sound one can tolerate to the faintest audible tone is over 100 dB. This represents over 10 log units of sound energy, a ratio of 10 billion to one. The dynamic range for the visual response of the eyes to different levels of light energy is equally broad. Thus exponents less than one have ecological significance for sensory systems that are tuned to a broad range of physical energy levels.

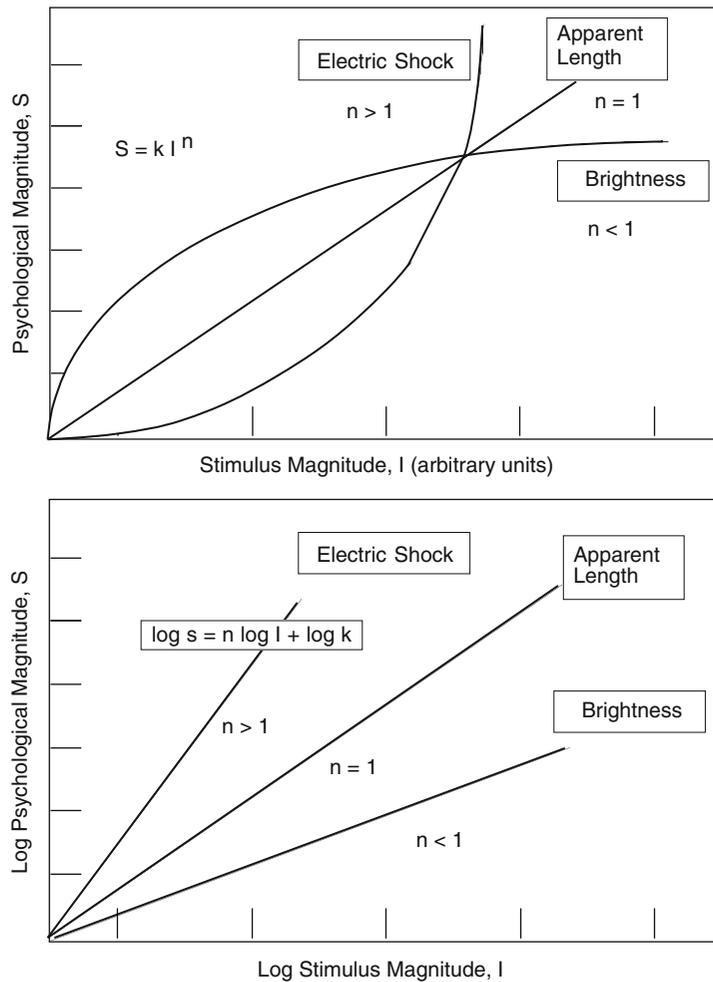


Fig. 2.3 Power function exponents less than, equal to, or greater than one generate different curves. In a log–log plot the exponent becomes the slope of a *straight line*.

Magnitude estimation as a test method and the resulting form of the power function formed an interlocking and valid system in Stevens' thinking. Power function exponents were predictable from various experiments. For example, in a cross-modality matching experiment, separate scaling functions were derived for two continua (e.g., brightness and loudness). One continuum was then scaled as a function of the other without using numbers. For example, a subject would be told to adjust the brightness of a light so it matched the loudness of a tone (fixed by the experimenter). The exponent in the matching experiment could be accurately predicted from the ratios of the exponents in the two separate scaling experiments.

When setting the sensations equal, the following relationships should hold:

$$\text{loudness} = \text{brightness} = k \log I^{n_1} = k \log I^{n_2} \quad (2.4)$$

and

$$n_1 \log(I_{\text{sound}}) + (a \text{ constant}) = n_2 \log(I_{\text{light}}) + (a \text{ constant}) \quad (2.5)$$

and

$$\log(I_{\text{sound}}) = n_2/n_1 \log(I_{\text{light}}) + (a \text{ constant}) \quad (2.6)$$

so that plotting a function of log sound intensity as a function of log light intensity would give a straight

line with slope equal to n_2/n_1 . This technique was very reliable (Stevens, 1959) and was often used as an undergraduate laboratory demonstration.

2.2.4 Critiques of Stevens

Other researchers were not so willing to accept the simple idea that the numbers applied to stimuli were in fact a direct reflection of the perceived sensation intensity. After all, the sensation was a subjective experience and the person had to decide what numbers to apply to the experience. So the simple stimulus–response idea was replaced by the notion that there were at least two separate processes: a psychophysical relationship translating stimulus intensity into subjective experience and response output function by which the subject applied numbers or some other response categories to the stimulus. Obviously, different scaling techniques could produce different response matching functions, so it was not surprising that an open-ended scaling task like magnitude estimation and a fixed-range scaling task like category ratings produced different psychophysical functions (a power function and a log function, respectively).

An extended argument ensued between the proponents of magnitude estimation and proponents of other scaling techniques like simple category scales (Anderson, 1974). The magnitude estimation camp claimed that the technique was capable of true ratio scale measurement, like measurements of physical quantities in the natural sciences (length, mass, heat, etc.). This was a preferable level of measurement than other techniques that merely rank ordered stimuli or measured them on interval scales (see Chapter 7). Opponents of these assertions remained unconvinced. They pointed out that the interlocking theory of the power law and the method that generated it were consistent, but self-justifying or circular reasoning (Birnbaum, 1982).

One problem was that category scales gave data consistent with Fechner’s log function. Indirect scales did as well, so these two methods produced a consistent system (McBride, 1983). Category scales already had widespread use in applied sensory testing at about the time Stevens was spreading the doctrines of ratio-level scaling and magnitude estimation (Caul, 1957). Given the argument that only one kind of scale could

be a true or valid representation of sensations and the fact that they were nonlinearly related (Stevens and Galanter, 1957) an “either/or” mentality soon developed. This is an unfortunate distraction for applied sensory workers. For many practical purposes, the category and magnitude scaling data are very similar, especially over the small ranges of intensities encountered in most sensory tests (Lawless and Malone 1986).

2.2.5 Empirical Versus Theory-Driven Functions

Both the log function and the power function are merely empirical observations. There are an unlimited number of mathematical relationships that could be fit to the data and many functions will appear nearly linear in log plots. An alternative psychophysical relationship has been proposed that is based on physiological principles. This is a semi-hyperbolic function derived from the law of mass action and is mathematically equivalent to the function used to describe the kinetics of enzyme–substrate relationships. The Michaelis–Menten kinetic equation states the velocity of an enzyme–substrate reaction as a function of the substrate concentration, dissociation constant, and the maximum rate (Lehninger 1975; Stryer, 1995). Another version of this equation was proposed by Beidler, a pioneering physiologist, for description of the electrical responses of taste nerves and receptor cells (Beidler, 1961). The relationship is given by

$$R = (R_{\max}C)/(k + C) \quad (2.7)$$

where R is response, R_{\max} is the maximal response, and k is the concentration at which response is half-maximal. In enzyme kinetics, k is a quantity proportional to the dissociation constant of the enzyme–substrate complex. Since taste involves the binding of a molecule to a protein receptor, it is perhaps not surprising that there is a parallel between taste response and an enzyme–substrate binding relationship. So this relationship has stirred some interest among researchers in the chemical senses (Curtis et al., 1984; McBride, 1987). In a plot of log concentration, the function forms an S-shaped curve, with an initial flat portion, a steep rise and then another flat zone representing saturation of response at high levels (see Fig. 2.4).

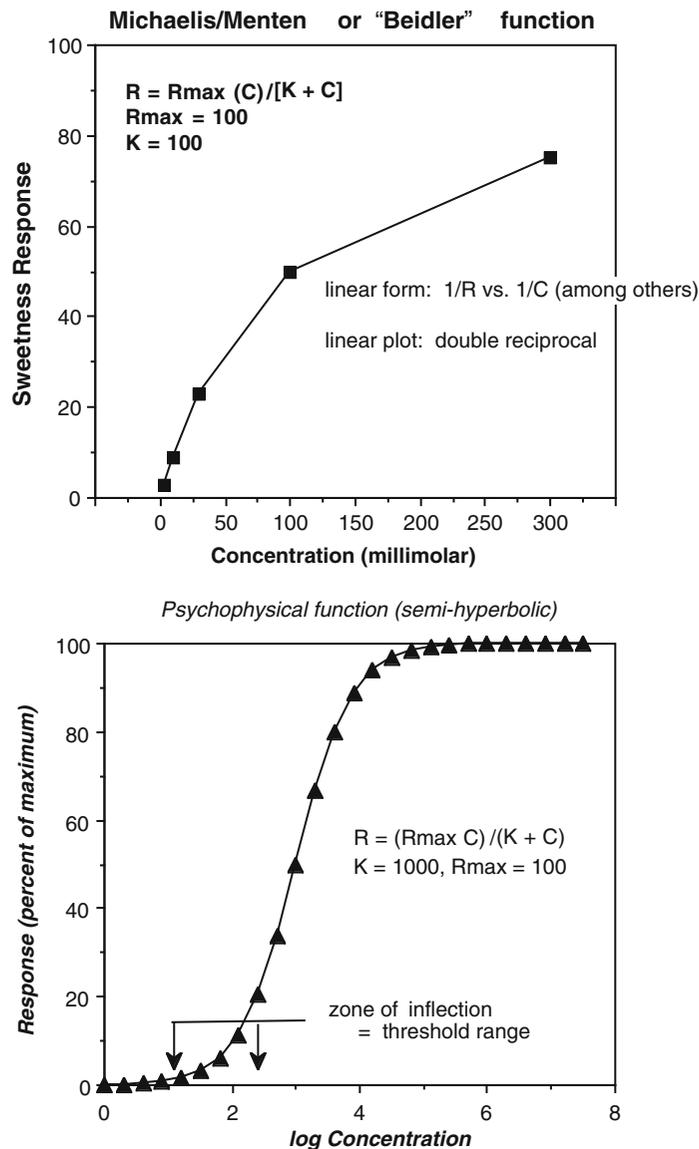


Fig. 2.4 The semi-hyperbolic relationship attributed to Beidler, cast in the same form as the Michaelis–Menten enzyme kinetic equation. This type of function is a common

form of a dose–response curve for chemical stimuli. In the lower panel the semi-log plot takes the form of an S-curve.

This is intuitively appealing. The response at levels below threshold should hover around some baseline and then grow faster as threshold is surpassed (Marin et al., 1991). The function should eventually flatten out as it approaches a maximum response as all receptor sites are filled and/or as the maximum number of taste nerves respond at their maximum rate. In other words the system must saturate at some point.

2.2.6 Parallels of Psychophysics and Sensory Evaluation

Each of the psychophysical techniques mentioned in this section has its parallel or application in applied sensory evaluation. The emphasis of sensory psychology is on studying the person as the research

object of interest, while applied sensory evaluation uses people to understand the sensory properties of products. Because any sensory event is an interaction of person and stimulus, the parallels in techniques should not surprise us. The major psychophysical research questions and methods and their sensory evaluation parallels are shown in Table 2.1. Threshold measurement has its applications in determining the minimum levels for impact of flavor compounds and the concentration ranges in which taints or off-flavors are likely to cause problems. Difference thresholds are similar in many ways to difference testing, with both scenarios making use of forced-choice or comparison procedures. Scaling is done in the psychophysics laboratory to determine psychophysical functions, but can also be used to describe sensory changes in product characteristics as a function of ingredient levels. So there are many points of similarity.

The remainder of this chapter is devoted to basic information on the structure and function of the flavor senses, since they have strong influence on the acceptability of foods. The visual and tactile senses are discussed only briefly, as separate chapters are devoted to color and visual perception generally (Chapter 12), and to texture evaluation (Chapter 11). For further information on sensory function the reader should go to basic texts on the senses such as Goldstein (1999) or the comprehensive *Handbook of Perception* (Goldstein, 2001).

2.3 Anatomy and Physiology and Functions of Taste

2.3.1 Anatomy and Physiology

Specialized sense organs on the tongue and soft palate contain the receptors for our sense of taste. Taste receptors are in the cell membranes of groups of about 30–50 cells clustered in a layered ball called a taste bud. These cells are modified epithelial cells (skin-like cells) rather than neurons (nerve cells) and they have a lifespan of about a week. New cells differentiate from the surrounding epithelium, migrate into the taste bud structure and make contact with sensory nerves. A pore at the top of the taste bud makes contact with the outside fluid environment in the mouth and taste molecules are believed to bind to the hair-like cilia at or near the opening. An illustration of this structure is shown in Fig. 2.5. Taste cells in a bud are not independently operating receptors, but make contact with each other and share junctions between cells for common signaling functions. The taste receptor cells make contact with the primary taste nerves over a gap or synaptic connection. Packets of neurotransmitter molecules are released into this gap to stimulate the taste nerves and send the taste signals on to the higher processing centers of the brain.

Table 2.1 Questions and methods in psychophysics and sensory evaluation

Question	Psychophysical study	Sensory evaluation examples
At what level is the stimulus detected?	Detection or absolute threshold measurement	Thresholds, taint investigation, flavor impact studies, dilution methods
At what level can a change be perceived?	Difference thresholds, just-noticeable-difference	Difference testing
What is the relationship between physical intensity and sensory response?	Scaling via direct numerical responses or indirect scales from difference thresholds	Scaling attribute intensity as in descriptive analysis
What is the matching relationship between two stimuli?	Adjustment procedures, trade-off relationships	Adjusting ingredients to match or optimize

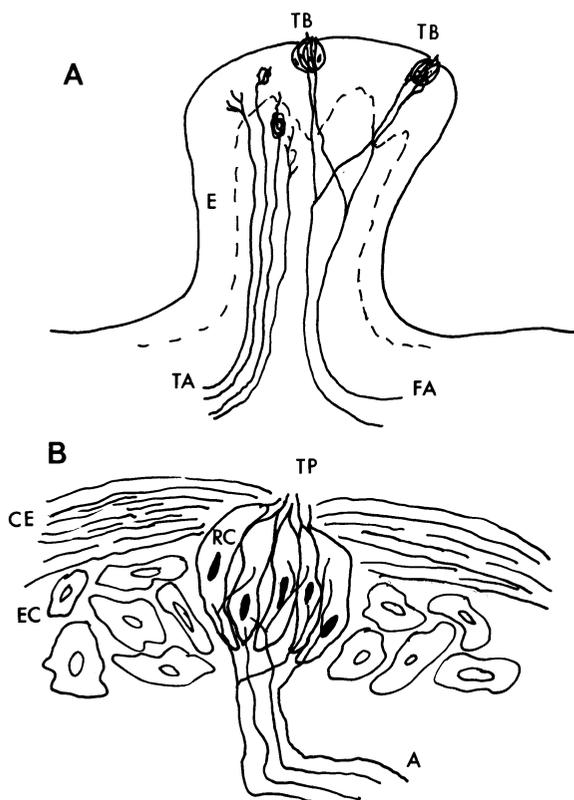


Fig. 2.5 (a) Cross-sectional drawing of a fungiform papilla. E, epithelium; TB, taste buds; TA, trigeminal afferent nerves terminating in various branched endings or encapsulated receptor structures; FA—facial nerve (chorda tympani) taste afferents terminating in taste buds. (b) Cross-sectional drawing of a taste bud. CE, cornified epithelium; EC, epithelial cells that may differentiate into taste receptor cells; RC, taste receptor cells, TP taste pore; A, axons from primary taste nerves making synaptic contact with receptor cells.

Through genetic research, the nature and types of taste receptor proteins have now been characterized. For sweet, bitter, and umami tastes, two families of receptor proteins are functional, the T1Rs for sweet and umami and the T2Rs for bitter tastes. These receptor proteins have seven transmembrane segments connected by intracellular and extracellular loops (hence “7TMs”). Figure 2.6 shows the arrangement of a 7TM with its genetically variable segments, which is also the structure of the family of odor receptors and the visual receptor, rhodopsin. The T1R proteins have about 850 amino acids and a large extracellular N-terminus, sometimes referred to as a “venus fly-trap domain” after the hypothetical pockets formed by the paired (dimer) forms of these receptors. The T2Rs

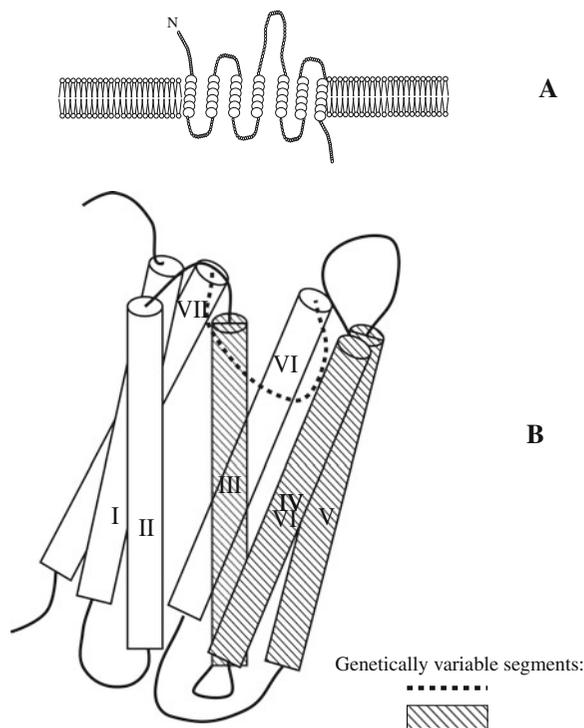


Fig. 2.6 (a) Planar schematic of a 7-transmembrane chemoreceptor protein. 7TMs have helical segments inside the membrane and several intracellular and extracellular peptide loops. The T1Rs for sweet and umami reception are associated as dimers with a long N-terminal; The T2Rs for bitter reception do not. (b) Schematic of the 7-transmembrane olfactory receptor, modeled after the structure of rhodopsin, the visual receptor protein. Transmembrane segments are symbolized by the cylinders and extracellular and intracellular loops by the heavy lines connecting them. Genetically variable segments include the barrels of segments II, IV, and V and the extracellular loop connecting segments VI and VII, making these sections candidates for a receptor pocket.

have about 300–330 amino acids and a short extracellular N-terminus (Bachmanov and Beauchamp, 2007). The two families can exist side by side in taste buds, but are expressed in different cells (Sugita, 2006). The family of T2Rs contains about 40 active human variants with 38 intact genes currently known (Bachmanov and Beauchamp, 2007). Different T2Rs may be co-expressed in the same cells. This may explain why most bitter taste substances are similar in quality and difficult to differentiate. The number and variability of this family may be responsible for the ability of mammals to react to a wide range of molecular structures among the various bitter substances. The hT2R38 variant has been identified as the receptor for molecules

such as PTC (phenylthiocarbamide or phenylthiourea) and PROP (6-*n*-propylthiouracil) to which there is a genetically based taste “blindness.” The mutations in hT2R38 responsible for this inherited insensitivity have been identified (Bufe et al., 2005; Kim et al., 2003).

The T1Rs comprise only three peptide chains in two combinations, forming heterodimers. One dimer is the T1R1/T1R2 combination that is sensitive to glutamate and thus functions as an umami taste receptor. The other dimer is a T1R2/T1R3 combination that functions as the sweet receptor. The umami and sweet receptors are expressed in different taste receptor cells. Both the T1Rs and the T2Rs are G-protein coupled receptors (GPCRs) as are olfactory and visual receptors. The G-protein is an intracellular messenger consisting of three subunits, associated to the receptor inside the cell membrane. Stimulation of the taste receptor (i.e., binding to the 7-TM) leads to separation of the G-protein subunits, which can then activate other enzyme systems within the cell, causing a cascade of amplified events. Notably, G-protein subunits may activate adenylate cyclase, leading to production of cyclic AMP and/or phospholipase C, producing inositol triphosphate (IP3) (Sugita, 2006). Both cAMP and IP3 cause further activation of intracellular mechanisms such as activation or inactivation of ion channels in the cell membrane. These events lead to calcium influx or release, which is required for binding of neurotransmitter vesicles (packets) to the cell membrane and release of neurotransmitter molecules into the synapse to stimulate the associated taste nerve.

Salt and sour taste mechanisms appear to work more directly on ion channels, rather than via GPCRs. Sodium entering the cell is responsible for a cell membrane potential change (an ionic/electrical gradient) associated with calcium influx. Various ion channels have been proposed for mediating salty taste. Protons for sour taste may enter taste receptor cells and then stimulate ion channels such as the family of acid-sensitive ion channels (ASICs) or potassium conductance channels (Bachmanov and Beauchamp, 2007; Da Conceicao Neta et al., 2007; Sugita, 2006). Evidence points to the involvement of members of the transient receptor potential family in sour transduction, specifically members of the polycystic kidney disease family of receptors (PKD, so named from the syndromes in which they were first identified) (Ishimaru et al., 2006). Recent work has also suggested a taste sensitivity to

free fatty acids, due to the presence of a fatty acid transporter, CD36, in taste receptor cells (Bachmanov and Beauchamp, 2007). This could serve as a supplement to the textural cues which are usually thought of as the main signal for fat in the oral cavity.

The taste buds themselves are contained in specialized structures consisting of bumps and grooves on the tongue. The tongue is not a smooth uniform surface. The upper surface is covered with small cone-shaped filiform papillae. These serve a tactile function but do not contain taste buds. Interspersed among the filiform papillae, especially on the front and edges of the tongue are slightly larger mushroom-shaped fungiform papillae, often more reddish in color. These small button-shaped structures contain from two to four taste buds each, on the average (Arvidson, 1979). There are over a hundred on each side of the anterior tongue, suggesting an average of several hundred taste buds in the normal adult fungiform papillae (Miller and Bartoshuk, 1991). Along the sides of the tongue there are several parallel grooves about two-thirds of the way back from the tip to the root, called the foliate papillae. Each groove contains several hundred taste buds. Other specialized structures are about seven large button-shaped bumps arranged in an inverted-V on the back of the tongue, the circumvallate papillae. They contain several hundred taste buds in the outer grooves or moat-like fissures that surround them. Taste buds are also located on the soft palate just behind where the hard or bony part of the palate stops, an important but often overlooked area for sensing taste. The root of the tongue and upper part of the throat are also sensitive to tastes. Frequency counts of taste buds show that people with higher taste sensitivity tend to possess more taste buds (Bartoshuk et al., 1994).

Four different pairs of nerves innervate the tongue to make contact with these structures. This may explain in part why the sense of taste is resistant to disease, trauma, and aging, in contrast to the sense of smell (Weiffenbach, 1991). The fungiform papillae are innervated by the chorda tympani branches of the facial nerves (cranial nerve VII), which as its name suggests, crosses the eardrum. This circuitous route has actually permitted monitoring of human taste nerve impulses during surgery on the middle ear (Diamant et al., 1965). The glossopharyngeal nerves (cranial nerve IX) send branches to the rear of the tongue and the vagus nerve (cranial X) to the far posterior areas on the tongue root. The greater superficial petrosal

branch of the facial nerve goes to the palatal taste area (Miller and Spangler, 1982; Nejad, 1986). Any one of the four classical taste qualities can be perceived on any area of the tongue, so the old-fashioned map of the tongue with different tastes in different areas is not accurate. For example, thresholds for quinine are lower on the front of the tongue than the circumvallate area (Collings, 1974).

Saliva plays an important part in taste function, both as a carrier of sapid molecules to the receptors and because it contains substances capable of modulating taste response. Saliva contains sodium and other cations, bicarbonate capable of buffering acids, and a range of proteins and mucopolysaccharides that give it its slippery and coating properties. There are recent suggestions that salivary glutamate may be capable of altering food flavor perception (Yamaguchi and Kobori, 1994). Whether saliva is actually necessary for taste response is a matter of historical controversy. At least in short time spans it does not seem to be required, as extensive rinsing of the tongue with deionized water through a flow system does not inhibit the taste response, but can actually sharpen it (McBurney, 1966).

2.3.2 Taste Perception: Qualities

Various perceptual qualities have been proposed as taste categories throughout history (Bartoshuk, 1978) but the consistent theme was that four qualities suffice for most purposes. These are the classical taste qualities of sweet, salty, sour, and bitter. Various others have been proposed to join the group of fundamental categories, most notably metallic, astringent, and umami. Umami is an oral sensation stimulated by salts of glutamic or aspartic acids. Astringency is a chemically induced complex of tactile sensations. These are discussed below. The metallic taste is occasionally used to describe the side tastes of sweeteners such as acesulfame-K and is a sensation experienced in certain taste disorders (Grushka and Sessle, 1991; Lawless and Zwillenberg, 1983). The classical four taste qualities are probably not sufficient to describe all taste sensations (O'Mahony and Ishii, 1986). However, they describe many taste experiences and have common reference materials, making them quite useful for practical sensory evaluation.

The umami sensation, roughly translated from Japanese as “delicious taste,” is attributed to the taste of monosodium glutamate (MSG) and ribosides such as salts of 5' inosine monophosphate (IMP) and 5' guanine monophosphate (GMP) (Kawamura and Kare, 1987). The sensation is distinguishable from that of saltiness, as direct comparison with equally intense NaCl solutions demonstrates. The sensation is sometimes rendered in English by the term “brothy” due to its resemblance to the sensations from bouillon or soup stocks. “Savory” or “meaty” are alternatives (Nagodawithana, 1995). The taste properties of glutamate and aspartate salts form the building blocks of flavor principles in some ethnic (notably Asian) cuisines, and so perhaps it is not surprising that Japanese, for example, have no difficulty in using this taste term (O'Mahony and Ishii, 1986). Occidental subjects, on the other hand, seem to be able to fractionate the taste into the traditional four categories (Bartoshuk et al., 1974). Many animals including humans possess receptors for glutamate (Scott and Plata-Salaman, 1991; Sugita, 2006).

2.3.3 Taste Perception: Adaptation and Mixture Interactions

The sense of taste has two important functional properties that also have parallels in the sense of smell, sensory adaptation, and mixture interactions. Adaptation can be defined as a decrease in responsiveness under conditions of constant stimulation. It is a property of sensory systems that act to alert an organism to changes; the status quo is rarely of interest. We become largely adjusted to the ambient level of stimulation, especially in the chemical, tactile, and thermal senses. Placing your foot in a hot bath can be alarming at first, but the skin senses adapt. Our eyes constantly adapt to ambient levels of light, as we notice upon entering a dark movie theater. We are generally unaware of the sodium in our saliva, but rinsing the tongue with deionized water and representing that concentration of NaCl will produce a sensation above threshold. Adaptation is easily demonstrated in taste if the stimulus can be maintained on a controlled area of the tongue, for example, when a solution is flowed over the extended tongue or through a chamber (Kroeze, 1979;

McBurney, 1966). Under these conditions, most taste sensations will disappear in a minute or two. However, when the stimulus is not so neatly controlled, as in eating or in pulsatile stimulation, the adaptation is less robust and in some cases disappears (Meiselman and Halpern, 1973).

One other important discovery accompanied experiments on taste adaptation. Concentrations of NaCl or any other tastant below the adapting level—of which pure water was the extreme example—would take on other taste qualities. Thus water after salt adaptation can taste sour and/or bitter. Water tastes sweet after quinine or acid and tastes bitter after sucrose (McBurney and Shick, 1971). Figure 2.7 shows the response to concentrations of NaCl after different adaptation conditions. Above the adapting concentration, there is a salty taste. At the adapting concentration, there is little or no taste. Below the adapting concentration there is a sour–bitter taste that is strongest when water itself is presented. Water can take on any one of the four qualities, depending upon what has preceded it. This should alert sensory evaluation workers to the need for controlling or at least considering the effects of taste adaptation. Both the solvent and the taste molecules themselves can elicit sensory responses.

A second feature of taste function is the tendency for mixtures of different tastes to show partially inhibitory or masking interactions. Thus a solution of quinine and sucrose is less sweet than an equal concentration of sucrose tasted alone (i.e., when the sucrose in the two solutions is in equimolar concentration). Similarly the mixture is less bitter than equimolar quinine tasted alone. The general pattern is that all four classical taste qualities show this inhibitory pattern, commonly called mixture suppression (McBurney and Bartoshuk, 1973). In many foods these interactions are important in determining the overall appeal of the flavors and how they are balanced. For example, in fruit beverages and wines, the sourness of acids can be partially masked by sweetness from sugar. The sugar thus serves a dual role—adding its own pleasant taste while decreasing the intensity of what could be an objectionable level of sourness (Lawless, 1977). Some of these mixture inhibition effects, like the inhibition of bitterness by sweetness, appear to reside in the central nervous system (Lawless, 1979) while others, such as the inhibition of bitterness by salt, are more likely due to peripheral mechanisms at the receptors themselves (Kroeze and Bartoshuk, 1985).

There are a few exceptions to the pattern of inhibition where hyperadditive relationships, sometimes

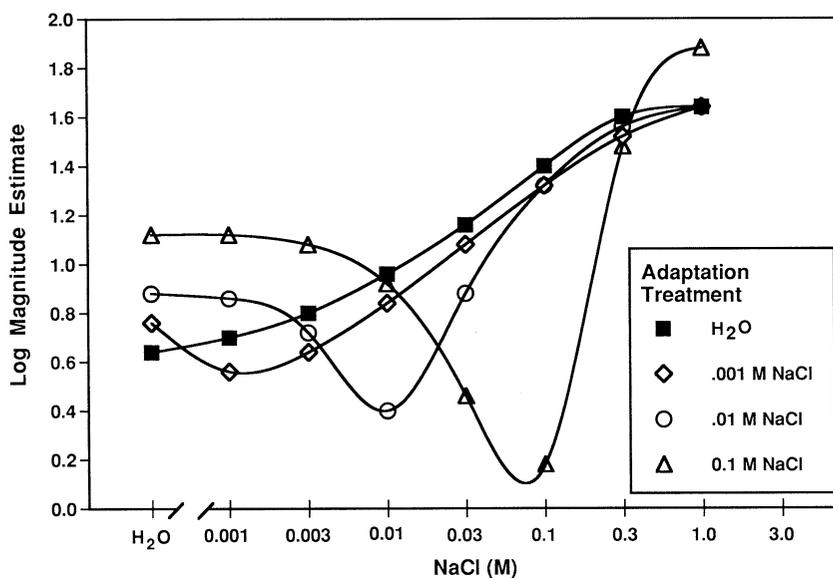


Fig. 2.7 Taste and water taste of NaCl following different adapting concentrations. The key shows the adapting (pretreatment) concentrations. Taste intensity reaches a minimum at each adapting level. Above the adapting levels, increased salty taste is

reported. Below the adapting level, sour–bitter taste is reported, reaching a maximum with water. (from McBurney (1966), copyright 1966, by the American Psychological Association, reprinted with permission).

called enhancement or synergism occur. Hyperadditive effects imply that there is a higher taste intensity in the mixture than would be predicted on the basis of simple addition of component effects. However, how this outcome is predicted is controversial (Ayya and Lawless, 1992; Frank et al., 1989b). The most well-known claim of synergy is the interaction of MSG with the ribosides mentioned above. These are clearly hyperadditive by any definition. Addition of even small subthreshold amounts in mixtures will produce strong taste sensations (Yamaguchi, 1967) and there is strongly interactive binding enhancement at taste receptors that could be the physiological reason for this effect (Cagan, 1981). A second area of enhancement is seen with sweetness from salt in low concentrations added to sugar. NaCl has an intrinsic sweet taste seen at low levels that is normally masked by the saltiness at higher levels (Bartoshuk et al., 1978; Murphy et al., 1977). This may explain some of the beneficial effects of small amounts of salt in foods. A third case of hyperadditivity appears in the sweetener mixtures (Ayya and Lawless, 1992; Frank et al., 1989b). The search for synergistic mixtures of sweeteners and of other flavors is ongoing, due to the potential cost savings in this food ingredient category.

Finally, one can ask what happens to mixture suppression when one or more of the components has reduced impact? Figure 2.8 shows a release from

inhibition that follows adaptation to one component of a mixture. Both the sweetness of sucrose and the bitterness of quinine are partially suppressed when present in a mixture. After adaptation to sucrose, the bitterness of a quinine/sucrose mixture rebounds to the level it would be perceived at in an equimolar unmixed quinine solution (Lawless, 1979). Likewise the sweetness rebounds after the bitterness is reduced by adaptation to quinine. These interactions are quite common in everyday eating. They can be easily demonstrated during a meal with tasting wines, since many wines contain sugar/acid (sweet/sour) taste mixtures. A wine will seem too sour after eating a very sweet dessert. Similarly, tasting a wine after eating a salad dressed with vinegar makes the wine seem too sweet and lacking in acid (“flabby”). These are simply the adapting effects upon the components of the wine, decreasing some tastes and enhancing others through release from inhibition. A similar effect can be seen in mixtures of three components, especially with salt. In a bitter-sweet mixture of urea and sucrose, for example, the usual suppression of bitterness and sweetness will be observed. But when a sodium salt is added to the mixture, there is a disproportionate effect of the salt inhibiting the bitter taste and consequently the sweet taste is enhanced (Breslin and Beauchamp, 1997). This effect is another explanation of the reported flavor enhancement in various foods when salt is added.

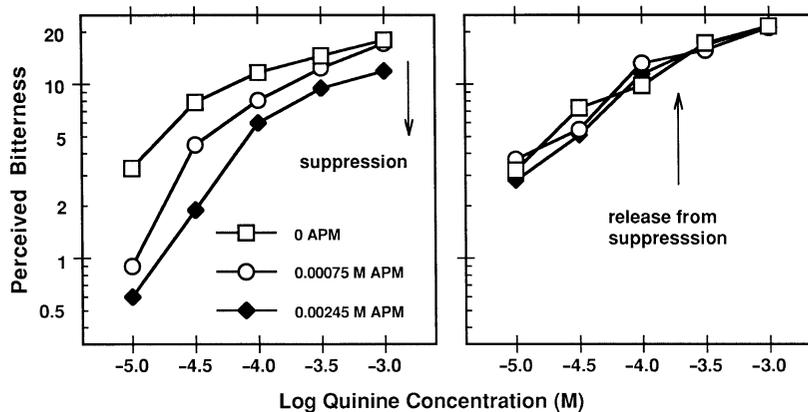


Fig. 2.8 Mixture suppression and release. The *left panel* shows perceived bitterness of quinine (*filled circles*) and mixtures with 0.00075 M aspartame (*squares*) and 0.00245 M aspartame (*open circles*) following adaptation to water. Mixture suppression is shown by reduced bitterness when the sweet taste is present

in the mixtures. The *right panel* shows the same items after adaptation to sucrose, reducing the sweetness and returning the bitterness to its unsuppressed level (from Lawless (1979), copyright 1979, by the American Psychological Association, reprinted with permission).

2.3.4 Individual Differences and Taste Genetics

Wide individual differences in taste sensitivity exist, particularly for bitter compounds. The best example of this is the genetically inherited insensitivity to compounds containing the functional group $-N-C \equiv S$ typified by certain aromatic thiourea compounds. This taste “blindness” was primarily studied using the compound phenylthiourea, originally called phenylthiocarbamide or PTC (Blakeslee, 1932; Fox, 1932). Due to the potential toxicity of PTC as well as its tendency to give off an odor, more recent studies have used the compound 6-*n*-propylthiouracil (PROP) which is highly correlated with PTC response (Lawless, 1980). Their structures are shown in Fig. 2.9. The minimum detectable concentrations (thresholds) of these compounds, PTC and PROP, follow a bimodal

distribution, with about 1/3 of Caucasian persons unable to detect the substance at the concentration detected by most people. Threshold tests as well as ratings for bitterness above threshold both allow differentiation into “taster” (sensitive) and “nontaster” (insensitive) groups (Lawless, 1980). Nontasters have a modification in the TAS2R38 taste receptor and show a simple Mendelian pattern of inheritance. Many other bitter substances such as quinine also show wide variation (Yokomukai et al., 1993), but none so dramatic as PTC and PROP.

Recent studies have identified hypersensitive groups of “supertasters” and counts of papillae and taste buds are correlated with taste sensitivity and responsiveness (Miller and Bartoshuk, 1991). Due to the enhanced trigeminal innervation in such individuals with a higher papillae density, it is perhaps not surprising that a relationship between PROP sensitivity and some lingual tactile sensations such as the sensitivity

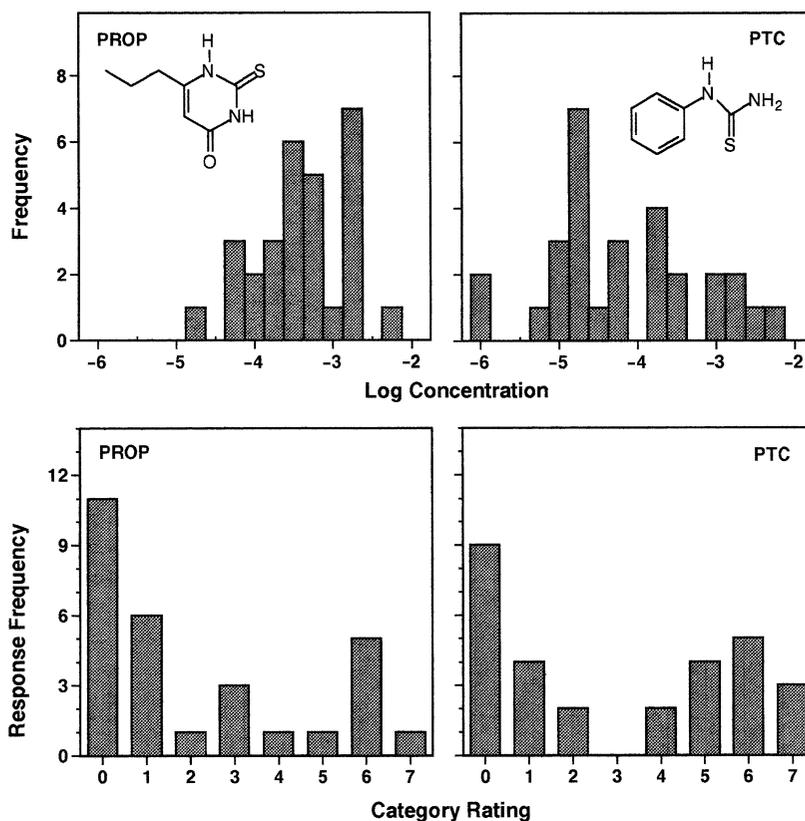


Fig. 2.9 PTC and PROP detection thresholds (*left panels*) and perceived intensity ratings (*right panels*) of 0.0001 M PTC and 0.00056 M PROP (from Lawless (1980), by permission of Information Retrieval Limited (IRL) and Oxford University

Press). Note that PTC gives a better separation of taster and nontaster groups, especially with the perceived intensity ratings.

to fat have been found. A large number of other correlates to PROP sensitivity have been observed including sensitivity to the bitterness of caffeine, saccharin, and responses to capsaicin (Bartoshuk, 1979; Hall et al., 1975; Karrer and Bartoshuk, 1995). However, many of these correlations are low and some lower than the correlations among traditional tastants (Green et al., 2005, see also Schifferstein and Frijters, 1991). The current view, then, is that taste and chemesthesis are mostly independent systems and the sensory professional should be cautious in trying to use any general marker like PROP sensitivity as a predictor of individual response (Green et al., 2005). A potentially important finding is that persons who are insensitive to a bitter compound such as PTC will not show some mixture suppression effects (since they perceive no bitterness, there is no inhibition) on other flavors (Lawless, 1979). This illustrates a more general principle, that depending upon what we *do not* sense in a product, the other flavors may be enhanced for us, in a similar fashion to the effect of release from suppression.

2.4 Anatomy and Physiology and Functions of Smell

2.4.1 Anatomy and Cellular Function

The olfactory receptors are located in two small portions of epithelium very high in the nasal cavity. This remote location may serve some protective function against damage, but it also means that only a small percentage of the airborne substances flowing through the nose actually reach the vicinity of the sensory organs. In order to counter this factor, the olfactory sense has several attributes that enhance its sensitivity. There are several million receptors on each side of the nose and they have a terminal knob protruding into the mucus with about 20–30 very fine cilia which “float” in the mucus layer (Fig. 2.10). One function of these cilia is to increase the surface area of the cell, exposing the receptors to chemical stimuli. The main body of the olfactory receptor cells lies inside the epithelium and they each send a thin axon into the olfactory bulbs.

Another anatomical amplification factor is that the millions of receptors send nerve fibers into a much

smaller number (perhaps 1,000) of glomerular structures in the olfactory bulb, after passing through a bony plate in the top of the nose. The glomeruli are dense areas of branching and synaptic contact of the olfactory receptors onto the next neurons in the olfactory pathway. Several thousand olfactory sensory neurons converge onto only 5–25 mitral cells in each glomerulus (Firestein, 2001). The mitral cells in turn send axons onto more central brain structures. The olfactory nerves project to many different sites in the brain, some of them closely associated with emotion, affect, and memory (Greer, 1991).

Unlike the taste receptors that are modified epithelial cells, the olfactory receptors are true nerve cells. They are unusual neurons in that they have a limited life span—they are replaced in about a month. The ability of the olfactory system to maintain its functional connections in the face of this turnover and replacement is a great puzzle of neural science. Other parts of the nervous system do not readily regenerate when damaged, so unlocking the mystery of olfactory replacement may provide benefits to those suffering from nervous system damage. The olfactory system is not immune from damage, however. A common injury occurs when a blow to the head severs the nerve fibers from the olfactory receptors as they pass through small passages in the bony cribriform plate on their way into the olfactory bulbs. This is sometimes self-repairing but often is not, leaving the individual without a functioning sense of smell, and therefore deprived of most food flavor perception for life. Sensory panel leaders need to be aware of the condition of total loss of smell, called anosmia, and screen panelists for sensory analysis duties with tests of olfaction such as a smell identification tests (Doty, 1991).

The mechanisms of odor reception are now well understood, starting with the discovery of a family of about 1,000 genes for olfaction in mammals, a discovery that earned Buck and Axel the Nobel Prize in 2004 (Buck and Axel, 1991). This may be the single largest gene family in the human genome. About 350 of these receptor types are active in humans. The receptors are G-protein coupled receptors, like the bitter receptors and visual receptor molecules. They have a sequence indicating seven transmembrane segments connected by intracellular and extracellular loops and have short N-terminals, like the bitter family of T2R receptors. Within the peptide sequences, there are from 10 to 60% variability (Firestein, 2001) with strong divergence in

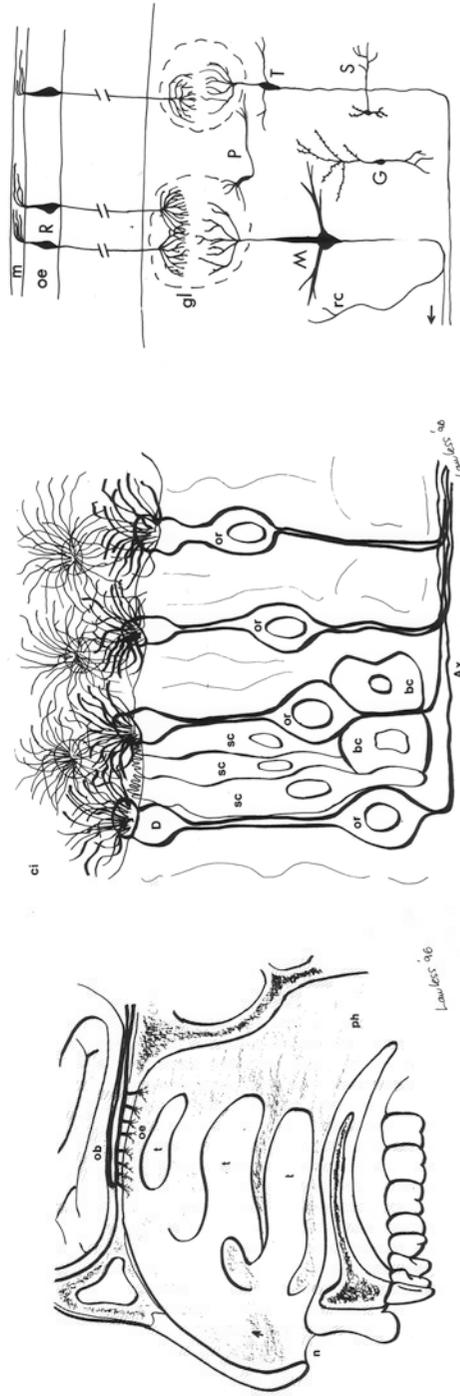


Fig. 2.10 *Left panel* gross nasal anatomy, n, external nares; t, turbinate bones or nasal conchae; ph, nasopharynx; ob, olfactory bulb at the base of the anterior cerebrum; oe, olfactory epithelium. Axon tracts leaving the olfactory epithelium pass into the bulb through small openings the cribriform plate. *Center panel* Diagram of olfactory epithelium. ci, cilia; D, dendritic termination of olfactory receptor cell; or, olfactory receptor cells; sc, supporting cells; bc, basal cells; Ax axon bundles. *Right Panel* basic cells types in the olfactory bulb. Olfactory receptors (R) send axons to glomeruli (gl) to make contact with apical dendrites of mitral (M) and tufted (T) cells, the output neurons from the bulb to higher structures. Cross-connections (some inhibitory) within layers are made by periglomerular cells (P), short axon cells (S), and granule cells (G) as well as recurrent collateral axons (rc), m, mucous layer containing olfactory receptor cell cilia; oe, olfactory epithelium.

the third, fourth, and fifth transmembrane regions (see Fig. 2.6). These three “barrels” face one another and may form a receptor pocket about 1/3 of the way into the membrane. Identifying the kinds of molecules (ligands) that bind in these pockets has proven difficult due to the difficulty in expressing olfactory receptors in model systems. In the one case in which this was successful, the receptor was found to be specifically tuned to octanal and very similar molecules (Zhao et al., 1998).

The intracellular mechanisms for stimulation are similar to those of the G-coupled receptors in taste. Binding to the receptor results in activation of the G-protein subunits, which in turn activate enzymes such as adenylyl cyclase. This turns ATP into cyclic AMP which in turn activates various ion channels. An influx of Na⁺ and Ca⁺⁺ ions causes the inside of the cell to become less negatively charged and when this membrane potential reaches a 20 mV threshold, an action potential is generated that travels down the nerve axon and results in neurotransmitter release. This is an amplification process, as the enzyme cascade can create about a thousand molecules of cAMP per second and hundreds of thousands of ions can cross through each open channel (Firestein, 2001). The calcium ions also open an outward flowing chloride ion channel, which serves as a kind of intracellular battery to reinforce the membrane potential change.

Different odor qualities are seen in spatial patterns (Kauer, 1987). Each odor receptor cell expresses only one type of receptor protein. Receptor cells with the same protein project to the same set of glomeruli. Similar odors also tend to map onto overlapping regions (Firestein, 2001). So different odors are represented by activation of different segments of the olfactory bulb. However, the matter is somewhat complicated by the fact that receptors are tuned to multiple odor molecules, and conversely, many odor molecules can stimulate a wide array of receptors. This has led to the combinatorial code for odor quality (Malnic et al., 1999). The brain recognizes the pattern of response across the array of neurons in order to “decide” on the odor quality or type. Viewed this way, olfaction appears to be the prototypical pattern recognition mechanism. Such a code can explain why some odors change in their quality when the concentration increases. Additional receptors with higher thresholds for that compound are recruited as concentrations increase, altering the patterned array.

2.4.2 Retronasal Smell

Arguably, the largest contribution to the diversity of flavors comes from the volatile airborne molecules sensed by the olfactory receptors. Whether sniffed through the external nares in the direction of normal inspiration or arising from odors present in the mouth, the vast diversity of what we come to know as food flavors is mediated by smell. Due to the tendency to localize aromatics from foods in the mouth, many people do not realize that the olfactory sense is responsible for sensing most flavors other than the simple five tastes described above. Much of what we normally speak of as taste is really smell (Murphy et al., 1977; Murphy and Cain, 1980). The lemon character of a lemon, for example, is derived not from lemon taste (which is only sour, sweet, and bitter) but from the terpene aroma compounds that arise in the mouth and pass up into the nasal cavity from the rear direction (retronasally), opposite to that from sniffing. This highlights the dual role of olfaction as both an external sensory system and an internal sensory system (Rozin, 1982).

A simple demonstration can convince anyone of the importance of this internal smelling or retronasal smell. Take a sip of a simple fruit beverage or juice while holding the nose pinched shut. Take care to note the sensations present in the mouth, primarily the sweet and sour tastes. Now swallow the sample and while keeping the mouth shut, release the nostrils and exhale. In about a second or so, the fruit flavor will appear. Pinching the nose shut effectively blocks the retronasal passage of flavor volatiles up to the olfactory receptors (Murphy and Cain, 1980). When that route is facilitated by swallowing and exhaling, the contribution of smell becomes clear. The tendency of people to label internal smells as “tastes” probably contributes to the claims of sweetness enhancement by volatile flavors such as vanilla and maltol. This is a simple mislocation and mislabeling of the sensation (see Chapter 9). Learning to distinguish aromatics from true tastes is one of the first tasks in panel training for any sensory analysis of food flavor. Note that volatiles in the oral cavity may also have stimulatory effects there, but these seem to be limited to trigeminal stimuli such as menthol (Halpern, 2008). In most respects, orthonasal and retronasal smells are qualitatively similar.

It has been claimed that most (or even all) of retronasal smell arises from a kind of pumping action of air into the nose when people swallow, a so-called swallow breath (Buettner et al., 2002). However, a simple demonstration of exhalation without swallowing shows that this is not the only mechanism for retronasal smell: Take a small volume of liquid into the mouth and swirl it around. Expectorate. Do not swallow! Breathe in while holding the nose pinched shut. Release the nasal pinch and breathe out. There will be a clear impression of the volatile flavors that are perceived by retronasal smell. This kind of exhalation-induced flavor perception (a matter of smell) is commonly practiced by judges such as wine tasters when they differentiate aroma in the glass from aroma in the mouth. So the swallow breath is not absolutely required for retronasal smell. The swallow breath may be an important part of perception during normal eating, but it may be supplemented by other mechanisms in both eating and formal sensory evaluations.

2.4.3 Olfactory Sensitivity and Specific Anosmia

The olfactory sensitivity of humans and other animals is remarkable. Our ability to detect many potent odorants at very low concentrations still surpasses the sensitivity of nearly all instrumental means of chemical analysis. Many important flavor compounds are detectable in the parts per billion range, such as sulfur-containing compounds like ethyl mercaptan, a cabbage or skunk-like compound, so potent that it is employed as a gas odorization agent. Some food flavors are even more potent, like the methoxy pyrazine compounds that occur in bell peppers. Other small organic molecules are not so effective at stimulating the olfactory sense. The vast array of terpene aroma compounds responsible for citrus, herbal, mint, and pine-like aromas are usually potent in the parts-per million range. In contrast, alcohol compounds like ethanol are only sensed when their concentrations reach parts per thousand, so although we may think of alcohol as “smelly,” in contrast to potent chemicals such as the pyrazines, it is not a very effective odor molecule.

A danger in flavor research is to assume that since a chemical has been identified in a product, and that chemical has an odor when smelled from a bottle that

resembles the natural flavor, it will necessarily contribute to the flavor in the natural product. For example, limonene has been often used as a marker compound for orange juice aroma, but analysis of orange samples shows that it is often present well below threshold (Marin et al., 1987). It has the status of a “red herring” or a misleading compound. The critical question is whether the concentration in the product exceeds the threshold or minimum detectable concentration. Compounds present below their thresholds are unlikely to contribute to the perceived flavor, although some summation of the effects of similar compounds is always a possibility. This kind of threshold analysis for estimating flavor impact is discussed further in Chapter 6. The approach uses “odor units”—multiples of threshold—as evidence of a potential sensory contribution.

Thresholds are highly variable both within and across individuals (Lawless et al., 1995; Stevens et al., 1988). Some individuals with an otherwise normal sense of smell are unable to detect some families of similar smelling compounds. This is a condition called specific anosmia, as opposed to general anosmia or a total inability to smell. Specific anosmia is operationally defined as a condition in which an individual has a smell threshold more than two standard deviations above the population mean concentration (Amoore et al., 1968; Amoore, 1971). Common specific anosmias include an insensitivity to the following compounds of potential importance in foods: androstenone, a component of boar taint (Wysocki and Beauchamp, 1988); cineole, a common terpene component in many herbs (Pelosi and Pisanelli, 1981); several small branched-chain fatty acids important in dairy flavors (Amoore et al., 1968; Brenndand et al., 1989); diacetyl, a lactic bacteria by-product (Lawless et al., 1994); trimethyl amine, a fish spoilage taint (Amoore and Forrester, 1976); isobutyraldehyde, responsible for malty flavors (Amoore et al., 1976); and carvone, a terpene in mint and other herbs (Pelosi and Viti, 1978, but see also Lawless et al., 1995). A sensory panel leader must be aware that each panel member has somewhat different olfactory equipment and that it may not be possible to force a panel into total agreement on all flavors. Also, a panelist with one specific anosmia may be a poor judge of that particular odor, but may function perfectly well on most other flavors. It makes little sense to exclude this panelist from participation unless the odor in question is a key component of all the

foods being evaluated. This diversity presents a challenge in panel screening and detection of outliers in data analysis.

The sense of smell has a rather poor ability to discriminate intensity levels. This is observed in several ways. Measured difference thresholds for smell are often quite large compared to other sense modalities (Cain, 1977) and the power function exponents are often quite low (Cain and Engen, 1969). Early experiments on the ability of untrained subjects to identify or consistently label odor categories showed that people could reliably identify only about three levels of odor intensity (Engen and Pfaffmann, 1959). However, not all of the problem may be in the nose. In reviewing the historical literature on differential sensitivity, Cain (1977) reported that the Weber fraction (Section 2.2.1) falls in the range of about 25–45% for many odorants. This is about three times the size of the change needed to discriminate between levels of auditory or visual stimuli. Much of the problem was due to variation in the physical stimulus as confirmed by gas chromatography. The sniff bottles' concentration variation was highly correlated with discrimination performance, with stimulus variation accounting for 75% of the variance in discrimination. Thus historical estimates of odor difference thresholds may be too high.

2.4.4 Odor Qualities: Practical Systems

In contrast to its limited ability to distinguish intensity changes, the sense of smell provides us with a remarkably wide range of odor qualities. Experiments on odor identification show that the number of familiar odors people can label is quite large, seemingly with no upper bound (Desor and Beauchamp, 1974). However, the process of labeling odors itself is not easy. Often we know a smell but cannot conjure up the name, called a tip-of-the-nose phenomenon, in an analogy to saying a word is “on the tip of your tongue” (Lawless, 1977). This difficulty in verbal connection is one reason why many clinical tests of smell use a multiple choice format (Cain, 1979; Doty, 1991) to separate true problems in smelling from problems in verbal labeling. Our sense of smell is also limited in the ability to analytically recognize many components in complex odor mixtures (Laing et al., 1991;

Laska and Hudson, 1992). We tend to perceive odors as whole patterns rather than as collections of individual features (Engen and Ross, 1973; Engen, 1982). This tendency makes odor profiling and flavor description a difficult task for sensory panelists (Lawless, 1999). It seems more natural to react to odors as pleasant or unpleasant. The analytical frame of mind for odor and flavor perception demanded in sensory analysis is more difficult.

In spite of the common adage in psychology texts that there is no accepted scheme for classifying primary odors, there is quite strong agreement among flavor and fragrance professionals about categories for smells (Brud, 1986). Perfumers share a common language, developed in part on the basis of perceptual similarities within categories (Chastrette et al., 1988) and upon the sources of their ingredients. However, these schemes are generally unfamiliar to those outside these professions and may seem laden with technical jargon. Odor classification poses several challenges and problems. First, the number of differentiable categories is large. Early attempts at odor classification erred on the side of oversimplification. An example is Linnaeus's seven categories: aromatic, fragrant, musky, garlicky, goaty, repulsive, and nauseating, to which Zwaardemaker added ethereal and burned. A second impediment to the understanding of odor classification outside the flavor and fragrance world is that many of the original categories derive from the source materials of vendors of such ingredients. Thus they have a class for aldehydic (from aldehydes used as perfume fixatives, later an important ingredient in perfumes such as Chanel No. 5) and a class for balsamic fragrances. This nomenclature can seem a bit mysterious to the outsider. Balsamic fragrances include pine-woody sorts of smells combined with sweeter smells like vanilla. This example raises the question whether the perfumery categories can be broken down into more basic elements. Another approach to the problem proposed that odor categories be based on specific anosmias, since they may represent lack of a specific receptor type for a related group of compounds (Amoore, 1971). However, such attempts so far reduce to systems that are too small.

Nonetheless, there is considerable agreement among workers in different fields about quality categories for smells. For example, Table 2.2 shows a practical descriptive system for fragrances in consumer products derived solely from the experience

Table 2.2 Odor category systems

Functional odor categories ^a	Factor analysis groups ^b
Spicy	Spicy
Sweet (vanilla, maltol)	Brown (vanilla, molasses)
Fruity, non-citrus	Fruity, non-citrus
Woody, nutty	Woody
	Nutty
Green	Green
Floral	Floral
Minty	Cool, minty
Herbal, camphoraceous (other)	Caraway, anise
	Animal
	Burnt
	Sulfidic
	Rubber

^aDescriptive attributes derived via principles of non-overlap and applicability to consumer products

^bFactor analysis groups derived from ratings of aroma compounds on 146 attribute list

and intuition of the panel leaders during training. The second system is based on a categorization of tobacco flavors derived from a factor analysis of hundreds of odor terms and aromatic compounds (Civille and Lawless, 1986; Jeltema and Southwick, 1986). Given the different approaches and product areas, the agreement is surprisingly parallel. The terms for the tobacco work were derived from the ASTM list of odor character notes that contain 146 descriptors. This list provides a useful starting point for odor description (Dravnieks, 1982) but it is far from exhaustive and contains both general and specific terms. Other multivariate analyses of fragrance materials have yielded systems with similar categories (<20) (Zarzo and Stanton, 2006).

Other terminology systems for aromatic flavors have been developed for specific industries. This narrows the problem somewhat and makes the task of developing and odor classification system more manageable. One popular system is shown in Fig. 2.11 for wine aroma, arranged in a wheel format with hierarchical structure (Noble et al., 1987). A similar approach was taken with a circular arrangement of beer flavor terms (Meilgaard et al., 1982). The outer terms represent fairly specific aroma notes. Each outer term has an associated recipe for a flavor standard to act as a prototype/standard for training wine panelists. The system has embedded category structure that makes it easy to use. Interior terms act as more general categories subsuming the more specific outer terms. The

more general terms have practical value. Sometimes a wine may have some fruity character, but this will not be sufficiently distinct or specific to enable the panelist to classify the aroma as a specific berry, citrus, or other fruit. In that case there is some utility in having panelists simply estimate the general (overall) fruity intensity. Different parts of the wheel may apply more or less to different varietal wines and slightly different versions may evolve for different wine types, e.g., for sparkling wines.

2.4.5 Functional Properties: Adaptation, Mixture Suppression, and Release

An important operating characteristic of the flavor senses is their tendency to adapt or to become unresponsive to stimuli which are stable in space and time. This is perhaps most obvious for olfaction in everyday life. When one enters the home of a friend, we often notice the characteristic aroma of the house—the residual smells of their cooking and cleaning, personal care products, of babies or smokers, of pets or perfumes. These odors seem to characterize and permeate a house in its carpets and draperies. After several minutes, these aromas go largely unnoticed by a visitor. The sense of smell has adapted. There is no new information coming in, so attention and sensory function turn in other directions. In smell, like taste and the thermal senses, adaptation can be profound (Cain and Engen, 1969).

The sense of smell also shows mixture interactions. Odors of different qualities tend to mask or suppress one another, much like mixture suppression in taste. This is how most air fresheners work, by a process of odor counteraction via intensity suppression. The effect can easily be seen in two component mixtures where the odors are very different and easily separated perceptually, like lavender oil and pyridine (Cain and Drexler, 1974). Figure 2.12 shows pyridine/lavender mixtures, estimates of the intensity of the pyridine component at different levels of lavender, and estimates of the lavender intensity at different levels of pyridine (from Lawless, 1977). Odor intensity decreases as a function of the concentration of the other component. Such intensity interactions are most likely common in all complex food flavors.

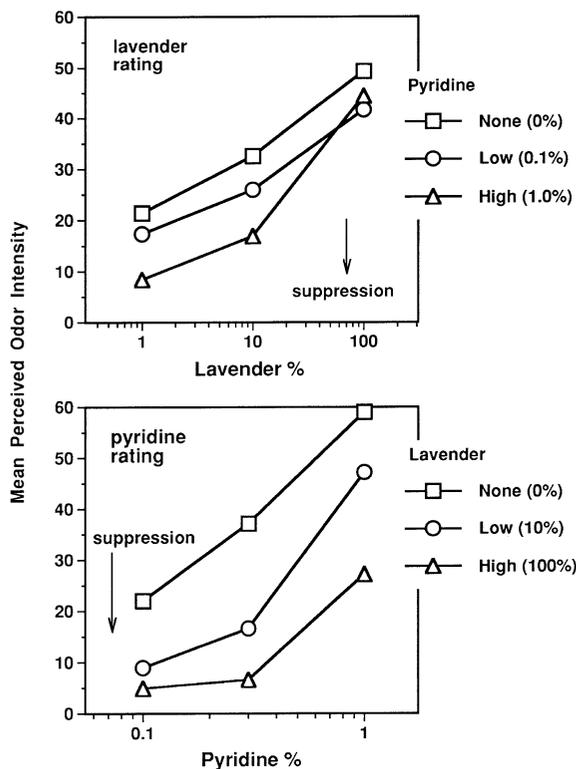


Fig. 2.12 Odor mixture inhibition in mixtures of lavender oil and pyridine. Decreased intensity of lavender is seen as a function of mixture with pyridine odor (*upper panel*) and decreased pyridine odor as a function of mixture with lavender (*lower panel*) (from Lawless, 1977 with permission).

Odor quality interactions are less predictable. Some odors seem to blend while others remain distinct. In general, odor mixtures bear a resemblance in their character to the quality characteristics of the individual components. For example, Laing and Wilcox (1983) showed that in binary mixtures, the odor profiles were generally similar to or predictable from the profiles of the components, although any intensity mismatch tended to favor the dominant component at the expense of the weaker item. This would suggest that emergent qualities or deriving a completely new odor as a function of mixing is rare. However, anecdotes exist about multicomponent mixtures in which the odor of the emergent pattern is not clearly present in any single component. For example, a mixture of ten or so medium chain aldehydes (C6–C16) produces a smell reminiscent of old wax crayons (Lawless, 1996). Furthermore, natural flavors consist of mixtures of many chemical components and no single

chemical may possess the odor quality characteristic of the blend. The odor of cocoa is a distinctive smell, but it is difficult to find any single chemical component which produces this impression. In an analysis of cheese aroma by gas chromatographic sniffing, the components had no cheese aromas in their individual characteristics (Moio et al., 1993). Burgard and Kuznicki (1990) noted that such synthesis may be the rule: “Coffee aroma is contributed to by several hundreds of compounds, a great many of which do not smell anything like coffee” (p. 65).

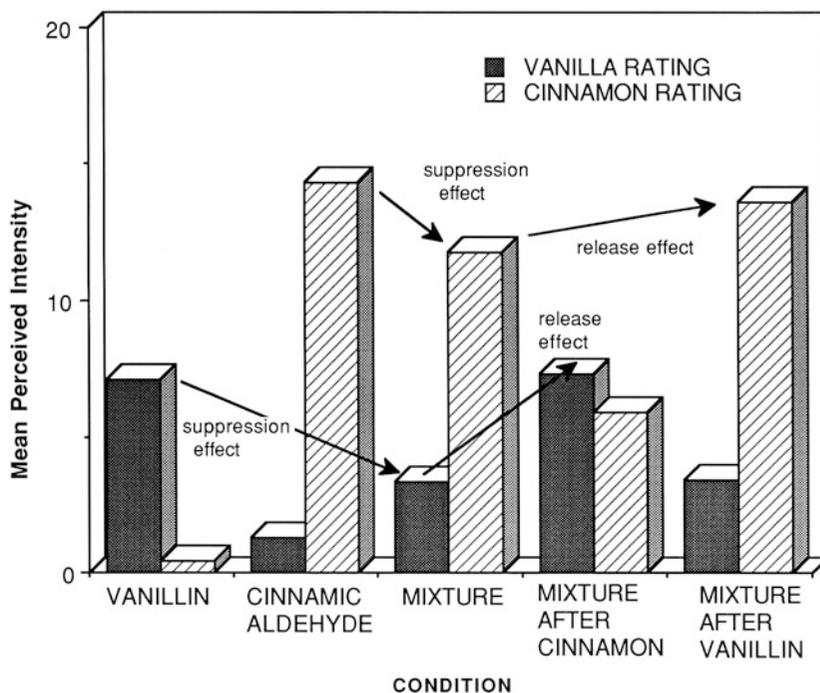
2.5 Chemesthesis

2.5.1 Qualities of Chemesthetic Experience

A variety of chemically induced sensations can be perceived in the oral and nasal cavities as well as the external skin. These chemically induced sensations do not fit neatly into the traditional classes of tastes and smells. They are called chemesthetic sensations in an analogy to “somesthesis” or the tactile and thermal sensations perceived over the body surface (Green and Lawless, 1991; Lawless and Lee, 1994). Many of these sensations are perceived through stimulation of the trigeminal nerve endings in the mouth, nose, or eyes. They include the heat-related irritative sensations from chili pepper and other spices, the non-heat related irritations from horseradish, mustard, and wasabi, the lachrymatory (tear-inducing) stimuli from onions, the cooling sensations from menthol and other cooling agents, and irritation from carbon dioxide. Other classes of sensations that are sometimes grouped with these are astringency, which is a chemically induced tactile sensation and the so-called metallic taste. Others could be added, but they are beyond the scope of this text. The ones discussed here are the common and major types of experiences found in foods and consumer products.

The importance of chemesthesis is evident from anatomical and also economic considerations. Much of the chemesthetic flavor sensations are mediated by the trigeminal nerves and the size of the trigeminal tracts relative to the other chemical sense nerves is impressive. One study found three times as many trigeminal fibers in the fungiform papillae of the rat than the facial

Fig. 2.13 Odor mixture inhibition and release following adaptation in mixtures of vanillin and cinnamaldehyde. *Open bars*, perceived intensity of vanilla odor; *Hatched bars*, perceived intensity of cinnamon odor. After adaptation to vanillin, the cinnamon odor returns to its unmixed level. After adaptation to cinnamaldehyde, the vanilla odor returns to its unmixed level (from Lawless (1984) with permission of the Psychonomic Society).



(taste) nerve fibers innervating taste buds (Farbman and Hellekant, 1978). So these papillae are not just taste sensory organs, but might be more accurately classified as organs for the perception of chili pepper burn (Lawless and Stevens, 1988). Even the taste bud itself seems organized to provide trigeminal access to the oral milieu. Trigeminal fibers ascend around the taste bud forming a chalice-like structure (Whitehead et al., 1985), possibly enhancing their access to the external environment.

The economic impact of trigeminal flavors on the food and flavor industry is growing. Carbon dioxide is a trigeminal stimulus and the carbonated beverage business—soda, beer, sparkling wines, etc.—amounts to huge sales worldwide. Putting aside CO₂, we can ask about the economic impact of individual spices or their use in various products. In the United States, so-called ethnic foods are experiencing a period of rapid growth due to a continuing influx of immigration of peoples from cultures with hot spicy cuisines and a growing trend toward less neophobic and more adventurous dining on the part of many Americans. Sales of salsa have surpassed the sales of ketchup since 1992. New programs of research have added whole new categories of chemesthetic flavorants, such as “tingle” compounds.

2.5.2 Physiological Mechanisms of Chemesthesis

A variety of specialized nerve endings from the tactile somatosensory systems can be observed histologically in skin and other epithelial tissues. For purposes of nociception, especially those induced by chemicals, it has long been thought that free nerve endings are the likely sensors. Generally, the nerve fibers involved in nociception are small diameter and slowly conducting c-class nerves. Many of the chemesthetic sensations are mediated by a special family of receptor proteins known as Transient Receptor Potential (TRP) channels (Silver et al., 2008). These proteins form cation channels and consist of four associated subunits. Each subunit contains a long peptide with six sections that cross the cell membrane and each contains a single pore region. Originally discovered in *Drosophila* photoreceptors, a wide variety of these functional channels have been found in various organs and many different cells (Patapoutian et al., 2003; Venkatchalam and Montell, 2007). The first chemoreceptive TRP to be characterized was the TRPV1, a so-called vanilloid receptor that is sensitive to capsaicin as well as acidic pH, heat, and mechanical stimulation. One member

of the TRPM family, TRPM8, is sensitive to menthol and other cooling compounds. TRPP3 channels have been implicated in sour taste transduction as they are responsive to acids, and may form a functional sour receptor. A type of TRP channel which is responsive to a very wide range of chemical stimuli including irritants and pungent stimuli such as wasabi and horseradish is the TRPA channel (Tai et al., 2008). TRP channels may also act in concert with the GPRC's to affect taste cell transduction for sweet, bitter, and umami tastes (TRPM5). The capsaicin-sensitive TRPV1 channel and the TRPM5 channel found in some taste receptor cells may participate in the sensing of some aspects of complex tasting divalent salts (iron, zinc, copper, etc.) (Riera et al., 2009). Because some TRPs are sensitive to both temperature and chemical stimulation, simultaneous or sequential combinations cause enhancements. For example, capsaicin can enhance heat pain from thermal stimulation, probably through a common action on TRPV1 channels and menthol can enhance cold-induced pain, probably through common action on TRPM8 channels (Albin et al. 2008). For a review of these important chemoreceptive mechanisms, see Calixto et al. (2005), Silver et al. (2008), and Venkatachalam and Montell (2007).

2.5.3 Chemical "Heat"

An actively studied category of chemesthetic sensations are those that arise from pepper compounds such as capsaicin from chili peppers, piperine from black pepper, and the ginger compounds such as zingerone. The potency of capsaicin is noteworthy, with thresholds below 1 ppm. This is about 100 times as potent as piperine and other irritants, based on dilution to threshold measures such as the Scoville procedure (discussed in Chapter 6). In pure form, capsaicin causes a warm or burning type of irritation with little or no apparent taste or smell (Green and Lawless, 1991; Lawless, 1984). The most obvious sensory characteristic of stimulation with the pepper compounds is their long-lasting nature. Stimulation with capsaicin, piperine, or ginger oleoresin at concentrations above threshold may last 10 min or longer (Lawless, 1984). So these flavor types are well suited to the application of time–intensity profiling (see Chapter 8). Other irritants such as ethanol and salt produce less persistent effects over time.

The temporal properties of capsaicin are complex. When stimulation is followed by a short rest period, a type of desensitization or numbing of the oral tissues sets in (Green, 1989). Application of the red pepper compound, capsaicin, to the skin or oral epithelium has profound desensitizing effects (Jansco, 1960; Lawless and Gillette, 1985; Szolcsanyi, 1977). This nicely parallels the animal experimentation showing a generalized desensitization after injection with capsaicin (Burks et al., 1985; Szolcsanyi, 1977), which is believed to result from the depletion of substance P, a neurotransmitter in the somatic pain system. Since effects of substance P have also been linked to the functioning of endorphins (Andersen et al., 1978), there is a suggestion that the kind of craving or addiction that occurs for spicy foods may be endorphin-related. High dietary levels of capsaicin also result in a chronic desensitization, as shown in psychophysical tests (Lawless et al., 1985). Figure 2.14 shows a desensitization effect seen in sequences during a psychophysical study, and also the apparent chronic desensitization that occurs in people who consume chili peppers or spices derived from red pepper on a regular basis (Prescott and Stevenson, 1996). Sensitization is also observed when the rest period is omitted and stimulation proceeds in rapid sequences; the irritation continues to build to higher levels (Stevens and Lawless, 1987; Green, 1989). These tendencies to sensitize and desensitize make sensory evaluations of pepper heat somewhat difficult if more than one trial per session is required. A calibrated descriptive panel may be useful, one whose abilities can help bridge the time delays required between repeated observations.

In addition to their numbing and sensitizing effects, irritant stimulation in the oral or nasal cavity evokes strong defensive reflexes in the body, including sweating, tearing, and salivary flow. There is a strong correspondence between sensory ratings of pepper heat intensity and the evoked salivary flow from the same subjects taken simultaneously with ratings (Lawless, 1984). This provides a nice demonstration that sensory ratings should not be dismissed as merely "subjective" in that they have obvious correlates in "objectively" measurable physiological reflexes.

An unresolved question in the realm of chemical irritation is the degree to which different sensory qualities are evoked (Green and Lawless, 1991). This is difficult to study due to a lack of vocabulary to

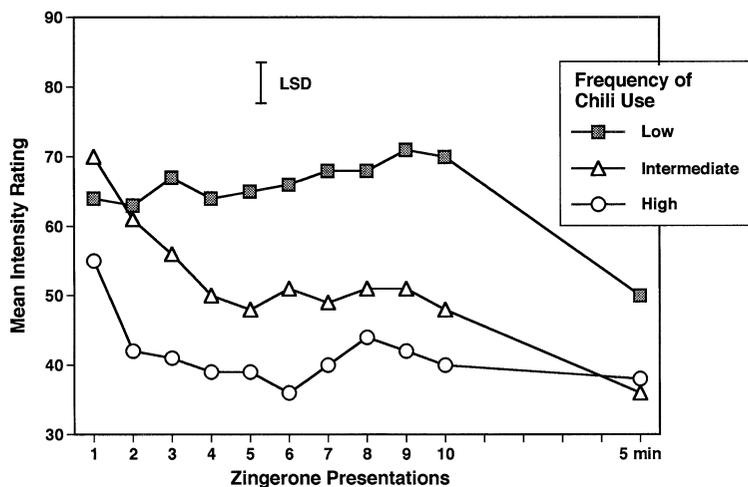


Fig. 2.14 Zingerone desensitization as a function of dietary use, numbers of exposures and a break in stimulation. The differences in the height of the curves demonstrate the chronic desensitization that is correlated with high dietary intake of pungent spices. The symbols at the far right demonstrate the within-session

desensitization that occurs during a hiatus in stimulation, as commonly seen with capsaicin, the irritant component of red (chili) peppers. The latter effect is more pronounced for those with low dietary intake. From Prescott and Stevenson (1996) with permission.

describe, at least in English, the experiences from pepper burn, CO₂, mustard, and so on. Experience with spices suggests that there are a variety of irritative flavor experiences and not all irritations are the same. Studies of synergistic interaction in mixtures and potentiation with different irritants in rapid sequences are suggestive of the possibility of multiple receptor mechanisms for oral chemical irritation (Lawless and Stevens, 1989, 1990). Direct measurement of qualitative differences was attempted in a descriptive study by Cliff and Heymann (1992) using a variety of irritant flavor materials. They found evidence for differences in lag time (short versus long onset) and burning versus tingling sensations among the irritants tested. A lexicon for carbonation was developed by Harper and McDaniel (1993) and involved descriptors for cooling, taste, trigeminal (bite, burn, numbing), and tactile/mechanoreception properties.

2.5.4 Other Irritative Sensations and Chemical Cooling

The trigeminal flavor senses also affect food flavor in other ways. Even such benign stimuli as NaCl can be irritative at high concentrations (Green and Gelhard, 1989). Carbon dioxide is a potent irritant in the nasal cavity, as are many organic compounds (Cain

and Murphy, 1980; Cometto-Muñiz and Cain, 1984; Cometto-Muñiz and Hernandez, 1990). Completely anosmic individuals can detect many odor compounds, presumably from the ability of odorants to stimulate the trigeminal nerve branches in the nasal cavity (Doty et al., 1978). There is an irritative component to many common odorants and flavor compounds. A variety of highly reactive sulfur compounds have been identified in other irritative spices and food flavors, such as compounds from horseradish, mustard, and the lacrimatory (tear-inducing) factor from onions and related vegetables (Renneccius, 2006). Ethanol and cinnamaldehyde are other examples of other common flavors that are irritative (Prescott and Swain-Campbell, 2000).

Carbonation, or the perception of dissolved CO₂, involves a truly multimodal stimulus. In addition to the tactile stimulation of mechanoreceptors, CO₂ acts on both trigeminal receptors (Dessirier et al., 2000) and gustatory receptors (Chandrashekar et al., 2009). Both of these chemical sensations involve the enzyme carbonic anhydrase, which can convert CO₂ to carbonic acid. For the sense of taste, the stimulation with CO₂ appears to involve the extracellular anhydrase enzyme and the transient receptor potential (TRP) mechanism (PDK2L1) of sour receptor cells (Chandrashekar et al., 2009). This is consistent with the enhancement of sour taste by CO₂ and suppression of sweetness (Cowart, 1998; Hewson et al., 2009). The role of nociceptors in

CO₂ perception is further substantiated by its desensitization by capsaicin (Dessirier et al., 2000).

Using the method of magnitude estimation, Yau and McDaniel (1990) examined the power function exponent (see Section 2.2.4) for carbonation. Over a range of approximately one to four volumes CO₂ per volume of H₂O, sensation intensity grew as a power function with an exponent of about 2.4, a much higher value than in most other modalities. The exponent is consistent with high sensitivity to changes in carbonation levels. Given the involvement of TRP mechanisms in both nociception and temperature sensing, interactions between carbonation and temperature might be expected. An enhancement of irritation, tactile sensations, cooling, and cold pain have all been observed with carbonation of solutions served at low temperatures (Green, 1992; Harper and McDaniel, 1993; Yau and McDaniel, 1991). Yau and McDaniel (1991) noted a small increase in tactile intensity at low temperatures (3–10°C). This may be an example of a phenomenon called Weber's illusion, in which Weber noted that a cold coin seemed heavier than a warm one, an early clue to the overlap in tactile and thermal sensing mechanisms.

Menthol, a compound that has both odor properties and is capable of causing cool sensations, is a trigeminal stimulus with obvious commercial significance in confections, oral health care, and tobacco products (Patel et al., 2007). Menthol has been found to interact with thermal stimulation in complex ways. Menthol enhances cool stimuli as would be expected, but can either enhance or inhibit warm stimuli depending upon the conditions of stimulation (Green, 1985, 1986). The sensory properties of menthol itself are complex, inducing a number of cooling, warming, aromatic, and other sensory effects depending upon the isomer, concentration, and temporal parameters (Gwartney and Heymann, 1995, 1996). A large number of hyper-potent cooling compounds have been patented, many of which can produce cooling without the odor sensations of menthol (Leffingwell, 2009; Renneccius, 2006).

2.5.5 Astringency

Tannins in foods are chemical stimuli and yet the astringent sensations they produce are largely tactile.

They make the mouthfeel rough and dry and cause a drawing, puckery, or tightening sensation in the cheeks and muscles of the face (Bate Smith, 1954). There are two approaches to defining astringency. The first is to emphasize the causes of astringent sensations, i.e., those chemicals which readily induce astringency. For example, ASTM (1989) defines astringency as “the complex of sensations due to shrinking, drawing or puckering of the epithelium as a result of exposure to substances such as alums or tannins.” A more perceptually based definition is that of Lee and Lawless (1991): “A complex sensation combining three distinct aspects: drying of the mouth, roughing of oral tissues, and puckery or drawing sensations felt in the cheeks and muscles of the face.” Principal component analysis has shown these sub-qualities to be independent factors and furthermore, distinctly separate from taste sensations such as sourness (Lawless and Corrigan, 1994). The fact that astringent sensations can be sensed from areas of the mouth such as the lips, that are lacking in taste receptors, further substantiates their classification as tactile rather than a gustatory sensations (Breslin et al., 1993).

The mechanisms for astringency involve the binding of tannins to salivary proteins and mucins (slippery constituents of saliva), causing them to aggregate or precipitate, thus robbing saliva of its ability to coat and lubricate oral tissues (Clifford, 1986; McManus et al., 1981). We feel this result as rough and dry sensations on oral tissues. Other mechanisms may also contribute to astringency in addition to the binding of tannins to salivary proteins (Murray et al., 1994). Acids commonly used foods also induce astringency in addition to their sour taste (Rubico and McDaniel, 1992; Thomas and Lawless, 1995). The astringent impact of acids is pH dependent (Lawless et al., 1996; Sowalski and Noble, 1998) suggesting that a direct attack on epithelial tissues or a pH-dependent denaturation of the lubricating salivary proteins may also occur.

The interaction of mucins and proline-rich proteins (PRPs) in saliva with tannins may be a key part of astringency mechanisms as protein content is a correlate of sensory response (Kallikathraka et al., 2001). Binding of polyphenols to PRPs is well known in the beer and fruit juice industries as it can give rise to turbidity known as chill-haze (Siebert, 1991). A similar visible haze generation reaction has been shown to occur with tannic acid mixed with saliva (Horne et al., 2002). Haze development of saliva is an *in vitro*

measure, a correlate of predicting individual responses to astringency in products such as wine and a potential measure for screening and selecting panelists for astringency evaluation (Condelli et al., 2006) as well as analysis of wine samples. The individual differences show an inverse relationship: panelists with high haze development and higher salivary flow rates are less reactive (have lower ratings). Their enhanced mucin or protein content may provide greater “protection” of oral surfaces against astringent compounds. Another important individual difference in astringent reactions is salivary flow rate (Fisher et al., 1994). Individuals with a higher flow rate tend to “clean up” faster after astringent stimulation. Repeated stimulation with astringent substances tends to cause a buildup of tactile effects rather than a decrement as one might see in taste adaptation or capsaicin desensitization. Figure 2.15 shows an increase in astringency upon repeated stimulation, as might happen with multiple sips of a beverage such as wine. Note that the pattern changes as function of tannin concentration, interstimulus interval between sips and to a small extent, as a function of the volume tasted (Guinard et al., 1986).

2.5.6 Metallic Taste

Another quality of chemical sensations that is sometimes referred to as a taste are the metallic sensations that arise from placing different metals in the mouth or from contact with iron or copper salts. Two common reference standards for metallic taste in descriptive analysis training are (1) rinses with ferrous sulfate and (2) a clean copper penny (Civille and Lyon, 1996). Research now shows that these are quite different sensations in terms of their mechanisms, although they both are described as “metallic” perhaps because they may occur at the same time.

The so-called metallic taste after rinses with ferrous sulfate solutions is actually a case of retronasal smell. The sensation is virtually abolished if the nose is pinched shut during tasting (Epke et al., 2008; Lawless et al., 2004, 2005). Because metal salts are not volatile, this olfactory sensation probably arises from the ferrous ions catalyzing a rapid lipid oxidation in the mouth, creating well-known potent odor compounds such as 1-octen-3-one (Lubran et al., 2005).

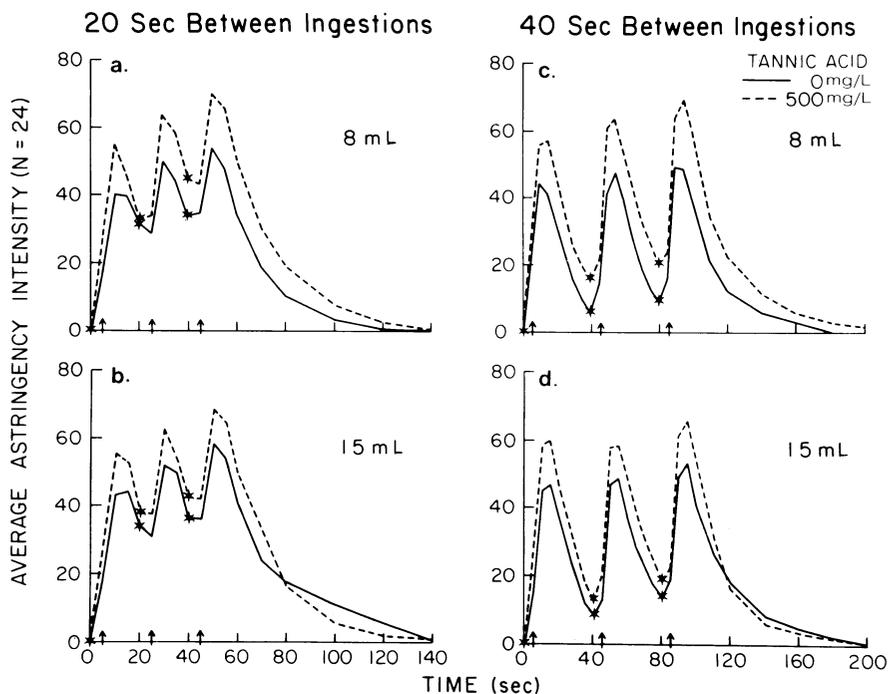


Fig. 2.15 Average time–intensity curves for astringency in wine with 0 or 500 mg/l of added tannic acid upon three successive ingestions. Sample uptake and swallowing are indicated

by a *star* and *arrow*, respectively. From Guinard et al. (1986) by permission of the American Society for Enology and Viticulture.

A second kind of metallic sensation is the one that arises from the “clean copper penny.” If one scratches the copper off part of the surface of a US penny, exposing the zinc core, the metallic sensation increases dramatically (Lawless et al., 2005). Due to the different electrical potentials of the different metals, a small current is created, making this a case of electrical taste stimulation (McClure and Lawless, 2007; Stevens et al., 2008). In the clinical literature on electrogustometry, in which electrical taste stimulation is used for diagnostic tests, the term “metallic” is often reported. The sensory analyst should be careful to distinguish between these two kinds of sensations. If the sensation is abolished or dramatically diminished by nasal occlusion, then it is a case of retronasal olfactory sensations, possibly due to potent lipid oxidation products. If not, there may be metals in the system leading to small electrical potentials. There is also the possibility of a third kind of metallic sensation that may be a true taste, but this is still controversial.

2.6 Multi-modal Sensory Interactions

Food is a multi-modal experience, so it should come as no surprise that the sensations from one sensory modality may influence judgments and perceptions from another. Through our experience, we learn about the pairings of colors and tastes, colors, and odors and come to have expectations about what sensations may accompany one another. Through repeated pairings or through natural co-occurrence of different tastes and flavors, an association can be built up leading to integration of those experiences (Stevenson et al., 1999). Brain imaging of regions of the frontal cortex supports that notion that the merging of these sensations into coherent percepts are “real” perceptions and not just some kind of response bias (Small et al., 2004). Interactions between sensory modalities and their possible neural substrates have been reviewed by Delwiche (2004), Small and Prescott (2004), and Verhagen and Engelen (2006). The discussions that follow will focus on those interactions that have been most heavily studied and are most relevant to foods: taste/odor, flavor/irritation (chemesthesis), and color/flavor. Other inter-modality interactions are discussed in the review papers mentioned above.

2.6.1 Taste and Odor Interactions

An reliable observation from the psychophysical literature is that sensation intensities of tastes and odors are additive or slightly hypo-additive (Hornung and Enns, 1984, 1986; Murphy et al., 1977; Murphy and Cain, 1980). The pattern of results is that intensity ratings show about 90% additivity. That is, when framed as a simple question about the summation of gustatory and olfactory intensity ratings in producing overall ratings of flavor strength, there is little evidence for interactions between the two modalities.

However, there have been many other studies showing enhancement of specific taste qualities, notably sweetness, in the presence of odors. An important tendency, especially among untrained consumers, is to misattribute some volatile olfactory sensations to “taste,” particularly retronasally perceived odors. Retronasal smell is poorly localized and often perceived as a taste from the oral cavity. Murphy and coworkers (1977, 1980) noted that the odorous compounds, ethyl butyrate and citral, contributed to judgments of “taste” magnitude. This illusion is eliminated by pinching the nostrils shut during tasting, which prohibits the retronasal passage of volatile materials and effectively cuts off the volatile flavor impressions.

Another observation is that harsh tastes can suppress and pleasant tastes can enhance ratings of volatile flavor intensity. Von Sydow et al. (1974) examined ratings for taste and odor attributes in fruit juices that varied in added sucrose. Ratings for pleasant odor attributes increased and those for unpleasant odor attributes decreased as sucrose concentration increased. No changes in headspace concentrations of volatiles were detected. Von Sydow et al. interpreted this as evidence for a psychological effect as opposed to a physical interaction. A similar effect was found for blackberry juice flavor at varying levels of sucrose and acidity (Perng and McDaniel, 1989). Sucrose-enhanced fruit flavor ratings while juices with high acid level showed lower fruit ratings.

When retronasal smell is permitted, a common finding is that sweetness is enhanced (Delwiche, 2004) and odors are enhanced as well. The effect depends upon the specific odor/taste pairings. Aspartame enhanced fruitiness of orange and strawberry solutions (sucrose showed no effect) and a somewhat

greater enhancement occurred for orange than for strawberry (Wiseman and McDaniel, 1989). Sweetness was enhanced by strawberry odor, but not by peanut butter odor (Frank and Byram, 1988). Some authors have argued that the sweetness enhancement depends upon the congruence and/or similarity of the taste and odor. This makes sense because many odors are referred to as smelling like tastes, such as the sweet smell of honey or the sour smell of vinegar (Small and Prescott, 2005). The spatial and temporal contiguity of odors and tastes when foods are consumed may also be important in facilitating this effect.

The degree of cultural experience panelists have with particular combinations seems important. There is an influence of learned expectancies (Stevenson et al., 1995). The pattern of learned correlations may determine how and when effects such as sweet taste enhancement are seen. Common experience with the co-occurrence of sweet tastes and caramelization odors, for example, may drive some sweetness enhancement effects. The influence of associative learning is shown by the fact that sweetness enhancement is predicted by initial sweetness ratings of odors and that pairings of formerly neutral odors with a sweet taste will induce this enhancement effect (Prescott, 1999; Stevenson et al., 1998).

Is this effect a true enhancement or simply an inflation of sweetness ratings due to taste/smell confusion? Evidence for the “reality” of the effect comes from the observation that a sweet smelling odor can suppress the rated sourness of a citric acid solution, just like a sweet taste would (Stevenson et al., 1999). A number of brain imaging studies have identified multi-modal neural activity in brain regions such as the orbitofrontal cortex (see Small and Prescott, 2005; Verhagen and Engelen, 2006). This has led to the interesting speculation that sniffing a sweet odor might evoke the entire experience of a taste/odor pairing (i.e., a flavor) that has been encoded in memory (Small and Prescott, 2005). Dalton et al. (2000) showed that detection thresholds for an odorant were reduced when subjects held a taste in the mouth, but only when the taste was congruent. However, in another study, sweetness enhancement by subthreshold odors was not observed (Labbe and Martin, 2009).

These interactions change with instructions and with training. In one study, citral–sucrose mixtures were evaluated using both direct scaling and “indirect” scale values derived from triangle test performance

(Lawless and Schlegel, 1984). A pair which was barely discriminable according to triangle tests received significantly different sweetness ratings when separate taste and odor attributes were scaled. Focused attention produces different results than appreciation of the product as a unitary whole. Sweetness enhancement by ethyl maltol decreased when panelists were trained to distinguish tastes from smells (Bingham et al., 1990). In another study, sensory profile training did not seem to promote the associative learning needed for odor/sweetness enhancement (Labbe and Martin, 2009). Along these lines, having subjects take an analytic (rather than synthetic) approach to odor/taste mixtures negates the odor-enhanced sweetness (Prescott et al., 2004). Taken together, these results show that attentional mechanisms or modality-specific training can alter the effect substantially.

A further consideration is that the responses that subjects are instructed to make also influence the apparent taste–odor interactions (van der Klaauw and Frank, 1996). Strawberry odor enhances the sweetness of sucrose–strawberry solutions (Frank et al., 1989a), an effect reminiscent of the enhancement reported by Wiseman and McDaniel (1989) and also the mislabeling of volatile sensations as taste intensity estimates seen by Murphy et al. (1977). However, when subjects are instructed to make total intensity ratings and then partition them into their components, no significant enhancement of sweetness is seen (Frank et al., 1990, 1993; Lawless and Clark, 1992). Odor–taste enhancement, then could in many cases merely be a case of response shifting, and not a truly increased sensation of sweetness at all.

This finding has broad implications for the ways in which sensory evaluations, particularly descriptive analyses in which multiple attributes of complex foods are rated, should be conducted. It also suggests some caution in substantiating claims for various synergies or enhancement effects in which ratings are restricted to too few attributes. Respondents may choose to “dump” some of their impressions into the most suitable category or the only allowable response if the attribute they perceive is otherwise unavailable on the ballot (Lawless and Clark, 1992). Alleged enhancements such as the effect of maltol on sweetness should be viewed with caution unless the response biases inherent in mislabeling smells as tastes can be ruled out. These effects are discussed at length in [Chapter 9](#).

2.6.2 Irritation and Flavor

Two other groups of interactions between modalities are important in foods. One is the interaction of chemical irritation with flavors and the second are effects in flavor ratings caused by changes in visual appearance. Anyone who has compared flat soda to carbonated soda will recognize that the tingle imparted by carbon dioxide will alter the flavor balance in a product, usually to its detriment when the carbonation is not present. Flat soda is usually too sweet. Decarbonated champagne is usually very poor wine.

Several psychophysical studies have examined interactions of trigeminal irritation from chemicals with taste and with odor perception. As in most laboratory psychophysics, these studies have focused on perceived intensity changes in single chemicals simple mixtures. The first workers to examine effects of chemical irritation on olfaction found mutual inhibition of smell by carbon dioxide in the nose (Cain and Murphy, 1980). This occurs even though the onset of the sting from carbon dioxide is delayed somewhat compared to the onset of smell sensations. Since many smells also have an irritative component (Doty et al., 1978; Tucker, 1971), it is probable that some of this inhibition is a common event in everyday flavor perception. If a person had decreased sensitivity to nasal irritation the balance of aromatic flavor perception might be shifted in favor of the olfactory components. If irritation is reduced, then the inhibitory effects of irritation would also be reduced.

Does chili burn mask tastes in the mouth, the way that carbon dioxide sting masks smell in the nose? Partial inhibition of taste responses has been found following pretreatment of oral tissues with capsaicin, particularly inhibition of sour and bitter tastes (Karrer and Bartoshuk, 1995; Lawless and Stevens, 1984; Lawless et al., 1985; Prescott et al., 1993; Prescott and Stevenson, 1995, but see also Cowart, 1987). Note that capsaicin desensitization takes several minutes to develop, i.e., it depends upon a delay between treatment and test stimuli (Green, 1989). Such a temporal gap would have occurred to varying degrees in pretreatment experiments with tastants. Also, since capsaicin inhibition is most reliably observed for substances sometimes reported as partially irritative, the inhibitory effect seen in pretreatment studies may be due to desensitization to an irritative component

of the “tastants,” rather than a direct effect on gustatory intensity per se (e.g., Karrer and Bartoshuk, 1995).

Tastes can modulate or ameliorate chili burn. There are folk remedies in various cultures, such as starchy corn, ghee, pineapple, sugar, and beer. Systematic studies of trying to wash out chili burn with different tasting rinses have shown some effect for sweet (most pronounced), sour, and perhaps salt (Sizer and Harris, 1985; Stevens and Lawless, 1986). Cold stimuli provide a temporary but potent inhibition of pepper burn, as known to many habitués of ethnic restaurants. Since capsaicin is lipid soluble, the Indian remedy of ghee (clarified butter) has some merit. Sour things stimulate salivary flow, which may provide some relief to abused oral tissues. The combination of fatty, sour, cold, and sweet suggests chilled yogurt as a good choice. A culinary practice of alternating cool, sweet chutneys with hot curries would seem to facilitate these interactions.

2.6.3 Color–Flavor Interactions

Finally, let us consider the effects of appearance on flavor perception. The literature concerning color–flavor interactions is quite extensive and interested researchers are cautioned that it is complex and at times contradictory (e.g., Lavin and Lawless, 1998). We make no attempt here to provide a comprehensive review.

Humans are a visually driven species. In many societies with mature culinary arts, the visual presentation of a food is as important as its flavor and texture characteristics. A common finding is that when foods are more deeply colored, they will obtain higher ratings for flavor intensity (e.g., Dubose et al., 1980; Zellner and Kautz, 1990). Effects of colored foods on flavor intensity and flavor identification are discussed in Stillman (1993). Miscolored foods or flavors are less effectively identified (Dubose et al., 1980). However, the pattern of results is mixed and inconsistent in this literature (see Delwiche, 2004). Once again, learned associations may drive the patterns of influence. Morrot et al. (2001) found that more red wine descriptors were used by a panel when a white wine was intentionally miscolored red.

An example of visual influences on food perception can be found in the literature on perception of

milks of varying fat content. Most people believe that skim milk is easily differentiated from whole milk or even from 2% low fat milk by appearance, flavor, and texture (mouthfeel). However, most of their perception of fat content is driven by appearance (Pangborn and Dunkley, 1964; Tuorila, 1986). Trained descriptive panelists readily differentiate skim milk from 2% on the basis of appearance (color) ratings, mouthfeel, and flavor. However, when visual cues are removed, discrimination is markedly impaired (Philips et al., 1995). When tested in the dark with cold milk, discrimination of skim milk from 2% milk drops almost to chance performance, a result that many skim milk drinkers find difficult to swallow. This research emphasizes that humans react to the ensemble of sensory stimulation available from a food. Even “objective” descriptive panelists may be subject to visual bias.

2.7 Conclusions

An important knowledge base for any sensory professional is an appreciation of the function of the senses through which we obtain our data. Understanding the physiological processes of the senses helps us take into account the limits of sensory function and how sensations interact. The historical underpinnings of sensory methods lie in the discipline of psychophysics, the systematic study of relationships between stimulus and response. Psychophysical thinking, then, is not just about methods for sensory testing, but a view of sensory function that looks at relationships among *variables*. This is a valuable point of view that can enhance the contribution of a sensory group to their product development clients. One of our industrial colleagues used to ask his product developers not to send him products to test. At first glance such a statement seems outrageous. But the key was in his next request: “Send me *variables* to test.” This approach is advantageous as it brings a deeper understanding of the relationships between ingredient or process variables and sensory response. It moves the sensory specialist beyond simple hypothesis testing and into the realm of theory building and modeling, in other words more like engineering than the all too common pattern of simple yes/no hypothesis testing.

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