

# Better Fruits and Vegetables through Sensory Analysis Minireview

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The flavor quality of many fresh fruits available to consumers today is generally believed to have deteriorated. While agricultural and postharvest practices certainly contribute to poor flavor, a large part of the problem is the challenge of breeding for and accurately assessing such a complex, multigenic trait in a natural product such as a fruit. Here we address the parallel challenges linked to measurement of flavor and human preferences, particularly as it applies to a complex, whole food in which many chemicals and sensations are synthesized into a distinct and recognizable flavor profile. What is flavor? What contributes to the pleasure evoked by flavors? We examine interactions between taste and olfaction as well as psychophysical measurement limitations that confound efforts to understand human flavor preferences. The ability to address these questions in a whole food presents exciting opportunities to understand the basic principles of how we select the foods that we eat.

## The Pleasures Evoked by Taste and Olfaction

Genetic approaches to flavor improvement have proven to be very challenging, in large part due to the complexity of assessing the phenotype [1,2]. The palatability of fruits and vegetables can best be understood by an examination of the components of flavor. While appearance, texture and chemesthesis (e.g., irritation) make important contributions, the core contributors to flavor are taste and olfaction. The taste qualities sweet, salty, sour and bitter have been considered ‘basic tastes’ since the 19<sup>th</sup> century. Some experts choose to add other oral sensations to the list (e.g., metallic, fatty, umami); however, the key feature in comparisons of taste and olfaction is that the number of distinct taste qualities is small compared to the huge number of distinct olfactory qualities.

Understanding the role of olfaction in flavor requires a distinction between ortho- and retronasal olfaction. Sniffing draws odorants into the nose through the nostrils where it passes over the turbinate bones (which add turbulence to the air flow), the sample then rises to the top of the nasal cavity and contacts olfactory receptors in the olfactory mucosa — this is called orthonasal olfaction (smell). Odorants emitted from foods in the mouth are forced upwards, behind the palate and into the nasal cavity from the rear by chewing and swallowing — this is called retronasal olfaction. The ultimate sensation of flavor results from the central integration of taste and retronasal olfaction.

Although retro- and orthonasal olfaction have long been known to have different properties [3], the proof that the brain processes them in different areas was only demonstrated relatively recently by fMRI studies; taste and retronasal olfaction presumably are integrated to produce flavor at the brain locations where these inputs converge [4]. The

pleasures evoked by taste and olfaction follow different rules, making understanding the pleasure evoked by the flavors of fruits particularly interesting.

The pleasure evoked by taste is hard-wired in the brain. Newborn infants make faces consistent with pleasure to sweet and displeasure to bitter. In fact, sweet receptors are present prior to birth — injection of saccharin into amniotic fluid will induce a fetus to swallow, suggesting that sweet is affectively positive even before birth [5]. Hard-wired affect for taste makes biological sense; the pleasure associated with food-associated sugars and dilute NaCl ensure intake of these critical nutrients. On the other hand, the displeasure associated with bitter protects from poisons [6].

The pleasure of olfaction is widely believed to be largely, if not entirely, learned, and this learning has biological importance. Odors paired with benefit (e.g., calories) come to be liked [7], while odors paired with illness (particularly nausea) come to be disliked [8]. Although it is clear that olfactory affect is easily learned, is there any evidence that some odorants evoke affect that is hard-wired?

Some studies on human infants and young children (1–2 years old) show that they can discriminate among odorants, but they do not show the affective responses (preference or rejection) characteristic of adults. As children grow, they begin to show preferences similar to those shown by adults [9]. This makes biological sense, since the plasticity of olfactory pleasure allows an organism to adapt to its environment by learning to like/dislike odors based on the consequences associated with those odors. However, some investigators argue that difficulties testing infants and young children limit the conclusions that olfactory affect is entirely learned, and take the position that some odors may be ‘inherently pleasant or unpleasant’ [10].

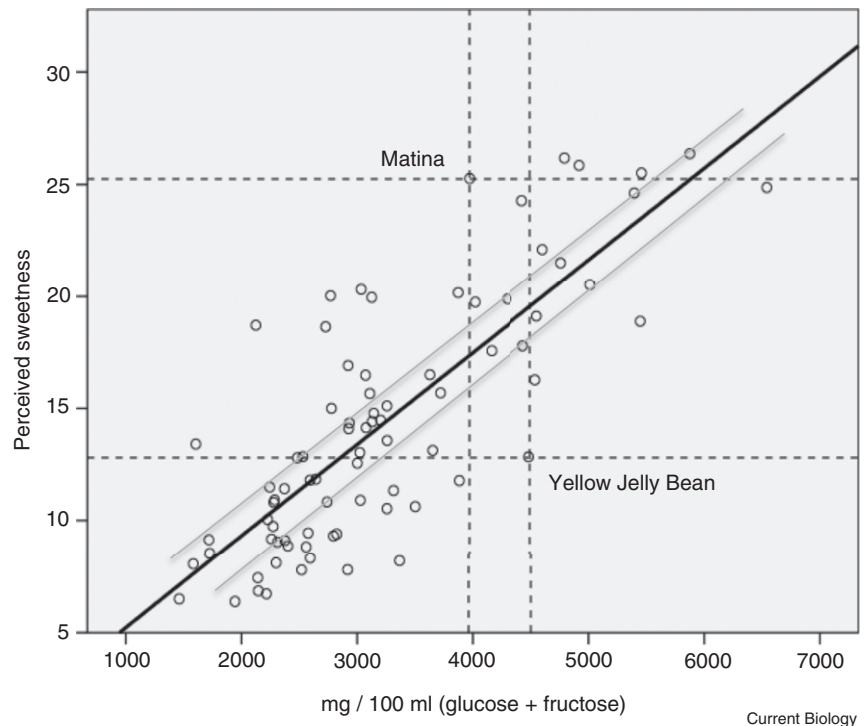
While there is no evidence for innate olfactory affect in humans, many of the most important flavor-associated volatiles in fruits are derived from essential nutrients. It would clearly be biologically wise if these cues for nutritional quality had hard-wired affect [11]. In this context, it is interesting to examine comments by Aristotle made in *On Sense and the Sensible* [12] describing two groups of odors. The first group is associated with foods whose pleasantness is associated with nutrition. The pleasure evoked from odors in Aristotle’s first group sounds remarkably like conditioned preferences. The second group of odors, restricted to humans, are “agreeable in their essential nature, e.g., those of flowers.” Could the pleasure of Aristotle’s second group (e.g., flowers) represent hard-wired olfactory affect evoked by volatiles that are cues for essential nutrients? It is provocative that the volatiles identified as cues to nutrients tend to be described as floral. This is an area that deserves further study.

The hedonic properties of flavors do not simply reflect the hard-wired affect of taste and the learned affect of olfaction. ‘Evaluative conditioning’ refers to the fact that neutral stimuli can take on affect when they are paired with stimuli that have hedonic properties (either positive or negative) [13]. This is relevant to the hedonic properties of flavors since neutral olfactory components may be rendered hedonically positive by association with sweet taste [14]. Thus, the palatability of fruits consists not only of the palatability contributed by the

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Figure 1. Perceived sweetness of 80 tomatoes as a function of the sugar concentrations in the tomatoes.



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hard-wired taste affect (e.g., sweet) and the learned affect (association of odors with calories), but also by the palatability of odors contributed by evaluative conditioning.

### Flavors in Tomatoes

The tomato is a complex, whole food with a unique flavor profile that results from integration of multiple diverse chemicals, including sugars, acids and volatiles. The challenge with determining the relative contributions of such a large number of different chemicals to flavor and liking is that the individual constituents cannot be manipulated in isolation. Rather, we must rely upon variation in chemical composition derived from genetics and environment. In a recent study, 80 different tomato varieties were grown, harvested and subjected to chemical (concentrations of sugars, acids, glutamate and 61 volatiles) and sensory (sweetness, saltiness, sourness, bitterness, umami, overall palatability and overall tomato flavor) analyses [15]. Through correlation of chemical composition and sensory evaluation, the contributions of individual chemicals to flavor were evaluated. Not surprisingly, palatability of tomatoes rose as a function of sugar concentration. Plots of palatability as a function of the concentration of each volatile revealed that palatability increases for some volatiles, decreases for others and remains unchanged for a third group. The data can be used to generate a 'recipe' for the ideal tomato, increasing volatile concentrations with positive correlations and decreasing those with negative correlations [16].

### Volatile-enhanced Sweetness

The tomato data provide an unexpected look into the phenomenon of central integration of taste and retronasal olfaction. This interaction has remarkable consequences — some taste and retronasal olfactory stimuli can intensify one another. As early as 1955, the food industry noted intensification of some volatile sensations by addition of small amounts of sweeteners [17]. Recognition of the ability of volatiles to enhance taste came later; the effects were small and even initially called an 'illusion' [18,19]. In addition, some sweetness enhancement was attributed to 'dumping', [20] that is, when asked to rate the sweetness of a complex sensation, if there is no opportunity to rate all of the sensations, subjects may 'dump' non-sweet sensations into the sweet category. The early studies tended to focus on fruity volatiles/flavorings (citral [21]; amyl acetate (banana) [19]; strawberry [22,23]; peach [24]; raspberry, passion fruit, lychee [23]), supporting the idea that experiencing fruit volatiles at the same time as sweet taste somehow leads to volatile-enhanced sweetness.

Taste/retronasal olfaction integration is important in the context of sweetness of commercial fruit crops. Studies on

tomatoes using expert panels suggested that 'fruity' volatiles increased sweetness [25]. Similarly, 'spiking' deodorized tomato purees with a few specific volatiles increased sweetness [26]. Complementary studies of mutant tomatoes reduced in fruity carotenoid-derived volatiles suggests that these fruits were perceived as less sweet [27]. Most recently, multiple regression analyses of the data generated in the tomato study described above revealed seven volatiles that contribute to tomato sweetness independently of sugars [15,28].

Figure 1 shows the variability of the perceived sweetness of different tomato varieties — Matina and Yellow Jelly Bean. Matina is perceived as roughly twice as sweet as Yellow Jelly Bean, yet actually contains less sugar. Each of the seven volatiles that contribute to tomato sweetness is at least twice as abundant in Matina as in Yellow Jelly Bean. This relative abundance seems to be generalized. A comparison of concentrations of each of the seven volatiles in tomatoes more than 1.5 units of perceived sweetness above or below the regression line (i.e., tomatoes outside the gray lines in Figure 1) indicated that all seven volatiles were significantly ( $p < 0.05$ ) more abundant in the sweeter tomatoes (Fisher exact test of distribution differences for tomatoes above and below the gray lines). All of these results suggest significant enhancement of perceived sweetness by specific volatiles present in the tomato.

Have fruits evolved to produce volatiles that enhance the perception of sweetness and thus palatability to animals? Do we unconsciously learn that certain volatiles are paired with sugars in whole foods? The discovery of tomato volatiles that enhance sweetness offers additional perspective to the phenomenon of volatile-enhanced taste. First, the volatile-enhanced sweetness in tomatoes was not an artifact of dumping since subjects rated flavor as well as taste. Second, some but not all of the volatiles that enhanced sweet were fruity. For example, one of the tomato volatiles (isovaleric

acid) smells like 'dirty socks' or 'cheese'. Few would expect such an odor to enhance sweet through experience.

### 'Typical' Flavors of Specific Fruits and Volatiles — Chemosensory Mixtures

Since the 19<sup>th</sup> century, mixtures of sensory stimuli in a given domain have been classified as analytic or synthetic. Mixing lights of different colors is the classic demonstration of synthesis. For example, mixing red and green lights results in yellow light, even though yellow is not perceptually similar to red or green. In contrast, combining sounds of different frequencies is the classic example of analytic mixing. When high and low notes are simultaneously struck on a piano, we hear high and low notes; the identity of each note is not lost in the mixture. The key element of the definition of synthesis is that the identity of the components *cannot* be perceived in the mixture.

Opinions have been mixed with regard to classification of taste and olfaction as analytic or synthetic. It would seem at first glance that taste is analytic. A mixture of sugar and quinine tastes sweet and bitter. However, this simplicity can blur with components of unequal intensity — stronger tastes can suppress weaker ones such that the simplified mixture is misinterpreted as synthetic [29], but there is no evidence for genuine synthesis in taste.

Suppression also occurs in olfactory mixtures. If strong and weak odorants are mixed, the strong will predominate, possibly abolishing the weaker. Laing and his colleagues [30] showed that as the number of odorants of equal intensity in a mixture increases (up to five), the ability of subjects to identify each odorant decreases. Recently, Sobel and colleagues [31] created mixtures of 30 odorants of equal intensity. These mixtures were relatively weak and tended to lose individuality; even when such mixtures were made up of very different odorants they were perceptually similar. He concluded that it was the olfactory equivalent of white [31]. This conclusion seems to contradict the fact that our world is filled with olfactory mixtures that have very specific qualitative identities: strawberry, tomato, roast beef, etc. However, these specific identities result from mixtures in which the components are not of equal intensity and may not cover a broad qualitative range. Olfaction is unique in that new distinctive real-world olfactory mixtures can continually be created, not only through new mixtures of available odorants, but also through the creation of new molecules that evoke olfactory sensation. This amazing ability of the olfactory sense allows us to learn to recognize new olfactory objects as needed for our well-being and even survival.

Recent work has given us a picture of how olfactory information is sorted and stored in the brain. While there are tens of thousands of volatiles in the world, there are only about 350 olfactory receptor genes expressing olfactory receptors. Rather than recognize whole molecules, olfactory receptors bind active groups on volatiles. Appropriate combinations of receptor binding can represent many volatiles. All of the receptors of a single type project to two matching glomeruli in the olfactory bulb. When a given odorant stimulates a combination of receptors, the pattern of glomeruli that respond creates a rough image of the structure of the odorant. These odor images are stored in memory [32]. If a positive experience results when an odor image is stimulated, subsequent encounters with that odor will be pleasant. Similarly, if a negative experience results, subsequent

encounters will be negative. This system works equally well with simple compounds or mixtures.

### Genetics and Experience in Fruit and Vegetable Preferences

Hard-wired liking of sweet and disliking of bitter will impact liking for specific vegetable and fruit varieties. Genetic variations in our ability to taste sweet and bitter are likely to play a role. For example, some individuals experience more intense taste sensations than do others — we call these individuals 'supertasters'. They dislike bitter vegetables more than others do [33]. Humans have ~25 different genes for sensing bitterness. The biological function of this variation appears to provide for adaptation to environments with different toxins [34]. The variability across individuals in the ability to taste specific bitter compounds is likely to be a very interesting source of individual variation in preferences for specific vegetables and fruits [35,36].

Genetic variation in olfaction is also likely to play a role in preferences. For example, there is large variation in perception of  $\beta$ -ionone within human populations [37].  $\beta$ -Ionone varies considerably across tomato varieties [15], and can be shown to contribute to tomato sweetness independently of sugar. Thus, variability in the ability to perceive  $\beta$ -ionone as well as variability in the concentration present in specific tomatoes may provide another source of variability in tomato perception and preference. Given that the pleasure evoked by volatiles is likely learned, conditioned preferences should also play a very important role in preferences for fruits and vegetables.

### Measurement of Sensation and Preference

Any effort to understand sensory and hedonic variation in responses to fruits and vegetables begins with measurement. In an effort to identify the most important volatiles for 'fresh tomato flavor and aroma', Buttery and colleagues utilized 'odor units' to rank order the contributions of the ~400 volatiles detected in a fruit [38]. The odor unit is the log of the concentration of an odorant divided by the odor threshold. Using this ranking system, they identified the ~15 volatiles that they predicted would contribute to tomato flavor. Unfortunately, this method incorrectly assumes that thresholds predict suprathreshold-perceived intensities. Figure 2 shows an example of two odorants, A and B, that both have the same odor thresholds (10 odor units) and are at the same concentrations in a tomato (60 odor units). Both odorants have the same log odor units: 0.78 (log (concentration in tomato/threshold)). However, the perceived intensity of odorant A grows much more rapidly than that for odorant B. Thus, odorant A makes a much more important contribution to flavor than does odorant B. Psychophysicists have long criticized the use of thresholds to draw conclusions about suprathreshold perceived intensities (for examples, see [39–41]).

Reliance on thresholds to characterize sensory ability dates back to an era prior to the development of modern suprathreshold psychophysics. We now have powerful psychophysical tools to study taste, aroma and flavor. Of special importance, we use methodology devised to permit valid comparisons across individuals and groups. This methodology is particularly appropriate in studies with fruits and vegetables where the ability to provide stable sensory and hedonic assessment across seasons is paramount.

### Measurement Theory

Gustav Fechner is considered to be the father of psychophysics [42]. His primary focus was on the threshold: the absolute threshold (the lowest stimulus intensity perceptible) and the relative threshold (the amount a stimulus had to be increased to produce a perceptible increase). He called the relative threshold the “just noticeable difference” or “jnd.” Fechner used the jnds to quantify suprathreshold perceived intensities. The perceived intensity for a given stimulus was the number of jnds between the absolute threshold and that stimulus. This view held until S.S. Stevens pointed out a fatal flaw in the jnd unit — it lacked ratio properties [43]. That is, a stimulus at 8 jnds was more than twice as intense as a stimulus at 4 jnds, as if the psychological size of the jnd grew as stimulus intensity rose.

Stevens devised direct methods that had ratio properties. With his most popular method, magnitude estimation, subjects assign numbers to sensations such that one sensation that is twice as intense as another is assigned a number twice as large. Stevens used this methodology to compare the relation between stimulus intensity and sensation intensity (called psychophysical functions) for a number of sensory domains [43]. In some domains, perceived intensity grows much faster than in others — that is, the slope of the psychophysical function is much steeper. In the chemical senses, olfactory functions tend to have lower slopes than do taste functions. Within taste, bitter stimuli tend to have the lowest slopes; that is, bitterness grows very slowly as concentration increases.

Stevens was not particularly interested in individual differences, but some of his students and colleagues were (for example, [44]). Comparisons across individuals cannot be made directly since we cannot share experiences with one another. Unfortunately, labeled scales (category scales, visual analogue scales) have been used as if they provide valid comparisons across individuals/groups. They do not. The labels on such scales (e.g., weak, strong, etc.) can denote different absolute perceived intensities to different individuals [45]. If we had a universal standard that we knew was perceived the same by all, we could make absolute comparisons for any sensations of interest by asking subjects to rate sensations of interest relative to that standard. Such a universal standard does not exist, but we can come close by selecting standards not related to the sensations to be compared (for the earliest use of this method see [46,47]). This methodology, formalized as ‘magnitude matching’ [48] led to the discovery of supertasters — individuals who experience the most intense taste sensations.

Hedonic scaling is subject to the same limitations as sensory scaling with regard to valid comparisons across individuals [45]. Valid hedonic scaling allows insights into group differences in food palatability; for example, supertasters experience more intense pleasure and displeasure from food. Older hedonic scaling methods (e.g., Natick 9-point hedonic scale) cannot show this difference [49].

### Application of Scaling to the Tomato Problem

It is clear that we cannot predict preferences solely on the basis of chemical composition. Our knowledge of how the brain integrates the multiple chemical inputs into a flavor image is insufficient. Until the rules for integration are defined, the only way to predict liking is empirical. Thus, a statistically sufficient number of samples exhibiting significant chemical variation must be sampled. Magnitude

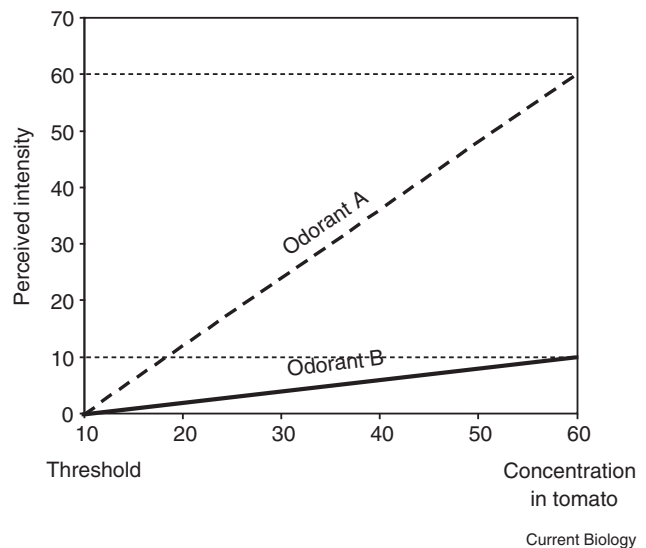


Figure 2. Illustration of the dangers of using thresholds to characterize importance of sensory contributions.

The importance of an odorant to the tomato depends on the shape of the function relating perceived intensity to concentration. The steeper function (odorant A) produces a more intense sensation in the tomato (60 as compared to 10).

matching methodology permits sampling of large numbers of samples across individuals and seasons. In the tomato preference study [15], we used magnitude matching to ultimately determine the contributions, or lack thereof, of over 70 different chemicals to consumer preferences. We also used these methods to ask different groups of subjects to describe the ‘best tomato ever tasted’. Females reported significantly higher ratings than males. Similarly, supertasters and ‘foodies’ (individuals who experience the greatest pleasure from food) exhibited different preferences [50]. These kinds of comparisons could be useful for those interested in different market segments.

### Conclusions

The ability to compare large numbers of samples in a large population facilitates identification of the most important drivers of human preferences for a whole food product. This finding alone permits breeders to focus attention on a limited set of chemicals to improve flavor. These analyses have, in turn, uncovered important processes that the brain uses to integrate diverse chemical signals into a unified image of a food. The better we understand the rules for how this integration occurs, the better our ability to predict what we like will be.

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