Cambridge University Press
978-1-108-71407-5 — Chemical Senses in Feeding, Belonging, and Surviving
Paul A. S. Breslin
Excerpt
More Information

1 Introduction

In this Element, I discuss the physiological and social roles of taste and the proximal chemical senses. First, I discuss from a chemosensory perspective how we perceive food and people when we contact them. These perceptions help us identify what we are eating and with whom we are present and serves as an analysis of the complex scene. Second, I consider the influence of taste in food choice, metabolism, and nutrition. Next, the impact of taste and the proximal chemical senses in social interactions is considered, including social eating. Then, I discuss the role of taste and the proximal chemical senses in emotion, which includes the emotions related to feeding and social interactions. Throughout, I propose and illustrate the influence of the proximal chemical senses in the rich interconnections of all of these ideas; a set of experiences, emotions, and perceptions that influence each other fluidly. The continuous interplay of sensation, perception, feeding, social gathering, bonding, sex, and emotions place the proximal chemical senses in a position of central influence for guiding and shaping human feeding and social interaction, two biological pillars that uphold survival of the individual and the species.

2 The Chemical Senses

2.1 Taste

Traditionally, we understand taste as a distinct oral sensory system or modality; it is well-known as one of the five senses. Taste, however, is inexorably linked to and integrated with olfaction and somesthesis (the skin senses) as we normally experience them from food in the mouth. This is both how the brain utilizes afferent taste signals and how we experience them in daily life. Hence, taste is one of several "proximal" chemosensory modalities that work in concert (see 2.4 The Proximal Chemical Senses). To separate taste from these other senses is to take it completely out of context. Whereas the traditional reductionist approach of isolating systems for study has been common among many laboratory scientists, this Element will explore these senses together because their comingling and merging is how we normally experience taste and the other upper airway senses, their perceptual constructs, and their associated behaviors.

These senses, while served by different nerves, are united as a functional group. For example, all taste stimuli also activate the somatosensory system, since the compounds must be carried on substrates or in solvents that are orally "felt." Furthermore, most sapid compounds have associated odors, presumably due to highly correlated volatile impurities and decomposition products. Where food is concerned, whenever taste is involved, smell and touch are also involved (as are vision and hearing to varying degrees). Further, the occasion of dining

Cambridge University Press
978-1-108-71407-5 — Chemical Senses in Feeding, Belonging, and Surviving
Paul A. S. Breslin
Excerpt
More Information

with another person (a topic examined later in this Element) may allow us to taste and smell the food, as well as smell the person with whom we dine, resulting in a complex integrated chemosensory “scene,” which we chemically sample, analyze, and perceptually synthesize. Thus, when the term “taste” is used in this Element, it means taste as well as its epithelial sensory companions of touch and smell when pertinent, which is most of the time. Historically, taste, olfaction, and somesthesis were all conceived as being unified operationally as “the epithelial senses” of the upper airways and consequently were grouped together by Emil von Skramlik as “*der Niederen Sinnes*” (the lower [skin] senses)(Von Skramlik, 1926). These he contrasted with the distal “higher” senses of vision and hearing.

2.2 Olfaction

Olfaction is the sensation of airborne chemicals acting in the olfactory epithelium on olfactory receptors that lie high in the nasal cavity, almost between the eyes, and give rise to odor sensations. Typically, these compounds are small and volatile. There are, however, exceptions to this rule, such as when large non-volatile molecules or particles are stirred-up with mechanical disturbance, such as by wind, or when they are given high energy, such as when cooking with oil. There are two air passageways that lead to the olfactory epithelium: one via the nostrils, called the orthonasal pathway; and one from inside the mouth and back up through the nasopharynx, called the retronasal pathway. Most food odors arising during eating and chewing are retronasal odors. Otherwise, almost all odors, including food odors, are orthonasal. Examples of olfactory qualities/objects we experience include the odors of: wet dog fur, geranium flowers, cooked hotdogs, rotten eggs, babies’ heads, motor oil, feces, and hundreds more. It is worth noting here that names for olfactory qualities are associated in many cultures (but not all) with object names, as in the preceding list, and are, therefore, less abstracted than qualities from other sensory modalities, such as red, sweet, or warm (Cain et al., 1998).

2.3 Chemical Somesthesis (Chemesthesis)

Chemical somesthesis or chemesthesis are the sensations of chemicals acting on the epidermis (skin) and epithelia (lining of the inside of the mouth, throat, nose, eyes, etc.) that give rise to myriad skin sensations, including warm, cool, hot, cold, tingle, tickle, itch, sting, burn, touch, light pressure, deep pressure, vibration, buzzing, and others. Chemicals have been identified that can elicit each of these sensations from skin and epithelia. Compounds that stimulate chemical somesthesis may be volatile and nonvolatile. Common food-based examples of chemesthetic compounds and their sensations are: the warmth and burn of capsaicin from chili peppers, the cool of menthol from mint, the irritation and sting of allyl isothiocyanate from horseradish, and the tingle and buzz of sanshool from Szechuan peppercorns. These compounds are thought to activate sensory neurons via action on ion channels in nerve endings within the skin and epithelia.

2.4 The Proximal Chemical Senses

All of our sensory systems can be divided into proximal and distal sensing groups. That is, whether they are activated when we are close to the stimulus source or whether they can be activated when we are far from the source, respectively. Taste and the skin senses are generally considered proximal sensory systems (for nonaquatic animals; Caprio et al., 1993), since contact or close proximity with the source of the stimuli is usually required to activate them. In contrast, olfaction, vision, and hearing can sense stimuli when the source is far away. Importantly, these three distal senses play a dual role and operate when a stimulus source is nearby as well. Thus, when food or people are near us, all of our senses can be activated at once. Olfaction has the further proximal sensory distinction of operating from within our mouths and bypassing our external nose via the retronasal air passage. This “retronasal” olfaction is a specialized proximal division of the olfactory sense that enables a different and more intimate perception of what has contacted the inside the mouth (Welge-Lussen et al., 2009). Thus, the sensory systems of the tongue with the oral and nasal cavities (the upper airways) integrate to create “flavor” as a proximal, polymodal, synthetic, and unified sensory experience, such as the flavor “gestalt” we experience when eating hot apple pie (Breslin, 2013; Breslin & Spector, 2008).

3 Perception

3.1 Taste

When we perceive a single taste (a qualia) such as the taste of a NaCl solution or a sucrose solution, the qualia may be subdivided into multiple perceptual attributes of: (1) quality (e.g., salty, sour, bitter, sweet, savory); (2) intensity (e.g., barely detectable, weak, moderate, strong); (3) location (e.g., taste on the tongue tip, back of tongue, soft palate, pharynx); (4) temporal (e.g., short-lived or enduring as an “aftertaste”); and (5) hedonic (e.g., pleasant or unpleasant). All of these five attributes are neurally encoded, so that when physiologists record from a taste-sensitive neuron (unit) either peripherally or centrally, it is unclear initially which attribute(s) are encoded within the signal or even of

Cambridge University Press
978-1-108-71407-5 — Chemical Senses in Feeding, Belonging, and Surviving
Paul A. S. Breslin
Excerpt
More Information

their sensory modality: taste, tactile, thermal, or some combination. Many taste responsive units are also tactile and thermal sensitive. Further, it may be impossible to understand taste to the exclusion of understanding touch, thermal, and even olfactory inputs, since they surely cooccur with every stimulation (Robinson, 1988). The fact that touch and thermal inputs are manipulated to be consistent across stimuli does not render them absent from what is encoded. There is a tendency among scientists to assume that a taste-sensitive unit carries information exclusively or predominantly about taste quality. But it is difficult to know the attribute(s) encoded within the signal simply from interpreting responses to a few stimuli.

Additionally, expectations of the perception will also guide interpretation of signals depending on whether we understand ourselves as tasting foods, medicines, or other people. Hence, it is inevitable that our responses to taste stimuli will only be normative and complete when we are fully aware of what we are tasting, so that expectations and interpretations may prime us for the stimulation (Kass et al., 2013; McGann, 2013). Understanding perception from the divisions of bottom up and top down do not quite make sense given that each controls the other from the outset, even before stimulation occurs in expectation of and according to our experience. Consider that top-down processing is clearly driven by previous experience. And while we might imagine that bottom-up processing is somehow purely the domain of receptor and afferent pathways, those too are modified as a result of their experience with stimuli and the constraints of the whole system. Bottom up and top down are oversimplifications of a vast array of reentrant neural subsystems. Those ideas represent a single time slice in an ongoing network of constant change. As such, these levels of analysis are illusory. Inevitably, the results of any animal or network-based experiment will incorporate some knowledge of what was – rather than merely what is – the state of the organism. It might be meaningful to describe a single experience as "mostly top down" or "mostly bottom up," but that experience has now changed the system leaving it newly modified for the stimuli that will follow.

3.2 Quality

Since Aristotle and even earlier, taste has been divided into major qualities (McBurney & Gent, 1979). These are most famously sour, salty, sweet, and bitter. Although early understandings of taste included astringent and pungent as taste qualities, these were later excluded as they could be elicited from nongustatory epithelia. Astringency can be classified as a somatosensation, related to oral qualities of mouth feel (e.g., lubricity, rheology, and tribology)

(Breslin et al., 1993; Green, 1993). But because these sensations can also be elicited from taste epithelia and, in particular, gain special access to neurons within the epithelium via taste pores, the roles of tactile, astringent, lubricating, fatty, and pungent sensations on taste may perhaps merge these modalities perceptually to some degree (see 3.4 Die Niederen Sinnes). A quality of taste, such as sweetness, is ultimately a perception that must be consciously and widely recognized as a distinct qualitative experience. For example, “metallic taste” (the experience of licking metallic zinc, copper, and some other metals) has been debated as to whether it is a unique taste, a somatosensation, or a combination of the two, but presently it is not clear to what sensory modality it belongs – that the sensation is experienced, however, is not in question (Lawless et al., 2004).

The main four taste qualities might not be the only taste qualities we can perceive. In fact, there might be a great many more. We tend to focus on these four because they are very common sensations we can clearly experience in isolation: the taste of acidic fruit juices, the taste of salt, the taste of honey, and the taste of medicines. Also, we tend to focus on the four main taste qualities because they can stimulate high maximum intensities; that is, we can experience all of them as strongly intense. Curiously, maximum perceived intensities differ from stimulus to stimulus and from quality to quality, so their robustness and salience differs. For example, of all of the high potency noncaloric sweeteners used to make diet sodas, none can reach a maximum sweetness intensity as high as that of the sugars sucrose or fructose. There are also taste qualities that have lower maximum intensities than sour, salty, sweet, and bitter; they are, therefore, less salient and garner less attention. Taste qualities that have lower maximum intensities include savory or umami (the taste of glutamate mixed with IMP or GMP), maltooligosaccharide taste (the taste of starch decomposition products or small glucose polymers), and nonsalty/nonbitter cation tastes (a subquality of calcium and potassium salts) (Chen et al., 2009; Lapis et al., 2017; Tordoff, 2001). There may even be tastes that have an intensity so low that we are not fully aware they have a unique quality, such as the taste of fatty acids from triglycerides and the taste of water. The latter two might be detectable and able to influence our perceived hedonics and preference for substances sampled without eliciting a unique conscious quality.

All of these taste sensations can be mapped into a theoretical taste space that is all inclusive of our perceptual experiences. Within this space will reside regions we may label with particular qualities, but this space will most certainly have more than four regions. It may have dozens of regions, some of which elicit taste sensations that have no quality. This is because some tastes may only influence our physiology or our affective processing and liking, yet they reside within this space. Taste space may also bleed into, intersect with, or be bent and warped by tactile and thermal spaces. Hence, we may need a partial return to Aristotle's claim that astringency and pungency are tastes. There will also be stimuli that occupy several regions of the taste space at once because they elicit multiple qualities. There are infamous examples of multiquality stimuli, such as the "sweeteners" saccharin and acesulfame, which elicit both sweetness and bitterness. But the most diverse multiquality stimuli are salts, such as NH4Cl, which can elicit three or four different qualities of taste at once (Murphy, Cardello, & Brand, 1981).

All taste stimulations by nutrients or toxins likely have physiological and metabolic consequences. The three caloric macronutrients (carbohydrates/ sugars, fats/fatty acids, proteins/amino acids) likely generate taste-triggered metabolic signals that prepare the body to process the incoming calories and also to drive liking and ingestion. All three generate taste signals, and for carbohydrates, there is evidence of metabolic priming (Mandel & Breslin, 2012). For the bitter-tasting toxins, especially when strongly bitter, there are physiological consequences that limit intake and absorption and can also induce feelings of nausea (Peyrot des Gachons et al., 2011). For sour stimuli, our inherent attraction and repulsion is determined by concentration (we tend to prefer lower concentrations [except for children, who can enjoy very high concentrations]) and contextual food cues such as presence in fruit (sweet paired) or fermented foods (savory paired). The physiological consequences of sour taste, however, are unknown at this time. For stimuli such as maltooligosaccharides, fatty acids, nonsodium cations, and water, there are metabolic consequences that arise even in the absence of clear and specific taste qualities. For example, maltooligosaccharides elicit an early insulin response from oral stimulation (Mandel & Breslin, 2012), even though their malty taste is weak at best (Breslin, Beauchamp, & Pugh, 1996; Lapis et al., 2017).

3.3 Hedonics and Preferences

Taste sensations elicit innate reactions of like and dislike depending on whether they signal nutrients or toxins, respectively. Hence, we are born liking and wanting to ingest sweet-tasting substances and disliking and wanting to reject bitter-tasting substances. We hypothesize that these taste-triggered facial reflexes are the foundation of human emotions via the facial efference theory of emotion (See 6 Emotions).

Our enjoyment, liking, and preferences for foods are also subject to social context and experiences. Foremost, the post–ingestive consequences of ingesting foods with caloric benefit or toxic effects strongly influence whether we will come to seek out these foods in the future via conditioned taste preference (Sclafani & Nissenbaum, 1988) or avoid them via conditioned taste aversion (Garcia, Hankins, & Rusiniak, 1976; Garcia et al., 1985), respectively. This plasticity in hedonics or liking allows humans to perceive certain chemosensory attributes, such as flavor, as unchanging, yet whether we seek these flavors or avoid them depends on their associations (Birch et al., 1990; Scalera, 2002).

Social context also plays a major role in our relation to food ingestion and liking. Rodents learn about safe flavors to eat from the mixture of flavor and hydrogen sulfide on the breath of other "demonstrator" animals (Galef & Kennett, 1987; Galef & Whiskin, 1997). We too learn from the habits and conversations of others about what is both safe to eat and good to eat. For example, we may learn to like foods of a culture different from our own that at first seemed unpleasant. Here, the practice of so many others and observation of their eating habits may help to teach us that the food is safe, nutritious, even delicious. This may also occur at a smaller scale from the feedback of others around a table either positive or negative regarding a particular food or dish. The flavor that we perceive is the combination of all oral stimulus sensations and retronasal inputs, as well as visual and auditory inputs. These may all be combined to yield our overall perception of the food's flavor. The multimodal sensory integration that generates flavor may be the most complicated sensory integration of which humans are capable, but whether we enjoy these flavors is largely based on our history with them.

Expectations influence the flavor we perceive as well. We come to expect a flavor based on verbal information. That is, labeling, marketing, and conversations inform us of what we are about to receive. This cues a mental flavor engram against which oral samples are compared. If the flavor memory or engram is not a close match to what we perceive, then we may perceive it as both "wrong" and unpalatable. As a *gedanken* exercise, imagine being offered a home-prepared tomato juice that was actually a pulpy orange juice that was dyed red. The mismatch from what was expected and what was perceived might be shocking and cause the opinion that the tomato juice was terrible, even though it may be perfectly pleasant tasting orange juice. Color may also lead to the perception of flavors that are not chemically present due to expectations. Thus, a sweet-and-sour-tasting, citrus-smelling beverage is ambiguously citrus fruit flavored, but may be perceived as lime flavored if green or grapefruit flavored if pink (Stillman, 1993).

3.4 Die Niederen Sinnes

Emil von Skramlik referred to the epithelial receptor systems as *die niederen Sinnes* or "the lower senses" (Von Skramlik, 1926). These he collectively believed were part of one overarching system of receptors embedded within an epithelial sheet that functioned together. Thus, chemicals, material substances (foods and beverages), temperatures, breaths, and so on all impact the epithelia at once and are processed collectively by the epithelial sheet and the brain. The tactile receptors, the thermal-sensing free nerve endings, the chemosensors, the nociceptors, as well as the taste and the olfactory receptors are all embedded within a continuous epithelial sheet, albeit not all in the same location. He envisioned that they operate as a sort of epithelial ecosystem, each perhaps occupying a different niche functionally but all working together as part of an integrated whole. There is also an epithelial cartographic component in that we tend to be able to identify the location of most epithelial stimulations. This conceptualization of the epithelium as an überorgan makes sense as this is how the physical world impacts us and it also happens to be how integrative areas of our brains, such as the insular cortices, process inputs from our upper airways. Hence, von Skramlik's conceptualization supports our use of taste perception as part of the proximal chemical senses in toto.

3.5 Perceiving Food and People: Scene Analysis

Unlike the role of conditioned taste preferences and conditioned taste aversions in which our attitude and affective processing for a food is altered by association, we may also come to have altered stimulus perception through learning and experience. The ability to "see" or perceive what we previously could not is a form of perceptual learning. The stimulus is not changing nor is its impact on our receptors. Rather, perceptual learning is a guided use of attention to features and attributes that permits us to focus on them. We do not perceive what we do not attend to, a phenomenon known as "inattentive blindness" (Lorig, 2012; Zucco, Priftis, & Stevenson, 2015). Experience and training usually serve to make us "experts" at perceiving, whether it is to see densities in mammograms or detect subtle off-notes in wines. As is typical of perceptual learning, once we learn the skill of guiding our attention to perceive features, it is difficult to stop attending to these features. Thus, once we learn that there is the necessary hint of cat urine odor in a fresh orchard peach, we will always know when it is there; just as once we learn to see and appreciate the subtle undertones of pinks, blues, greens and yellows in various shades of "the color white," we will see these hues in the whites around us in wall colors, clouds, book pages, papers, lights, and so forth.

As we gradually become familiar with the flavors and aromas of favorite foods and dishes as well as the fragrance and body odor of friends and acquaintances, we come to build our flavor and aroma engrams, which helps us know when foods are ready, ripe, and prepared correctly. This also provides

Cambridge University Press
978-1-108-71407-5 — Chemical Senses in Feeding, Belonging, and Surviving
Paul A. S. Breslin
Excerpt
More Information

a great advantage in recognizing when something has gone wrong, such as when food may be spoiled or when a friend may be sick. The perceptual learning about the proximal chemosensory signals of foods and friends and the building of their engrams enables us to identify situations that may be safe or harmful, and to be prepared for either outcome.

It is well recognized that humans have an extraordinary expertise for human faces and for facial recognition (Haxby, Hoffman, & Gobbini, 2000). We are quite simply experts at this – all of us. Although there may be an inborn preparedness to have this expertise, I believe this is another example of perceptual learning in which we stare into people's faces every day of our lives, and from this learning comes expertise. I believe humans have a similar expertise for food flavors. We eat food several times a day almost every day of our lives. Food flavors can be extremely complicated both chemically and perceptually. Yet we have mastery of the food flavors we experience with regularity. I believe our expertise for food flavors may even rival that of dogs' abilities to smell body odors of other dogs and animals.

Science has a strong tendency to isolate and identify. This has also been a standard part of perceptual science. Fortunately, more recent trends in perceptional research, and vision research in particular, have recognized that isolation is not the way in which our senses work. This Element makes a point of linking taste (per se), smell, and somatosensory stimulation to understand our perception of flavor and foods because these systems are not isolated. But, perhaps surprisingly, our discussion here has also been somewhat limited in showing the context of flavor stimulation. In the last decade, visual science has recognized the importance of scene analysis (Enns & Rensink, 1990; Wolfe et al., 2011). The scene analysis approach to chemosensory perception needs to be applied to flavor and all of chemosensory research as well. For instance, our familiarity and expertise with food flavors and also with human odors is useful in social situations in which we are around multiple dishes and multiple people. There exists in these situations a chemosensory scene that must be analyzed to enable us to determine the source and identity of chemicals. The task is made easier by the fact that not all objects are equiintense or equidistant from us. In addition, we are not static relative to the objects. Thus, we talk with one person and then another, or we may bring a food closer to us and into our mouths one at a time. Once a food or beverage is in our mouths, they can stimulate retronasal olfaction as well as taste and chemesthetic stimulation, which makes identification and recognition much easier. Our sensory systems and our brain may also be organized to process edible signals and social signals separately (Bender et al., 2009; Small et al., 2005; Welge-Lussen et al., 2009). There are many chemical cues, however, that are common to both foods and humans, and how we parse

Cambridge University Press
978-1-108-71407-5 — Chemical Senses in Feeding, Belonging, and Surviving
Paul A. S. Breslin
Excerpt
More Information

them perceptually will be based upon our expectations of what we are experiencing, such as cheese versus human feet. Note again that olfactory quality is intimately linked to source object, at least in Western culture, resulting in odd ambiguities of either smelling like stinky feet or good cheese.

3.6 Art and Gastronomy

Art is the skillfully executed, emotionally evocative, perceptual abstraction of the familiar and unfamiliar. Art is ancient; earliest observations of cave art appeared over 40,000 years ago. Art is ubiquitous and highly valued; every culture has some form of art and in all modern developed societies there are public art museums, theaters, and concert halls. People and civilizations invest in art as much as they do in gold and other precious metals. Art is a reflective and refined abstraction of our lives, a way to see ourselves in a new light, with a new perspective. It is a lens through which we can look into a mirror, or perhaps a mirror shard, and try to understand ourselves better. Art involves all of the senses and can take virtually any form; it can be flat, three dimensional, temporary, semipermanent, static or kinetic, paintings or movies, it can be inanimate or live, it can be music, dance, or literature, and can take place or be positioned anywhere. Art can be presented in any medium, and for the proximal chemical senses, it is most commonly presented in the medium of food . . . food and flavor as art.

Since gastronomy is the art of cooking, excellent gastronomy is not just food that tastes delicious, but food that invites you to appreciate that it is unusual, better, skillful, and draws in the consumer to wonder how is it different from the everyday and what makes it so unusual. Gastronomy can be interesting, unfamiliar, surprising, even shocking. But as is true of most art, gastronomy should cause the perceiver (or consumer) to be reflective: of the food, the flavors, the sources of foods and flavors, the scene, the culture, and the idea of how we relate to the world around us. And while gastronomy can challenge our perceptions and ideas of flavor and familiarity, comfortable flavors of “home cooking” sustain us just as the folk art on the refrigerator does.

Summary: Our perceptions of tastes and the chemical stimuli of the upper airways are highly integrated multimodal signals. So much so that it may be difficult to separate modalities from one another. How we come to perceive flavors and tastes, foods and friends, is highly malleable and will be based upon our familiarity, consequence learning, contextual learning, and perceptual learning and experience. The more familiar we are, the greater our expertise. When it comes to food flavors, all humans are extreme experts. This is useful for chemosensory scene analysis when we are surrounded by foods and people and