Other Tastes, Other Worlds

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The word taste has undergone many connotative changes with time. Originally in all Western European languages it meant nothing more than "to sense," to sense anything. Then, more specifically it came to mean touch and to test by touching, and, by transference, to appreciate. Within a biological and psychological context ambiguity still surrounds the word because taste and flavor are often employed interchangeably. For the discussion which follows it is necessary to agree upon a precise definition and to distinguish between taste and flavor. Taste will refer strictly to the interactions between chemicals and the receptors in vertebrate taste buds together with their nerves and central pathways, and between chemicals and gustatory receptors and neural pathways in invertebrates (*1*).

Summary. The idea of four primary tastes has influenced our concept of the gustatory world of all animals. It has also been the basis for constructing theories of gustatory neural integration. Since natural chemical stimuli are complex mixtures to which responses are multineuronal, difficult questions about integration arise. Answers are usually framed in terms of "labeled line" or "across-fiber" hypotheses. Comparative studies of vertebrate and invertebrate taste reveal in all receptors universal basic parameters that bear on the controversy. Comparative studies also place in more accurate perspective diverse chemically related ecologies and behaviors.

We are so accustomed to thinking of the chemical world that reaches our tongues in terms of sweetness, saltiness, sourness, and bitterness that we unconsciously extrapolate these subjective assessments to all animals. Or, at the very least, we tend to restrict our experimentation to those compounds which evoke four tastes in man. Comparison with other sense modalities where these matters have received more attention reveals something of the diversity that exists beyond our own sensory perception (Table 1). A fundamental difference, for example, is that pitch and hue correspond to points in a continuous series whereas the stimulus qualities of taste represent points in a discontinuous series.

The existence of dimensions of experience associated with the sensing of objects implies the existence of specific properties (wavelength, chemical species) appertaining to objects. The reverse is not true. The ability to discriminate these properties implies different sensing devices and means of coding and signaling differences to the central nervous system. It also implies a central ability to differentiate incoming signals. Thus, different frequencies of sound waves are distinguished as a consequence of different hair cells in the basilar membrane responding best to different frequency bands. Discrimination of different wavelengths of light by human beings is possible because there are different kinds of cones, each broadly tuned to a different range of the spectrum, and because other wavelengths can be coded as combinations of the inputs from the three cones. In a comparable sense taste qualities are experienced by human beings most probably as a consequence of there being categories of taste receptors tuned to different molecular species. There is no direct experimental evidence bearing on this point.

Neither hair cells nor cones respond to a single wavelength; rather, they respond better to one region than to another. Similarly taste receptors respond to more than one compound (or category of compounds) but better to one than to others. (The word "receptor" in this discussion refers to a cell that responds to impinging chemicals by depolarizing; it does not refer to a particular molecular site or mechanism in that cell.) This property of differential tuning within a more or less broad spectrum of sensitivity is a fundamental property of all receptors. Specificity of a receptor, that is, whether it responds to few or many chemicals, is thus a relative characteristic.

Let us now ask: What kinds and range of molecular species do different animals sense and what is the neural basis? Framed this way the question is straightforward; however, the frequency with which dimensions of stimulus and dimension of experience are interlocked or even confused in our thinking obfuscates the question. On the one hand, it may be maintained that particular stimulus discriminations and sensations can be investigated only in human subjects (*2*). On the other hand, it has been pointed out that "qualities are different because they eventuate in different kinds of behavior" (*3*). The two statements are not actually in conflict because the first equates sensations with responses to quality (presumably in the object) while the second excludes sensation. The confusion arises from use of the word quality to refer to properties of the objects sensed and to parameters of human sensations (see Table 1). Once the distinction is clear, it can be seen that the prerequisites for discriminating between stimuli within one modality are receptors that respond differently and selectively to the various stimuli. Equally necessary is a nervous system that does not lose the message in a tangle of synapses and nondiscriminating interneurons at higher levels. Differences in the response characteristics of receptors are of little value to an organism if some interneuron upstream treats all incoming messages alike. The experimental means of detecting this discriminative capacity are the demonstration of correlative differences in behavior—including verbal. That detection is possible in nonhuman animals is attested by the success that has attended analyses of color vision in diverse organisms.

It is clear that different species, different populations of a species, and different individuals within a population have different sensitivities (thresholds) to commonly encountered stimuli, that they "taste" different compounds, and that they are "blind" to different compounds. Within populations there is the usual variance about a mean; there are sexual differences, differences associated with age, with pathology, and with genotypes. The last is exemplified by the well-known difference in response to phenylthiourea and related compounds.

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We are concerned here, however, with differences in quality discrimination and threshold *among* species.

The task of comparison is confounded by the uncertainty that still surrounds our own gustatory experiences. How many taste stimulus dimensions do we perceive as qualitatively different? For Aristotle the answer was two. All sapid substances were either sweet or bitter. From the 16th to the 18th centuries as many as ten stimulus qualities were said to be detectable. Among the recorded tastes were pungent, tart, spicy, peppery, brackish, alkaline, ambrosial, nectareous, acid, metallic, soapy, nauseous, and dulcet. At this time no distinction between taste, flavor, and hedonic characteristics was being made. In 1916 Henning proposed that all perceived qualities could be derived from four primary qualities: sweet, sour, salty, and bitter (*4*). The implication is clear that man experiences more than four qualities. Left unanswered is the question of how so-called secondary qualities—that is, those that cannot be identified with the four primaries—are derived and whether they are unique qualities or mixtures. This controversial question, usually framed as "the labeled line hypothesis versus the across-fiber hypothesis," will be discussed later in this article.

Quite apart from the uncertainty of the derivation and nature of secondary qualities is a residual uncertainty about the verity of Henning's model. Although generally accepted, the model has not gone without challenge. Recently Schiffman and Erickson pointed out that the model is a closed system which by its very nature prohibits description of quality of sensation in any but four primaries (Henning's model is a tetrahedron with the four primaries at the corners and other qualities designated as points within these confines) (*5*). They suggested that taste qualities exist which cannot be accommodated by the old model. Although precautions were taken in their tests to eliminate olfactory contributions, activity from trigeminal receptors was present. The reality of four primaries is suggested by the fact that there are no words for tastes, as distinct from flavors, other than sweet, salt, sour, and bitter. There are no generally agreed upon gustatory equivalents of yellow, orange, pink, and brown, for example. The implied existence of four primary sensations also implies an equally limited number of stimulus dimensions perceived as distinct at the receptor level and, therefore, a limited number of receptor mechanisms for signaling to the central nervous system.

If it is assumed that for each primary chemical stimulus there must be a unique receptor preferentially sensitive to it, then the following conditions influence the character of the perceived world: (i) the number of different primary receptors; (ii) the kind of each receptor, that is, what species of chemical its structure (molecular or otherwise) will permit it to respond to; (iii) the width of the tuning curve (how many different chemicals it responds to) of each receptor; and (iv) the point of maximal response in the action spectrum. Additionally, if mixing of stimulus primaries is possible, as it is with wavelengths of light, even finer resolution of the taste world is possible.

Primary Receptors

Not all animals have the same number of primary receptors. It has been inferred that man has receptors for carbohydrates (sweet), acids (sour), salts (salty), and a number of compounds, of which quinine is an example, evoking the sensation bitter. There is, however, no direct proof. Electrophysiological recording from individual human taste cells would provide valuable information on this point. All animals appear to possess receptors for salts (as ascertained electrophysiologically in many cases), but although the "sweet tooth" is ubiquitous, some animals do not respond to sugars (*6*). Many other sensitivities have been found in insects, and many types of receptors have been discovered. This is especially true of caterpillars, where eight of the total complement of 11 oral receptors on each side are located on the maxillary mouthparts. The commercial silkworm, *Bombyx mori*, has three receptors for salts, one for deterrents (miscellaneous organic compounds), one for inositol, one for sucrose and glucose, one for glucose alone, and one for water (*7*). The caterpillar of the cabbage butterfly *Pieris brassicae* has two receptors for salts, one for deterrents, two for glucosinolates (mustard oil glycosides), one for sucrose and glucose, one for anthocyanins, and one for amino acids (*8*, *9*). A caterpillar may have as many as eight primaries. The number determines the size of its "window" looking out at the world.

Table 1. Comparison of dimensions of different sensory modalities.

Dimensions of stimulus	Dimensions of experience
Sound (periodic vibrations)	
Wave amplitude	Loudness
Wave frequency	Pitch
Harmonics	Timbre
Light (radiant energy)	
Wave amplitude	Luminosity (brightness)
Wavelength	Hue
Purity of wave	Saturation
Chemicals (taste stimuli)	
Concentration	Intensity
Molecular species	Quality (no word)
Purity of compound	Quality

Specificity

The specificity of receptors, that is, what kinds of compounds they respond to, varies widely from species to species and determines the direction in which the individual's window faces the world. We, for example, could just as well have been endowed with a receptor for fats, one for cellulose, one for starch, and one for chlorophyll. The insolubility of these materials in water is no obstacle because suitable receptors could have been evolved just as readily as those requiring aqueous solutions. Olfactory receptors operate very efficiently with water-immiscible compounds. The two species of caterpillars just mentioned have the same number of receptors but with sensitivities to different stimuli. Other insects have still different receptors, for example, one type for salicin and populin and others for sorbitol and for hypericin.

Width of Tuning Curve

The width of the tuning curve of each receptor as well as the point (compound) to which it gives its maximum response determines the resolution of the window. The width could be broad or it could be narrow as implied by the generalist-specialist doctrine of olfaction. A receptor could, in theory, respond to a single chemical compound. The width would then be deterministically small, thus giving the receptor absolute specificity. A problem arises here because the experimenter introduces a bias with his choice of test chemicals. Since we are dealing in taste with a discontinuous assemblage of compounds, and not a continuum as in vision and hearing, width of tuning curve refers to the number of compounds to which a receptor is sensitive. The butterfly *Pieris rapae* L., for example, has a receptor for sodium ions and a different receptor for potassium ions (*10*). This animal can differentiate between the two and does so in nature. The blowfly, on the other hand, detects sodium and potassium with the same receptor and does not distinguish between the two.

The butterfly *Pieris brassicae* and the moth *Mamestra brassicae* have specific (narrow) receptors for glucosinolates whereas a number of other insects, of which the blowfly is one, detect sinigrin and sodium chloride with the same receptor.

Point of Maximum Response

Tuning curves of receptors which are all sensitive to a given compound may yet be quite different from one organism to the next. They can differ in either of two respects. First, each could also be sensitive to identical groups of additional compounds but exhibit maximal responses to different members of the group as exemplified by the following two series in which the capital letter represents the "best" stimulus: aBcd; abcD. Second, each could be preferentially sensitive to the same compound but possess no other sensitivities in common (aBcde; Bfghi). For example, each of two animals could possess a receptor for carbohydrates, and this could be a primary (that is, carbohydrates would be the "best" stimulus); yet the carbohydrate receptor of one animal could respond to carbohydrates, saccharin, cyclamates, monellin, aspartate, D-leucine, D-alanine, D-tryptophan, and D-glycine, while that of the other animal could respond to carbohydrates, L-valine, L-leucine, L-isoleucine, L-methionine, L-phenylalanine, L-tryptophan and not to organic sweeteners. In fact, the first mentioned receptor could be that of man; the second is that of the blowfly. It follows that identity in nature, that is, equating one taste object with another, will be different for the two. For example, artificial sweeteners and sugar each taste sweet to man (even though some of the synthetics also have aftertastes), but in the case of the blowfly none evoke the same behavior as does sugar.

Given all of these differences in the peripheral sensory system an identical object in nature could present different faces to each animal even if only a single receptor were stimulated. This follows because a compound has more than one characteristic and the various receptors would be sensitive to different characteristics. For example, in one animal a receptor sensitive to the phosphate radical, and hence stimulated by sodium phosphate, might also respond to glucose diphosphate, "seeing" only the character phosphate, while in another animal a receptor sensitive to glucose would see only the glucose moiety and respond to glucose disphosphate as glucose. In other words, in a heterogeneous world each animal would accord unique values to different segments of that world. As a consequence, the behavior, other things being equal, would also differ. In reality, many different kinds of receptors are stimulated simultaneously, and the biases introduced by the properties of each single receptor—what it is sensitive to, how many things it is sensitive to (width of its action spectrum), and the character of the tuning curve—may be compounded in the central nervous system.

Neural Mixing

Equating receptors with primary stimuli and concluding that the discrimination of these stimuli depends solely upon the information from each receptor and where it is received in the central nervous system assumes that upstream of the receptor the integrity of the sensed information is maintained until it reaches a decision-making center. In many invertebrate chemosensory systems this is the case since each receptor has its own axon; there is no synapsing (at least in insects) outside of the central nervous system and there are no lateral connectives. Synapsing does, of course, occur within the central nervous system so neural mixing of messages which can occur in the mammalian system at the level of the taste cell (multiple innervation and cross innervation) is merely postponed.

The nature of neural mixing and the question of whether or not discrimination of additional stimulus qualities to the ones permitted by primary receptors (if they are tied only to a labeled line system) is possible, pose difficult problems. In the human visual system receptors are sensitive to the spectrum from about 380 nm to 780 nm. If all were identical, no differences in wavelength could be appreciated. With three kinds of receptors sensitive only to three separate parts of the spectrum, only three bands could be distinguished. Since each receptor responds best at one part of the spectrum but is also sensitive to others, and since the tuning curves of each overlap so that the entire spectral range is sensed, all regions including the areas of overlap can be distinguished if the information from all receptors is combined and integrated neurally. Does taste operate this way?

In vertebrates and invertebrates alike there is for each receptor a best stimulus and a range of secondary stimuli. There are various degrees of overlap of activity spectra. When more than one receptor is stimulated, patterns of neural activity involving multiple fibers are transmitted to the central nervous system. Consider, for example, two stimuli a and b, which are the best stimuli for receptors A and B, and a third stimulus c for which there is no specific receptor (that is, c is not the best stimulus for any receptor). Stimulus c could activate both A and B. It could, therefore, be distinguished from a and b as long as the central nervous system was able to tell which and how many receptors were acting. In human taste experience, stimulus c is often described as a mixture of a and b. It is described as salty-sweet and sweet-sour. It is as though the central nervous system adds but does not mix the information. Furthermore, no neural addition need be unique to a single compound; that is to say, an identical summed neural pattern could be constructed from any one of several compounds as long as proper adjustments in concentration were made to compensate for differences in stimulating effectiveness. In the blowfly, for example, more than one receptor (usually three) respond to sodium valerate, and an across-fiber pattern is generated. The same pattern can be obtained, after concentrations are adjusted, to formic acid, quinine, and several other unrelated compounds.

Two questions now suggest themselves. Do other animals detect and distinguish more stimulus qualities than there are numbers of primary receptors by combining neural input? If the answer is yes, does the new stimulus dimension evoke a new experiential quality (see Table 1)? For the moment the discussion will be restricted to stimulation by "pure" chemicals.

Attempts to answer these questions in the field of vertebrate gustation have led to the formulation of two hypotheses which are sometimes presented as being mutually exclusive. These are the labeled line hypothesis and the across-fiber pattern hypothesis. The modern concept of labeled lines is derived from the doctrine of "specific nerve energies" enunciated nearly 150 years ago by Müller (*11*). As then defined it stated that a nerve carries a unique message irrespective of the stimulus applied. Originally the concept was applied to sensory nerves. Later it was modified by others to refer to individual neurons. Thus, a receptor for which the best stimulus is salt would, regardless of the nature of the stimulus, deliver a set message. A further extension of Müller's doctrine stated that a fiber delivered its message to an identifiable locus in the central nervous system. At some point the sensation "salty" would be evoked or a behavioral response appropriate to salt would be initiated. If, however, the salt stimulated two nonidentical labeled lines, which at some point converged on a first-order interneuron, would the output from that interneuron be considered as a labeled line? In the original sense of the term, no; however, as pointed out above, the concept has now been generalized to any nerve fiber, central as well as peripheral, so the contemporary answer would be yes (*12*). The question is not one of semantics as much as it is one of how the central nervous system handles information arriving on a single labeled sensory neuron and how it handles multineuronal information.

The across-fiber pattern hypothesis originally suggested by Pfaffmann (*13*) and elaborated by Erickson (*14*) takes the position that information received by the central nervous system from more than one gustatory receptor forms a spatial pattern of activity across neurons which provides an identifiable experience corresponding to a particular pure compound. Thus, in some vertebrates potassium chloride initiates a different pattern across neurons than does sodium chloride, and the two salts can be distinguished even though there is no receptor specific to either one. Insofar as vertebrates are concerned there is little doubt that discrimination of patterns is possible. The essential question becomes, is the experiential result analogous to NaCl tasting like sodium plus chlorine or tasting like salt? In short, is a pattern a simultaneous reading of several labeled lines providing a mixed experience or is it a mixing providing a unique experience? The controversy between the two current schools of thought has not been resolved.

The uncertainty in the vertebrate field might suggest that the problem is intractable when investigated in other animals. Analyzing the gustatory behavior of invertebrates against this background, while it may not resolve the fundamental problem, does broaden our concepts of the potentialities of the gustatory sense.

Returning to the first question, do animals detect and distinguish more stimulus qualities than there are numbers of primary receptors, some partial answers have been obtained from studies of the blowfly. The blowfly possesses four primary gustatory receptors: water, sugar, salt I, and salt II. The distinctive properties of the two salt receptors are not clearly understood. This uncertainty tends to confuse the issue; however, the fly is able to distinguish water, sugars, and salts. With the two salt receptors it may be able to distinguish some salts from others on the basis of different anionic moieties (*15*). In any case, there are at least three fiber types. Any compound, even such bizarre stimuli as the anesthetic halothane, that stimulates the water receptor is interpreted behaviorally as water (*16*). A water-deprived fly responds to the message from the water receptor by drinking. Any compound that stimulates the sugar receptor is interpreted behaviorally as sugar. A water-satiated but food-deprived fly, which no longer responds to input from the water receptors, responds to messages from the sugar receptor by ingesting. A compound which is a second-best stimulus for the sugar receptor (for example, valine) is responded to as though it were a low concentration of sugar, the best stimulus. In short, there are labeled lines recognized by the central nervous system and capable of evoking specific behavior when activated.

What happens, however, if the fly is presented with a chemical compound with different properties than any of the above, which is not a best stimulus for any of the receptors but which stimulates two or more submaximally? A number of mono- and dicarboxylic acids fall into this category; they stimulate the salt, "anion," and water receptors. Electrophysiological monitoring of responses of tarsal receptors coupled with behavioral observations have shown that these acids can be distinguished from salts even though there is no specific acid receptor (*17*). The behavioral response to salt is retraction of an extended proboscis (or failure to extend a retracted proboscis). The response to acid is extension (characteristically different from the extension to water and to sugar) and regurgitation. For the fly, therefore, the answer to the first question is that at least one stimulus dimension, that characteristic of acids, can be discriminated in addition to the number permitted by the number of primary receptors. Because of the nature of the receptors that contribute to the compound message the new stimulus dimensions are undoubtedly quite different from species to species.

The second question, does this new stimulus dimension evoke a new dimension of experience, cannot be answered. In the present state of our knowledge the kind of behavior evoked by multiple firing of several receptors cannot be duplicated exactly by a compound that stimulates only one receptor. Sodium chloride cannot mimic formic acid. One can always argue reasonably that the finite solubility of the salt is a limiting factor and that acids are distinguished simply because they overload the information channel with noise rather than cause a specific pattern to be transmitted. On the other hand, there are compounds, such as some sodium salts of fatty acids, which also initiate multireceptor responses at frequencies comparable to those evoked by acids but do not elicit aversive responses. The differences in behavior strongly suggest subtleties of pattern and different dimensions of experience but clearly require more intensive investigation.

Different electrophysiological responses to sugar have also been reported. Fructose and galactose each stimulate two kinds of cells in the blowfly whereas glucose stimulates one (*18*). At the concentrations tested the sugars can be distinguished. No tests have been made, however, to ascertain whether or not the sugars can be exactly matched by adjusting their concentrations nor whether, if so, the neural input becomes the same at the equated concentrations.

Mixed Stimuli

Up to this point, I have been considering the gustatory world as composed of simple, singular stimuli. This simplification has enabled us to dissect the properties and capabilities of gustatory systems. Rarely, however, does a wild animal encounter singular stimuli, that is, pure compounds. In a natural habitat the stimuli affecting the gustatory system are mixtures, often incredibly complex, of many compounds. The receptor determinants involved in sensing mixtures include those already mentioned but at least three others in addition. These are the absolute threshold, the time course (adaptation) of response, and the capacity of the receptor to engage in synergistic and inhibitory interactions with multiple compounds. Differences in receptor thresholds from one animal to another obviously play a role in determining which dimension of the world each senses. Furthermore, in any one gustatory system differences in thresholds of two or more receptors which respond to the same stimulus can also determine the nature of multineuronal input. For example, an animal may have two populations of salt receptors with different but overlapping ranges of thresholds. This phenomenon of stimulus fractionation not only extends the range of detectable concentrations but enlarges discriminatory potentialities. At low concentrations one receptor may respond and at high concentrations the other, while in the middle range both respond. On the basis of labeled lines the central nervous system theoretically could distinguish low concentrations of salt from high by which neurons were firing. On the basis of across-fiber patterns it could distinguish the middle range from the extremes as well. Although the three ranges could be distinguished with a single receptor simply on the basis of frequency of firing, a two-receptor system provides opportunities for qualitative as well as quantitative (intensity) discrimination.

In those cases where evidence suggests that multineural patterns are significant, differential rates of adaptation become extremely important. As Schoonhoven has indicated, patterns may change with time because of this (*9*). Not only may receptors adapt at their own characteristic rates to the same compound but receptors with different specificities may also adapt at different rates to their respective best stimuli. As a consequence, a receptor which is making a maximum contribution to a pattern during the first moment of stimulation may be contributing only minimally a second or more later.

With mixed stimuli the opportunities for interaction at the receptor level are many, but the mechanisms are not well understood. Various kinds of inhibition have been reported. The water receptor of *Phormia* is inhibited by ions above a critical concentration and by nonelectrolytes (*19*). The sugar receptor is inhibited by high concentrations of salt and the salt receptor by high concentrations of sugar (*20*). Mannose inhibits the fructose site of the sugar receptor but not the glucose site (*21*). Glucose and fructose act synergistically. The salicin receptor of *Manduca* is inhibited by caffeine (*9*). Behavioral studies have shown that there is synergism between sugars and amino acids and sugars and sinigin, but the site of interaction has not been identified (*22*).

All of the receptor properties and interactions discussed form the basis for different perceptual capacities from species to species. In normal ecological situations the multidimensionality of gustatory stimuli together with the heterogeneity of receptors mandate a patterned neural response. Clearly different neural patterns can be distinguished as indicated by differences in evoked behavior. The crucial question already alluded to in the section on pure stimuli is whether the central nervous system adds or mixes the incoming messages. Different behavior does not necessarily answer the question in favor of one interpretation or the other.

Consider the case of the caterpillar of the swallowtail butterfly *Papilio troilus*. The two plants, sassafras (*Sassafras albidum*) and spicebush (*Lindera benzoin*), upon which it feeds evoke from the gustatory system a multireceptor patterned response. Unacceptable plants also evoke a patterned but different response. Among the cells responding in each situation is one preferentially sensitive to sugar and one preferentially sensitive to salts. If the saps of certain unacceptable plants are mixed with a sugar solution, the sensory pattern is altered and the mixture is accepted. The most obvious change in the pattern is an enhancement of the contributions of the sugar receptor. There is an absolute change in the number of action potentials it generates per unit time as well as a change in the ratio of response vis-à-vis the other receptors. The addition of salt or acid renders an acceptable plant unacceptable and alters the absolute and relative contribution of the salt (or deterrent) cell. These results are compatible with either theory. One could argue that the central nervous system is simply adding information from labeled lines signaling acceptance, to that from labeled lines signaling rejection, the final behavioral outcome being the sign of the sum. Yet, one could also maintain that a much greater subtlety is encoded in the pattern. It would appear that the ultimate resolution of this problem must await more intensive analysis of sensory patterns or direct electrophysiological analyses of central neurons, or both.

Conclusion

The hypothesis of four primary taste stimulus qualities derived from human experience has undoubtedly influenced our concept of the gustatory world of animals and formed the substrate upon which theories of neural integrative properties relevant to gustation have been erected. Insofar as the operations have been restricted to human beings the results have been illuminating. When they begin to serve as models for other gustatory systems, even in other mammals, the implied universality requires that some of the fundamental aspects of human and other receptor systems be examined more closely and on a comparative basis. When this is done, it immediately becomes apparent that some basic parameters common to all receptors must be taken into consideration. These include, at the peripheral level, receptor specificity, widths of tuning curves, and points of maximal sensitivity. As soon as one realizes that the normal response to the chemical world is multineuronal, one must add threshold, adaptation, and synergistic and inhibitory interactions. The question of the nature of central integration and the relative importance of labeled lines and multineuronal patterns adds another dimension of complexity. Whether the two ideas represent two possible universal mechanisms or relate only to human experience remains to be seen. If we are dealing with something fundamental, then from a theoretical point of view it is possible that this parameter can be studied more profitably in invertebrates. At most, comparative studies of gustatory systems may lead to the solution of some problems basic to all chemoreception. At least, by freeing us from the straitjacket of four primary tastes they place in more accurate perspective diverse chemically related ecologies and behaviors.

References and Notes

1. I am arbitrarily exempting all aspects of temperature, texture, and those features of stimulation involving the trigeminal nerve and associated human sensations described as burning, peppery, piquant, and so forth. In short, I am regarding as flavor the complex sensations evoked from simultaneous stimulation of gustatory (sensu stricto), olfactory, temperature, and mechanoreceptors as well as free nerve endings. I am also excluding hedonic assessments such as bad, nauseous, and pleasant. My purpose in being so unnaturally restrictive, in isolating one component of a composite system that assays food, is to simplify and keep within reasonable bounds the task of comparing the responses of a variety of unrelated animals to one common parameter (that is, chemicals in solution) of their chemical environment.
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