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A study of the science of taste: On the origins and influence of the core ideas

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Abstract: Our understanding of the sense of taste is largely based on research designed and interpreted in terms of the traditional four "basic" tastes: sweet, sour, salty, and bitter, and now a few more. This concept of basic tastes has no rational definition to test, and thus it has not been tested. As a demonstration, a preliminary attempt to test one common but arbitrary psychophysical definition of basic tastes is included in this article; that the basic tastes are unique in being able to account for other tastes. This definition was falsified in that other stimuli do about as well as the basic words and stimuli. To the extent that this finding might show analogies with other studies of receptor, neural, and psychophysical phenomena, the validity of the century-long literature of the science of taste based on a few "basics" is called into question. The possible origins, meaning, and influence of this concept are discussed. Tests of the model with control studies are suggested in all areas of taste related to basic tastes. As a stronger alternative to the basic tradition, the advantages of the across-fiber pattern model are discussed; it is based on a rational data-based hypothesis, and has survived attempts at falsification. Such "population coding" has found broad acceptance in many neural systems.

Keywords: across-fiber pattern; basic tastes; distributed neural coding; population coding; psychophysics; receptors; reductionism; systems biology; taste

> "Science is made up with facts as a house is made from stones. But a collection of facts is no more a science than a pile of stones is a house."
>
> —Poincaré, *Hypotheses in Physics* (1952)

1. Introduction

Over a century of research and understanding in the field of taste has been largely contained within a four-taste model, now referred to as the "basic tastes," using the words sweet, salty, sour, and bitter, or stimuli representing these words. This model holds that there are only these few tastes, and each taste has receptor and neuron types specifically serving it. At the neural level this model is equated with the "labeled-line" idea that each taste has its own dedicated neural line into the brain. There is a very different approach that does not involve basics, but posits a continuum of tastes served by "across-fiber patterns" of activity over populations of neurons.

There has been a long-standing controversy between the basic tastes and the across-fiber pattern positions. Why has it lasted so long rather than being resolved by a few experiments early on? The position is taken in this article that the concept of "basic tastes" is not a proper scientific model because it is not potentially falsifiable. This model has been convenient enough to be easily adapted to any experimental situation, receptor, neural, or psychophysical. But the vagueness and flexibility that provide this convenience prevent it from being adequately defined, which is a fundamental fault in science. A proper definition of the idea is taken here to mean that it is based on an underlying data-based and rational hypothesis that generates precise definitions of the terms used, and thus provides the context for tests that could possibly falsify the idea (Popper 1963). The basic tastes model does not include these provisions, and therefore such tests have not been carried out. Under these conditions, there can be no resolution of the controversy. On the other hand, the across-fiber pattern model meets these two requirements of science, a rational data-based definition and testability. This model has been supported in a variety of attempts at falsification.

The major thrust of this article is to critically examine the across-fiber pattern and basic tastes models of the organization of taste. The across-fiber pattern model will be cast in the format of Young's theory of color perception,

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and the basic tastes model will be drawn on the backdrop of Hanig's famous experiment on the distribution of taste sensitivities across the tongue.

The argument will be made that, although the idea of basic tastes has directed our research for over a century, we do not know what basic tastes are; we do not know the origins, rationale, or definition of this idea, and thus we do not explicitly know how to test it.

2. "Basic Tastes"

2.1. Background

The origins of the idea that there are a few basic tastes predate modern science by at least two millennia. The evolution of the concept is rooted in ancient cultural and philosophical thought long before the advent of the scientific method. It also appears to be derived from the characteristics of our cognitive abilities. These may be the primary root reasons for the development of the idea of basic tastes, but it is clear that this model has never been construed as a scientific hypothesis to be tested.

2.2. Basic tastes from antiquity

In China during the early Han dynasty, the first two or three centuries B.C., two ways of organizing experience were formalized. These were the Yin–Yang dichotomy, and the five ways of wu xing (Unschuld 1993). Prominent in the latter were the five tastes, sweet, sour, salty, bitter, and acrid. Both of these aspects of knowledge are evident in modern thought.

The Yin–Yang idea points to the importance of differences, meaning that a concept cannot exist without something different from it; "day" would not exist without "night," "high tide" needs "low tide," good and bad depend on each other, male and female, red depends on green, and there would be no "salty" if there were no other taste. This differentiation provides the logical basis for taste discrimination and its quantification in the across-fiber pattern theory (see Sect. 6.4 on Quantification).

2.3. Basic tastes and information theory

But why did the Chinese create the idea of five tastes? The reason is not immediately obvious. Perhaps it is clear from simple sensory experience that five tastes are distinct perceptual entities, like pigs, pineapples, and planets. Or it may be that the ancient Chinese had jars of spices on the table that included a sugar and a salt, a citrus juice, bitters, and something acrid (pepper?); they needed – and we need – words to communicate about these important substances. Still the main reason for the idea of five tastes may have been that the traditional Chinese method of organizing experiences, the "five ways" demanded by wu xing. But then where did *these* five ways come from?

By the 20th century the idea of basic tastes had not evolved much beyond asking how many there are. Boring (1942) stated that the general consensus was that there are four. Of relevance here, in an information theory approach, Miller (1956) showed that human memory limits the contents of facile categorizations to about seven members each. His research provides one very practical rationale both for the invention of the five ways of Chinese thought, and for our four or five basic tastes. Our limited ability to remember the contents of a category containing more than "the magical number seven plus or minus two" of unrelated items certainly could have influenced our understanding in the field of taste, as it does in many other aspects of our description of the world.

As examples of the ubiquity of such categorizations, we have seven days in the week, seven sins and seven virtues, and Newton's seven colors – all arbitrary man-made rubrics. The many geological time periods are packaged into groupings and subgroupings of seven or less each. The standard format of scientific papers also has about six sections – Introduction, Methods, Results, Discussion, Summary, and Conclusions – which is very useful. But why is this format so useful? We have not been able to deal with the 365 days of the year without dividing that number into small categories; four seasons of three months each, each month consisting of about four weeks, each week of seven days. The year is a natural phenomenon – once around the sun – but these other terms are not. Aristotle, the great classifier of all things into short lists, proposed seven tastes. These short lists seem to make good intuitive sense. But are there *really* seven seas and seven continents? And is the Mediterranean Sea *really* made up of seven mini-seas? Should we anticipate seven tastes?

3. Hanig and basic tastes

3.1. Hanig sets the stage

The modern empirical history of basic tastes is herein taken rather arbitrarily as starting with a seminal experiment by Hanig (1901). He demonstrated that the areas of sensitivity of the tongue to the basic tastes differ, with sweet largely in the front, bitter in the back, and salty and sour on the sides. Although their points of maximum sensitivity differ, their total distributions overlap greatly. It has been data of this sort that has supported the idea that we can sense only these "basic" tastes – the main assumption of the basic tastes doctrine. Subsequent research in taste largely followed his format. In the present article Hanig's work is used as a short-hand rubric for the idea of basic tastes.

An attempt to define the idea of basic tastes would be helpful here, although it will become clear throughout this article how nebulous and indefinable this idea is. But at this point, the idea of basic tastes may be put simply: The basic tastes are all we can sense, thus all tastes are reducible to only these few separate and distinctly different sensations.

3.2. Following Hanig

The idea of four basic tastes gave us a very convenient structure for research. The job then was just to find evidence for them. And we did.

3.2.1. Psychophysics. The field of psychophysics followed Hanig in general form; subjects can describe tastes in the terms of the basic words (Halpern 2002a).

Textbook treatments often state that it is generally accepted, or that it is a fact, that there are only four tastes for humans (e.g., Bartoshuk 1988; Bernstein et al. 2006; Geldard 1964; Graham 1990; Kandel et al. 1991; Moncrieff 1956; Osgood 1956; Pfaffmann 1951, 1954; Shepherd 1994; Smith & Davis 2000; Smith & Scott 2001; Steward 2000). Throughout these texts, definitions of "basic tastes" are notably absent. But the influence of the idea of a few basic tastes has been so strong that Hanig's broadly overlapping areas of sensitivity have sometimes been redrawn into four discrete and nonoverlapping areas on each side of the tongue, and these drawings make excellent illustrations for text books (e.g., Bear et al. 1996; Graham 1990; Kandel et al. 1991; Shepherd 1994; Steward 2000). It should be pointed out that Hanig's data have been reproduced accurately in some cases (e.g., Geldard 1964; Purves et al. 2001), and properly corrected in another (Smith & Margolskee 2001).

3.2.2. Receptor organization. Much research on taste receptors has been presented in tacit or explicit support of the basic tastes idea; experiments have been routinely designed and interpreted in terms of a small number of "basic" typologies. For example, when appropriate techniques had been devised, there began a protracted search for the basic taste receptor mechanisms or cells, such as for "sweet" (Birch 1977; Eggers et al. 2000; Shallenberger & Acree 1967, 1971; Tateda 1965). Current data on receptors using molecular genetic techniques (Chandrashekar et al. 2006; Zhang et al. 2003) have been taken to support basic tastes in that there are receptor mechanisms that are described as specific to two of the basic tastes, sweet and bitter (Zhang et al. 2003; Zhao et al. 2003), with similarly specific neural pathways (Sugita & Shiba, 2005) and behaviors related to these receptors and pathways (Mueller et al. 2005; Zhang et al. 2003; Zhao et al. 2003). A neutral search without the bias to find basic receptors would have been preferable. It might be that with at least 40 years of research directed toward finding the receptors for the basic tastes, acceptable receptors for each would eventually be found.

3.2.3. Neural organization. The history of the search for neuron typologies to correspond with the basic tastes began with the first recordings from individual taste neurons over 60 years ago (Pfaffmann 1941) and continues to the present (e.g., Boughter & Smith 1998; Boughter et al. 1999; Lemon & Smith 2005, 2006; Scott & Giza 2000; Smith & Scott 2001; Smith et al. 2000; St. John & Smith 1999). The "labeled-line" coding idea in taste holds that each neuron represents only the basic taste to which it responds best, giving us four groups of neurons (Frank 1974, 2000). Mathematical techniques have been used to categorize data on neural responsiveness into a few types to support this position (Scott & Giza 2000; Smith & Davis 2000; Smith & Margolskee 2001; Smith & Scott 2001; Smith & St. John 1999; Smith & Vogt 1997; Smith et al. 2000). As with basic taste receptors, there is a lack of an a priori rationale, a rational definition of what neuron groups are, and critical testing with control groups.

3.2.4. Summary. For about a century the field of taste has rather uncritically been guided by the idea of four basic tastes. We went in with Hanig's orientation, and then showed that there were indeed four basic tastes. It is not easy to estimate the degree of bias that this assumption may have brought to the field of taste, and the corollary degree of bypassing of data and theory to the contrary.

3.3. Hanig omitted control groups

Unfortunately, Hanig's format did not provide the essential perspective of control tests demanded by science. If his findings were to have any relevance to the basic tastes model, it would have been necessary to learn if other tastants, for example KCl and $CaCl_2$, proline, and lysine, also had differentially distributed sensitivities across the tongue. If they were distributed in this way, the implications of his data for the basic tastes idea would have been nullified. No one has completed his research with the required control studies. Why not?

Since Hanig, there has been a routine omission of control groups in research using the basic tastes for its organization. This omission is notable in the three areas of research just noted: psychophysics, and receptor and neural organization. The effect of omitting control groups is to support the basic tastes model, rather than to question it. This format is not helpful in science.

4. Extra-curricular support for Hanig

Two of our approaches to knowledge – our language and our experimental methods – have guided us toward Hanig's position.

4.1. Language

4.1.1. Cognitive characteristics of humans. The limits of human cognition mentioned earlier (Miller 1956) give a logic to the idea that there would be just a few named tastes, up to six or seven, but not 20. If there were indeed these higher numbers of basic tastes of some sort, they might be too many for us to be aware of them – or even to know to look for them. The five rather than 105 ways of Chinese thought might have derived in part from this cognitive constraint. We cut up reality into a few words in order to understand and communicate. To follow such an arbitrary linguistic force in science is a problem worth study.

4.1.2. Words as hypotheses? The taste words have served as scientific formats in that we follow them. The Eskimos have multiple words to communicate about snow. But these important words do not necessarily invoke a science about multiple kinds of snow. Analogously, our use of a few basic taste names does not indicate more than that we need such words to communicate about taste. Although necessary for communication, there is no reason that these words should have served as meaningful hypotheses about the nature of taste.

4.1.3. Words versus reality. There is the very strong problem that we tend to believe in the reality and validity of our words. Our language is necessarily limited to discrete words that usually seem to have clear and straightforward meanings. May we assume that the words "liberal," "love," "intelligence," "clear," "understand," "define," or "reality" are clearly understood and defined, and are accurate representations of reality? And "salty" or "basic taste?" Our words are designed to serve us, but are not necessarily the best scientific representations of the nature of things. We may think that we get words from the dictionaries, but they are merely compendiums of the words we use, such as the taste words. Allowing scientific theory to be constrained or led by the terminology in common use would have made our current understanding of mathematics or physics impossible.

Many scientists have been critical of the influence of our words on our understanding. Speaking about geological time periods, S. J. Gould (1994) discussed words used to invent categories:

> The human mind seems to work as a categorizing device. . . . This deeply (perhaps innately) ingrained habit of thought causes us particular trouble when we need to analyze the many continua that form so conspicuous a part of our surrounding world. Continua are rarely so smooth and gradual in their flux that we cannot specify certain points or episodes as decidedly more interesting, or more tumultuous in their rates of change, than the vast majority of moments along the sequence. We therefore falsely choose these crucial episodes as boundaries for fixed categories, and we veil nature's continuity in the wrappings of our mental habits. . . . We must also remember another insidious aspect of our tendency to divide continua into fixed categories. These divisions are not neutral; they are established for definite purposes by partisans of particular viewpoints.

The close correspondence between Gould's comments and the probable continua in taste, including inflection points as the corners of Henning's tetrahedron (1916) is of note. Henning described the world of gustation as a *continuum* of tastes in three dimensions – a tetrahedron, defined by "sweet, sour, salty, and bitter" at its four corners.

Gould could have been writing about Aristotle, the great categorizer. In addition to his seven tastes, Aristotle wrote that there are five elements, earth, air, water, fire, and aether; this was a good beginning as he identified the major forms of matter – solids, gases, liquids – and energy. Aether was the astronomical material. He even categorized categories into ten kinds, such as substance, quality, quantity, relations, etc.

Another critic of the uncritical belief in words, G. Kimble, wrote (1996):

> Language is the agent of cognition, the currency of thinking, the tool-box of communication and the custodian of culture. To be useful, it must map onto the world with some precision. Unfortunately, however, the fact that it does so encourages the faith that the fit is perfect and that truth is in the dictionary: If there is a word for it, there must be a corresponding item of reality. If there are two words, there must be two realities and they must be different.

William James (a foundational psychologist and brother of the author Henry James, who may have been a greater but less systematic psychologist than William) recognized the problem (1890): "Whenever we have made a word . . . to denote a certain group of phenomena, we are prone to suppose a substantive entity existing beyond the phenomena. (And) the *lack* of a word quite often leads (to the idea) that no entity can be there . . ." The relevance of these comments for the naming of tastes is clear.

Proper concern has occasionally been voiced over the problematic adequacy of the "basic" words to represent tastes (Beidler 1974; Purves et al. 2001). And eloquently presaging the words of Henning (1916), Brillat-Savarin (1886) pointed out that the four basic tastes "are only a convenient way to talk about a much larger array of taste sensations."

It is interesting to note that Richard Feynman did not discover certain revolutionary aspects of quantum mechanics in terms of words, and then decide how to interpret the words. He just imagined the atom, and "watched" its behavior. But he did have to translate these discoveries into words – although they were clearer in graphs. We may well follow his direction in taste, that is, to lead, not to follow, the words. In the field of physics it has been realized that our common words are not always reliable or sufficient, and may be misleading, so neutral words such as "quark" are sometimes invented.

Beyond these, it might be useful to consider that even our most basic and secure word-concepts, mass, time, distance, and energy, are based on man's conception of the nature of things. They seem too good to be less than totally true in their general or particular usages, and quite real independent of our naming them. But they are only our words, rubrics facilitating our understanding, and our communications (or miscommunications) with each other. Our understanding of even these "basic" physical concepts is changing; they are not as simple and real as these distinct words make them seem.

In summary, it might be helpful to worry about allowing common usage words such as "sweet" and "sour" guide our research and understanding. These words could provide a problem rather than the solution.

4.1.4. Why *these* taste words? Imagine the wordsmiths of ancient China developing a communication system for the tastes of things; what words would they choose? Which foods would they name? They might devise names for the good things to distinguish them from the bad: sweet versus sour or bitter. And names for that all-important substance, salt; wars have been fought over the possession of salt as a seasoning and as a preservative. These four would very probably be at the top of any culture's list of taste words. Other words might be invented by culture, depending on the local foods available.

In fact, words for the four "basics" appear to be found quite uniformly in all languages – and are evident in English as well as foreign dictionaries. These include, at least, Afrikaans, Arabic, Albanian, Chinese, Danish, Dutch, English, French, German, Greek, Hebrew, Hindi, Hungarian, Indonesian, Irish, Italian, Japanese, Latin, Maori, Nepali, Oromo, Papua, Persian, Polish, Portuguese, Russian, Samoan, Sanskrit, Scotch, Serbo-Croatian, Slovak, Spanish, Swahili, Swedish, Tagalog, Urdu, Vietnamese, and Yiddish. There are some exceptions, such as omissions of "salty," even in the presence of the noun "salt" and the verb "to salt," and sometimes confusions between "sour" and "bitter;" but these may be errors in the editing of the dictionaries. And, as in English, there are very many culturally idiosyncratic taste words beyond the basic four in each language. In Korean there are words for bland and spicy. In Basque there is one word for bitter/sour. The Indonesians have the word "pahit," which has no translation in English. A thorough cross-cultural study of taste words and their meanings might prove useful.

Does this apparent ubiquity of usage of the four basic taste words indicate something very obviously true, four separate sensations that sum up all tastes? Or could they represent four specialized physiological processes? These propositions lack testable rationales that are independent from the invention of words for communication. It might be doubted that scientists in each of these cultures independently proposed these words as scientific hypotheses.

4.2. Our methods fit Hanig's orientation

Of course, all of our knowledge comes in terms of what we can measure, and thus what we can measure can determine how we think. What we measure depends on our techniques of measurement. Thus the techniques of measurement that are available can set the arena into which our discourse falls. These techniques include the biological and mathematical methods at hand. Then the characteristics of our language bias our understanding of the data.

4.2.1. Biological techniques. All of our biological techniques have forced our thinking into a search for a neural structure for a named function; we can scarcely avoid taking this position (Erickson 1978). As examples of the techniques at hand, the earliest of the modern biological techniques were those of Gall and Flourens at the beginning of the 19th century (Erickson 2001). Gall, a comparative neuroanatomist, attempted to measure variations in the relative sizes of human brain areas in relation to the talents of these individuals. His contemporary, Flourens, ablated various parts of animal brains to assay the function of each. Because of the nature of their techniques, their answers were necessarily in terms of what "word-as-function" existed in which "word-as-structure." Gall opted for a strict localization of many functions: math, language, sex, avarice, and memory as examples. Flourens won that argument for the time, stating that, on the contrary, the brain was something of a bowl of relatively homogeneous soup. Both were probably correct in part, Gall presaging the labeled-line point of view, and Flourens the distributed models. Later, section of the dorsal and ventral roots showed that the former had a sensory function, and the latter were motor. Then electrical stimulation of the brain also dictated locations for functions, for example, that the various muscles or movements were represented in different points in the brain. The electrical recording methods – gross and microelectrode – were, again, necessarily locationist in their conclusions. Brain imaging, borrowing a clinical tool that favors locationist data, shows that the various searched-for functions are relegated to differing named brain structures. But why not search for avarice or patriotism or fishing? Why expect worded functions to be in circumscribed and easily namable localized structures? Chemical tracing of neural pathways is also locationist with the pathways being the structures considered. In the labeled-line model, the basic tastes become the functions to be identified with the structures that are individual receptors or neurons.

It is probable that none of these new localizing techniques produced false or trivial data. But the proper interpretation of each species of data turned out to be more complicated than had been acknowledged. Does each new technique, now the molecular/genetic studies, show us a new reality? The position taken here is that any of these techniques might have given us a very advanced answer if we had known exactly what the question was. Otherwise the techniques may at least temporarily direct our ideas rather than vice versa. We cannot know the best technique, or even an appropriate one, until we know what we are looking for.

In physics on the other hand, techniques are continually being developed to meet the explicit issues raised by their formal hypotheses. Particle accelerators were invented to address very specific issues, topics such as the structure and mechanics of atoms and their components. Scientific physics, although not clearly older than the science of taste, might be considered more advanced.

4.2.2. Mathematical techniques. Various mathematical methods have been used to provide support for the basic tastes idea, rather than test it. Prominent among these has been multidimensional scaling, cluster analysis, and factor analysis. Although these techniques can be used to suggest directions for further hypotheses and research (Uslander, in Kruskal & Wish 1978), they cannot prove or disprove the reality of any groupings, including those used to support the basic tastes model (Aldenderfer & Blashfield 1984; Sarle 1987; Sokal & Sneath 1963). This issue depends on a prior formal definition of what groups are (Erickson et al. 1993) that might then be tested by these mathematical techniques. To use these techniques to determine if groups exist is like asking a road map to tell us where we are going, which they cannot do, rather than to legitimately ask it about the lay of the land for our consideration.

The exemplary presentation for the use of multidimensional scaling uses linear distances between cities to recover a correct map; importantly, this provides no conclusions about groups of cities, such as the Washington, DC–Boston corridor. Such linear distances are also possible in handling taste data in multidimensional spaces (Erickson 1986; Erickson et al. 1993; Schiffman & Erickson 1993). Factor analysis, although used to support the idea of groupings, is not relevant to this issue; this technique only indicates the number of factors underlying the data – for example, three strong factors might be used to successfully represent data of no groupings, or of many groupings.

But correlations have been routinely used (e.g., Geran & Travers 2006; Gilbertson et al. 2001; Lemon & Smith 2005; Scott & Giza 2000; Smith & St. John 1999) instead of the linear distances between objects for which multidimensional scaling methods were devised. Correlations are indicative of nonlinear degrees of relationships, incorrectly displacing the points into a "groupy" appearance towards the edges of the now nonlinear space (Erickson et al. 1993). Correlations are completely inappropriate for multidimensional scaling, but still they are used to support the basic tastes model. This adds to the previous problem that these plots are incorrectly used to provide conclusions about groupings.

Even random data sets will always contain apparent structure, appearing as grouped in both multidimensional scaling and cluster analyses, whether based on linear distances or correlations (Erickson et al. 1993). Indeed, the published graphs purporting to establish the presence of groups with these methods could just as well be representing random or regularly arranged "checkerboard" data. These groupings are only in the eye of the beholder.

In summary, basic taste "groupings" or "typologies" derived from these mathematical methods are completely unfounded (Erickson et al. 1993), but have been used as key support for the basic tastes doctrine. Why?

5. Following Hanig has been problematic

A variety of problems attendant on following Hanig's lead are evident, but ignored.

5.1. Lack of controls

As mentioned in Section 3.3, Hanig set the stage for omitting control groups. This, in itself, disqualifies most data since then used to support the basic tastes position.

5.2. Undefended assertions

There is a general uncritical acceptance of the reality of basic tastes (Sect. 3.2.1). The many textbook statements that there are four basic tastes do not define what a basic taste is. They do not discuss the lack of the necessary underlying testable hypotheses or the absence of controls, although ad hoc reasons, such as control of food intake, may be offered in support of the idea. This procedure of only supporting the basic tastes position has become routine (Amrein & Bray 2003; McBurney 1974, 1978; McBurney & Gent 1979; Scott 2004) instead of fairly testing it. When both sides of this issue are represented, the lack of support for the basic tastes position becomes evident (Schiffman & Erickson 1980).

By contrast, in the field of physics, some textbooks, and certainly discussions of the history of physics, point out where the idea of atoms came from, what data support that idea, how falsifications were attempted, and in what ways it is a heuristic idea. Could that be done in taste? Probably not within the present structure in this field.

5.3. Data are ignored

In order to follow Hanig, much data and logic contrary to the basic tastes position have had to be jettisoned.

5.3.1. Receptors and neurons. In studies supporting the few basic tastes position, the data that falsify that position are often not addressed. As a recent example, data from molecular studies define several receptor mechanisms. Conclusions were drawn that taste receptor cells and neurons are not broadly sensitive to a variety of tastants (Chandrashekar et al. 2006; Zhang et al. 2003; Zhao et al. 2003). Without denying the *data* about taste receptors, the *conclusion of narrow tuning* is clearly falsified. That receptor cells and neurons are broadly responsive constitutes one of the clearest and most substantial arrays of data in taste stretching over 50 years (e.g., Brasser et al. 2005; Caicedo & Roper 2001; Caicedo et al. 2002; Dahl et al. 1997; Erickson 1963, 2000, 2001; Gilbertson et al. 2001; Herness 2000; Lemon & Smith 2005, 2006; Pfaffmann 1941, 1955; Rolls 2005; Stapelton et al. 2006). In an important analogy, color vision receptors may be described in terms of single photo-chemicals, but they each respond to very broad arrays of wavelengths; likewise, that chemoreceptor mechanisms exist does not indicate that the receptors and neurons each respond only to one taste. It would be useful if these molecular data were rationalized with what is known about taste. When such important and relevant data are ignored (e.g., Amrein & Bray 2003; Scott 2004), the analysis in support of basic tastes does not fail – and perhaps cannot fail.

One issue should remain clear. The molecular data show that there are at least two types of taste receptors, and this is to be expected. The breadth of responsiveness of receptor cells and taste neurons is a different issue.

5.3.2. Psychophysics: How many tastes? That there are only four tastes, and that these four will completely account for all other tastes, has been stipulated as the core assertions of the basic taste model. This model, seldom defined, is perhaps given its most articulate presentation by Halpern (2002a). There may be no more, or other, than these four tastes. But if these untested assumptions are removed, any taste has equivalent opportunity to serve as a basic. In English there are at least 31 words used to describe tastes without resorting to nontaste adjectives. These words are all potential candidates for basic tastes in that several of them might account for other tastants as efficiently as do the basics. But such tests with other than the basics have not been performed. A preliminary example showing how such tests could be done is presented in Section 7.

And there is evidence that there are other than the four basic tastes, or that the four basics will not account for all tastes. Umami is the foremost example. Metallic (Critchtey & Rolls 1996; Lawless et al. 2005) and fat (Chale-Rush et al. 2007; Gilbertson et al. 1997; Mattes 2005; McCormack et al. (2006) are possible candidates as tastes separate from the basics. However, because of the lack of a definition of what a taste is, fat may serve only as a flavorant (Pittman et al. 2006) for the reasons given by Halpern for umami (2002b). That water might be a separate taste has a long history, now with some empirical support (Gilbertson 2002). Di Lorenzo et al. (1986) showed that in rats a conditioned taste aversion to ethanol (EtOH) did not generalize to any of the basic tastants or combinations of any two of these, except that it did generalize to a mixture of sucrose and quinine (QHCl); thus EtOH appears to be a separate nonbasic taste, and the taste of a sucrose/quinine mixture is not clearly reducible to the basics. If a continuation of such findings are readily absorbed into the basic tastes model, it will be a negation of its major raison d'etre – that there is a defined and limited set of basic tastes.

Spurious suggestions for new basic tastes might occur as a result of the lack of a clear definition of what a basic taste is. To be noted here is Halpern's cogent argument that umami is not a taste, but a flavorant (2002b) importantly affecting the tastes of other stimuli. Although monosodium glutamate (MSG) has a taste – disagreeable and not clearly a combination of the basics – umami is a flavor that only appears when small amounts of MSG are added to foods. What exactly is a taste, or even a basic taste?

It should also be noted that although Boring (1942) did not touch on the lack of a definition for basic tastes, he did correctly comment that Hanig's data did not limit the number of tastes, for example to four.

5.4. Logic is ignored

The primary logical fault with the basic tastes position is that – as previously mentioned – it does not have a rational and testable definition. We do not know what "basic tastes" are, but that does not appear to be a topic of concern. This fault runs through the following discussion.

In addition to not addressing contrary data, articles supporting the basic taste idea do not address the logical strength of coding in populations (e.g., the across-fiber pattern theory) and the corresponding logical weaknesses of the labeled-line basic tastes position (Erickson 1968, 1977, 1982a, 1982b, 1984b, 1985a, 2000, 2001; Erickson et al. 1990; Erickson & Covey 1980; Erickson et al. 1980; Ishii & O'Mahoney 1987; O'Mahoney & Ishii 1987; Schiffman & Erickson 1980, 1993). It is to be noted next that there is a general acceptance of some form of population coding throughout the field of neurobiology (see Erickson 2000, 2001).

The evidence for receptor or neuron types is held as a falsification of, or at least awkward for, across-fiber patterning (Scott & Giza 2000). However, the original presentation of across-fiber patterning was in terms of a few receptor and neuron types (Erickson 1963). This model requires receptor types in nontopographic sensory systems such as color vision and taste (Erickson 1968). It is odd that groupings have been used as an argument against this theory (Smith & Scott 2001).

The basic tastes assumption has provided an illogical format for neuron categorization. The fact that each taste neuron or receptor is more sensitive to one of the basic tastants than others (Frank 1974, 2000) is logically inescapable; how could a neuron not be more sensitive to one tastant than others? And this must be as true for any other set of tastants as for the four basics, qualifying any set of four stimuli as basics; but, again, these control studies of trying other tastants are absent. And in Frank's model the side-band responses to the non-"best" stimuli are considered to be noise, or the tastes of the basic stimuli must be assumed to be a combination of several tastes (Bartoshuk 1988) – both unparsimonious ad hoc assumptions apparently devised to support the basic tastes model. The fact that larger amounts of data, from more than the four basic stimuli, can be expressed along a continuum in the same form as Frank's plots (Erickson 1967; Scott & Erickson 1971) is not addressed in the basic tastes model.

Although both the rationale and control experiments are missing, Frank's data have been cited as strong support for the idea of labeled lines, and thus basic tastes. Other methods of obtaining data in support of neuron types or groupings have been undertaken, also without independent rationale and definition (e.g., Smith et al. 2000; St. John & Smith 1999).

The similarity of the specific taste receptor data to the characteristics of color vision provides another area for an unbiased critique of the basic taste model. Adaptation, or the genetic absence, of the long-wavelength visual receptors, results in a strong diminution or absence of responsiveness to a range of "reds," analogous to the taste effects seen in mice missing a taste receptor (Zhang et al. 2003; Zhao et al. 2003). In this situation, responses of cells to other wavelengths may vary from not affected to very affected depending on their wavelength. The across-fiber pattern model would accommodate increases in saturation in the perception of shorter wavelength stimuli along with decreases in saturation in longer wavelengths. Similar effects in taste are evident, and not surprising. Resolution of this issue in taste would require close attention to the responses to systematically varied stimuli other than the basics (analogous to variations in wavelength), and a rationalization of the conclusions of specificity in taste with the contradictory historical findings.

The assumption that there are only four tastes has a strong but illogical effect on psychophysical data collection (Erickson et al. 1990). The finding of "suppression" between tastes (Bartoshuk 1988) required the prior assumption of the existence of a few perceptually distinct basic tastes that cannot each be modified in mixtures. In that idea, only the basics should be sensed, so only changes in the strength of the basic tastes in the mixtures could be accepted as data. Any change in taste quality, such as synthesis of different tastes (Erickson et al. 1990; Schiffman & Erickson 1980), was not admissible. If the subjects are only given the basics for use, then they can respond only in terms of the basics. But given other standards for use, they possibly would have used those – there was an omission of this key control group. But if the doctrine of basic tastes is not assumed, then mixtures of "basic" or other tastants could be understood to produce a changed across-fiber pattern with some similarity to, or correlation with, each of the components. A new and intermediate taste, no longer a basic taste, should be sensed, usually *similar* to both components, but not just suppressed versions of basics. For perspective, if the descriptions of colors are limited to only a few basic terms or color samples, then the ratings for colors intermediate to these "basic" colors are reduced (Erickson 1977); these could be inappropriately considered "suppressed."

So in addition to the prior assumption of basic tastes, the idea of suppression requires an additional assumption that these tastes are somehow related while also being distinct and separate. No additional assumptions are required in the across-fiber model, as the continuum requires that tastes be related. Parsimony has proven useful in science.

The lack of linking hypotheses is one of the most serious of the problems with the logic of basic tastes. This model encompasses four unrelated events at various levels of meaning. First, it holds that only four tastes are *perceivable*. This is extended without explanation to the *neural* level, where four different sets of sensory neurons each exclusively represent one of these tastes. It is also held for the *receptors*, and then *receptor mechanisms*, as well as for *stimuli*, without articulating the relationships between these levels.

5.5. Convenience

It may be that the most generally persuasive drawing power of the basic tastes model is that *without a formal restraining definition, this model is very convenient in designing experiments, and it easily categorizes any data – especially from experiments cast in the four tastes format*. The design is thus very straightforward and is supported by our words and techniques. And this procedure, as Hanig's, seems to validate the basic tastes idea without test. Arguments in favor of the basics position flow easily from this context, encouraging a lack of attention to contrary matters of data and logic. It is certainly hard to think of a simple model different from that provided by the basic tastes to guide our research and understanding – and against which the basic model might finally be tested. It is improbable that an ultimately successful science was ever built on convenience.

5.6. Formality and science

In the remainder of this article the term "formal" will refer to the use of data-based, rational and heuristic hypotheses that provide clear enough definitions of their terms to be potentially falsifiable. Hanig's work does not fit into this definition. The core orientation herein is that formal definitions are required for taste to qualify as a science, just as they are in physics. One aspect of this process is that it provides the essential groundwork for control experiments, as illustrated in Section 7. But first, some previous experiments with controls will be discussed.

6. Previous control tests of taste models

The major tenet of this article is that models of taste must be testable, which means potentially falsifiable. There have been a few unbiased tests of differential predictions between the basic tastes and across-fiber pattern models. The topics are the required singularity of basic tastes, the presence of tastes other than the basics, taste as a continuum rather than four separate tastes, and the possibility of quantification. The findings uniformly falsified the basic taste model and/or supported the across-fiber pattern model. A brief discussion of these will lead to an illustrated proposal (Sect. 7) for a test of more generally accepted aspects of the basic taste model, the ability held for only the basics to account for other tastes, and that only the basics are perceived in other tastes (Halpern 2002a).

6.1. Singularity of tastes

If there are only four (or a few more) basic tastes, then each should be sensed as being singular because each is not more than one taste (Erickson 2000; Erickson & Covey 1980; Erickson et al. 1990; O'Mahoney et al. 1983). On the other hand, if each stimulus that was not basic were composed of several of the basics, it should be perceived as "more-than-one" taste. The across-fiber pattern model indicates that any tastant, basic or nonbasic, might be sensed as singular (Erickson 2000; Erickson & Covey 1980; Erickson et al. 1990; O'Mahoney et al. 1983). This is testable. Previous studies (Erickson & Covey 1980) have demonstrated that the basic tastes are judged as only relatively singular (by around 80% of the subjects). This research also showed that the nonbasics are somewhat less singular than the basics (about 50% of the subjects reporting singularity), but not clearly "more-than-one" as would be predicted in the basic tastes model.

And certainly mixtures of tastes should contain more than one basic taste, and thus be rated as more-than-one. However, it was shown that mixtures of several tastants can be perceived as being relatively singular (Erickson 1982a; Erickson & Covey 1980; O'Mahoney et al. 1983; Schiffman & Erickson 1980). Indeed, mixtures of two basics can appear to be as singular as the individual basic components of that mixture; for example, the singularity of mixtures of HCl with either NaCl or Q_2SO_4 were equivalent to the singularity of those basics when tasted alone.

As controls on these methods (Erickson 1982a), individual tones were routinely rated as one stimulus, and multiple tones were rated as more-than-one; this complexity increased with the number of tones in the "mixture." That is, the tonal stimulus appeared to be "analyzed" into its components, all components remaining clear and unchanged as predicted for tastes in the basic model. However, increasing the number of components of a taste mixture does not show this increase in complexity. Instead of being analyzed into its components, a new somewhat singular but nonbasic taste was "synthesized" in mixtures of two, three, or four components. Like taste, a nonbasic color resulting from the combination of two "basic" colors (Erickson 1977; Erickson & Covey 1980), such as a blue-green, was also rated as singular – this being an example of the synthesis of a sensation different from either of the "basic" components (Erickson et al. 1990). "Analysis" is predicted for topographic systems such as auditory tones, and location on the skin or retina. "Synthesis" is predicted for the nontopographic systems such as color, taste, the vestibular sense, kinesthesis, and olfaction. These unbiased methods could have falsified the across-fiber pattern theory, but instead supported it and falsified this aspect of the basic tastes position.

On the other hand, and in partial support of the basic tastes model, mixtures of sucrose or fructose with any one of the other three basic stimuli were rated as strongly less singular (around 39% to 64%) than either of the components alone (about 85% each for the sugars), suggesting that these sensations do indeed remain somewhat independent and singular. Also, when these sugars were mixed with any nonbasic stimulus, the combinations were rated as less singular than either component, an indication of semi-independence. Also, quinine behaved somewhat like the sugars in that, in mixtures with sucrose or NaCl, the singularity of the mixture was greatly reduced – as it should be in the basic tastes doctrine; however, the combination of QHCl with HCl remained singular. These data are suggestive of the receptor specificity claimed for sweet and bitter (Zhang et al. 2003). It was concluded that although NaCl, HCl, and QHCl were interrelated, sucrose might well stand further apart, perhaps not being on the same dimension as the others (Erickson & Covey 1980). That sucrose and quinine might lie outside the continua of the other tastants had been suggested (Erickson et al. 1965). Further control studies could provide clarity here.

6.2. Tastes other than the basics

The singularity of nonbasic tastes and mixtures, just noted, is indicative of the synthesis of a different taste, this taste necessarily being something other than and in addition to the basics (Erickson 1977; Erickson et al. 1990; O'Mahoney et al. 1983; Schiffman & Erickson 1980).

The question of whether the basic tastes are the only tastes perceived in mixtures, as held in the basic tastes model, has also been tested (Erickson 1982a; Erickson et al. 1990). Subjects very rarely fail when asked to identify one of the four basic tastes alone. But when mixed with another basic taste, the failure rate in identifying a stimulus increased dramatically, indicating that that basic was not clearly and separately experienced in the mixture. In a control study, a simultaneous "mixture" tone did not generate this confusion in the identification of a given tone.

These findings together suggest that there are more than just the four basic tastes.

6.3. A continuum of tastes, not just four

As proposed by Henning (1916), many tastes comprise a continuum in the shape of a tetrahedron defined at its four corners by sweet, sour, salty, and bitter; this continuum is explicitly composed of *many singular* tastes, not just those tastes at the four corners. But the four corner-tastes were later held to be the only tastes possible, and called the "basics" (Bartoshuk 1988). Henning's continuum is a clear contradiction of the basic tastes position, while being a core aspect of the across-fiber pattern theory.

That multidimensional scaling solutions are possible indicates that the spaces are continuous. If the data were unrelated, solutions of low dimensionality would be impossible. This invalidates the basic tastes idea that the few tastes are independent of each other. Interrelatedness along a continuum is a core part of the across-fiber pattern model.

That taste is probably organized as a continuum also shows up in reports of neural activity. For example, Frank's data (1974, 2000) on the responses of individual neurons to the various basic tastes derives from a continuous organization presented as her baseline (Woolston & Erickson 1979); she demonstrates that neurons will show decreasing responsiveness with increasing distance from the "best stimulus," a "neural response function" along these continua (Doetsch & Erickson 1970; Erickson 1967, 1968, 1974, 1978, 1982, 1984b, 1985b, 1986; Erickson et al. 1965). This is contrary to the basic tastes position and in accord with the across-fiber pattern theory (Erickson 1967; Erickson et al. 1965; Scott & Erickson 1971. But her data have been accepted as strong support for the basic tastes position instead. Why?

In this basic tastes orientation, the fact that many of these neurons respond best to stimuli other than the basics is not considered because the topic is restricted to basic stimuli. The desired results are on the whole mathematically assured once the best stimulus of these four is found; that the other three stimuli are less effective is therefore not surprising. However, this relatedness may be extended to provide the same coherent organization for at least 16 stimuli across a continuum when the requirement is dropped that only the four basic stimuli be considered (Doetsch & Erickson 1970; Erickson et al. 1965, 1967, 1968; Erickson et al. 1965; Scott & Erickson 1971). Plots similar in form to Frank's were obtained, but for many stimuli. These are the smooth, bell-shaped neural response functions that describe the responses of individual neurons along the taste continua, as they appear for color vision receptors and neurons. These much more extensive and powerful neural response functions are neither expected nor checked for in the quadripartite logic.

It is important to note that even Hanig's data are what would be expected from a continuum (Schiffman & Erickson 1980), as would Frank's groupings (Schiffman et al. 1979; Woolston & Erickson 1979).

6.4. Quantification of neural information

There has been no definitive attempt to quantify taste information in the quadripartite model. On the other hand, the across-fiber pattern theory has provided a testable method to quantify the differences or similarities between any stimuli, including tastants. The general idea for the representation of the differences in quality and intensity for any two discriminable tastants is that they must provide neural responses that are somehow different from each other. This is the meaning of the Chinese Yin/Yang differentiation required for our understanding of any concept; to exist, "sweetness" must have another taste different from it. People with only the "red" receptors can see no colors at all. So as to create the most bias-free measure (no prior assumption of what constitutes the difference, such as groupings) the different across-fiber patterns set up by two tastants are superimposed, and the absolute difference between them, say in impulses/second, is measured.

The quantification given in the across-fiber pattern model may be best presented first by example, and then formalized. The across-fiber patterns shown by Lemon and Smith (2005) provide the first demonstration. In their Figure 3, the basis for the quantitative differences between two stimuli is given by the differences between the pairs of curves. The difference between sucrose and fructose is small, as would be the difference between KCl and HCl. The difference between HCl and sucrose is large. As absolute differences in impulses/time, these would be linear distances, and could be appropriately used for multidimensional scaling. Other examples that could be analyzed this way may be seen in the across-fiber patterns presented by Boughter and Smith (1998), Boughter et al. (1999), Dahl et al. (1997), Schiffman et al. (1979), Smith & Li (1998, 2000), and Smith et al. Figure 2 (2000). This approach has been found to be a useful heuristic (Dahl et al. 1997; Erickson 1982b, 1986; Ganchrow & Erickson 1970; Schiffman et al. 1979).

Stated in general terms, the *total amount* of activity set up by a given stimulus, here a tastant, is its *neural mass.* These are the areas under each across-fiber pattern curve discussed above. (Lashley [1931] noted the importance of "neural mass" in the handling of high levels of information of importance to a species.) The absolute difference in impulses/second (or some other measure) between this profile and the profile set up by a second stimulus is called the *neural mass difference* (Erickson 1986). In the across-fiber pattern theory, the prediction is made that the perceived differences between two stimuli is a positive function of the amount of this neural mass difference. As an example, two sodium salts of similar concentration would produce small neural mass differences, and would thus be predicted to be poorly discriminable from each other.

The total neural mass produced by a stimulus is taken to be indicative of intensity. If the neural masses produced by two stimuli are different, that indicates a difference in intensity. Both intensity and quality give neural mass differences information about discrimination between stimuli. If it is desired to inspect only taste quality differences, leaving out intensity differences, the neural masses – representing intensity – can be brought to the same level by multiplication through one of them.

As examples, just noticeable differences in the color of a stimulus, or the location of a visual or somesthetic stimulus, would require the same neural mass differences. In the topographic systems (Erickson 1968), such as visual or somesthetic location, very many neurons are available; therefore they may be narrowly tuned and still evoke enough neural mass to differentially define the event. For usable events in nontopographic systems such as taste or color, few neurons are available, so to produce sufficient neural masses with their concomitant neural mass differences, they must be broadly tuned. This broad tuning would bring many neurons into play to provide the necessary neural mass (Erickson 1968, Figures 2 & 3).

7. A more definitive control?

7.1. A proposed control experiment

A model might be evaluated by the degrees to which it can encompass and predict large amounts of useful data. Such tests, described in Section 6, appear to controvert the basic tastes doctrine. An even stronger test would be to inspect the standard textbook definition of the basic tastes. Are the “basics” the only ones that can *account for other tastes* (Pfaffmann 1951, 1954), or might they be more efficient at this than other tastants or words? And are the basic tastes *the only tastes perceivable* in other tastants and mixtures (Bartoshuk 1988; Halpern 2002a)? The following sketch, an example extended from the control formats in Section 6, is presented as a tentative illustration of how such an experiment might be done, and the rich vein of information to be expected from such experiments.

7.2. Introduction to the illustration

The key aspect of this demonstration was that control groups composed of tastants not considered to be basics were included to compare with the performance of the basic tastes. If the few-basic tastes position is correct, then the experimental basic words and stimuli should account very strongly or completely for various other taste stimuli, and the four controls using nonbasic stimuli should completely fail, or nearly so. If there were no clear differences between the experimental and control groups in effectiveness in accounting for other stimuli, the basic tastes position in this definition would be considered falsified – and this is how the results came out.

7.3. Materials and methods

Two *experimental* groups of subjects used the basic taste words and stimuli as “Standards” to account for the “Comparison” stimuli (Fig. 1, panels E1 and E2), and four *control* groups used from two to five “Standard” stimuli not considered to be basic (Fig. 1, panels C1 to C4) to account for the same Comparison stimuli.

The subjects were Duke University undergraduate students earning experimental credit in a course. Each subject participated in only one of the six groups. There were 31 subjects in the basic words (Fig. 1, E1) and 26 in the basic stimuli (E2) groups, and 22, 18, 12, and 13 in the 2, 3, 4, and 5 nonbasic controls (C1–4). Using these Standards, each subject was asked to account for the tastes of the 10 Comparison stimuli (Fig. 1 abscissae). To avoid biasing the subjects towards use of the basic tastes model, it was expressed only in the first control (E1) in which the subjects were asked, but not taught, to

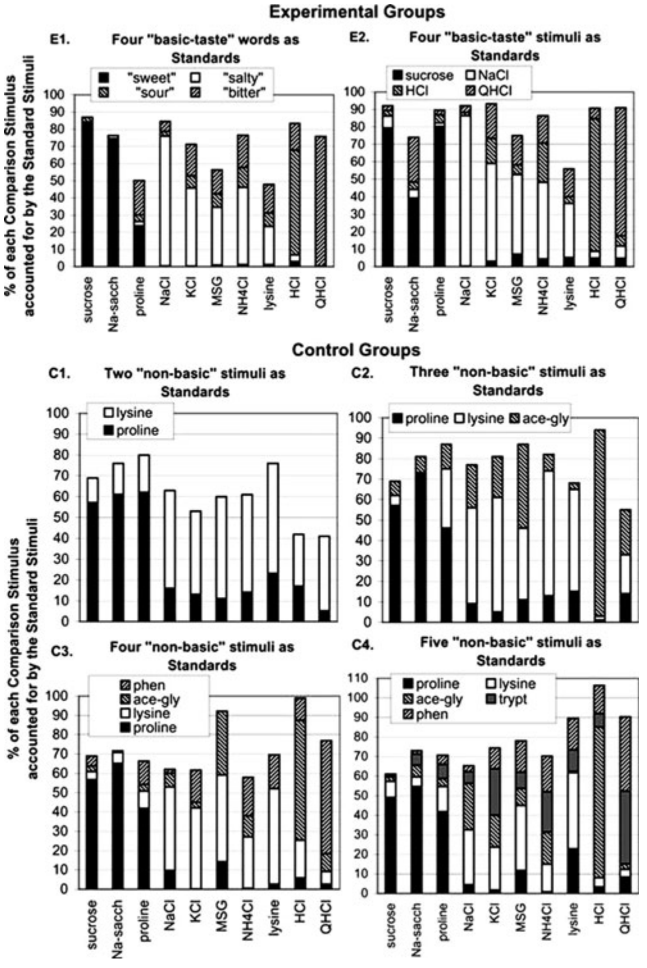

Figure 1. Accounting for ten Comparison taste stimuli with basic and nonbasic Standard tastes; the experimental design and results. In the six panels, the first two, E 1–2, give the results from the two experimental “basic tastes” groups, and C 1–4 each give the results from one of the four “nonbasic tastes” control groups. In panels E 1 and E 2 the four basic words (sweet, sour, salty, and bitter) and stimuli (QHCl, HCl, NaCl, and sucrose) were used as Standards to describe the tastes of the ten Comparison stimuli. In the rest of the panels (C 1–4), from two to five stimuli not considered to be basic were used in the same role as Standards.

use the words sweet, sour, salty, and bitter as Standards. The sip and spit method was used with partially filled 3 oz. paper cups, and distilled water rinses. The subjects were instructed to taste each Standard and Comparison stimulus – with rinses – as many times before and during the experiment as necessary to remain familiar with them. They recorded the percent to which each Standard word or tastant accounted for the tastes of the Comparison stimuli.

The stimuli were: 0.002 M quinine HCl (QHCl), 0.0025 M sodium saccharine (Na-sacch), 0.01 M monosodium glutamate (MSG), 0.03 M HCl; 0.03 M l-phenylalanine (phen), 0.05 M l-tryptophan (trypt), 0.1 M l-lysine, 0.1 M n-acetylglycine (ace-gly), 0.1 M NH_4Cl, 0.2 M NaCl, 0.3 M KCl, 0.6 M sucrose, and 0.6 M l-proline.

7.4. Main results

The main issue was to compare the performance of the two experimental basic taste groups (Fig. 1, panels E1–2) with the four control nonbasic taste groups (C1–4). Contrary to the basic tastes idea, the data for the control groups overlap those of the experimental groups.

As examples of the data, the subjects rated the taste of NaCl (Fig. 1, E1, fourth column) as 0.3% sweet, 75.6% salty, 2.8% sour, and 5.8% bitter for a total of 84.5%, leaving 15.5% of its taste not accounted for. On the other hand, the four basic taste stimuli (E2) accounted for a total of 93.7% of the taste of NaCl.

Averaged over all the Comparison stimuli, the basic words (Fig. 1, E1) were relatively ineffective as Standards, accounting for 69% of the Comparison stimuli, and the basic stimuli (Fig. 1, E2) were relatively effective, accounting for 84%. Although the nonbasic Standards should not have accounted for the Comparison stimuli, they were competitive with the basics; the 2 nonbasic stimuli accounted for 62% of the Comparison stimuli (Fig. 1, C1), the 3 nonbasics for 81% (C2), the 4 nonbasics for 73% (C3), and the 5 nonbasics for 78% (C4).

To be noted is the overlap in effectiveness between the basic (E1–2) and nonbasic (C1–4) Standards, and the general increase in effectiveness as the number of nonbasic Standards was increased from two (C1) to five (C4).

Individual subjects occasionally accounted for more than 100% of a Comparison stimulus. For example, one subject rated KCl as 30% accounted for by lysine, 50% by tryptophan, and 50% by phenylalanine (total = 130%), and another rated MSG as 30% lysine, 10% tryptophan, and 80% phenylalanine (120%). These aspects of the data are hidden within the averaged data in Figure 1, but were strong enough to appear in the averaged data as 109% of HCl accounted for in Figure 1, C 4. This is discussed further in "A Completion Effect," Section 7.8.

7.5. This psychophysical definition of basic tastes was falsified

The definition that basic tastes (Fig. 1, E 1–2) will account for the tastes of a variety of taste stimuli, and that nonbasic controls (C 1–4) cannot, was falsified; each of the experimental and control groups accounted for considerable and overlapping proportions of the Comparison stimuli. This is illustrated in Figure 1 in that the columns have substantial height in both the experimental and control groups; no basic group (E1–2) achieves 100% in accounting for any Comparison stimulus, and no nonbasic group (C 1–4) completely fails with columns at 0%. For this finding of broad overlap no statistical assay was needed. If a rational statistical definition of basic tastes were offered, for example, if a reason was given why basic tastes should do better than nonbasics at $p < .01$, or that the basics should be at 100% and the nonbasics at 0%, those predictions might be testable. At any rate, it is doubtful that the basic words could be found more efficient than the 3, 4, or 5 nonbasic stimuli, as the latter have higher raw data averages.

The present format is different from Hang's (1901) and those in other psychophysical articles supporting this model that followed him, in that it used controls, and could have supported or falsified the basic tastes model.

7.6. An inconvenient truth

After the experiments it became disconcertingly clear that the subjects were biased towards the idea that the four basic tastes should account for the Comparison stimuli! We failed in our efforts to keep this issue balanced between the experimental and control groups, and so the data are probably skewed in favor of basic tastes. Many of the subjects commented on this issue in debriefing, such as "Aren't there just four tastes?" They reported that they had learned from textbooks, in middle school through college, that there are four basic tastes. This unexamined bias may be unavoidable in all psychophysical studies involving the basic tastes. The future researchers in the field of taste will be drawn from such students.

This bias could account in part for the use of basic words and stimuli herein, and the relative singularity of the basics, and would raise the issue of whether the use of basic words is learned, or a sensory verity. These questions might be approached experimentally, but the cultural "common truth" of basic tastes would be hard to null out.

7.7. Further tests of the basic tastes model

7.7.1. A definition of "basic tastes." To test the four tastes model in somewhat more detail, as clear a statement as possible of the idea was sought. Two relevant tenets of the model at the psychophysical level, as cogently summarized by Halpern (2002a), are (a) that the four basic tastes completely account for all tastes, and (b) that the basics are clearly and separately perceivable, unchanged, as the only components of mixtures and other stimuli. (He also points out that in this model each receptor and neuron is specifically tied to only one of these tastes). It is clear from his article that the terms "taste" and "basic tastes" have not been formalized beyond functions (a) and (b), and no control experiments have been done to test other words or stimuli as basics, other numbers of nominee basic tastes, or whether they are indeed clearly discernable in mixtures or other stimuli. To the extent that Halpern's two statements might be taken as possible tests of the model, it is further falsified as follows.

7.7.2. The accounting was not total. In regard to Halpern's tenet (a)., first, the basic tastes did not completely account for the Comparison stimuli. But must the basic tastes be held to exactly a 100% accounting of other tastes in the present format? Would 95% do? It could easily be that there is an inherent lack of clarity of tastes, say in comparison with our abilities to report that a shape is a square, a straight line, or a point, that would somewhat degrade the subjects' acuity in tasting. Perhaps the performance of the basic tastes herein is the best the subjects could be expected to do, and that these data are equivalent to a perfect accounting. But the nonbasic Standards accounted for the Comparison stimuli at about the same level as the basics; either way, the control and experimental groups are roughly equivalent in this limited set of data.

7.7.3. Tastes other than the basics were perceived. In regard to Halpern's tenet (b), the psychophysical basic tastes model holds that the basic tastes are clearly and separately perceivable, unchanged, as the only components of other taste stimuli and mixtures. This did not hold in the present data. After the experiment proper, the subjects in the four and five nonbasic controls (Fig. 1, C 3–4) were asked to describe their nonbasic Standard stimuli freely, that is without the instructions to use the basic words. In the basic tastes model, only the basic words should have been used – but only 65 % of the words used were basic, and 35% were not. These nonbasic words included alcohol, alkaline, aspirin, bad, bad soda, baking soda, bland, cottony, chalk, citrus, crap, dentist work, fresh, ginger ale, medicine, metally, milky, mineral, mouth wash, nasty, not good, Nutra Sweet, old, pastry, plastic, spicy, Sweet 'n Low, and tangy. Acid, lemon, and vinegar were counted as basic words for sour. The fact that words other than the basics can account for tastes has been shown (Schiffman & Erickson 1971; Schiffman & Dakis 1975). A more complete treatment of this issue would be interesting, perhaps using some nonbasic words; and such a procedure would provide a reasonable control for the basic words protocol (Fig. 1, E1). The present data suggest that the basic tastes do not come naturally as the only verbal descriptors subjects find appropriate; and this in turn suggests that their exclusive use in psychophysical studies may have resulted, to some degree, from directions to use only these words, guaranteeing a successful outcome in terms of basic tastes.

7.7.4. Inconstant accountings. And, as was true in describing the nonbasic Standard stimuli with words (7.7.2), the Comparison stimuli did not appear to be perceptually made up of the basic stimuli. The basic tastes model requires that the non-basic stimuli should be completely describable in terms of the basic stimuli (Halpern's tenet (a). For example, the taste of proline should be composed of the basic tastes, mostly sweet and bitter (Fig. 1, E1, column 3). Furthermore, the amounts of each basic taste in proline should be definite to unequivocally define the taste of proline (Halpern's tenet b). If this is so, then accountings for Comparison stimuli by proline should also be definite, or fixed, because it represents fixed amounts of the basic stimuli. When used only with lysine, proline accounts for an average of 33% of each Comparison stimulus (Fig. 1, C3). If proline is composed of definite and fixed amounts of the basics, it should continue at 33% no matter how many Standards are used along with it. But this accounting drops progressively from 33% when there are only two Standards to 24%, 20%, and 20% of each Comparison stimulus when more Standards were added (not illustrated independently, but discussed next with reference to Fig. 2). Lysine also drops progressively in this series from an average of 28% to 30%, 25%, and 16% when used with one to four other Standard stimuli (Fig. 1, C1–4). So proline and lysine, as examples, are evidently not perceptually composed of definite amounts of the basic tastes as required in the basic tastes doctrine.

A similar effect might be found using various numbers of the five basic stimuli. For example, the degree to which NaCl accounts for another stimulus or mixture might depend on whether it was used alone, or along with one to four other basics. If the accountings by NaCl decreased in this series, both of the basic taste's primary definitions (Halpern's tenets a and b) would be negated. Such control experiments have not been done.

7.8. *A "completion" effect*

This failure to find fixed amounts of accounting for the Comparison stimuli by individual Standards is not in line with the basic tastes model. A reason for this failure may be provided by a look at the overall averages for the nonbasic Standards shown in Figure 2. The average decreasing effectiveness of each of the individual Standards as the number of Standards increases from 2 to 5, appears in the lower curve. On average, when two Standards were used they each accounted for about 31% of the taste of the Comparison stimuli; but with three Standards this decreased to 26% each, with four to 18% each, and decreased to 16% for each of five Standards. But this curve should be level if each nonbasic Standard was

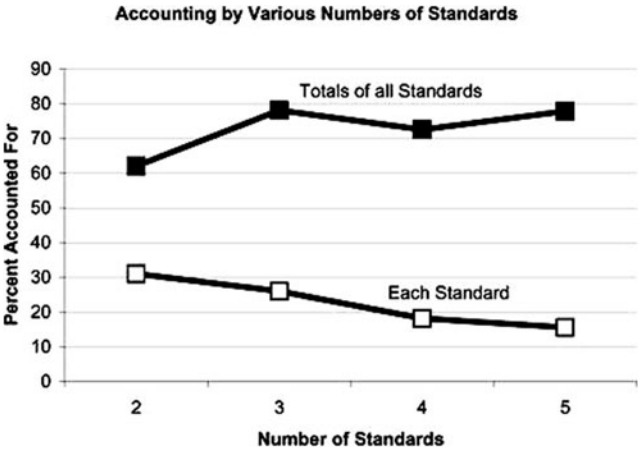

Figure 2. The degree to which each nonbasic Standard stimulus accounted for the Comparison stimuli depends on how many Standards were used (from Fig. 1, C 1–4). The lower curve shows that each Standard's account was not constant but decreased (averages) as the number of Standards increased. The upper curve shows that the total amount accounted for by all Standards may be approaching an asymptote of somewhat less than 100% as the number of Standards increases. The upper curve equals the lower curve times the number of Standards.

indeed made up of definite and fixed amounts of four basic tastes as held in the basic tastes doctrine.

The reason for this steady decline (lower curve, Fig. 2) may be seen in the totals accounted for with each set of Standards (top curve). The implication is that these totals may be rising towards "completion," which would be close to 100%. With only two Standards, the total amount of a Comparison stimulus accounted for is 62%; this rises to 78% with three Standards, 72% with four, and 80% with five Standards. It might be concluded that completely accounting for the taste of a Comparison stimulus was an implicit objective for the subjects. To do this, they would have to reduce the value given for each Standard when there were more of them; otherwise, the total could quickly rise to more than 100%. If each Standard were held to the 31% seen for two Standards, then when 5 standards were used, 155% of the Comparison stimulus would be accounted for. This might be perceived by the subjects as an excess to be avoided, a potentially strong effect in previous research of this nature. Those controls were missing.

In summary, subjects in psychophysical procedures may take on two conflicting goals; to veridically report how well each Standard accounts for a Comparison stimulus, and to completely account for the Comparison stimulus with whatever Standards are available. The direction the subjects take in these kinds of experiments might depend heavily on the nature of the instructions given to them. Because the subjects were clearly aware of the idea and role of basic tastes before the experiment, their reports could be biased towards the completion usually required in studies of this sort (sect. 7.6). Support for this idea is seen in that subjects very rarely go over 100% in accounting for a Comparison stimulus (Fig. 1 C4, HCl). Further discussion and testable speculations on the "completion" effect are contained in the Appendix.

This problem may be summarized thus: If the subjects believe in four (or five etc.) basic tastes, and are given this number of stimuli to use, then they might for this reason complete the accountings with four (or five etc.) stimuli.

7.9. Singularity, or what is A taste?

As found in previous tests of singularity (sect. 6.1), neither were the basics singular (one taste) nor the nonbasics more-than-one (of the basic tastes), as required in the basic tastes doctrine. This was confirmed in the present data.

The perceived singularity of each of the 10 Comparison stimuli was determined in the basic words and stimuli controls (Fig. 1, E1 and E2) after the experiment proper. It is seen in Figure 3 that only 70% of the subjects found the basics NaCl, QHCl, and sucrose to be singular. The taste of the basic stimulus HCl was rated as less singular (43%) than the other basics, and also less singular than some of the nonbasic stimuli. The nonbasics were rated as singular to some degree; for example, KCl was rated as singular by 48% of the subjects. To the extent that the basic tastes model requires singularity (the model is not clear on this), these data falsify the model.

These are not statistical statements; as for Figure 1, the point of Figure 3 is not that one stimulus is statistically more singular than another, but that the data are intermingled between basic stimuli and the nonbasics. Also it seems clear, as nonstatistical statements, that the basics do not rest at complete singularity (left column) and the nonbasics do not rest at completely more-than-one (right column), as might be held in the basic tastes doctrine. It is hoped that this conclusion will be tested in future studies.

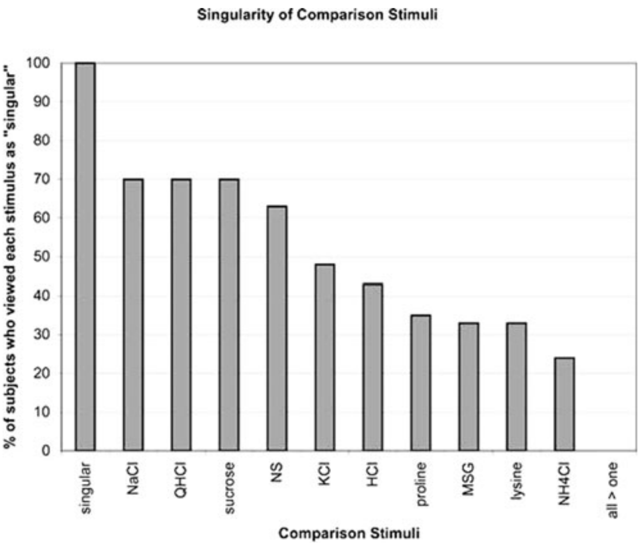

Figure 3. Comparison stimuli rated as "singular" or "more-than-one;" data from the basic tastes protocols (Fig. 1, E1, E2). The left column indicates how the ratings would appear for a hypothetical stimulus that was rated as singular by all subjects, and the right column illustrates the data for a stimulus that was always rated as more-than-one. No stimulus is completely either singular or more-than-one, the only two outcomes that would be predicted in the basic tastes model.

Some of the singular ratings of the basics may be accounted for by the fact that the subjects were biased towards the verity of basic tastes, as mentioned in Section 7.6.

7.10. Other comments on the experiment

It could be argued from the basic tastes model that the nonbasic stimuli could account for the Comparison stimuli because each was composed of set amounts of basic tastes. If this argument were made, it must equally be argued that the basic tastes might function because they were composed of various amounts of the tastes of the nonbasics. To remain unbiased, the argument cannot be made in one direction only, in support of the idea of basic tastes. The basic tastes position may not be assumed valid while testing its validity.

If words are not trustworthy vehicles of communication between what we perceive and what we report, should less than the expected basic tastes outcomes be taken very seriously? Might nonverbal methods, not using the basic words, give different, more valid results?

Were the protocols appropriate for the questions asked? It could be argued that the present procedures did not properly examine the basic taste model – but it must be admitted that the effort was made. This then raises the good question of how this idea might be more properly tested. This is not as clear as it should be. It is hoped that other more substantial and appropriate experimental protocols will be pursued.

The present data are not as forceful as the previous findings in other psychophysical studies in supporting the basics view. This may be because herein the subjects were not instructed on how to use the basics. That the data are as supportive as they are may result in part from the fact, mentioned in Section 7.6, that the subjects expected that their responses should be in terms of the basic tastes. This issue could be tested.

7.11. Do these data falsify the Basic Tastes model?

These data and discussion falsify the basic tastes model *as it has been presented thus far*. But, strictly speaking, without a clear rationale and definition of what "basic tastes" are, the model can neither be falsified nor supported. It is in a fatal limbo. This may be seen as a serious problem by some in the field of taste and by others from various fields, as well. It is hoped that a clear and testable underlying hypothesis and the resulting definitions will be elaborated and tested. These could lead to a clearer view of the nature of taste.

8. A promising alternative to basic tastes: Thomas Young

The previous sections of this article have addressed the many serious shortcomings of labeled-line models of neural information, and the basic taste model in particular. What would be a more substantial alternative of broader applicability? The present section presents such a model based on Young's theory of color vision.

8.1. A definition of "theory"

In this article it is held as an essential part of investigating the basic tastes that there must be a rational, data-based hypothesis from which the basic terms are derived, and that makes the hypothesis and its terms testable. The term "formal" was used to introduce this idea in Section 5.5. The following quote from Young's theory of color vision, first presented in 1802 and 1807, meets these requirements in brief, forceful and elegant fashion. Because it meets these requirements, Young's statement is classed as a "theory" in this article.

8.2. Young's theory

Young's is a model of scientific thinking in the neurosciences that has seldom, if ever, been equaled; perhaps it had something to do with the fact that he was a polymath linguist who knew the vagaries of words. His interpretation of the Rosetta stone, although incorrect in detail, showed that he understood both the "labeled-line" and "population" implications of the symbols encountered (Erickson 2001). Here the "labeled-line" idea means that each of a limited number of symbols of determinate meaning will represent an equally limited number of events; three color receptors could signal only three colors. "Cleopatra" would be represented by one dedicated symbol, as the $ sign. The "population" idea means that a limited number of symbols (individual letters), each of indeterminate meaning but taken in combination, can represent an enormous number of different events; three color receptors could represent a continuum of colors. "Cleopatra" would be spelled out.

In the 1802 passage we will quote, note that Young first presents the *rationale* for the hypothesis – its economic necessity, that there cannot be enough color-coded private "labeled lines" to have one for each perceivable color from each point on the retina. The words in parentheses are by the present writer. Then he proposes the testable *solution* to this problem: If each of a very few (three) receptor types are relatively responsive to many wavelengths, each different from the other two in the placement of this responsiveness along the continuum, an unequivocal code in the pattern of activity across these receptor types for each color will result. Illustrations of Young's theory are given by Helmholtz (1924) and are found in many other texts (relevant discussion is provided by Erickson 1968, 1974, 1982b, 2001; Erickson & Schiffman 1975). In the 1807 quote, Young states that his economical logic would give the receptor types the ability to represent very many different colors at each point on the retina, a continuum.

His hypothesis for the encoding of color is succinctly put in what are arguably the two most powerful sentences in the history of neurobiology.

> "Now, as it is almost impossible to conceive each sensitive point of the retina to contain an infinite number of particles (receptors), each capable of vibrating in perfect unison (responding) with every possible undulation (wavelength), it becomes necessary to suppose the number limited, for instance (to three); and that each of the particles is capable of being put in motion less or more forcibly, by undulations differing less or more from a perfect unison; for instance, the undulations of green light will affect equally the particles in unison with yellow and blue, and produce the same effect as a light composed of those two species; . . ." (1802).
>
> "the different proportions, in which (the motions) may be combined, afford a variety of traits beyond all calculation." (1807).

8.3. The implications of Young's theory

Young's was an unusual mode of thinking, not common since, in that it did not depend on available *techniques* or *words* of problematic meaning. *His idea was driven by a precisely defined logical problem, given a straightforward solution, and the complete theory can best be conceptualized graphically, without words.* His entire comment sets in its most elemental form the *rationale* of across-fiber pattern coding throughout the brain, to provide the means for the immense power of the brain to handle extremely large amounts of information (Erickson 2001). This model is particularly applicable for the most complex of the brain's functions where the amount of information far outweighs the number of basic "labeled" neurons available (Erickson 2001). And it is nicely testable.

His idea solves these problems by letting the information remain in the population form from its "first representation" to its "destination," unchanged in general across-fiber pattern format, such as from sensory input to behavioral output. Very few transforms would be required, even into the level of motor responses (e.g., the problem of the "binding" together of the various aspects of a stimulus is eliminated) (Erickson 1974, 1978, 1982a, 1984b, 1986, 2000, 2001). The data in all neural systems, including taste, fit this model. But the solution to this problem would be impeded by linear gatherings of information reduced to bits traveling along many labeled axons and across many synapses to a final neuron labeled "grandmother," which is the general tenor of the basic tastes position.

Young's theory not only predicted the general broad form of the response characteristics of the receptors and neurons across wavelengths ("neural response functions," Doetsch & Erickson 1970; Erickson 1968, 2000, 2001; Erickson et al. 1965), but also their broadly-tuned character at more central levels; at no place in the brain could they return to "labeled-lines," as that would destroy Young's economic ability to represent large amounts of information.

This economic statement provides perhaps the most important, or only, rational and testable hypothesis of sensory coding, and neural functioning in general. Very many colors can then be represented in the across-fiber pattern of activity across only three receptor types, just as a 3-digit number (base 10) can represent 1000 different events, and 10^{11}, even more. This model thus presents the heuristic question of how many different levels of activity may be represented in the firing of a neuron, or a population of neurons. In this model, a relatively small number of neurons could hold massive amounts of information with redundancy, even in the presence of noise (Erickson 1985b, 2001).

But the simplicity of the model, which Young set in the context of three neurons, while making the idea altogether clear and generalizable to other more complex situations, also makes it easy to ignore when considering larger issues.

The across-fiber pattern idea of the neural representation of information closely parallels Young's theory. The rationale and successfully predicted data are of the same nature in both color vision and taste. The quotes we cited could well be used in taste, exchanging taste terms for visual terms.

8.4. Across-fiber patterning and Young

8.4.1. The across-fiber pattern model. Although this model has been presented a number of times (Erickson 1963, 1968, 1974, 1978, 1982b, 1984b, 2001), it might best be summarized here as an extension and detailed elaboration of Young's theory. It is based first on Young's concern for an economy of neural resources, and also on an economy of neural principles.

Concerning an economy of *neural resources*, Young's idea is that a continuum of wavelengths may be represented most economically in the pattern of activity across three broadly tuned color receptors. In the across-fiber pattern model, this idea is generalized to all neural systems, sensory, motor, and probably most others in which an efficient economy in the representation of sometimes great amounts of information is required.

Concerning an economy of *principles*, it seems probable – at least as a first approximation – that once the nervous system found an efficient way to represent information, it would conserve that method across systems to whatever extent is possible – or reinvent it. The across-fiber pattern model is applicable to all systems thus far considered.

8.4.2. Generality of across-fiber patterning. This possibility of the great generality of the across-fiber pattern model is not always immediately obvious. Some of the continua are laid out as maps across neural tissue, such as across the skin surface, retinal location and muscle location (which muscle?), and in other systems the continua are not laid out spatially, such as color, temperature, taste, flexion and extension, and vestibular sensitivity; the entire continua are to be found at each point in a spatial map. The former have been termed "topographic" systems, and the latter "nontopographic" systems (Erickson 1968). As examples, the entire nontopographic color continuum is found at each point in the topographic retinal maps, and the taste continuum at each point on the tongue and its projections in the skin maps. But in both cases, the neural information is in the form of across-fiber patterns.

As another point where the neural systems appear to require different mechanisms, the tuning of the neurons in spatial maps appear to be narrow with respect to the total continuum, whereas for the nonspatial codes imbedded therein the neurons must be broadly tuned to complete the continuum with the few neurons available at that point – Young's point. Relatively narrowly tuned spatial somesthetic and visual neurons are broadly enough tuned to provide a continuous and economical representation of those spaces, finer than the distances between receptors. In a two-dimensional sheet such as skin or retinal location, as few as three neurons could provide the information about the location of many different stimuli within their areas of sensitivity by the unique pattern of activity across them, as the location of a ship can be determined by distances from three known points. Population coding applies identically in both spatial and nonspatial situations.

Such population coding, of which the "across-fiber pattern" theory is an explicit and highly detailed example, has been widely advocated in all sensory systems, including the chemical senses. It has been widely accepted in olfaction (Buck 2004; Malnic et al. 1999) for at least 50 years (Adrian 1955), and in taste for over 40 years (e.g., Erickson 1963, 1968, 2000; Scott & Giza 2000; Smith et al. 2000). It is also appropriate for most other sensory, motor, and molar neural functions (Covey 2000; Erickson 1968, 1974, 1978, 1984b, 2001). The great utility of Young's idea has been rediscovered independently by many investigators (see Erickson 1974, 1978, 1982b, 1984b, 1985a). As they were not aware of Young's work and others, they independently invented various words to name it. These names include, at least, the following: distributed, combinatorial, ensemble, parallel, and population coding. Some used the population idea without naming it, including Adrian, Doetsch, Hartline, Johansson, Llinas, Merzenich, Mountcastle, Nafe, Sperry, and Tower in sensory systems, and Georgopoulos, Law, Lee, and McIlwain in motor systems. Among others, Goldman-Rakic, Hebb, and Lashley utilized this general idea for broader brain functions (Erickson 2001). The across-fiber pattern term was first introduced by Erickson (1963, 1968). In that there are no clear and substantively different definitions of the other terms, they are assumed to be similar to across-fiber patterning. However, across-fiber pattern coding is more precise in that it states exactly how the individual neurons contribute to the overall code, whereas the other terms simply state that the code is distributed over a population of neurons. Definitions of these other terms would be extremely salutary, including how they differ from across-fiber patterning and from each other. To the extent that there is one idea, the use of one term would be simplifying and clarifying.

This model also addresses some important molar issues that are rarely touched on because they are hard to address. These issues include the neural representation of "concepts" or "equivalence," as well as "memory" and "readout," and a solution to the binding problem (Erickson 1974, 1982b, 1984b, 2001).

Whatever the reasons for this ubiquitous neural commonality of proposed strategies in representing information, it would be surprising and unparsimonious if an entirely separate mechanism had evolved for taste (Erickson 1968, 1978, 1984b, 1986, 2000, 2001). Across-fiber patterns are appropriate for very high to low levels of information (input-output variance). The neural strategies for yes/no situations could require only labeled-lines, an across-fiber pattern reduced to one neuron, each neuron having one designated function, as in pheromone-based behavior, the giant axon escape reactions in crustaceans (Erickson 2001), or the specificity for l-arginine of neurons in the channel catfish (Caprio 1978). This would be equivalent in Young's model of language for one determinate symbol to represent Cleopatra. Such possibilities are not in conflict with the across-fiber patterning model, wherein individual neurons may be entirely "specific" where the level of information becomes minimal, one bit, as discussed in Section 6.4 (Erickson 1968).

8.5. Across-fiber patterning and taste

The original datum driving the "across-fiber pattern" theory (Erickson 1963, 1968) was the broad responsiveness of individual taste neurons (Erickson 1963; Pfaffmann 1941, 1951, 1954, 1955). This has been elaborated extensively, both empirically and logically (e.g., Boughter et al. 1999; Erickson 2000; Scott & Giza 2000; Smith et al. 2000). With this broad sensitivity, the stage is set for the encoding of many tastes with few neurons – and the taste neurons are notoriously few.

8.5.1. Across-fiber patterning requires receptor and neuron typologies. The original presentation of across-fiber patterning was in terms of Young's typologies (Erickson 1963). All data on receptor types are predicted or accommodated by the across-fiber pattern model on logical and economic grounds (Erickson 1968, 2000, 2001). For example, receptor and neuron types are required for nontopographic sensory systems such as color vision and taste, for Young's economic reasons (Erickson 1963, 1968). The necessity for types here lies in the paucity of neurons available at each point on the tongue. On the other hand, topographic systems, such as skin or retinal location, although fully using across-fiber pattern codes, do not find broadly tuned typologies necessary because, with the abundance of receptor surface and neuron quantity, Young's economy is not as strong an issue (Erickson 1968).

As discussed earlier (sect. 4.2, techniques) the existence of groups or types of taste receptors or neurons has not been established. This lack does not disqualify the idea of typologies, but only makes the point that they have not been formally defined, and so the issue has not been resolved.

8.5.2. Fuzzy set types. Young's idea exists in a somewhat different approach to typologies, that of "fuzzy sets." This idea presents a logic for a few underlying *processes* rather than a few cell types. These processes are shared in various "fuzzy" degrees by all cells, allowing for idiosyncrasy between cells without losing the advantage of typologies. They have been presented as mathematical abstractions that account for the amount and time course of taste responses (Buhusi 2000; Erickson et al. 1994, 1995, 1996). This procedure assigns relative values in each of these few time course and amplitude sets to describe each cell's response. The success of this approach in accounting for the amount and time course of each cell's responses suggests that further investigation in this line might be useful. This approach could clarify the problematic issue of the labeling of types of cells as a different issue from that of the labeling types of underlying processes.

8.5.3. Breadth of tuning of receptors and neurons. The across-fiber pattern theory proposes broad tuning of receptors and neurons. There is a long and detailed history showing the multiple sensitivities of taste receptors (Herness 2000), and the clearly validated multiple sensitivity of afferent taste neurons (Erickson 2000; Gilbertson et al. 2001; Lemon & Smith 2005, 2006). That the breadth of sensitivities of individual cells, or their participation in the various sets of underlying processes, vary from only one to all the stimuli used is not a problem for this theory; there is breadth in each cell, but it appears to be variable between cells within the very limited range of stimuli tried thus far.

8.5.4. Developments in across-fiber pattern coding. Erickson (2000, 2001) pointed out that the across-fiber pattern model would find its most important application in more molar functions of the nervous system where information demands are very high, and rapidity of handing of this information is very important (Erickson 1974, 1982b, 1984b). Simon and his coworkers (2006) are taking a broader look at food intake as a "distributed" code. They describe not just the encoding of tastants, but the whole distributed oral input during ingestion in parallel and simultaneous with postingestive properties of tastants. This population approach will certainly be expanded to include all the sensory input and motor output necessary for ingestion, and similarly on to other large behavioral issues such as decision-making, memory, and language. A basic-taste, labeled-line direction would prevent access to these ultimately unavoidable molar issues. On the other hand, population codes represent large amounts of information simultaneously at all neural levels (Erickson 2001). This is the current issue of reductionistic versus systems biology.

9. Summary statements

The basic taste model has been entrenched in our culture and thought since before the dawn of the scientific method. It appears to have been "grandfathered" into our current scientific thinking without being subjected to the same rigorous standards of testing that we would apply to any novel model used to explain available data. We seem to have found the right answer without having asked the right question, or any question at all. The ongoing wide acceptance of and compliance with this model has probably resulted in a distortion and restriction of our scientific understanding. The effect of this broad acceptance on our understanding of taste is hard to estimate.

A preliminary demonstration of a test of a psychophysical use of this model found it to be false within the limits of this definition and protocol. More complete tests of this model are encouraged in all areas of taste – receptor, neural, and psychophysical – as a part of normal scientific procedure. An essential part of these tests would be the inclusion of control groups.

The across-fiber pattern model meets the requirements of definition and testability demanded by science. It has proven to be heuristic, and to be applicable to broad ranges of neural systems. This great breadth of relevance speaks to the validity of this model.

10. Conclusions

In its most general sense, this article is a search for the necessary systematic approach to the study of taste that will usefully inform and coordinate all its parts. This broad view suggests that it would be essential to consider venues other than the basic tastes model.

Certainly the basic taste words will never be lost to familiar conversation; we need them. But the cultural truth and convenience of a few taste words appears to have overridden their scientific inspection. How could we proceed in science if we were denied these words? But the need for common taste labels does not validate the basic taste idea as a guiding scientific model.

This review of the concept of basic tastes calls for control experiments based on rational and heuristic hypotheses from which are drawn clear and testable definitions of the major concepts (e.g., basic tastes, population models, or other hypotheses). The great leaps in knowledge in physics have required the strong understanding that it is essential to continuously examine by testing and, if necessary, to be willing to modify or even delete their most basic concepts. We might well emulate that vigorous science.

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APPENDIX: A “COMPLETION EFFECT” AND “OVER-ACCOUNTING” IN TASTE PSYCHOPHYSICS (SEE SECT. 7.8)

Although not set forth formally, it appears that an assumption of the basic tastes position is that each basic taste is perceptually nonoverlapping with the others, and that together they must exactly add up to the whole (100%) of any taste. There are many reports to support these ideas.

However, a “completion” effect as described herein points to the fact that in accounting for the taste of a Comparison stimulus with several Standards, the subjects appear to be trying to *completely account* for the tastant rather than, or in addition to, giving perceptually veridical descriptions of the Comparison stimuli in terms of the Standards. This is suggested by the present data; with increasing numbers of Standard stimuli, the value given each stimulus decreases, with the result that, or perhaps so that, a 100% accounting is approached. If this is even partly correct, it would have an obscure but very fundamental impact on the historical and modern conceptualization of the nature of taste.

Then the fact that some of the accountings in the 4 and 5 nonbasic controls were somewhat greater than 100% might be expected on the grounds that the amounts of the Standard stimuli contained in the Comparison stimuli indeed summed to more than 100%. For example, this was seen in the group data average of 105% accounting for HCl with 5 nonbasic Standards (Fig. 1, C-4). This *over-accounting* effect also was occasionally obtained by individuals when using the basic stimuli and words.

But suppose there were *overlap* between tastes (for example with “sour” and “bitter,” or HCl and QHCl), and three Standards each accounted for 40% of a Comparison stimulus. If summed linearly (as if they did not overlap in their tastes) they would then account for 120% of a Comparison stimulus; this was apparently sometimes the case, especially with larger numbers of Standard stimuli. On the other hand, with overlap between the tastes of these three Standards, each partly accounting for the *same* aspects of a taste, these three together might actually have accounted for a total of only perhaps 70%, leaving 30% unaccounted for. This means that an assumption of linear summations seen in the literature (sweet + sour + salty + bitter = 100% of a tastant, Bartoshuk 1988) may be invalid.

The “distinct and nonoverlapping tastes” aspect of the basic tastes idea represents “crisp” sets of tastes wherein a linear summation to exactly 100% is expected in that model. But with overlapping or “fuzzy” taste sets, a linear summation in the analysis of the data values could inappropriately amount to the more than 100% – as in the present research.

Open Peer Commentary

Insights from the colour category controversy

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Abstract: There are striking parallels between the basic tastes debate and the debate on human colour categorisation. Colour categories show a remarkable cross-cultural similarity, but at the same the time exhibit seemingly inexplicable large interpersonal variations. Recent results suggest that colour categories are the result of cultural learning constrained by the neural substrate of colour perception.

The discussion on the basicness of taste at its different levels – perceptual, neurophysiological, psychophysical, linguistic, and cultural – is in many ways reminiscent of the discussion on colour categories. Colour perception is perhaps better understood and less controversial than taste perception. It is accepted that our retina has four types of photoreceptors, three of which are involved in chromatic perception, and the neural coding and transmission of colour perception is well understood (e.g., Gegenfurtner & Sharpe 1999). However, the cognitive aspects of colour perception and the nature of colour categories in particular have been under debate for more than 50 years (for an overview, see Hardin & Maffi 1997).

Colour categories cut up a continuous chromatic experience into concepts that can be associated with linguistic terms. Just as with basic tastes, some colours are considered to be primitive (white, black, red, green, blue, and yellow) and all other colour experiences can be described in terms of these primitive colours. These colours have been identified as being psychologically opponent (Hering 1964) and neural coding for these opponent channels has been identified in the brain (De Valois et al. 1966). This precludes other colours from serving as primitive colours (but see Jameson & D'Andrade 1997).

When considering linguistic colour category systems across cultures, one could at first be tempted by the rather varying colour lexica and their referents across cultures to conclude that the colour continuum is arbitrarily cut up by linguistic categories (e.g., Gleason 1961). This Whorfian view was challenged by Berlin and Kay (1969) who demonstrated how a set of different languages spoken in different cultures have basic colour terms of which the referents are remarkably similar. This was reconfirmed almost 30 years later in a statistical study using data from a large set of languages from non-industrialised cultures (Kay & Regier 2003; Lindsey & Brown 2006; Regier et al. 2005). This universalist view holds that these regularities in referents of colour terms result mainly from regularities in the neural coding of colour; and as the neural coding is largely genetically determined, so are colour categories. Nevertheless, there is considerable evidence that colour categories are plastic, that they are learned, and that they change as a result of learning experiences. These learning experiences typically involve language, and, as such, colour cognition is brought into the realm of linguistic relativism. In a series of recent reaction time experiments (Drivonikou et al. 2007; Gilbert et al. 2006; Roberson & Hanley 2007) subjects were asked to find the odd-one-out in a set of otherwise identical colours. The odd-one-out belongs either to the same linguistic colour category of the distractors (i.e., blue or green) or falls just outside the category; the perceptual distance was, of course, kept identical. When the target appears in the right visual field, subjects were faster at spotting the odd-one-out when it belongs to a different category. This is not observed when the target belongs to the same category, when the target is presented in the right visual field, or when the subjects are distracted with a linguistic task. As language is situated in the left hemisphere, information in the right visual field travelling to the visual cortex via the left hemisphere is more under the influence of lexical representations. This suggests that language, and lexical representations in specific, have an impact on natural categorisation.

These experiments, however, do not inform us on how natural categories are formed; for this, insights can be gained from computer simulations (Belpaeme & Bleys 2005; Dowman 2006; Jameson 2007; Lammens 1994; Puglisi et al. 2007; Steels & Belpaeme 2005). These studies typically involve modelling a large population of individuals interacting with each other and trying to reach a consensus on colour terms. As colour terms refer to colour categories, the process of arriving at a linguistic consensus on colour terms affects the categorisation of colour. The interest of this type of simulations lies in the fact that the evolution of colour typology can be studied diachronically and under a varying set of ecological, perceptual, and social conditions.

Simulations in which human-like colour category systems emerge from linguistic interactions about colour are presented in Steels and Belpaeme (2005) and Belpaeme and Bleys (2005). In these simulations colour categories are situated in a semantic colour space, which is implemented using a three-dimensional CIE L*a*b* colour appearance model (Fairchild 1998). The colour space models colour perception numerically, has an opponent character, and, importantly, is not symmetrical. The colour space thus forms a bias on colour category acquisition, which, together with the linguistic interactions in a situated environment, nudges colour categories towards certain locations in the colour space. It is important to note that language seems to play an important role in binding colour categories of individuals together. Without language, individuals will be able to learn a category for, say, reddish hues, but the categories would be insufficiently coordinated to allow communication about "red." Lexical terms thus not only serve as a conduit for learning categories, but also serve to coordinate categories between individuals.

In light of what we know about colour categories, it is very likely that the basic tastes are indeed, as Erickson seems to suggest, the product of a cultural agreement made on top of an innately fixed psychophysical substrate.

Salty, bitter, sweet and sour survive unscathed

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Abstract: Types of sensory receptor can only be identified by multidimensional discrimination of a familiar version of a sensed object from variants that disconfound putative types. By that criterion, there is as yet no evidence against just the four classic types of gustatory receptor, for sodium salts, alkaloids, sugars, and proton donors.

The causal theory of perception is a dead-end. By itself, processing in the brain can never show how many types of taste there are. Philosophers (e.g., Hamlyn 1957) and psychologists (e.g., Gibson 1979) have long pointed out that visual perception cannot be projection onto a cinema screen in occipital cortex. This is a matter of logic, not science: the problem remains how we perceive the picture in that neural firing (even with "binding" across modules in visual areas). Equally, how does a taster get a taste out of a pattern across fibres? All that can be said from Erickson's account is that one pattern is transformed into another across-fibre pattern until we get to the neuromuscular transmission pattern that produces what speakers of the language have learnt to recognise as a name for a taste.

How we achieve knowledge of the world through the senses is an issue in the first instance of purely psychological science – characterising the unconscious and conscious cognitive processing that accounts for the externally observable performance of the individual. It is sensed materials in items of food and drink (Booth 1994) that are perceived through gustation (Freeman et al. 1993), as well as for olfaction (Booth et al. 1995) and touch (Booth 2005; Richardson-Harman & Booth 2006). So the prior question is how people distinguish sources of tastes. Measurement of the mental causation involved is required in order to work out how the brain processes the signals on which such achievements depend.

Nobody has proposed a single fibre from a tastant receptor to a taste word. Despite caricatures by textbooks and even some neurophysiologists (e.g., Lemon & Smith 2006), a "labelled line" could not have meant a single fibre. This idea was put forward before the cell doctrine was established. The issue is whether any aspect of a human taster's performance can be controlled by a discrete signal from some set of compounds applied to the tongue. Like so many psychophysicists, Erickson neglects the cultural and cognitive aspects of sensory description. The design of his experiment fails to measure the way in which the assessor and the investigator "communicate" about reality by saying that a sample tastes sweet, salty, metallic, savoury, or whatever. Even on a simplistic behavioural account, the assessor has to have learned an association between materials containing compounds that stimulate the same type of gustatory receptor and the word that is used to name that set of tastants in the tasted sample. In cognitive reality, the naming of a taste can only succeed in the context of other sensory and conceptual processing, not least being the profile of activation of other receptor types that is almost inevitable by any one compound (Booth 1995; Booth & Freeman 1993). Taste descriptors are a very mixed bag too, from biologically functional tastes like salty and bitter, through flavours and textures like lemony and astringent, to culinary concepts like savoury.

The hypothesis of four basic tastes emerged from nineteenth-century experimental psychologists 'exploitation of chemists' recent success in preparing pure compounds, instead of the unknown mixtures available to earlier cultures. Neither Erickson's approach nor the continuing ill-conceived advocacy of a fifth "umami" taste (Booth et al., submitted) is a biosocially adequate way to challenge that number four. Definitions of conceptual categories or counts of words do not address the factual question of how the compounds control the words. A control group is not the issue either. The problem is proper design of samples to be tasted by any one assessor (Booth et al. 2003).

Taste is not measured by arbitrary calculations from responses to under-designed samples. The experimental results in Erickson's review, even when reported in full, would be scientifically very thin. He asked students to "account for percentages of the taste" of a solution. It is well known that averaging such integrative responses across individuals creates artefacts and that totals of percentage judgments (let alone their group averages) do not measure performance. A treatment of such data without unwarranted assumptions would be to compare the largest percentage given by each individual between the same number (four) of criterial and non-criterial compounds. Considering that these are grouped data from an under-specified task, there are remarkable mutual dominances of sucrose and the sweet amino acid, proline, of the two sodium salts, NaCl and MSG, and of the two nitrogenous compounds quinine and ammonium chloride. Unfortunately, the only acids used were the "dirty" tasting HCl, the complex-tasting MSG, and the chloride salt of the weak base, ammonia. Nevertheless, the taste predominant in HCl uniquely was clearly evident in both MSG and NH_4Cl. Thus, a valid interpretation of the data presented by Erickson supports the classic four types of tastant.

It should also be noted that MSG gave no evidence of being a fifth taste. Rather, it reduces to a balance of NaCl-dominated lysine, acids-dominated acetylglycine, sucrose-dominated proline, and quinine-dominated phenylalanine, as we have claimed (Booth et al., submitted; Freeman et al. 1993).

Erickson does not take account of the only method yet found for identifying discrete types of taste (or of colour, shape, aroma, musical chord, etc.). This is to show that there are ranges of concentrations of different tastants at which discrimination fails, in the general case among mixtures (Booth et al. 1995; 2003; Booth & Freeman 1993) or in the special case of two or more single compounds of the same type (Breslin et al. 1996). The concentrations do not need to be matched empirically: it is much more efficient to estimate the indiscriminable ratio(s) by interpolation, using the determinate calculation of multi-psychophysical discrimination distances from the internal standard (Booth et al., submitted; Booth & Freeman, 1993). Until Erickson's tastants are tested this way, there are no perceptual data by which to evaluate the molecular evidence for gustatory receptor types on the human tongue and to start tracking multiple-fibre codes around the brain.

Criteria for basic tastes and other sensory primaries

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Abstract: Primary, or basic, colors have been discussed for centuries. Over time, three criteria have emerged on their behalf: (a) their physical mixture yielding all other spectral colors, (b) the physiological attunement of receptors or pathways to particular wavelengths, and (c) the etymological history of the color term. These criteria can be applied usefully to taste to clarify issues.

Erickson argues against salt, sweet, bitter, and sour as being "basic" tastes. His control tests with proline, lysine, and other chemicals are particularly useful, but his empirical facts are also not surprising. What Erickson and I find surprising is that a notion of four pure, labeled-line, basic tastes would have survived so long, given Pfaffman's (1941) early support for what is now called across-fiber patterning. More broadly, why does the notion of basic sensations persist in any modality?

The larger history across the sensory modalities offers some insight. At least since Boyle (1663/1999), basic colors were called *primaries*, and this idea appeared in perception textbooks up until the 1980s. But the terminology was confusing, because Locke and Boyle's distinction of primary (objective) and secondary (subjective) "qualities" (see Herrnstein & Boring 1965, pp. 14–17) made some secondary qualities into primary sensations. Thankfully, the notion of color primaries disappeared from textbooks. Nonetheless, *basic* colors remained.

But talk of primaries, if by another name, is unavoidable. Primaries are steeped in history and inveigle theory. Historically, there are at least three criteria for primariness. Consider color. Young, building on Newton, argued that three widely spaced colors could serve as primary colors and generate (almost) all chromatic secondary colors. Thus, criterion (a), *physical mixture*, became the first, and oldest, criterion for determining what a basic sensation (a primary) is versus what can only be derived from them (a secondary). Erickson tests a correlate – singularity (primaries should be singular) – and finds little evidence for this in taste. But there isn't much evidence supporting its diagnositicity in color either.

The next criterion came from Johannes Müller (see Herrnstein & Boring 1965, pp. 26–33), who popularized the idea now known as the labeled line. Let us call this criterion (b), *physiological attunement*. That is, certain neural pathways are uniquely attuned to certain physical states – particular chemicals, chromatic frequencies, whatever. Ignoring Hering's evidence for four primary colors, these two concepts – physical mixture and physiological attunement – seemed congenially aligned.

Erickson reviews the attunement evidence for basic tastes, but finds the area insufficiently motivated.

The third criterion comes from language. Call it criterion (c), *cultural salience*. This is really the only one in which the tetrad of salt, sweet, bitter, and sour makes sense. Erickson notes that most languages have such words, but he doesn't pursue a deeper cultural context.

Back to color: The basic English color terms are red, yellow, green, blue, brown, black, gray, and white (Berlin & Kay 1969). Critically, their etymology is lost in the prehistory of the language. They are not related to any object. All other color terms are borrowed from objects – orange from the fruit, violet and pink from their respective flowers, indigo from a plant. Such nonbasic color terms are legion – silver, gold, navy, turquoise, mauve, khaki, burgundy, chartreuse, olive, lavender.

Back to taste: Salt, sweet, bitter, and sour are primaries by this definition in English (all are Teutonic), and surely in very many other languages. The reason is that these terms are enwrapped in the needs and desires of members of many cultures, and have remained so for a long time. Consider: Salt licks were always highly prized locations for human beings, and are so named (e.g., Salzburg, Alsace, and any English town ending in "wich"). Salt has served as money, it featured in Norse mythology and in the Bible, and salt taxes spurred Gandhi's fasts (Kurlansky 2002). All of this would seem to make salt salient across a wide range of cultures.

Sweet has always been linked with ripe fruit, and over the last four centuries, with cane sugar and sucrose. The growth of cane sugar consumption has been astonishing. Mintz (1985, pp. 5–6) noted that in England, cane sugar went from a nobleman's privilege in 1650 to supplying one fifth of the calories of the English diet by 1900 – about the level for U.S. teenagers today. How could sweet not be a cultural primary?

Bitter is a term that has been associated with beer (as in a pint of ale) for many centuries. Until the 19th century, beer was the universal beverage in Northern Europe, particularly among the lower classes. Beer soup was a typical breakfast beverage, and the average daily beer consumption was three liters (man, woman, and child; Schivelbusch 1992). From the 17th century onward chocolate and coffee joined the bitter mix, both soon to be sweetened with cane sugar. Like sugar and at about the same time, chocolate and coffee entered into Western culture as a noble treat, unaffordable to all but the few, only to become necessities for all nearly two centuries later. Indeed, one could argue that salt, sweet (cane sugar), and bitter (chocolate and coffee), along with spice tastes, drove the earliest successes of globalized markets.

Sour is intimately associated with acids and fermentation. All cultures have fermented (soured) foods – milk (to make yoghurt), cereals (to make bread), maize, cassava, and so on. Fermentation and salting were the earliest food preservative processes used by humankind. Such a great gain for nutrition would remain salient in a culture for a long time.

Are there other basic tastes covered by this criterion? Acrid, no, defined as bitter; fat, no, derived from fed (fatted = well fed); metallic, no; umami, not in the West; water, likely not (salt:salty ≠ water:watery). So Erickson is right – the evidence from (a) mixture and (b) physiological response does not favor any basic tastes. But the evidence for (c), the cultural salience of four tastes, remains strong.

Some colors meet all three basic criteria, although caveats are needed. The best green wavelength to mix with a given red to produce the best yellow is not the green that maximally triggers the middle-wavelength receptor, and is not the green that is the prototype on a Munsell color chart. As Erickson notes, logic should drive our science, but depending on whether one's frame of reference is the logic of physical mixture, of receptor physiology, or of language and culture, one will get differing results. To keep these separate is to advance the science on all fronts.

Basic tastes as cognitive concepts and taste coding as more than spatial

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Abstract: Erickson's treatise intertwines and confuses two major, but separable, issues: whether there are basic tastes and how taste stimuli are encoded. The idea of basic tastes may reflect a natural process of concept formation. By only discussing two spatial coding schemes for taste, Erickson ignores the temporal dimension of taste responses and the contribution of neuronal cooperativity.

Erickson's ambitious treatise on the idea that there are a few basic tastes challenges our assumptions about the organization of the taste system. In this regard, his arguments are thought provoking and deserve to be taken seriously. However, we offer the following comments in the spirit of joining in a lively debate about these issues.

Erickson confuses the question of whether there are basic tastes with the question of how taste stimuli are encoded by the nervous system. These are two separable issues, and their comparison is akin to comparing apples to oranges. Even if there were a "continuum" of tastes, there might still be separate groups of cells associated with each taste stimulus. So the argument that there are not (only) four or five basic tastes does not necessarily impact the labeled-line theory. Nor does it provide support for the across-fiber pattern theory since there are other mechanisms and schemes that Erickson did not consider that may also be used to encode taste.

As Erickson notes, the idea that there are only a few basic tastes goes back far in history. He argues rather convincingly that our language limits our thinking about taste and that it also guides our scientific inquiries. However, the converse could also be true. That is, it may be that our language related to taste is the result of our perception of the taste world and the brain's ability to recognize the similarity among tastes to form natural categories that logically organize our taste world. So, we may learn that sucrose, saccharin, and proline are sweet, just as we learn that collies, dachshunds, and Great Danes are dogs; they share common features. Erickson's argument that we as humans are naturally prone to organizing experiences into groups does not mean that groups don't exist.

His more cogent argument concerns the question of whether these psychophysical groups of tastes, that is, "taste qualities," should restrict our quest for separate receptors associated with each group. Certainly, the finding of a family of bitter receptors, rather than just one (Mueller et al. 2005), argues that the taste experience may be far more nuanced than just the four or five basic taste qualities. Moreover, the recent discovery of fat receptors located on taste receptor cells (Gilbertson et al. 2001) may provide an impetus to broaden our definition of what a taste actually is. As Erickson correctly points out, we don't really have a formal definition of what constitutes a taste.

In his discussion of his psychophysical experiment, Erickson argues that these data falsify the idea of four basic tastes on several counts. First, his subjects could do just as well at "accounting" for the array of tastants using "non-basic" taste stimuli as they did using the "basics" (by which we presume he means prototypical exemplars of the basic taste qualities). However, his non-basics were not shown to be independent from his basics; on the contrary, his non-basics evoked taste sensations that were similar to one or more of the basic taste qualities. So the observation that subjects could do just as well using non-basics as basics is not surprising and does not falsify the basic grouping of tastes. Second, Erickson argues that since the accounting was not total there must be other tastes that can account for the missing quality. This point is related to his next argument that taste qualities were present that were not related to the basics tastes. However, examination of the other descriptors offered by the subjects only underscores the multimodal nature of taste stimuli; tastants can evoke thermal, tactile, and olfactory sensation in addition to taste.

Labeled-line versus across-fiber pattern theories. Erickson paints a dichotomy between the labeled-line theory and the across-fiber pattern theory and sets them up as a debate that is still raging unresolved in the literature. We would argue that both the dichotomy and the debate are straw men.

Consider first the differences between the labeled-line theory and the across-fiber pattern theory. These theories are by no means mutually exclusive and are therefore difficult to disentangle. Both are spatial theories in that they rely on the identities of the neural elements that produce activity. So, even if there were a labeled-line code, with different neuron types encoding different taste stimuli (basic or not), such an arrangement would obviously result in different across-fiber patterns of activity. Conversely, if the activity across all cells were the critical conduit of information, then if two patterns were different, there would necessarily be some cells that fired more for one stimulus than the other and these cells could be called labeled lines. For example, Smith et al. (1983) showed that cells that responded most to sucrose in the hamster brainstem were essential for the tight association of across-neuron patterns of sweet-tasting stimuli in a multidimensional taste space. Moreover, if all cells were broadly tuned so that they participated equally in multiple discriminations, the information that they could convey would be limited: the more broadly tuned the cells, the more homogeneous the contribution to the across-fiber pattern and the more ambiguous the message. After all, as Erickson himself points out, it is the *differences* between across-fiber patterns that convey information and these differences must arise from cells that show differential sensitivity across tastants.

Both the labeled-line and across-fiber pattern theories use as their basic data point some measure of response consisting of the number of spikes in an arbitrary time period during which the tastant is on the tongue. This measure assumes that the activity is integrated over this time interval. The Neural Mass Index, which Erickson argues is a better indicator of similarity among tastants than the Pearson correlation also contains the implicit assumption of integration over time. In all of these conceptualizations the temporal patterns of activity and potential cooperativity among neurons are ignored, even as these measures are emerging in the literature as informative coding mechanisms in the central nervous system (Di Lorenzo & Victor 2003; 2007; Katz et al. 2001; 2002; Roussin et al. 2008).

The labeled line / basic taste versus across-fiber pattern debate: A red herring?

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Abstract: Why has the labeled line versus across-fiber pattern debate of taste coding not been resolved? Erickson suggests that the basic tastes concept has no rational definition to test. Similarly, however, taste neuron types, which are fundamental to the across-fiber pattern concept, have not been formally defined, leaving this concept with no rational definition to test. Consequently, the two concepts are largely indistinguishable.

The original conception of across-fiber patterns (AFPs) described by Erickson was based on Young's theory of color vision, which included the idea that the eye is provided with three distinct sets of broadly tuned receptors (Young 1802; 1807). Although Erickson agreed that receptor or neuron types are similarly required for taste, he stated their existence has not been established, as they have not been formally defined. This failure to formally define taste cell types results in an AFP theory that is not testable, and therefore, AFPs suffer the same deficit Erickson ascribed to the concept of labeled lines / basic tastes (LLs). A serious consequence is that the LL and AFP models of taste coding are largely indistinguishable, creating confusion at both theoretical and empirical levels.

The relationship between the two models can be compared to alternating perceptions of a Necker cube, an analogy used famously by Dawkins (1976) to suggest that what appeared to be two different theories were actually only two different ways of looking at the same theory. For instance, LL and AFP information could be encoded within the same neural representation: the rich information contained in an AFP could be utilized by brain circuits that discriminate tastes, and in parallel, best-response neuron activity embedded within that AFP could be used to convey categorical information for circuits that make rapid yes/no decisions, such as an infant's acceptance of sweet tastes and rejection of bitter ones. In instances where virtually all of the AFP information is carried in the best-response neurons, the AFP and LL signaling are nearly identical – tuning this narrow may actually occur for sweet taste in primate primary taste fibers (Danilova et al. 2002). Similarly, Erickson suggested that neural approaches for yes/no circumstances could require only LLs in the form of an AFP reduced to a single neuron and that this possibility is consistent with the AFP model.

The lack of uniqueness of LLs and AFPs leaves open the possibility of interpreting any data as being for or against either model. This is illustrated here by reviewing the types of evidence that have typically been taken as support for the LL model, followed by a demonstration of how this evidence can be turned on its head to fit nicely into an AFP framework.

Groupings of taste stimuli into basic tastes using cluster analysis of neuron responses to multiple basic taste stimuli have been largely replicated across species and nervous system levels (e.g., Scott & Plata-Salaman 1999). Moreover, their validity has been strengthened by showing that conditioned taste aversions (CTAs) involving a basic taste generalize to taste stimuli in the same basic taste category, but not to those of other categories (e.g., Nowlis et al. 1980). Erickson rightly argues that although these cluster analyses may separate neurons, they do not define types. Nevertheless, he suggests that if the neurons within one group responded similarly to manipulations of the taste system, and neurons of other groups responded differently, such evidence would favor neuron types (Scott & Giza 2000).

Indeed, CTA, pharmacological, nutritional, and hormonal manipulations, especially of salt- and sweet-responsive neuron groups, including sodium deprivation, lingual amiloride or gymnemic acid application, deoxycorticosterone acetate (DOCA) priming followed by intracerebroventricular renin, and intravenous insulin or glucose, have provided such evidence (Chang & Scott 1984; Giza & Scott 1987a; 1987b; Hellekant et al. 1998; Jacobs et al. 1988; McCaughey & Scott 2000; Scott & Giza 1990; Verhagen et al. 2005). These findings are strengthened by functional-anatomical relationships of taste pathways that are consistent with LLs, including the innervation of single or small numbers of taste buds by primary taste neurons in some species, transynaptic neural tracing demonstrating differential projections of sweet and bitter receptors, differential localization of the activation of brainstem sensory neurons by bitter versus sweet or acidic stimuli, and unique regions of cortical activation associated with each basic taste (Accolla et al. 2007; Harrer & Travers 1996; Sugita & Shiba 2005; Travers 2002; Zaidi & Whitehead 2006).

Mouse transgenics have also been used to selectively manipulate individual taste receptor cell types, and the results have been taken by some to be a hands-down win for LLs (Chandrashekar et al. 2006). Knockouts of sweet or bitter taste receptors and ablation of cells expressing sour receptors each resulted in loss of sensitivity to the respective basic taste without affecting responses to other basic tastes (Damak et al. 2003; Huang et al. 2006; Zhao et al. 2003). Consistent results have been obtained using genetic "rewiring" of taste pathways: Expression of a bitter receptor in taste cells normally expressing only sweet receptors resulted in "rewired" mutant mice, which readily ingested a bitter stimulus that was aversive to normal mice (Mueller et al. 2005).

Additionally, one of the biggest stumbling blocks for LLs has been data suggesting taste receptor cells are broadly tuned (e.g., Gilbertson et al. 2001). However, it has recently been shown that each taste receptor type occurs in a different population of taste receptor cells (Chandrashekar et al. 2006), and about 80% of Type II taste receptor cells, each of which contains only one type of taste receptor, respond to only one basic taste (Tomchik et al. 2007), suggesting that taste receptor typologies – potential substrates for LLs – exist.

In total then, the empirical data seem quite strong in favor of LLs. Why then hasn't the knockout punch to the AFP model been delivered? It could be argued that manipulation of a specific taste neuron, receptor, or receptor cell type would not only affect a LL, but could also have a specific effect on AFP coding. For example, in the genetically "rewired" mice described earlier, sweet-best neurons would become bitter-best neurons, and cells in the population that normally responded in any degree to sweet receptor activation would now respond in a similar degree to bitter receptor activation. Consequently, a bitter taste would now evoke the AFP normally activated by sweet taste. Therefore, as a result of the failure to develop formally sound definitions for AFP and LL models, this genetic manipulation, or, in fact, any selective manipulation, cannot distinguish these models.

Taste learning in rodents: Compounds and individual taste cues recognition

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Abstract: Contrary to the outstanding simplistic view of the taste system, learning studies show a more complex picture. Behavioral data using conditioned taste preference and aversion tasks support the idea that mixtures involve complex interactions between individual taste cues. Evidence from taste conditioned blocking, taste perceptual learning, and taste learned preferences is considered to support such a view. Greater support for research in taste learning and memory is required for a complete understanding of taste recognition.

The article by Robert P. Erickson raises a most relevant issue concerning certain neglect about research on taste when compared with other sensory systems. As Erickson proposes, this neglect may have been due in part to previous misconceptions about the simplicity of taste detection and perception. Its primitive phylogenetic and ontogenetic origin may have contributed to the current state of affairs, since primitive is often misinterpreted as simple. Or, conversely, the complex nature of the processes involved in taste sensation, perception, and cognition may have hindered a more advanced knowledge in the taste field. Although the scenario appears to be simpler at the periphery, since distinct receptors and cells have been identified for some specific tastes – a finding common across species from *drosophila* to mammals – central taste processing involves complex reciprocal interactions among different brain levels. There are data supporting distinct subsets of neurons maximally responsive to the quality and also to the hedonics of specific tastes, originating at the brain-stem level (Yamamoto 2003). Moreover, at higher brain levels, taste perception engages combination, comparison, and interactions not only across taste qualities, but also from other sensory modalities, motivational state, and memory. A critical feature adding complexity to taste sensation is the dynamic nature of the gustatory system, as it is modified by learning, even at the lower brainstem level (Yamamoto & Yasoshima 2007). Moreover, in spite of a general misconception about the low cognitive level of taste memory, it shows complex learning phenomena dependent on the hippocampal system (Gallo et al. 1999), and it shares molecular mechanisms with other complex types of memories (Shema et al. 2007).

Considering this complex scenario, it does not seem probable that a unique theory, either labeled-line or population coding, will be solely enough for explaining taste sensation and perception. The article by Erickson offers a much-needed opportunity for debate on the topic. Among the various issues the target article raises, that of the singularity of mixtures merits attention. It is stated that mixtures are mostly perceived as being singular. This assertion seems to be mainly based on psychophysical studies in humans. However, there is a bulk of evidence from behavioral studies in animals that may offer additional insights. The evidence shows that, depending on the behavioral procedure and the requirements imposed by the learning task, compounds may be treated either as a single configural cue, or as a combination of individual taste cues. In any of the cases, the mixture cannot be reduced to the sum of the elements. However, several phenomena that have been demonstrated in rodents by using conditioned taste preference and aversion tasks, support the idea that the segregation of individual taste cues in mixtures may take place as long as the task would require such discrimination.

First, in conditioned blocking, previous training with an individual member of a compound modulates learning about another member of the compound. Thus, a previously learned aversion or preference to an individual taste A retards the acquisition of a new learned response to a different taste B if the later is presented in a compound AB (Balleine et al. 2005; Gallo et al. 1999). The blocking phenomenon would not appear if the compound had been sensed as singular and the individual basic components had not been recognized by the animals.

A second example of phenomena showing the possibility of taste segregation in mixtures is perceptual learning. On the one hand, perceptual learning takes place when complex stimuli are required to be discriminated. The effect consists in facilitating the learning discrimination by previous non-reinforced exposures. On the other hand, previous non-reinforced exposure may retard learning if simple stimuli are used – an opposite well-known effect termed latent inhibition. Both perceptual learning and latent inhibition have been demonstrated with taste cues and taste compounds. The fact that previous exposures to the mixtures do not induce latent inhibition, but rather increased learning discrimination, does not support the idea that they are perceived as singular cues. Although different explanations have been proposed for explaining taste perceptual learning, the evidence does not support the idea that configural cues are generated by the presentation of mixtures, nor the latent inhibition of the common element as the sole explanation. Rather, a reduction in generalization between the taste mixtures by previous exposure, that it comes from interactions between the unique elements, has been proposed (Mackintosh et al. 1991).

Finally, the basic conditioned taste preference tasks are clear evidence showing that taste mixtures are not always sensed as individual cues. Learned taste preferences for an individual taste cue, such as quinine or saline, are developed by mixing each with sucrose. The effect cannot be explained by a sensory preconditioning effect in which the taste becomes associated with the positive hedonic features of sucrose, but by associations with the reinforcing caloric properties. Whatever the explanation, if the mixture would have been sensed as individual and distinct of the components, no learned preference to the individual components should be evident.

Overall, the animal behavioral data support the fact that individual taste cues can be perceived as distinct within taste mixtures. Further insight into this issue could be gained by research on preverbal human newborns and children. The fact that they can discriminate the basic tastes is supported by their distinctive facial response patterns. Recording behavioral reactions to taste mixtures could provide useful information.

A complete understanding of taste processing requires a multidisciplinary approach that integrates results from molecular biology, genetics, electrophysiology, neuroimaging, behavior, and psychophysics, both from evolutionary and developmental perspectives. Efforts aimed to increase research funding and give more attention to taste training at school are desirable because chemosensory processes are profoundly influencing our everyday life.

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The nature of economical coding is determined by the unique properties of objects in the environment

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Abstract: The physical properties that signify objects differ dramatically, so that the organization of sensory systems must reflect those differences. Although all senses may encode peripheral sensory information using across-fiber firing distributions, an economical coding system for each sense will necessarily differ. An economical code must maximize information about objects, whether they are predators or foods.

While all senses have been optimized through evolution to provide unique information for survival, they must simultaneously be general-purpose systems that can respond to an ever-changing environment (Handel 2006). For this reason, it seems inevitable that peripheral receptors must respond with differential excitations to varying stimuli (although there may be a small set of receptors that are narrowly tuned, Wilson 2007; Xu et al. 2005). That, in turn, results in an across-fiber firing distribution representing the entire sensory continuum. Although across-fiber patterning appears to provide a functional mechanism for all senses, I argue that the properties of the sensory environment determine the number and distribution of the peripheral receptors and the subsequent computations that integrate the excitations of those diverse receptors. The issue of economy of coding can be understood only in terms of the goal of detecting objects in the environment.

1. Number of receptors. Why are there only three cones? The spectra of natural light and the reflectance of most materials are continuous and smooth (Judd et al. 1964; Wandell 1995). Typical excitations can be reproduced using different amounts of three independent functions: one function to represent the overall illumination level, one function to represent the blue-yellow contrast, and one function to represent the red-green contrast (Ruderman et al. 1998). That both the illumination and reflectance functions can be represented by a small number of independent functions suggests that only a small number of receptors would be necessary to recover the illumination-independent color. However, the excitations of the three cones overlap to such a degree that there is a high correlation among the firing rates. The subsequent opponent color processing acts to decorrelate the responses of the receptors and yield independent contrast functions.

Why are there so many sound receptors? Sounds range from nonharmonic noise (wind) resulting from continuous frequency excitation to harmonic timbres produced by vibrating objects. For vibrating objects, the source excitation (e.g., vocal fold vibration) occurs at discrete non-overlapping (typically harmonic) frequencies, but the sound body resonances (the filter) occur at multiple overlapping frequencies based on the shape and material. Normally, the resonances create multiple excitation peaks at widely spread frequencies separated by regions of low amplitude. Neither the source spectra nor the filter spectra can be modeled by a small number of independent linear functions. To distinguish among different timbres (i.e., different sound objects) therefore requires many receptors (roughly 3,000 receptors/ear), necessarily tuned to narrow overlapping frequency bands to pick up the resonance peaks. (If important sounds were nonharmonic, then fewer receptors would be necessary).

What this means is that the organization of the visual and auditory periphery seems tuned to the properties of the environment. Economy of coding is not about the number of receptors; it is about the picking up of the redundancies that signify objects (Barlow 2001). Is this tuning also true for taste? Is there a reason for the small number of taste receptors? Furthermore, since there is no continuous physical attribute underlying the various tastes that would support excitation and inhibition among adjoining receptors (as found for seeing and hearing), would a cross-fiber patterning explanation require that all the peripheral taste receptors interact with each other? The across-fiber excitatory and inhibitory interactions found for vision and audition generate cells at higher levels with unique properties such as motion detection. Is this also true for taste, or is there just a simple population code? Without a physical continuum would it be possible to construct taste metamers analogous to color metamers, given the small number of different taste receptors?

2. Distribution of receptors. Young (1802) argued that it would be physically impossible to have enough unique color detectors at each retinal point to account for color perception. Although the cones in the fovea underlie color perception, they are also responsible for the fine-grain shape and motion perception that creates figure-ground organization. I would argue that it is this latter function that is critical to survival and that color constancy enhances our ability to segment objects in spite of changes in shape resulting from motion, occlusion, or other variation. From this perspective, the color detectors occur throughout the fovea because they augment figure-ground organization. If only the background was colored but not the objects, then labeled-line color receptors could be localized at discrete points on the retina.

Here again, economy is about maximizing information. The perceptual goal is to construct a stable visual world in spite of the constant flux. If objects and backgrounds were not usually colored differently and if more independent functions were necessary for color perception, then a different receptor organization would have emerged. I feel that an economy argument for an across-fiber explanation of taste must go beyond the number of receptors. If taste perception is not about identifying foods, then I wonder if analogies to other senses are appropriate.

3. Perceptual constancy. Although we believe that color is an inherent property of objects, in reality perceived color is based on our inferences about the illumination and surrounding colors. It is a second-order calculation based on the relative ratios of absorptions in different parts of the field. Color matching under different illuminations requires imagining what the standard would look like under the second illumination, not matching cone absorptions. In this target article, Erickson presents results illustrating that the description of tastants is similarly context dependent. Are such judgments possible with a population code or must they also be based on higher-level excitation ratios?

In sum, senses convey specific survival information, as well as respond to an evolving environment. But, as I have argued earlier, it is the particulars of the environment that determines the organization and distribution of the receptors and the subsequent transformations at later neural regions. The neutral excitation at the eye (a photograph) or ear is transformed into a set of parallel intensity contrasts at multiple resolutions that segment sensory experience into objects and properties regardless of scale (De Valois & De Valois 1988; Lewicki 2002). I would expect similar sorts of transformations for taste, and deriving those transformations is necessary to create an adequate theory of taste perception.

Basic tastes and unique hues

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Abstract: The logic of the basic taste concept is discussed in relation to the physiology and psychophysics of color vision. An alternative version of the basic taste model, analogous to opponent-process theory is introduced. The logic of quality naming experiments is clarified.

Erickson mounts a vigorous attack on the concept of a basic taste in all its forms. My concern is not with the physiology of the taste receptors, but with a psychophysical conception of basic tastes. Color vision provides an interesting point of comparison that may help illuminate some of the issues, a comparison Erickson himself makes in several places. As is discussed at some length in the target article, the receptors that underlie color vision have broad and overlapping spectral tuning. Information about the spectral composition of the stimulus is not signaled by activity in any one of the three receptor types, but rather, is embodied in the pattern of activity across all three receptor types. Nothing follows from these facts about the receptors, however, as to the central encoding of spectral information and the structure of color experience. The same set of receptors could drive a system that encoded spectral information more centrally in terms of relative amounts of three basic hues or by a representation that treats each spectral mixture as unique and singular. In fact, the receptor outputs are recombined starting in the retina to form three new channels that encode spectral information in terms of sums and differences of the receptor outputs. Similarly, the structure of taste experience is not fixed by the number of receptor types or by their tuning. Even if the taste receptors themselves are narrowly tuned, it would not follow that the central representation is in terms of neurons with similar narrow sensitivity, nor that taste experience consists in combinations of a small number of specific tastes. Although these points are not incompatible with the target article, its attack on the basic taste concept in all its forms is carried through so ruthlessly that the impression is left that there are strong connections between the different basic taste concepts.

There is another more substantive way in which the comparison with color may be helpful. Although it is true that each color experience is singular in the way mentioned in the target article, it is not true that color experience is unstructured. The prevailing theoretical perspective in color science, opponent process theory, conceives of color experiences as encoding color in terms of two opponent hue channels, yellow-blue and red-green, and a non-opponent achromatic channel (Kaiser & Boynton 1996, pp. 250–59). Thus, the experience of orange combines yellowness from one chromatic channel and redness from the other, plus some amount of whiteness from the achromatic channel. It is not that orange is experienced as being some kind of mixture of a pure red and a pure yellow, but rather that there is a hue attribute, yellowness, that is shared by a large number of hues, including orange, and a different hue attribute, redness, which is also possessed by many hues including orange. In one sense, there are basic colors, in that color is represented using a very small number of basic attributes. In another sense, there are no basic colors because nothing is seen as having more than one determinate color. There is some ambiguity in the taste literature, including the target article, as to which sense of basicness is at stake.

Finally, I will comment on the experimental illustration found in section 7 of the target article. The first condition involved using basic taste names to account for the taste of a stimulus. The remaining conditions involved accounting for the taste of the stimulus in terms of sets of tastants, both basic and non-basic, depending on the condition. There is no reason to think the two types of tasks are comparable, so the tastant conditions cannot serve as controls for the naming condition. Erickson interprets the failure to reach 100% in the naming condition as significant, but this feature of the data is uninterpretable given the lack of controls. Similar experiments done using names for the four opponent hues have provided useful support for the opponent process theory, but only by looking at how subject performance changes as the set of available hue names is varied (Sternheim & Boynton 1966). It is also worth noting that nothing regarding the basic taste concept follows from the fact that English contains taste words other than the names of the putative basic tastes, contrary to the suggestion in section 7.7.3. Even if it is true that every taste is experienced as some mixture of the four basic tastes, it wouldn't follow that there would be no use for words specific to those mixtures. It is not even a direct consequence of the basic taste model that the names of the basic tastes are more commonly used than the names of mixtures. The only relevant claim is that it should be possible to describe any taste completely using only the basic taste words, not that there is no other way to describe tastes.

Neither the comparison with color nor the difficulties with the experimental illustration provide positive evidence in favor of any basic taste concept. If it is to be rejected, however, it needs, as Erickson argues, to be clarified, and the rejection should be on the basis of data that are properly controlled and genuinely in conflict with predictions of the model.

Taste quality coding in vertebrate receptor molecules and cells

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Abstract: Recent work on receptor molecules and cells used prototypical sweet, salty, sour, bitter, and umami stimuli. Labeled-line coding was supported, but it remains possible that the molecules and cells could respond to other tastants. Studies with other tastants are needed. The sensory message might contain two codes – one for attraction or aversion, the other, across-fiber patterning of stimulus quality.

1. Introduction. Whether taste quality is coded by specific biological units (labeled lines) or across multiple units (across-fiber patterning) has long been debated by researchers. Erickson argues cogently that the concept of "basic tastes" is a poorly defined hypothesis, and consequently, researchers do not know how to test it or the related hypothesis of labeled lines for those tastes. He refers briefly to recent research on taste receptor molecules. We will discuss the molecular receptor work further and also new work on taste bud cells. These two lines of research are elegant and exciting! They have yielded important new information about taste transduction and the processing of information in the vertebrate taste bud. They have the potential also to test coding mechanisms at the receptor level, but as yet, they do not clearly do so.

2. Receptor molecules. Molecular studies have identified two families of G-protein-coupled receptors, which are expressed in distinct cell types. Two receptors of one family are thought to mediate two basic tastes: sweet and umami. A second family of several receptors is thought to mediate the bitter tastes. The functional roles of these molecules have been examined by expression profiles, imaging of calcium responses to tastants by cultured cells containing the molecules, and studies of behavioral and neurophysiological responses to tastants in animals who did not have the intact molecules, such as naturally occurring mutants and genetically created "knock-out" mice. Labeled lines were inferred (reviewed in Chandrashekar et al. 2006). It is disappointing that the stimuli used to show the presence or lack of responses were only compounds known to elicit, or potentiate the presumed basic tastes – sweet, salty, sour, bitter, and umami (e.g., see Li et al. 2002; Zhang et al. 2003). Thus, these studies assumed the hypothesis of basic tastes and collected data to support it and the labeled-line hypothesis, but did not test the hypotheses. It remains possible that the molecules could respond to other tastants.

The putative sweet receptor is a heterodimer (T1R2/T1R3), which contains multiple sites for binding sweet compounds consisting of a variety of structures. These include pockets in the N-termini of both subunits for sugars, D-amino acids, and various "artificial" sweeteners, a cysteine-rich area in the T1R3 subunit for the protein brazzein, and the transmembrane region of T1R3 for Na-cyclamate, the sweet inhibitor lactisole, and perhaps also Na-saccharin and acesulfame-K (Galindo-Cuspinera et al. 2006; Jiang et al. 2004; 2005; Morini et al. 2005; Xu et al. 2004). Although not discussed in the literature, this complex molecule could bind various other stimuli, as well. The putative umami and bitter receptors also could bind other stimuli. One could propose the alternative hypothesis, that is, the receptor molecules are broadly tuned so as to participate in across-fiber patterning and thus would bind a variety of taste stimuli, perhaps responding "best" to one or another tastant. Then, a variety of tastants, including those known to elicit the basic tastes, other "singular" tasting compounds (as in Erickson), and those known to elicit complex tastes, could be tested. The results could allow the researchers to disprove one coding hypothesis and support the other.

3. Receptor cells. As noted by Erickson, a large body of data shows that taste neurons respond to more than one type of taste stimulus. In particular, rodent and frog data from many laboratories show that taste bud cells respond to more than one type of taste stimulus (reviewed in Herness 2000). Yet, a given receptor cell expresses only one type of receptor molecule (Chandrashekar et al. 2006). If the molecules are narrowly tuned for a basic taste quality, then the cells should be narrowly tuned, as well. Recent work combined calcium imaging in mouse lingual slices and molecular techniques to address this paradox. Two types of taste bud cells – "receptor cells" and "presynaptic cells" – were found. Most receptor cells responded to only one of stimuli for sweet, umami, or bitter tastes, whereas the presynaptic cells responded to stimuli for all the basic tastes, including sour and salty. It was proposed that presynaptic cells receive inputs from receptor cells via ATP and that both the receptor and presynaptic cells transmit information to afferent fibers (DeFazio et al. 2006; Tomchick et al. 2007). Again, only stimuli known to elicit the basic tastes were used. Moreover, as specific responses occurred in only 82% of the receptor cells, it seems possible that if more broadly tested, receptor cells might show broader response profiles. One would like to see the receptor cells tested with a variety of tastants, as suggested for the receptor molecules.

4. Coding mechanisms. Sugita (2006) suggests that sweet and umami modalities mediate attraction, while bitter mediates aversion, and salty and sour mediate attraction or aversion, depending on the concentrations. Indeed, expression of a receptor that binds spiradoline, a tasteless compound, in mouse bitter- or sweet-receptor expressing cells led to behavioral rejection of spiradoline in the former case, and attraction in the latter case (Zhao et al. 2003). In the mid-20th century, fly taste receptor cells initially were thought to code for two modalities – "acceptance" and "rejection." Fly researchers limited their choice of stimuli to the four basic tastes, and the "sugar," "salt," "water," and "fifth" receptor cells became viewed as labeled lines. Data indicate that the sugar and water cells mediate behavioral attraction, the fifth cell mediates rejection, and the salt cell mediates attraction or rejection depending on the concentration (reviewed in Dethier 1976). Dethier (1974) questioned whether the "rigid specificity" of these labeled lines "existed more in the minds of investigators than in the receptors themselves." He showed that the cells responded to a variety of unusual compounds and natural foods with spectra of activity that were unique, with little or no overlap. Dethier proposed that the taste sensory message in flies is two-fold: first, there is coding for acceptance or rejection, and second, across-fiber patterning might provide the "potential for discrimination among many substances." Perhaps labeled lines and across-fiber patterning provide similar separate messages in vertebrates.

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Mathematical techniques and the number of groups

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Abstract: Cluster analysis, factor analysis, and multidimensional scaling are not good guides to the number of groups in a data set. In fact, the number of groups may not be a well-defined concept.

As a statistician I will comment only on the statistical aspects of Erickson's article, notably section 4.2.2, "Mathematical techniques." I agree with Erickson's general sentiment that cluster analysis, factor analysis, and multidimensional scaling are unreliable indicators of the number of groups of neurons or of any other objects to which we apply the techniques. It is well known, for example, that the apparent number of groups found by cluster analysis can depend strongly on details of the clustering algorithm that are unrelated to the science in question. For example, one must make decisions about whether to analyze the original data, standardized data (rescaled so the mean is 0 and the variance is 1), or correlations. One must also decide how to measure the distance between clusters. Should it be Euclidean distance, or something else? Should it use average linkage, complete linkage, or single linkage? These choices all give different views of the data. The choice matters, but none is guaranteed to be the best or to be the only reasonable way of looking at the data. To illustrate, I refer to two figures from *The Elements of Statistical Learning* (2001) by Hastie, Tibshirani, and Friedman. Figure 1 (Figure 14.5 of Hastie et al. 2001) shows the results of clustering either with or without standardizing first. The results are quite different, and in this case the unstandardized result is correct. Figure 2 (Figure 14.13 of Hastie et al. 2001) shows three cluster analyses of one data set. The analyses differ in whether they use average, complete, or single linkage to measure distance between clusters. Again, the results are quite different. The point is not to say which is best; it is to say that results depend on seemingly innocuous choices and that none gives a complete picture of the data.

Factor analysis and multidimensional scaling are subject to some of the same vagaries. For example, answers depend on whether we analyze raw data, rescaled data, or correlations, whether we assume normality in factor analysis and what loss function we use in multidimensional scaling. Each gives a different view of the data; none is necessarily the best. One analysis may appear to show four well-distinguished groups but another may appear to show eight, three, or none at all. Faith in the results of any particular analysis may often prove unfounded. The number of groups in multidimensional data can depend on who is looking, with what techniques, and for what purpose.

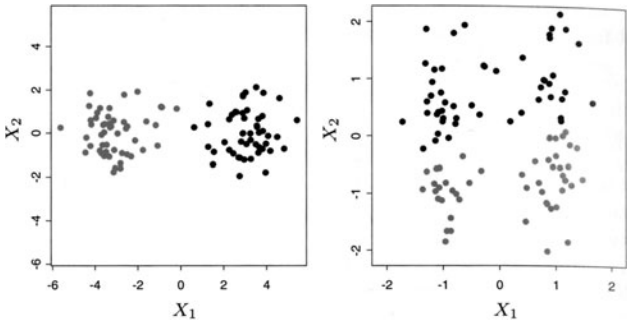

Figure 1 (Lavine). Simulated data: On the left, K-means clustering (with $K = 2$) has been applied to the raw data. The two [shades] indicate the cluster memberships. On the right, the features were first standardized before clustering. This is equivalent to using feature weights $1/[2 \cdot var\ (X_j)]$. The standardization has obscured the two well-separated groups. Note that each plot uses the same units in the horizontal and vertical axes. (From Hastie et al. 2001. With kind permission of Springer Science and Business Media.)

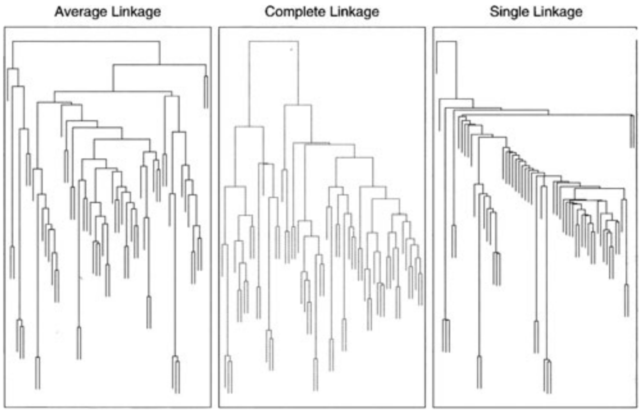

Figure 2 (Lavine). Dendrograms from agglomerative hierarchical clustering of human tumor microarray data. (From Hastie et al. 2001. With kind permission of Springer Science and Business Media.)

On the analysis of spatial neural codes in taste

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Abstract: The two most popular, yet opposing, models of taste processing, the labeled-line (LL) and across-neuron pattern (ANP) theories, are variants of spatial neural coding. Analyses whose outcomes have been argued to support either theory have sometimes glossed over important caveats and considerations that may drastically impact interpretation. Some of these issues are discussed here.

Both the LL and ANP theories rely on certain common assumptions, including the concept of pooling the activities of neurons. Under LL theory, neurons are pooled into groups or "types", in which there are as many different types of cells as there are taste qualities. Here, each type is composed of neurons that share a common optimal stimulus and it is the quality of only this stimulus that a type encodes. On the other hand, ANP theory posits that taste qualities are encoded by the pooled response of many like-tuned and heterogeneously-tuned neurons, which gives rise to a pattern of activation across the population. Curiously, ANP theory also relies on the concept of neuron types. For ANP theory to work, the pool of neurons that generates the patterns must be composed of cells with different tuning characteristics: There must be a mix of different types of cells to get unique patterns for different stimuli. Indeed, there are variants of ANP theory in taste that define explicit roles for groups of differently tuned neurons in generating distinct ANPs (Smith et al. 2000).

But the way that neural groups and pools are typically defined and/or interpreted in the taste literature is subject to caveats that are sometimes overlooked or not explicitly acknowledged. One issue stems from the fact that neural data sets in taste are usually composed of many neurons sampled from many animals. The taste response characteristics of central gustatory neurons are influenced by a number of factors and neural responding could vary widely among animals as a function of variables that are not usually controlled, such as satiety state (Giza et al. 1992). Such variation could induce vast differences in the sensitivities of neurons that are not exactly a result of strict differences in the efficacy of sensory input. With just this in mind, it becomes questionable as to whether or not sets of neurons generated from many-animal data sets indeed reflect accurately those that would be observed across many neurons in an individual animal. Newer recording and optical technologies may prove fruitful in monitoring the activities of many neurons simultaneously.

Spatial codes that require cells to be segregated into defined types must assume that all neurons composing a type serve the same function and that the response properties of cells within a group are orthogonal. These assumptions refer to the independence of responses that is implied to exist among cells that are of a common type. These assumptions, however, cannot be easily validated using traditional taste data sets. There is presently only very limited means of relating the tuning properties of taste neurons to their function, such as, for example, whether they contribute to taste perceptual identifications or oromotor responding. What is more, there is not a method to determine independence among the activities of taste neurons based on their stimulus-response characteristics. For example, two cells with common tuning that would be grouped together and assumed independent under a classic typing scheme could actually be synaptically related, where one cells serves as a driver for the other. Here, there is not independence in the firings of these cells but statistical dependence, whereby a spike in the presynaptic cell increases the probability of firing in the follower neuron. To resolve response relationships among cells would depend on knowing the architecture of the neural circuit into which the cells are embedded, the exact locale of each neuron in the circuit, and the patterns of connectivity among cells. Data on these topics for taste nuclei are scant at best.

Models of coding must also account for the variability in responding that is inherent to taste neurons. A recent study revealed that in many gustatory neurons the response to a given stimulus can vary widely from trial to trial (Di Lorenzo & Victor 2003). For some cells, within-neuron response variability impacted the definition of their best stimulus, where variability in responding rendered a changeable best stimulus over trial blocks. This observation poses a clear challenge to a LL mode of operation. It also could be a potential issue for discriminating certain stimuli under an ANP code, particularly stimuli that are perceptually distinct but generate ANPs that differ only mildly. Tastants classified as bitter or sour are examples of such stimuli. Studies of central taste neurons in rodents have shown that ANPs evoked by these stimuli, as based on single-trial data, are strongly correlated (Lemon & Smith 2005). Factoring in a certain element of across-trial response variability among neurons renders a variance about the neural mass calculated from a stimulus pattern: ANPs to certain bitter and sour tastants could actually at times be more similar than the strong correlation already revealed by the single-trial data. This becomes paradoxical when viewed against behavioral data showing that rats can readily discriminate between the tastes of sour and bitter tastants (Grobe & Spector 2006). Part of this conundrum lies in that it is not exactly clear how much of a difference between ANPs would be sufficient to compute perceptual taste discriminations.

Considerations for further development of spatial codes in taste might include quantifying neuronal responses along behaviorally relevant stimulus-response windows. For example, perceptual identifications of taste stimuli can happen in less than 1 second as indexed in rat behavioral experiments (Halpern & Tapper 1971), although many neurophysiological studies have quantified taste responses over 5- or 10-second periods. What is more, in some taste neurons there is a particular envelope to a stimulus response, wherein the magnitude of firing dynamically changes over the response time course in a stimulus-specific way (Katz et al. 2001). Such neuronal dynamics would suggest that the overall spatial neural signal, whatever its format, possesses a time-dependent plasticity that could be captured only by considering time as a factor in the code. These time dependencies in spatial activity might reflect parsing by the nervous system of different features about taste stimuli as related to ongoing streams of perceptual and behavioral processing (Katz et al. 2001). These are only a few issues associated with models of spatial coding in taste.

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The complex facts of taste

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Abstract: There is both empirical evidence that supports, and does not support, the four basic tastes, as well as the labeled-line and across-fiber pattern theories. All of these concepts have proven useful to researchers investigating taste coding, and should be appreciated for their heuristic value. Dismissal of any of them is neither supported by evidence nor productive.

Facts – empirical findings – are useless without appropriate accompanying theory. Employing the metaphor in the target article's Poincaré quotation, without theory the house is just a shapeless pile of stones. However, when theory is unsupported by empirical findings, there are no stones with which to form the house. Both good theory and accurate facts are necessary to understand behavior. Taste perception's empirical findings are complex, and therefore the theories explaining those findings must also be complex.

The target article critiques the traditional position that there are four basic tastes largely based on the argument that empirical support for this position is lacking. For example, the article shows that the four basic tastes concept predated empirical research, and speculates that one (nonempirical) reason for there being four is the limits of human cognition – that we can only easily remember less than ten members of any category. However, it is not clear how that argument explains the existence of precisely *four* basic tastes. Amoore and his colleagues, close to half a century ago, postulated the commonly accepted seven basic odors.

Another argument made against the four basic tastes is that it is not possible to take substances representative of the four basic tastes, combine those substances, and be able to identify the original substances in the mixture. However, when two basic colors of paint, yellow and blue, are combined the result is green paint, whose origins would be undecipherable to anyone not trained in color mixture. Yet this does not mean that yellow and blue are not basic colors.

A more fruitful approach to the four basic tastes, one that is followed by many scientists, is to think of them as taste concepts that describe or account for other tastes (Logue 2004). Such an approach was used in the target article's experiment when the subjects stated what percentages of various comparison tastes were accounted for by different standard tastes. On average, the four basic tastes accounted for 84% of the comparison tastes, a greater percentage than for any other set of basic tastes or taste words. No statistical tests were reported, so it is difficult to confirm or disconfirm the target article's statement that "other stimuli do about as well as the basic . . . stimuli." Regardless, it appears that it was possible for the participants to account for the huge majority of several comparison tastes using the four basic tastes.

Examining participants' ability to use the four basic tastes to describe or account for other tastes involves using the four basic tastes theory as a heuristic. Any heuristic's value depends on the degree to which it helps us to understand data. Does the four basic tastes theory help us to generate new, productive experiments? Can it help guide neuroscientists in looking for specific brain structures? In fact, the four basic tastes theory does seem to have assisted neuroscience research. Scientists have found evidence of receptors and brain structures dedicated to at least two of the basic tastes (sweet and bitter; see, e.g., Sugita & Shiba 2005). Without the four basic tastes theory, scientists might have taken longer to find these neuronal pathways.

Just because the four basic tastes were postulated before there was empirical research to support them does not necessarily mean that they are inconsistent with subsequent empirical research. However, the target article also argues that the current empirical evidence does not support the four basic tastes theory. The difficulty with this argument is not that it is inaccurate – current empirical evidence is indeed not consistent with there being just four basic tastes. The difficulty with this argument is that it is not new. Bartoshuk's excellent (1988) chapter clearly demonstrates that through the centuries many basic tastes have been postulated and investigated in addition to sweet, sour, salty, and bitter. As just a few examples, for years scientists have believed that there is a fifth basic taste, umami (Smith & Margolskee 2001); for decades scientists have been investigating the taste of water (Bartoshuk 1988); and recently, the taste of polysaccharides has been added to the list (Sclafani 2004).

That there are basic tastes – four or some other number – is an essential component of the labeled-line theory of taste coding described in the literature and in the target article. Consistent with its critique of the basic tastes, the target article repeatedly raises concerns with the labeled-line theory, stating that evidence does not support it. However, there is significant evidence, some of which is cited in the target article, supporting the labeled-line theory. For example, the target article cites Zhang et al. (2003) as showing "data . . . suggestive of the receptor specificity claimed for sweet and bitter." We also know that individual neurons in the chorda tympani nerve and in the brain tend to respond more to one of the basic tastes than to the others (Pfaffmann et al. 1979; Scott et al. 1998; Scott & Plata-Salaman 1991).

Nevertheless, it is also the case that there are data that do not support the labeled-line theory. Most taste cells in mammals will respond to a wide variety of chemical substances (Scott & Plata-Salaman 1991). Such data tend to support what Pfaffman called the across-fiber pattern theory in 1941, in which tastes are coded by patterns of neuronal activation, rather than by labeled lines (Bartoshuk 1988).

Taste coding is not simple. Many, probably most, taste researchers believe that there are more than the four basic tastes of sweet, sour, salt, and bitter. In addition, it is not the case that there is no evidence for the labeled-line theory. It is also not the case that there is no evidence for the across-fiber pattern theory. The facts are that how our bodies code tastes provides evidence to support both theories, to a degree. Most scientists are sophisticated enough to perceive, appreciate, and work with this complexity, and they should be credited with evidencing this sophistication. In the meantime, consideration of the four (or more) basic tastes theory, the labeled-line theory, and the across-fiber pattern theory, is likely to continue to prove useful in generating empirical findings that will help advance our understanding of taste coding.

Language does provide support for basic tastes

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Abstract: Recurrent lexicalization patterns across widely different cultural contexts can provide a window onto common conceptualizations. The cross-linguistic data support the idea that sweet, salt, sour, and bitter are basic tastes. In addition, umami and fatty are likely basic tastes, as well.

Is the mapping of language onto the world arbitrary? Erickson takes the position in his article that language tells us nothing about the underlying nature of things. Words are uninformative, or worse, misleading for theories of taste. We disagree. Language can be a valuable tool for uncovering human conceptualization – when approached in the right way. We suggest here how we can use the language of taste to inform our scientific theories. But, first, some clarifications are in order.

Erickson's position is a realist one. He states that things – tastes – exist independently of our naming them. He contrasts this with the alternative nominalist position, that it is the words *sweet, sour, salty, bitter* that create the taste categories "sweet," "sour," "salty," and "bitter." He thinks nominalism cannot be true because experience is continuous, but words in language force arbitrary boundaries in service of communication needs, which can vary as a function of culture, experience, and availability of foodstuffs. More importantly, his realist position leads him to assert that there is no evidence for basic tastes because the linguistic categories that exist are just a matter of language usage not psychophysiology.

If we take single examples for individual languages, arbitrariness abounds. Keeping to gastronomy, in Japanese there is a word *pakupaku* which means 'to eat in big mouthfuls or take quick bites,' while in Hawaiian *muka* means 'a smacking sound with the lips, indicating that the food is tasty,' and in G|ui, a central Khoisan language spoken in Botswana the verb *k|'ōrē* means 'to have a good taste common to eggs, a certain caterpillar, or other specific food.' Why should Japanese, Hawaiian, and G|ui have precisely these words, and English none of these? Surely this demonstrates that language merely reflects cultural preoccupations and nothing more.

We agree that individual words by themselves cannot tell us anything deep about underlying cognition. But when different languages make the same distinctions again and again – despite variation in culture and ecology – there is something more to explain. Language discriminations have to be supported by the psychophysics, and recurrent patterns suggest uneven psychophysical continua, or salient prototypes (cf. the color domain, where language data have always been taken seriously; see Berlin & Kay 1969; Regier et al. 2005; 2007). Conversely, psychological foci for basic tastes are made plausible by their common lexicalization across languages. In the case of taste, language discriminations do not just reflect one great cultural tradition – they reflect 8,000 traditions, many quite unconnected to one another, and with different staples, cuisines, and so forth. If languages demonstrate recurrent taste categories, despite these differences, it suggests there are psychologically salient taste concepts being mapped onto language. So, what are the linguistic facts?

Sweet, sour, salty, and bitter are commonly labeled by distinct words in the many independent languages, as Erickson notes in his article, too. Moreover, some languages make lexical conflations across taste qualities, providing further tantalizing clues as to how taste qualities are conceptualized. Over 100 years ago, Myers (1904) devised a cross-linguistic questionnaire, which he sent to missionaries and European residents abroad, to investigate the taste words of people from different cultures. The results of that study show that sweet and salt are commonly conflated together, as are sour and bitter. Two other common conflations include salt, sour, and bitter together and sweet, salt, and sour together. These facts combined suggest that sweet and bitter are psychologically the most dissimilar and distinct tastes. Also, that sweet and salt are more similar to one another than to the other tastes, and that sour and bitter are likewise more similar to one another than to the others.

According to Erickson, these conflations are just arbitrary facts about particular languages. If that is so, it is hard to explain how these cross-linguistic tendencies also mirror naming behavior within single languages. English speakers naming different chemical solutions, for example, often make identification errors. Most commonly they confuse bitter and sour, but they also confuse sour and salt, and even occasionally salt and bitter. They do not, however, mistake bitter and sweet (e.g., O'Mahony et al. 1979). This parallelism between the English data and the cross-linguistic naming supports the idea that there are common psychological concepts underlying the linguistic systems of different languages.

Examining lexicalization patterns across a range of languages opens up the possibility of finding additional conceptualizations that just happen to be missing from a single language. The natural variation in languages means that there can be accidental lexical gaps. But large-scale cross-linguistic investigations can help us discover additional systematicities. Proof of how fruitful language data can be in informing scientific theory is the "discovery" of umami as a basic taste (Ikdea 1909/2002; Lindemann et al. 2002). Examination of the literature shows potential additional basics. These include astringent, mint, pungent, rancid, spicy, and fatty. Although many of these terms do not appear to encode pure taste sensations (as elicited by epithelial taste receptor cells, rather than olfactory or trigeminal stimulation), there is evidence that the set of basic tastes is larger than once thought. Work from our own lab suggests that fatty is a term that appears in the vocabularies of quite distinct cultural traditions, including Tzeltal speakers in Mexico and Yélî Dnye speakers of Rossel Island, Papua New Guinea, as well as in many of the Algonkian languages of North America (Chamberlain 1903). And just as we find conflations of sweet, salt, and such, there are other languages that show conflation of sweet and fatty, including the Toaripi in Papua New Guinea and Bau dialect speakers from Fiji (Myers 1904). Recent physiological evidence gives further substance to this idea. At least part of the gustatory experience of fat appears to be through activation of taste receptor cells (Gilbertson 1998). In support of this, "super-tasters" who are sensitive to the bitter taste of 6-*n*-propylthiouracil (PROP) are also sensitive to the difference in fat content between a 10% fat salad dressing and 40% fat salad dressing, whereas "non-tasters" of PROP are not (Tepper & Nurse 1997). A likely mechanism for this is the number of taste buds that tasters have and hence the number of fatty acid sensitive taste cells (Gilbertson 1998).

In sum, language patterning is part of the data that a good theory of taste perception is answerable for, and attention to it may yield insights into psychophysical processes.

And what about basic odors?

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Abstract: Erickson's article links the concept of four "basic" tastes to color perception as a sensory modality with similar problems of categorization. Such problems are also present for odors and olfaction. Olfaction is the sensory modality with the closest physical relationship to taste, and the sense organs of both permanently interact. We discuss the origins and influences of core ideas of the science of smell to add to the discussion of unresolved categorization problems in taste from another, closely related point of view.

When a food or beverage is placed into the mouth, flavor is experienced as a multitude of sensations, including taste, smell, touch, temperature, sight, sound, and sometimes pain/irritation (Delwiche 2004). Taste and smell particularly have many demonstrated psychophysical interactions (Small & Prescott 2005). Nevertheless, all so-called pure tastants used in many experiments including that of Erickson have been assumed to stimulate primarily taste buds and thus results on taste perception were ascribed almost exclusively to taste sensations. Some of these tastants, however, are also olfactory stimuli delivered to olfactory receptors by retronasal routes (Mojet et al. 2005). Additionally, there is increasing consensus that flavor perception is predominantly based on olfactory sensitivity (Mojet et al. 2005). For example, many patients confuse loss of smell as a gustatory problem (Hadley et al. 2004). Taste and smell interactions can happen at several levels of information processing before and at the cortical level. For a definitive example, when a subject is presented with a subthreshold concentration of an odor compound (i.e., benzaldehyde – a cherry/almond aroma) in conjunction with a subthreshold concentration of a taste compound (i.e., sodium saccharin – a sweet taste), subjects are able to detect the combination (Small & Prescott 2005). Erickson's neglect of the close and important relationship of taste and smell causes his results to be questionable both on methodological and theoretical grounds. Considering the close relationship of taste and smell, it is unclear why if both olfactory receptors and taste buds can perceive a large diversity of odor and taste qualities, respectively (Axel 2005), only taste has a limited number of basic elements (Hadley et al. 2004).

In olfactory research many efforts have been made in the last centuries to classify odors, though none of them have gained the wide acceptance as the model of four basic tastes. After the first odor classification by Linnaeus in 1756, researchers have proposed a number of basic odors comparable to that of basic tastes, ranging from 4 to 9. The existence of a limited number of odors called basic or primary or reference ("standard") odors, however, has been consistently questioned (Dravnieks et al. 1978; Zarzo & Stanton 2006).

In everyday life, tastes come principally from foods and beverages in discrete time periods, whereas odors are ambient. The relative inaccessibility of the olfactory epithelium compared to the tongue, as well as the higher technical effort needed to present odors compared to tastants, limited early work on olfaction. An experiment on odor perception analogous to that of Hanig (1901) on taste perception, whose misinterpretation led to the unproven but commonly seen tongue map of anatomical specialization for the different qualities of taste, simply did not occur.

In our opinion, Erickson's call for control experiments about the concept of basic tastes should be extended to presentation of single as well as combinations of tastants and odors. In such studies, three types of interactions between odor molecules in mixtures (i.e., synergy, suppression, and hypoadditivity), which originate from integration mechanisms taking place at the single olfactory sensory neuron, should be considered (Duchamp-Viret et al. 2003). Different concentrations of each molecule should be examined, because the ligand repertoire of odor receptors broadens at higher concentrations (Duchamp-Viret et al. 2000). A further observation of interest is that increases in odor and taste intensity ratings are stronger for harmonious taste/odor pairs or taste/odor pairs that are typically encountered together (Delwiche 2004). Tastant as well as odor grouping would both likely become more complex, particularly in view of these interactions.

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Basic tastes and basic emotions: Basic problems and perspectives for a nonbasic solution

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Abstract: Contemporary behavioral and brain scientists consider the existence of so-called basic emotions in a similar way to the one described by Erickson for so-called basic tastes. Commenting on this analogy, I argue that similar basic problems are encountered in both perspectives, and I suggest a potential nonbasic solution that is tested in emotion research (i.e., the appraisal model of emotion).

Basic tastes and basic emotions. Similar to the fact that the dominant model in taste science is the basic tastes model, the dominant model of emotion during the last century, and which is probably still the most influential in current emotion research, is the so-called basic emotions model (see Ekman 1992; 1999; Izard 2007). The contemporary version of the model is largely based on the interpretation made by Tomkins (1963) of the evolutionary perspective on emotion developed by Darwin (1872) concerning the functions of emotional expressions. The adjective "basic" is used in emotion research to express three postulates (see Ekman 1992). First, it is used to convey the notion that "there are a number of separate emotions which differ one from another in important ways" (Ekman 1992). Second, it is used to indicate that "evolution played an important role in shaping both the unique and the common features which these emotions display as well as their current function" (Ekman 1992). Finally, the term is also often used in reference to the notion that the existence of nonbasic emotions can be explained by combinations of the basic emotions (e.g., Tomkins 1963). Theorists differ on the number and nature of basic emotions that they propose, but the six following ones are often included: anger, joy, sadness, fear, and disgust (see Ortony & Turner 1990). These basic emotions, which are also sometimes called *primary* or *fundamental* emotions (see Ortony & Turner 1990) are often conceptualized as affect programs that are triggered by specific eliciting conditions to produce emotion-specific response patterns such as prototypical facial expressions, physiological reactions, and action tendencies, and for which specific neural systems exist in the brain (for discussion, see Grandjean et al., in press; Ortony & Turner 1990). Basic emotions are typically being characterized in this tradition as innate, easy, categorical, and immediate (see Russell et al. 2003). Interestingly, the notion of fundamental or basic emotions can first be found in the philosophical history of psychology; for example, Descartes (1649/1998, Art. 69) already distinguished between six primary emotions (admiration, love, hatred, desire, joy, and sadness) and assumed that all other emotions either belong to these families or are blends of these primary emotions.

It is striking that a very influential representative of the basic emotions model made the explicit analogy between basic emotions and basic tastes as an argument for the existence of basic emotions (Izard 2007). Indeed, Izard (2007) argued that "It is possible to argue by analogy that the capacity to discriminate among basic-emotion feeling states, like discriminating among basic tastes, is innate and invariant across the lifespan," and importantly that "the data relating to the underlying neural and behavioral processes suggest that the emergence of discriminable basic emotion feelings is analogous to that for basic tastes (. . .)." So, if Erickson is right in his criticism of the postulates concerning basic tastes, it means that Izard's (2007) analogy is strongly misleading for emotion researchers.

Basic problems. In their analysis of basic emotions, Ortony and Turner (1990) achieve a conclusion that is conceptually close to the one achieved by Erickson, namely that the basic emotions perspective is "an article of faith rather than an empirically or theoretically defensible basis." Recently, Grandjean et al. (in press) argued that the major drawbacks of basic emotion models concern (a) the lack of clear predictions on the eliciting conditions for basic emotions; (b) the absence of specific hypotheses for the expected prototypical patterning of emotion-specific responses; (c) the unclear criteria for defining basic and nonbasic emotions; and, (d) the unspecified central mechanisms, or affect programs leading to basic emotions. In terms of brain mechanisms involved, it is critical to notice that most of the recent cognitive neuroscience research on emotion has attempted to identify specific brain regions implementing these distinct basic emotions, with the view, for example, that signals of fear and disgust are processed by distinct neural substrates, namely, the amygdala and the insula, respectively (see Calder et al. 2001). Given the central importance of finding specific neuronal processes for basic emotions as evidence for the existence of basic emotions – just like it is the case for basic tastes – it is interesting to notice that, for example, Mineka and Öhman (2002) proposed that "the amygdala seems to be the central brain area dedicated to the fear module." However, an analysis of the literature concerning the brain mechanisms in emotion suggests that emotions are instead represented in a distributed way in the brain, and in particular that the amygdala is not specific to fear, but would be in fact critically involved in the processing of all events that are appraised as being self-relevant for the organism (Sander et al. 2003; 2005).

Towards a nonbasic solution. An alternative to the notion of the existence of independent discreet emotions is the view that there is a continuum for emotions, as argued by Erickson for tastes. The current emotion theory that, by analogy, corresponds closely to the view supported by Erikson as an alternative to the basic tastes model is the so-called appraisal model of emotion (see Ellsworth & Scherer 2003; Scherer 2001; Sander et al. 2005). It would take too much space to detail this model, but it is worth mentioning that a key aspect of appraisal is that the elicitation and the differentiation of an emotion depends on a multifactorial evaluation of the meaning and consequences of an event, given the individual's goals, needs, and values, as well as the current context. Such evaluation is central to componential appraisal theories of emotion, and allows us to conceptualize emotions along a continuum driven by the appraisal mechanisms, rather than along discreet categories of basic emotions. Such an approach conceptualizes the behavioral meaning of an event for the individual, and thus the resulting emotion, on the basis of multiple complementary criteria including novelty, agreeableness, goal conduciveness, coping potential, and norm compatibility (see Scherer 2001).

Conclusion. Although its origin remains to be understood, the analogy between the scientific conceptualizations of so-called basic tastes and so-called basic emotions is striking (see e.g., Izard 2007), and has even led to empirical research investigating which basic emotions are elicited by basic tastes (e.g., Robin et al. 2003). If neither the basic tastes model nor the basic emotions model were to be relevant theories to guide research, one can hope that mutual exchanges between the taste and emotion sciences would allow us to avoid the use of one to support the other.

The neural structure and organization of taste

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Abstract: Gustatory studies are predicated on the existence of basic tastes. Erickson questions this assumption and offers contrary evidence. Although Erickson may conflate certain concepts and demand uncommonly stringent requirements for basic tastes, his thoughtful article reminds us that the basic organization of taste is not yet settled.

During the 1970s and 80s, gustatory theory outran data. There was a lively debate over the fundamental structure of the taste system: Were there basic tastes? Gustatory neuron types? Was the afferent signal for a taste confined to one coding channel (labeled-line) or extended across the activity of all neurons (across-fiber pattern)?

That debate fractured and eventually wearied the field, which thankfully embraced a burst of empirical data from molecular biologists, electrophysiologists, and brain imaging scientists who turned their tools to taste. The path for the past 15 years has been one of discovery: How sapid stimuli are recognized, neural circuitry and neurochemistry organized, which areas process taste and its hedonic sequelae in primates, and which are driven by taste in humans.

Cheered by this progress, attention has shifted from theoretical debates to a practical appreciation of function. It was clear that some neurons are more important in representing a particular taste quality, but also clear that the signal could hardly be restricted to one channel. That compromise was enough of a theoretical platform to satisfy the empiricists, and the field thrived.

Yet, it is useful occasionally to return to our origins and ask whether a supposition accepted decades ago has limited us to discover only what was ordained by that supposition, in this case, that the system is composed of a small number of discrete basic tastes.

No one is better qualified to remind us of this than Robert Erickson, an early and consistent skeptic of basic tastes. Here, Erickson represents 45 years of theory and data in opposition to the notion and the degree to which its acceptance has shaped our understanding of taste.

Notwithstanding the clear value of this article, I offer four cautions. First, Erickson mixes three independent concepts: basic tastes, gustatory neuron types, and a labeled-line coding strategy. It is seductive yet facile to conflate them. Basic tastes provide the labels, gustatory neuron types offer the lines, and the labeled-line strategy appears to emerge intuitively. Yet, the existence of basic tastes and neuron types supports neither labeled-line nor patterning theories. Vision has basic (primary) colors, yet uses an across-fiber strategy.

The existence of basic tastes as the targets to be detected, and neuron types as the lines to be labeled, are necessary but not sufficient to support labeled-line theory. Patterning, however, is silent on the issue of neuron types. It makes no distinction between a gustatory dimension spanned by 1,000 neurons, each with a unique sensitivity profile, or by only five neuron types, each with 200 members. Patterning only requires that the information within neuron types be shared. Meaningful interpretations can only derive from a comparison of activity across neurons with different profiles, whether members of discrete types or not.

Second, Erickson dismisses the concept of basic tastes by imposing a definition, derived from other senses, that is recognized as too stringent for taste. Advocates rarely promoted the requirement that basic tastes in proper combination be capable of composing all other tastes, and certainly not that they be the only qualities that can be tasted. Erickson's point that arguments for basic tastes are contaminated with cultural and linguistic biases is well taken. But support extends beyond mere familiarity or the availability of descriptors to include distinct transduction mechanisms and the likely existence of gustatory neuron types (discussed later). Thus, qualities that have survived to be termed basic have an underlying neural machinery to support their status.

Erickson writes that we do not know what basic tastes are (true), yet, we appear unconcerned with that ignorance. Far from unconcerned, we regret that the evidence is so flimsy as only to support the notion that basic tastes are a convenient rubric for organizing studies, yet we are satisfied that recent advances imply that this effort is not misguided, even if it is not resting on the clear definition Erickson and others crave. Perhaps the field is beguiled by using basic tastes as a guide, but the concept has permitted an unprecedented rate of discovery.

Third, Erickson does not review data that have informed these issues with greater sophistication than is presented here. The existence of neuron types has been addressed in studies that transcend the attempt to classify response profiles. Taste cells are statistically separable into clusters, suggesting neuron types. Yet, those within each cluster are not functionally identical, permitting the argument that clusters reflect the scientist's eagerness to impose order on a system void of them. A resolution of whether neuron types exist could not be made on a taste system at rest. It had to be set into motion.

Taste neurons change responsiveness when the animal is subjected to alterations in physiological state (Hajnal et al. 1999; Jacobs et al. 1988; McCaughey & Scott 2000), conditioning paradigms (Chang & Scott 1984), and taste modifiers (Scott & Giza 1990). Taking advantage of this convenient discovery, the question of the existence of taste neuron types could then be recast as follows: As the system changes to accommodate these manipulations, do the neurons within one putative cluster change as a group, in a manner different from, even opposite to, the accommodation made by cells in other clusters? Such common purpose would imply a functionally distinct group, and so would argue for gustatory neuron types. In each case, the answer was affirmative. Gustatory neuron types are likely.

Finally, Erickson overreaches in proposing that all sensory and motor messages are encoded in patterns. There is inevitably spread across receptors in any interaction with the environment. When that distribution is as narrow as the receptor physiology allows, and when mechanisms such as lateral inhibition are employed to tighten it further, it may fairly be represented as a labeled line. Erickson, on Thomas Young's shoulders, offered a profound insight with the dichotomy between topographic and nontopographic modalities. He might continue to embrace that dichotomy here and recognize that certain processes are best served by specificity.

Such, however, is not the case for taste, the breadth of whose neurons virtually requires that the encoded quality be read across them. The discipline of taste was, and remains, largely sympathetic to Erickson's position and grateful for his contributions.

Should labeled lines and pattern models be either-or? Issues of scope and definition

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Abstract: Erickson's conclusion that if basic tastes are not appropriate at one level, reference to labeled lines is inappropriate at any level, depends on matters of definition and scope. His population model mirrors Young's theory of color perception. However, there is evidence for distinct pathways to the cortex for two cone-opponent and one achromatic channel. Depending on the use made of key terms, sensory systems may display both across-fiber and labeled-line features.

Erickson's article raises important semantic issues, some of which echo lucid arguments previously put forward by him about the extent to which findings at one level of analysis are often applied, inappropriately, to a different level of analysis. For example, Erickson (1977) cited "Brewster's Fallacy," whereby Brewster inferred, from studies at the psychophysical level, that at the stimulus level, there were three kinds of light – red, yellow, and blue. Some of the arguments in the present article are complicated by the opposite tendency. That is, implicit in the text is the assumption that if the notion of basic tastes is not appropriate at one level, reference to labeled lines is inappropriate at any level. Whether this is the case or not depends, in large measure, on matters of definition and scope.

Young's insightful model of color vision predated the validating discovery of separate cone photopigments and their associated genes, producing three populations of receptors, each of which, though broadly tuned, have identifiable response characteristics. Such individuality is required to produce the pattern across which a perceptual interpretation is made. The need for these distinct lines of input is evident when one of them is missing in color deficient individuals. Unless the term "labeled lines" is restricted to very narrowly tuned outputs that run uninterrupted from the periphery to consciousness, then identifiable, arguably labeled, lines are required at certain levels within any across-fiber pattern model. To that extent it is probable that both vision and taste involve some short-distance labeled lines. It may be appropriate to consider the three visual photopigments the basis for three short-distance labeled lines, and the ganglion cells the basis for a subsequent layer of opponent-process labeled lines. Notwithstanding, in agreement with Erickson, it would clearly be inappropriate to call red, green, and blue lights basic visual stimuli. In a similar vein, although basic tastes generally imply labeled lines at the neural level, the reverse need not be true. Separately identifiable output lines, if they exist, need not imply a fixed number of basic tastes. In vision direct use is not made of the pattern of responses across the receptors. In principle, as Young concluded, color experience could be explained by the ratio of responding across three broadly tuned color receptors. Despite the economy of this idea, it is clear from both psychophysical data, and the discovery of color opponent output cells, that in practice no such simple pattern directly feeds color experience. Mullen and Kingdom (2002), for example, have obtained evidence for distinct pathways from the retina through the lateral geniculate nucleus to the cortex for two cone-opponent systems, as well as an achromatic channel. Commonalities among mechanisms across sensory systems are, as Erickson maintains, most likely. In the end, and depending on the particular use made of key terms, most sensory systems are likely to display both across-fiber and labeled-line features. This may be especially true of taste responses, which represent but one component of the overall integrated flavor experience created by complex interactions with other senses (Stillman 2002).

Important differences between visual and chemosensory stimuli limit comparisons between processes at the receptor level in taste and in vision. In color vision the stimulus consists of a continuum of wavelengths. There is not an obvious continuum for chemosensory stimuli, and so the pattern of stimulation is likely to be fed by receptors that differ more than those in color vision, as revealed by studies that have identified both ionic and metabotropic mechanisms at work in taste receptors. Erickson may be correct in maintaining that perceptual basics do not exist, and that in any case the concept of basic tastes is not potentially falsifiable. However, this does not negate the possibility that at the receptor level some basic functional categories, for example, receptors responding to acids, might exist. Conceivably they could, by their mode of operation, contribute to the pervasive nature of basic taste words, inadequate though that vocabulary is for describing taste, let alone flavor, experience.

In recent years the labeled-line versus across-fiber pattern argument has, due in no small measure to the work of Erickson himself, become somewhat of a straw man. Few contemporary researchers or textbooks adopt a narrowly defined labeled-line approach with respect to taste perception. Notwithstanding, the force of Erickson's persuasive and illuminating arguments, namely, that research has become hide-bound by the notion of a set number of perceptual basics, has the potential to broaden the perspective researchers bring to bear on both research design and the interpretation of data.

Synthesizing complex sensations from simple components

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Abstract: The target article suggests that taste is not based on the traditional four basic tastes, but rather is a continuum subserved by cross-fiber integration. This commentary describes evidence indicating that the traditional concept is valid, and that with suitable precautions, it is possible to match natural substances using mixtures representing fundamental tastes.

Although the target article suggests an across-fiber model as an alternative to the widely held belief that there are four basic tastes, I believe that these two concepts are not incompatible.

Erickson states that his model is "based on Young's theory of color vision." Thomas Young reasoned that because there are a very large number of hues, it is almost impossible to conceive of a separate receptor for each of these hues, and that there may be only three types of "particles" (or receptors), each having a primary or greatest sensitivity to one hue, but also a broad but lesser sensitivity to the others.

Thus, according to Young's theory, no single receptor can by itself provide information concerning a particular hue: He stated that a "blue" receptor could respond to the presence of a low level of blue light, as well as a higher level of light corresponding to other hues. As pointed out in the target article, in keeping with Young's multisensitivity concept, neurophysiological measurements have shown that single gustatory nerve fibers and their associated receptor cells can respond to more than one of the putative primary or basic tastes, but with a different sensitivity to each taste. As with hues in vision, it is only by cross-fiber integration at higher levels of the nervous system that perception of basic tastes could emerge. Hence, the target article's cross-fiber model does not rule out the concept of basic taste qualities.

In the "cross-fiber" quote from Young cited in the target article, it is stated that green light can stimulate two receptors with their primary sensitivities to yellow and blue light, respectively, resulting in the "cross-fiber" mixture being perceived as green. Young, despite his brilliance, was wrong, being misled it seems by the subtractive color mixture produced by mixing blue and yellow paints. As subsequently pointed out by Helmholtz, blue and yellow *lights* are complementary, and when rays producing these two hues are viewed separately, then mixed, pale yellow, pale blue, or white is seen depending on the relative proportions. The reason for pointing out Young's mistake is not to show that even a genius can blunder, but rather to demonstrate that it is not always possible to analyze mixtures into their primary components through introspection.

Despite this inability to determine basic constituents, Section 7 of the target article reports experiments in which subjects attempted to describe complex tastes in terms of their components. In discussing the results in Section 7.6, entitled “An inconvenient truth,” it is stated, “After the experiments it became disconcertingly clear that the subjects were biased towards the idea that the four basic tastes should account for the Comparison stimuli.” It was concluded, “This unexamined bias may be unavoidable in all psychophysical studies involving the basic tastes.” However, the problems in these experiments do not invalidate the use of other means of supporting or refuting the concept of basic taste qualities.

There is another way to test the validity of the basic four-component theory of taste. This is to use a variant of the procedure employed by Helmholtz to confirm the validity of the trichromatic theory. If the theory of basic tastes is correct, it should be possible to match the taste of any substance by using a mixture of chemicals each representing one of the basic tastes. With your indulgence, I’ll explain why I believe that this can be done using appropriate conditions.

Back in the early 1950s, armed with a fresh PhD in organic chemistry, I was hired by a major food company, and given the assignment of preparing a survey of the literature on taste perception. After two years spent in New York City libraries, I prepared a 318 page monograph spanning the period from the mid-19th to the mid-20th centuries (Warren 1953). I became convinced (or biased) of the validity of the concept of basic tastes, and using this concept, set about trying to match the taste of the powdered “instant” coffee produced by the company.

Padded nose clamps were used to block the aroma, and food dyes were employed to match the appearance of coffee (as well as conducting the experiments in dim red light). Results obtained by a panel made it clear that the major components of the coffee taste were bitter and sour, but that using magnesium sulfate (called “bittersaltz” in German) and hydrochloric acid produced very different sensations than coffee because of the quick onset of their tastes; coffee had a much slower onset of sensation and a blending of components. The molecular weight of components appeared to determine the time course of their sensations. For example, bitter substances with high molecular weights (e.g., naringin, derived from the white pulp of grapefruit) and synthetic sucrose octaacetate had much longer onset times and persistence of their tastes, lingering even after rinsing with water. Similar time constraints based on molecular weight applied for sour substances. Despite the fact that coffee is a complex mixture of many sour and bitter components, presumably each with their own onset times, an acceptable match to the instant coffee was obtained when the representatives of bitter and sour components each had a molecular weight between 150 and 200.

Author’s Response

The pervasive core idea in taste is inadequate and misleading

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Abstract: The target article described the ubiquitous and often undefined idea of “basic tastes” as the basis for sensory coding in taste, and its attendant problems. The commentaries cover the full range of reaction to this argument, from full support, to qualification of the level of analysis to which “basic tastes” apply and the nature of empirical support, to full denial of either the characterization of the literature or that such characterization reveals any problem. Many commentators, and I, go on to propose other types and sources for taste analysis, which I relate to the “across-fiber pattern model.”

For over a century, our understanding of the nature of taste has been extensively guided by the concept of basic tastes. In the target article, I argued that the use of this model has usually been so implicit that the extent of its influence is not obvious, that the idea itself was not founded on a rational basis, and that it has no testable definition.

But, is my concern realistic for precisely defining the context-giving terms “basic taste,” “across-fiber pattern,” or any other fundamental term, or can we proceed directly to the collection of interesting data without such academic concerns? This turned out to be a large issue for many of the commentators, and thus provided the orientation for many of the responses.

The target article generally emphasizes the necessity of greater clarity in taste research. In analysis of no other sensory system do we find a few sensory “basics”; this is a failed concept in olfaction, and is not the same idea as that used for “basic” colors. I consider that just in raising these issues, the article and the commentaries met their goal. I thank all the commentators for their sometimes surprising, but always thoughtfully illuminating, approaches. I recommend each contribution as worthy of careful study.

R1. Is a theory of taste desirable?

There is wonderment expressed by **Di Lorenzo & Chen**, **Hilbert**, and **Scott**, that I treat research at all levels, from transduction mechanisms to psychophysical organization, with the one model of “basic tastes.” Therefore, a good place to start my responses would be with a justification of this overall monothematic structure of the article.

First, the fact that the taste system functions in a deterministically cooperative way, each level bound with the others, leads to the idea that one model should accommodate the whole. Also, it is clear that for over a century, research in most areas of taste has been guided and constrained by this one “basic taste” model. The experiments from receptor events to behavior have been designed in terms of basic tastes, and the data in all areas came out in terms of the basic tastes.

Whether or not the basic taste term was used, it is clear that that is the basis of how our field evolved and continues. Although rather *implicitly*, basic taste receptors are fit into the labeled-line model, which has been presented as the neural equivalent of psychophysically defined basic tastes. And this model has the great advantage of simplifying experimental design and thus facilitating the rapid collection of data.

But I believe we will eventually benefit from a properly founded *explicit* and broadly applicable theory of taste, such as the across-fiber pattern model; something that can give a necessary and testable structure to this field.

This model is not designed to pursue particular topics, such as the search for typologies, or the neural representation of specific information, but as an approach to a theory that will encompass all aspects of neural information, including taste. The across-fiber pattern model has been described in detail (Erickson 1963; 1968; 1974; 1978; 1982a; 1984b; 2000; 2001). Its intended role as a guide towards and structure for empirical studies is stated clearly in the prefatory quote from Poincaré.

R2. The basic tastes model reigns

The idea that basic tastes have been the guiding force in the field of taste was noted by Bartoshuk 20 years ago (1988). For example, although in 1916 Henning adamantly opposed the idea of four tastes, espousing instead the idea of a taste continuum (see sects. 4.1.3 and 6.3 of the target article), he illustrated it by labeling the four corners of a tetrahedral continuum with the basic tastes! But with what other tastes or stimuli could Henning have illustrated his model? This may be why Henning is incorrectly quoted as supporting the basic tastes model (Bartoshuk 1988), and why research has continued to follow that format.

Does the basic tastes model still give the field its format? **Stillman** notes we are "hide-bound" by the basic taste orientation, reflecting almost all the commentaries. The only areas of research not affected by this idea might be some applied studies, such as of variations of the threshold for a given basic taste with age, and of the anatomy of the taste pathways; but even these often draw in the idea of basic tastes.

R3. Relating levels

Could we study one area, say psychophysical events, and ignore or even deny the fact that these events derive from the characteristics of the receptors and other factors such as our culture and language (sect. 7.6)? Although a psychophysical study can be successfully conducted without addressing the transmitters involved, that study must not avoid the other known aspects of the taste system. This would be analogous to studying the behavior of oxygen as a reactive gas, as if this were separate from the study of its atomic structure. The usefulness of relating different levels of study is clear in several commentaries.

Di Lorenzo & Chen, **Gallo**, **Kennedy & Gonzalez**, **Lemon**, and **Scott** usefully relate psychophysical and neural events, as does **Hilbert** for color vision. Di Lorenzo & Chen intertwine three levels of organization in suggesting that our language may reveal the relationship between neural organization and psychophysics. **Belpaeme** proposes a direct dependency of language on neural events. **Booth** conflates many levels of influence into the understanding of taste processing, including, at least, cognitive processes, learning, other senses, and biosocial influences. **Sander** usefully makes the conflation between behavior (emotions) and neural structures, as well as between taste and the emotions. Whenever I use the term "labeled-line," I refer to its conflation with "basic tastes."

Warnings about the problems inherent in drawing casual relations are sounded by **Di Lorenzo & Chen**, **Hilbert**, and **Scott**. **Stillman** makes the cautionary point that the lack of perceptual basic taste groupings does not negate the possibility of receptor categories. And **Cutting** carefully refuses to equate the various definitions of basic tastes that do not properly fit together (sect. R5.2).

Clearly, drawing relations between the various aspects of a field is essential for a strong science of taste. But the *implicit assumption* that the basic taste model justifies these conflations is at best very problematic; this is especially so in its lack of clear linking hypotheses to relate the different levels (sect. 5.4). For example, what links the activity in labeled-lines to the perception of only a few basic tastes? The across-fiber pattern theory *explicitly hypothesizes* the nature of these relationships (see sects. R10.6 and R10.7).

R4. The role of hypotheses

My view is that good hypotheses are needed for the testable definitions and predictions required in any field of science. **Scott**'s commentary is particularly useful in that our different views of science highlight and clarify each other.

R4.1. On hypotheses and definitions

Scott avers that my concern with detailed hypotheses and "too stringent definitions" of terms get in the way of data collection – which contains the real discoveries. But I doubt that even a simple data collection can be devised without some notion of the meaningful context for the data, and it bodes ill if this context is not spelled out. For example, what does it mean that we have data supporting the idea of neuron groupings, or a cortical area for "sweet?" Are these just data, or does it go deeper than that? The prior, but unasked, questions should have been: "Why should we search for groupings of neurons?" and "What do we mean by 'group?'" As affirmed in many of the commentaries (sect. R5), we have a poverty of clear definitions, and the underlying hypotheses are very vague at best. Simple data collection is easy, but not simple.

R4.2. On breadth

Again, in distinction to **Scott**, I believe that *breadth* is important for a hypothesis. He states that I over-reach in applying the across-fiber pattern theory to other sensory systems, and indeed I apply it beyond input to central mechanisms, as well as to behavior. Several of the commentators also take broad views, including at least **Belpaeme**, **Cutting**, **Di Lorenzo & Chen**, **Gallo**, **Handel**, **Majid & Levinson**, **Sander**, **Stillman**, and **Roessner, Rothenberger, & Duchamp-Viret** [**Roessner et al.**] (sect. R7; sect. 2.1).

R4.3. On predictions

As suggested by **Hilbert** and **Sander**, it requires clear hypotheses to provide the essential *predictions* to validate an idea (sects. 6 and 7). I welcome these comments. The across-fiber pattern model has provided predictions of core issues in the field that are testable, and these have been met with some success.

R4.4. On control experiments

Although it was stressed as a major problem throughout the article, and was the point of the experiment (sect. 7), there was little commentary on our general and long-term poverty of the control experiments essential for validation of any hypothesis or conclusion. Because disagreement is the best instigator to commentary, perhaps there is no disagreement that, in simply accepting the basic tastes model without test, we do indeed have a long-term and continuing lack of important control studies.

R5. The role of definitions

Let us define our terms. I may have lost most of my audience with that line! I sense that there is little interest in my esoteric enthusiasm for clear hypotheses and shades of meaning of terms like "basic tastes." Why not just collect the interesting data (sect. R4)? I feel that our routine laxity about the meaning of the core words we use, and the models that employ these words, has produced great problems with much of what we have learned about taste. This view is verified in the differences among the definitions used in the commentaries summarized next. A route towards clarification is contained in the Summary Comment.

R5.1. Are clear definitions desirable?

The first question concerning definitions is whether they are to be desired at all. I was unaware that it is generally recognized that my definitions of basic tastes are too stringent (the same as those of Bartoshuk [1988] and Halpern [2002a]) (sects. 3.2.1 and 5.3.2), as claimed by **Scott**. He avers that data are equivalent to discovery, that clear definitions slow the production of data, and thus that the accepted lack of a clear definition of basic tastes has encouraged a rapid accumulation of discovery. In this sense he touts the practicality of vague definitions. I cannot agree.

My view that good definitions of terms and hypotheses are of importance is evidently shared by several of the commentators; these include at least **Di Lorenzo & Chen**, **Fox**, **Gallo**, **Handel**, **Hilbert**, **Kennedy & Gonzales**, and **Stillman.** I have attempted to make the across-fiber pattern model as clear as I can, thus making it possible to suggest various falsifiable tests of it (sects. 6 and 7). Tests of the basic taste model, attempted in section 7, are technically impossible because of its vague definitions.

R5.2. Basic tastes

A central point of this article is that the core idea of basic tastes has wandering and weak definitions. This is confirmed in the variety of ways it is treated in the commentaries.

Scott points out that there is a *general acceptance* of the fact that *we have no usefully clear definitions of basic tastes*. In my view, if this is true and we cannot do any better, the concept should be dropped – science questions definitions rather than searching for their support. **Kennedy & Gonzalez** confirm this vagueness of basic tastes and would like improvement. **Booth** decries the lack of a good definition and describes a novel and interesting direction that might provide clarity. The previous and present attempts to test the basic tastes idea (sects. 6 and 7) showed that its vagueness prevents a proper test. Scott regrets this vagueness in that it inhibits support of the basic taste idea.

Hilbert details two definitions of basics from *color vision* that are similar to those used in taste: (1) many colors or tastes can be rated on their basics, and (2) they can be perceived separately in mixtures. He strongly points out that it is not usually clear which definition is implied in taste, including in this article. **Logue** also relates the idea of basics in taste and color vision. She points out that both tastes and colors can get lost in mixtures; but because there are basic colors, should we not agree on basic tastes? However, **Cutting** points out, these "basic" terms may not be equivalent. Color basics can be mixed to match other colors, but a failure of this fact in taste may simply mean that these basic terms are not defined well enough for a direct comparison.

Cutting presents a *review of the meanings of the "basic" and "primary" concepts*; this is certainly useful when considering the meaning of the term "basic taste," which has also been "primary taste." He states that a cultural definition of basic tastes makes sense in that it clearly aligns with the needs and desires of the people in their own culture – salt and sugars are important in our lives; this is in close agreement with my discussion of the role of culture and language in our classifications (sect. 2). He suggests that two other definitions have no support at this time: taste mixture studies, as in defining basic colors, and labeled lines. Perhaps he would agree that, if clarified, these two might fit in with the cultural definition. But because of the present lack of clarity, he disagrees with some others who hold that acrid, fat, metallic, umami, and water are basic tastes; indeed, how can we explore for new basic tastes when we do not know what they are?

Sander provides a useful perspective on basic tastes from what turns out to be the closely allied definitions of *emotions*. Not surprisingly, the number of basic emotions that have been proposed is around six (sect. 2.3), and this position has received support in its analogy with the basic tastes. This analogy makes the basis for the basic emotions especially interesting reading. In a stance similar to Henning's (1916), Sander concludes that emotions are not distinctly different, but like tastes are verbal descriptions of rather factitious points along a continuum.

Warren brings into focus a surprisingly testable but largely untested prediction from the core definition of basic tastes; that is, they may be combined to form all other tastes. He provides an interesting example of how this prediction can be tested. But the number of successes can be counted on one hand. I would guess that there have been very many tests of this most obvious and important prediction from the basic tastes model, but that those scientists found it did not work, and did not publish. But falsified predictions are at the heart of science, and these would have been most prominently published were this physics. We do not have a *Journal of Negative Results*, but imagine how informative one could be! Perhaps an internet *JNR*?

R5.3. Groups/types

The idea of basic tastes strongly leads to the assumption of underlying anatomical basic taste groupings or types, such as labeled lines or specific receptors (sect. R3). My considerable concern with groupings centers on the ease with which groupings of many sorts can be developed absent a critical rationale (sect. 3.2).

As examples, **Fox** and **Gallo** accept groupings of specific receptors, and they and **Di Lorenzo & Chen** support labeled-line groups. **Scott** has searched for neural groups with mathematical analyses such as multidimensional scaling and cluster analysis, and then when those failed (sect. 4.2.2), he searched for other support and found it in an influence of motivational state on neural responsiveness; **Fox** suggests that the latter definition supports the former. These commentators also cite successful anatomical and receptor classifications. But an inspection of a clearly nonbasic continuous sense, audition, shows that if only four disparate tones were used, say 500, 1,000, 1,500, and 2,000 Hz tones, they serve well as "best stimuli" for auditory neurons, and a different neural cortical location would be found for each; then are these "basic" tones? There is probably a neural area, best-neuron type, and receptor type for lysine; but this control was never performed because lysine is not a "basic." We find what we look for.

Fox claims that the across-fiber pattern model fails in that there is no sufficient definition of the groups necessary for it. He does not note that groupings define the labeled-line view, whereas in the across-fiber pattern model they are only necessary in nontopographic systems such as color vision and taste, where they have been defined.

Lemon and **Lavine** offer strong caveats against accepting mathematical analyses as support for the idea of groupings in taste. Lemon points out that the measures of neural responses as seen in repeated measures, even in the same animal, are inherently too unstable to properly define "best stimuli," and comparisons across animals result in additional problems. And, of course, best stimuli change with variations in stimulus intensity, and with the stimuli chosen for searching for the best stimulus; if only basics are used, one of them must be best. Also, Lavine makes the point that the common use of certain mathematical procedures to support the classification of data into groups is invalid; he cites multidimensional scaling, cluster analysis, and factor analysis as culprits. **Fox** agrees, as do I (sect. R6; sect. 4.2.2).

It is probable that the search for support of classifications has been driven by desires to demonstrate that basic-tastes groups exist. A motivated search for groupings, without strongly specifying what a relevant grouping would be, is bound to succeed.

R5.4. Labeled lines

The following definition of "*labeled line*" generally follows that suggested by **Di Lorenzo & Chen**, **Fox**, **Lemon**, **Scott**, and **Stillman**: A labeled line is a neuron whose activity is labeled in its meaning. In taste the meaning is to represent one of the basic tastes. As I understand it, the meaning of activity in a labeled line is set whatever stimulus evoked the activity, be it the best stimulus or other, and it is not interpreted in terms of activity in other neurons (as in the across-fiber pattern model), or by the temporal pattern of its activity. The label is fixed. But perhaps this definition could use some serious tuning-up.

In support for the labeled-line idea, **Di Lorenzo & Chen**, **Fox**, and **Stillman** suggest that a broadly tuned neuron's "best stimulus" could make it useful as a labeled line. Di Lorenzo adds that even if there are many more tastes than just the basics, there could be a labeled line for each. Depending on the number of separate tastes, this could encumber many labeled lines in a relatively sparse sensory system. Her quantitative prediction is worth study. **Scott** accepts any relatively narrow tuning as a labeled line.

In comparison with the across-fiber pattern model, these definitions absolutely distinguish the labeled-line from the across-fiber pattern model in that in the latter, each broadly-tuned neuron participates with others in the representation of many different stimuli, and responses to all stimuli, of whatever magnitude, are accepted as information. The identity of the best stimulus is not relevant as in the labeled-line view. I discuss labeled lines in the article as the extension of an across-fiber pattern model to a homogeneous group of neurons wherein the information is reduced to one bit – only one message (sect. 8.4.2).

In criticism of the labeled-line idea, **Lemon** notes that "best stimuli" are too unreliable to serve as indicators for labeled lines. Then what can the meaning be of activity in a labeled line? And if a broadly tuned neuron's meaning is considered to be only that of its best stimulus, responses evoked by other-than-best stimuli would produce confusion and wasted effort for the nervous system. On the other hand, broad tuning is accepted "as-is," an integral and functional part of across-fiber pattern coding.

Kennedy & Gonzales quote one of the wise old men in taste, Dethier (1974), that the "rigid specificity" of labeled lines "existed more in the minds of investigators than in the receptors themselves." This rings a bell with **Sander**'s comment that the six basic emotions perspective is "an article of faith rather than an empirically or theoretically defensible basis."

Beyond that, **Scott** and **Stillman** state that few scientists are concerned with a good definition of labeled lines. They do not give a reference, but if this is true, is there no real, good, and generally accepted definition of labeled lines? Does no one care? I suggest that a critical and testable definition should be developed before we are led further by this idea.

R5.5. Across-fiber pattern

The definition of information representation in the across-fiber pattern model is simply this: The information in a neural message is defined by a unique pattern of activity across neurons. Details of this idea are given in sections R9 and R10, and sections 6, 7, and 8 of the target article. **Booth** makes a perceptive and exact statement of one important aspect of the across-fiber pattern model; that is, the neural patterns hold from receptor to behavior without "read-out" points in their journey (Erickson 2001). It is nice to have that spelled out.

R5.6. Labeled-line versus across-fiber pattern?

Fox and **Di Lorenzo & Chen** suggest that the two models are largely indistinguishable because they are both spatial, and because of the lack of strong definitions to separate them. This alone should make clear how essential stringent definitions are to our science. Di Lorenzo & Chen also suggest that labeled-line and across-fiber pattern coding are not different in that the responses in a broadly tuned neuron may be interpreted as a labeled line according to that neuron's best stimulus. **Fox** and **Kennedy & Gonzalez** make the same point, while opting for both the across-fiber pattern and labeled-line models. **Booth** reasonably questions both labeled-line and across-fiber pattern models to the extent that there is a lack of good definitions.

Several commentators pose the possibility that labeled-line and across-fiber patterns can exist in parallel. As **Kennedy & Gonzalez** point out, this idea has been around for a long time; they align with Dethier (mid 1970s) in proposing two coding mechanisms corresponding to (a) acceptance/rejection and (b) the encoding of many taste stimuli. The first might be called two labeled lines providing the minimal information required for simple yes or no responses (sect. 8.4.2). For the second, Dethier invoked the across-fiber pattern code. This sensibly suggests that the two ideas are distinctly different, while possibly coexistent.

R5.7. Taste continuum

Whether or not taste can usefully be defined as a continuum is a clear point of distinction between the basic-taste and across-fiber pattern models; the former cannot tolerate a continuum, whereas the latter embraces it. But, as is clear from the commentaries of **Handel** and **Stillman**, it is hard to believe that taste could be a continuum (sect. R9). **Sander** supports the idea of a taste continuum in its similarity to a continuum of emotions (sect. R7.3), and I find it probable in taste (sects. R5.8, R9, and R10.3; sects. 6.3 and 8.4.2). So this is an important but very tricky issue. Give me a moment.

Because chemicals are discrete entities, how could they be considered as a continuum? The elements find their best organization when considered by mass, as in their representation in the periodic table. They do not *form* a continuum, but are most productively considered as being *members* of a continuum. This is how I use it in taste. I think it is premature to assert that there is not a continuum of taste without test.

The presence of a taste continuum is evident in the neural data (Erickson 1967). When considered beyond the four basic stimuli, the neural responses are seen to conform to neural response functions tuned broadly across some continuum, much like the color receptors (sect. 6.3). If we pretend that we do not know the wavelength continuum, the responses of color receptors can be used to generate an illustration of that continuum, as well as the bell-shaped characteristics of the color receptors. In this pretend situation, physicists could be asked to define the color continuum. These same methods generate a taste continuum from the neural responses of taste neurons, as well as demonstrate their bell-shaped neural response functions across this continuum. Given a broad enough range of stimuli – certainly beyond the four basics - chemists could be asked to identify this continuum. The fact that mathematical solutions such as multidimensional scaling (sect. 4.2.2) succeed *at all* in taste – even if in a distorted and not clearly interpretable form (e.g., not being able to prove the existence of neural groups) – indicates that there is indeed a useful underlying continuum. If taste data are viewed in this manner, the chemistry, neural organization, and psychophysics of taste may gain clarity they would not get if we just stick to the basics.

Di Lorenzo & Chen claim that labeled lines are not incompatible with a continuum; they could just appear at certain points along it. But this is hard to rationalize with the definition that activity in a labeled line is unrelated to activity in other labeled lines, whereas a continuum is a specification of relationships.

R5.8. Breadth of tuning

The terms "narrow" (or specific) and "broad" are commonly used to describe the tuning of individual afferents. It is certainly not always clear what those terms mean, or why we should care. "Broad" seems to refer to neurons sensitive to large portions of the stimulus continuum, such as with color receptors, and "narrow" indicates neurons sensitive to a small portion, as in tactile or visual location.

But a more explicit prediction for breadth of tuning in the across-fiber pattern theory is in order here (sect. 6.4). In this model, proper breadth of tuning is a strictly mathematical issue. The tuning should be sufficiently broad to gain enough *neural mass* to make the necessary discriminations. What is enough mass? In color, the few neurons available at each retinal point must be just broadly tuned enough to provide the mass out of which can be carved the sufficient *neural mass differences* required for signaling changes in wavelength. On the other hand, in representing visual location, there are so many neurons available that broad tuning across space would result in an unnecessary, indeed overwhelming, incoming neural mass.

In finer detail, quantification in the across-fiber pattern model suggests that any discriminable change, wavelength, location, taste, or other, depends on the same amount of neural mass difference – a constant, X. In the uniform darkness of the brain, where one system cannot be seen as different from another, just X is what the nervous system needs to detect a change, whether visual location or taste. It can just notice X. This quantifiable hypothesis can be tested.

Back to the vernacular, that taste receptors and neurons are broadly tuned seems to be accepted by almost all but the molecular biologists (sect. 5.3.1), and now the molecular findings have been reconciled with this clearly established breadth (Tomchik et al. 2007). But the role of this breadth is debated. None of the commentators deny the necessity of broad tuning in the across-fiber pattern model for taste, and **Logue** points out that such breadth is contrary to the labeled-line code. But **Di Lorenzo & Chen**, **Fox**, **Gallo**, and **Kennedy & Gonzales** suggest that better sense could be made out of broadly tuned neurons if they were considered as labeled lines according to their best-of-the-basics stimuli (sect. R10.2).

R5.9. Singularity

The labeled-line model indicates that only individual basic tastes should be perceived as singular, whereas the across-fiber pattern idea predicts the singularity of many tastants and mixtures. Tests of this difference should be a primary effort for evaluation of the models, but they are seldom attempted. Therefore, I find **Gallo**'s attempt to test one of these core aspects of basic tastes particularly gratifying. (**Warren** tested the other core definition (sect. R5.2). More tests should be considered essential, and are not complex.

As context, I have shown that human subjects may sometimes classify an individual stimulus or a mixture as singular, and at other times as more-than-one (sect. R9; sects. 3.2.1, 4.1, 6.1, and 7.9). Using rats, **Gallo** finds that although complex stimuli can be rated as singular, as in the across-fiber pattern model (sects. 6.1 and 7.9), the basic components of a mixture can also be identified, supporting the basic taste idea. The result depends on the context. To provide him with a possibly passable example, a complex object, such as a car, might be seen as a single object, or as more-than-one (windows, tires, or such), depending on how the question is asked. But if simultaneous activity in four labeled lines were reported as singular, that would be equivalent to perceiving them as an across-fiber pattern. This is a topic in taste that could use further study.

R6. Misleading methodology

The basic taste methods have uncritically supported the basic tastes model, and thus have certainly distorted the field. To illustrate this position, imagine a color mixture experiment in which the subjects are limited to responding only with the basic color terms, red, green, yellow, and blue. When asked to rate a mixture of green and blue, they are only allowed to respond with the words green and blue, and cannot say "a singular hue something like blue and green, but not exactly either." If allowed, they would also respond that these colors are reduced in basics saturation, as less blue or less green; this is illustrated in studies of color-naming (Erickson 1977). This procedure is standard in taste studies; the subjects are not allowed to rate a taste mixture of HCl and NaCl as a unique taste, but must respond in terms of the basic tastes, sour and salty – thus always supporting the basic taste idea.

This pervasive but faulty methodology of using only basic tastes has led to strongly biased support for the basic tastes model. *This one surprising error appears to have largely provided the shape of the field as we know it.*

As a good example of this bias, **Kennedy & Gonzales** point to the fact that the molecular studies (sect. 5.3.1) supporting the idea of specific basic taste receptors would very probably have shown broad tuning if a range of stimuli beyond the basics had been used. They state that in studies of the receptor molecules, the researchers "assumed the hypothesis of basic tastes and collected data to support it and the labeled-line hypothesis, but did not test the hypotheses." **Majid & Levinson** also cite the need for a larger array of taste stimuli beyond the basics. I suggest the employment of systematic variations of taste stimuli of some variety, at least beyond the four basics (sect. 5.4). And now it has been shown that the receptor cells are broadly tuned (Tomchik et al. 2007).

There have been many attempts to find the groupings required by the basic taste model. Many researchers, including **Scott** herein, have sought these groups through improper use of mathematical techniques such as multidimensional scaling, cluster analysis, and factor analysis (sect. R5.3; sect. 4.2.2). **Fox**, **Logue**, and **Scott** cite the findings of CNS areas devoted to particular basic tastes as supportive of the basic tastes model. It is probable that when searching for labeled areas, using basic tastes *or others*, they will be found. The necessary controls using other than basic tastes are lacking.

All such findings supporting the basic tastes idea, and most of those of the last century, were directed by the context of the basic tastes hypothesis in which they were generated. Thus, this model has very extensively and uncritically supported itself.

R7. Informing ourselves more broadly

The value of a broad view of taste is emphasized in several commentaries, such as those by **Booth** and **Gallo**, and others mentioned next. They represent the systems approach to science in distinction to the reductionistic or molecular approach. Just as psychophysical, neural, and receptor events must inform each other, related areas of study also provide important insights into the realities of the nature of taste. However, **Handel** cautions that comparisons between systems can be problematic when the systems differ, and **Scott** laments the broad applicability of the AFP theory beyond taste (sects. R4.2 and R9).

R7.1. Insights from studies of language

A primary thesis of the article is that the discrete nature of our language may inappropriately drive us to use the concept of a few discrete basic tastes (sects. 3.2.1 and 4.1). But several commentators also point out that language may properly elucidate certain aspects of taste.

Di Lorenzo & Chen usefully intertwine our words, psychophysics, and neural organization, such that the basic taste words may reveal our perceptions of genuine aspects of neural organization. This idea would be interesting to formalize as a testable hypothesis. Their position relates to the *relativism* and *nominalism* of **Belpaeme** and **Majid & Levinson**, discussed next.

From studies of color-naming, **Belpaeme** (sects. R3 and R9) takes a *linguistic-relativism* position that our language modifies innate biologically driven perceptual organization, and can shed light on this organization. He contrasts this with my *universalistic* approach, which is that the taste sensations are driven only by biology. He describes procedures in color-naming that could be useful in taste studies.

In a related view, **Majid & Levinson**'s *nominalist* position is that words actually create valid basic taste categories (sect. R5.2), and that this has cross-cultural support. For example, the same confusions between bitter and sour exist across cultures, and common patterns of taste words across cultures support the idea of umami and others as basics. He contrasts this with my *realist* position, which is that events – here tastes – exist independently of our naming them. These views of **Majid & Levinson** and **Belpaeme** seem strongly related to that of **Cutting** (sect. R5.2) on the force of our culture on the organization of taste.

This commonality of taste perceptions across cultures is neurally meaningful. For example, bitter and sour stimuli produce somewhat similar across-fiber patterns, and thus they can be confused with each other. Why they have separate names is important, but that does not mean that they are as discriminable from each other as either is from a sweet stimulus. Useful taste names should not be taken as a rejection of a taste continuum any more than color names are a rejection of a color continuum; but neither should these names be taken as proof of only a few basic sensations.

On the other hand, in his unique search for definitions based on his experience with color vision (sect. R5.2), **Cutting** shows how only the cultural definition provided by language gives support for the idea of basic tastes, and that the definitions based on stimulus mixtures and labeled lines are not supportable. He raises the good questions of how one definition may be compared to others, or support be found between them, and comments that they certainly should not be confused with each other.

R7.2. Insights from the study of emotion

Sander describes several useful and interesting parallels between the studies of emotion and taste. In a comparison with taste, there are currently considered by some to be six basic emotions; this is directly in line with Miller's prediction of about that number (sect. 2.3). The idea of neural areas for basic tastes (sect. R5.3) has suggested that neural areas may also be found for specific emotions. Sander shows these arguments to be problematic, and that a continuum of emotions is a more reasonable view, as suggested for taste in the target article (sects. 6.3 and 8.4.2). As the two fields seem to be somewhat in the same position, he suggests that better communication between them would be helpful.

Importantly, the prior categorization of emotions into basic groups is being questioned rather than assumed, an obviously good tactic for basic tastes.

R7.3. Insights from a broader view of sensory input

Many commentators advocate the advantages of taking broader views across sensory systems. **Handel** makes useful comparisons with audition, and **Belpaeme**, **Cutting**, **Fox**, **Handel**, **Hilbert**, **Logue**, and **Stillman** with color vision. The AFP theory applies across sensory systems (sect. 8.4.2).

As an informative example of the utility of a broad point of view, **Roessner et al.** point to the relationships between taste and its close ally, olfaction. We have much to gain from careful comparisons of the two. Obviously, taste stimuli have olfactory components, taste and olfaction cooperate in food intake and other functions, and they are both chemical senses.

Given this close cooperation, it is informative to note that they are anatomically very separate at the input end; taste is directed into the hindbrain and moves anteriorly into the forebrain, in company with vision, audition, and somesthesis. Olfaction, the most ancient of the senses, enters and forms the most anterior part of the brain. But even though separate, taste and olfaction seem driven to cooperate; how and why this cooperation happens is certainly worthy of study.

Olfaction is not the only sense that cooperates with taste. For example, it is clear that input into the hindbrain taste relay comes not only from olfactory input (Van Buskirk & Erickson 1977a), but also from the nasal trigeminal system (Van Buskirk & Erickson 1977b) and from the stomach (Glenn & Erickson 1976; sect. 8.5.4). The study of taste would certainly benefit from a broader view of interactive sensory inputs.

R8. Critique of the basic tastes model

Some critiques of the basic taste format are brought together here in brief form. Foremost, this model has directed research and understanding throughout the history of taste. The simplicity and convenience of this model has made it very attractive. However, **Stillman** suggests that the labeled-line idea may not be as broadly accepted as I indicate.

As a *primary criticism* of this model, **Kennedy & Gonzalez** note that good definitions are an essential requirement for the evaluation of models, and that the basic tastes model is quite undefined. The lack of defined linking hypotheses for the interactions between different areas of research is part of this problem (sect. 5.4). But as **Scott** notes, these weak or missing definitions facilitate support for the model.

The lines of evidence that have been used to *support* the basic tastes model include all psychophysical studies that use only basic tastes (sect. 3.2.1); the idea of groupings (sect. R5.3; sect. 3.2.3); the labeling of broadly tuned neurons or neural areas by their best stimuli by **Di Lorenzo & Chen**, **Fox**, **Logue**, and **Scott**; and **Logue**'s conflation of basic colors and tastes. **Cutting** finds support for basic tastes only in their cultural definition.

R9. Critique of the across-fiber pattern model

As with the critique of the basic tastes model (sect. R8), the relevant aspects of the AFP model that were detailed elsewhere are briefly compiled here.

Concerning the *breadth* of the AFP model's applications, **Scott** (sect. R4) complains that I over-reach in proposing that all sensory messages are encoded in patterns. But a good hypothesis covers large areas of investigation, thus providing parsimony of concepts. In this sense, the across-fiber pattern is a good model (Erickson 2000; 2001) in that the nervous system will probably stick with a good method of representing information once it has found one, and the AFP model applies to all systems; both vision and taste, as well as movement, are built on the same principles, as are fish, fowl, and elephants. Of course, retinal disparity and sensitivity to differences in timing of auditory inputs are quite unique, but still the AFP model is appropriate for them.

Handel, Hilbert, and **Stillman** doubt that the across-fiber pattern model is appropriate for color vision at the central levels (beyond the receptors); however, these neurons are as broadly tuned across wavelengths as are the receptors, and thus fit the AFP model. **Sander**'s review of the study of emotions suggests the across-fiber pattern model's breadth of application.

Lemon raises the issue of *quantifiability* as important for a model. The AFP model is clearly quantifiable, giving predictions for test (sects. 6 and 7).

Young's model is based on the idea of *economy* of neural resources, so this very important asset is part of the AFP model (sect. 8).

Predictions are an essential part of a good hypothesis (sect. R4; sects. 6 and 7). The AFP model is strongly predictive of a variety of findings. These include the probability of a *continuum* underlying the sense of taste (sect. 6.3), denied by **Handel** and **Stillman**, but supported by **Sander** via the emotions; *broad* tuning of receptors and neurons in some nontopographic systems such as taste; *narrow tuning* of receptors and neurons in topographic systems such as location in somesthesis and vision; compatibility with a *temporal code*; and the existence of *types* of receptors and afferents in nontopographic modalities such as color and taste. **Scott** has over time cited the evidence both for and against typologies as denials of the across-fiber pattern model (sect. 5.4).

The idea that taste mixtures could be perceived as *singular* has been successfully tested (sect. R5.9; sects. 6 and 7). And **Hilbert** points out that colors are singular – a successful prediction from the across-fiber pattern theory.

R10. Misunderstandings about the across-fiber pattern model

The AFP theory is very largely misunderstood. This is clearly borne out in the diversity of viewpoints expressed in the commentaries. I hope that this brief discussion will provide some clarity.

R10.1. Typologies/groupings

A number of important differences appeared among the commentaries on the relationships between across-fiber pattern coding and groupings.

The AFP model is designed for the representation of information broadly throughout the nervous system, not just for taste (sect. R58; sect. 8). The general requirement for typologies in this model derives from the paucity of receptors or neurons available in nontopographic modalities, such as color vision and taste. Also, the body might find it too genetically expensive to generate many different pigments, each specifically or maximally sensitive to only a very small section of the continuum – or to generate a receptor for each tasteable listing in the Merck Index. Thus, the representations of colors and tastes are argued to employ a few broad and cooperative types of receptors and neurons.

On the other hand, in the topographic modalities, there are very many neurons available to encode the spatial maps of location across the retina and skin. It would be anatomically difficult to have each of these be broadly tuned across the body; for example, a "nose-tip-best" neuron extending its gradually descending sensitivity down to the ankles. And, because of the generosity of neurons, there would be sufficient neural mass generated by point stimulation of the skin to provide for discrimination of location (sect. 6.4). For both reasons, groupings are not called for, and are indeed counter-productive, for topographic modalities.

Thus, as pointed out from 40 years ago (Erickson 1963; 1968) to the present (Erickson 2000; 2001; and the present article), the AFP theory is not silent on the issue of typologies as **Scott** avers, but instead is very explicit. The intent is to be sufficiently explicit that the idea can be further considered and tested.

Di Lorenzo & Chen point out that although groupings have not been defined or demonstrated (**Lavine**), it does not mean that they will not be; certainly true (sect. 8.5.1). But instead of a search for any typology, which must succeed, I hope that the rationale for groupings and their definitions will first be sufficiently explicated that the idea can be tested. Groupings are not contrary to across-fiber patterning and are the definition of labeled-line coding (sects. 4.2 and 8.5.1).

Lemon suggests that the AFP theory needs groupings to get unique patterns of neural activity. But unique patterns underlie all discriminable inputs whether or not there are groupings. The across-fiber patterns for each discriminable tactile stimulus or auditory frequency are unique, but there are no groupings of these neurons.

Interestingly, **Handel** gives a rationale different from Young's for the neural typologies in color, and the lack thereof for auditory tones. He points out that differences in the physical characteristics of the stimuli demand three types of color receptors and many types for tones. The fact that the former is nontopographic and the latter is topographic leads to the same conclusions from the AFP theory of taste. How these two disparate orientations come to the same conclusion is an interesting question.

R10.2. Breadth of tuning

The fact that neurons are broadly tuned is generally accepted, but it is often a cause of broad concern. It may be that it is intuitively difficult to see how this breadth is anything but noise that needs to be silenced.

Di Lorenzo & Chen take this view in their claim that breadth of tuning results in a loss of information. This is addressed in section 6.4 where breadth is shown to be the basis for the subtle coding of large amounts of information, and previously, where it was shown that breadth of tuning causes no loss of information (Erickson 1968, Fig. 2). In brief, as breadth increases, the neural mass increases, whereas the neural mass differences – the basis of discrimination – remain constant (sect. 6.4). This happens because recruitment of additional neurons as breadth of tuning increases just compensates for the loss of neural mass differences obtained from each neuron.

One approach to clearing up the noise, as voiced by **Di Lorenzo & Chen** and **Fox**, is that the nervous system might interpret all activity in broadly tuned neurons – whatever stimulus caused it – as representing their "best stimulus," making them labeled lines. Similarly, **Stillman** defines any well-identified group as representing labeled lines, even if broadly – tuned, such as color receptors. But even with such blunt tuning, the color receptors still provide for acuity approaching 1 mμ – expected only in the AFP model.

Scott accepts any narrowly tuned neuron as a labeled line. He claims that I should admit that this narrowness of tuning, evident in topographic systems, is an exception to across-fiber patterning. But the tuning there is still much too broad to account for the accuracy of tactile localization (sects. R5.8 and R10.1), as was noted by Adrian, Mountcastle, and Sperry, as well as many others (see Erickson 2001); each of these scientists saw the need for a version of across-fiber patterning even for this "narrowly tuned" system.

Both broad and narrow tuning require AFP coding (sects. 8.4 and 8.5).

R10.3. Color vision

The analogy between the neural coding for color and that for taste is a fairly common theme among the commentators. That the form of the neural representation of color changes from three bell-shaped neural response functions at the receptor level, to a two (or four) opponent process representation beyond, causes **Handel**, **Hilbert**, and **Stillman** to question whether the AFP model could hold throughout the visual system. The tuning is broadly bell-shaped in the receptors, and broadly "S"-shaped centrally, with the Ss lying down across the wavelength dimension, inhibitory towards one end of the wavelength continuum, and excitatory towards the other (De Valois 1960).

The important aspect of neural response functions for color is that they be broad and simple, and indeed this is their characteristic peripherally and centrally. The AFP model is not concerned with the shape of the function, and thus is equivalently competent to represent wavelength both at the receptor level and beyond. Color is not the only dimension represented by other than simple bell-shaped neural response functions; for a review see Erickson (2001).

R10.4. Temporal codes

Di Lorenzo & Chen criticize the AFP model for excluding the possibility of temporal coding, and **Lemon** also raises this question. However, the across-fiber pattern model includes temporal coding (sect. 8.5.2; Erickson 2001). On the other hand, and from a more neutral perspective, it might have been pointed out that labeled lines cannot use information in a temporal pattern because their meaning is defined only by their best stimulus (sect. R5.4). The equation of both labeled lines and across-fiber patterns as spatial models (sect. R5.6) glosses over their very substantial differences, and should not be used to rule out temporal patterns in across-fiber pattern coding.

R10.5. Quantification

An important asset of the across-fiber pattern model is that it is inherently quantifiable, for example, in providing predictions about intensity thresholds, discrimination between intensity levels, and discriminability among different tastants (sect. 6.4). But **Lemon** suggests that some stimuli present rather similar across-fiber patterns that are not compatible with their perceptual distinctness. For example, although HCl and QHCl can be easily discriminated, the across-fiber patterns they produce are not as distinct as that caused by many other pairs of stimuli. There may be two issues here. On the one hand, these stimuli are similar in eliciting avoidance, and thus some similarity in their across-fiber patterns might be expected. On the other hand, they are motivationally charged stimuli, encouraging a high level of behavioral differentiation between them when needed. **Gallo**'s data on the rat's ability to pick out individual taste cues in a mixture suggests that quinine and HCl might be highly discriminated when this is demanded. Whatever the case, the across-fiber pattern model lays itself open to tests of its quantitative estimates of the differences between stimuli.

R11. Questions and comments about the experiment

This article is intended to advocate for hypotheses and basic terms that are sufficiently clear that they can be properly tested. Such a control study is offered to make the possibility of tests clear (sect. 7). This preliminary study is intended more to encourage other more fulsome studies than to settle the questions asked.

Several commentaries on this study suggest that there is a strong tendency to accept the basic taste idea rather than to test it. For example **Booth**, and **Di Lorenzo & Chen**, as well as others who previously viewed the article, point out that I should not have claimed that the nonbasic tastes could account for the various comparison stimuli; instead, I should have acknowledged that these tastes are effective only because they are composed of the basic tastes. *This criticism assumes the validity of the basic tastes idea while testing it! It suggests that control experiments are not called for because we know the basic tastes idea is true!* But, by the neutral position required in this situation, it could as well be claimed that the basic stimuli are only effective because they are composed of the innately effective nonbasic stimuli (sect. 7.10). This demonstrates that the basic tastes idea does, in fact, exert strong control over our research and understanding of taste. It is so strong, that there is evidently no desire to perform the required control tests.

Di Lorenzo & Chen state that, because the accounting by the basic tastes was not total, I infer other tastes. I do not mean to suggest this. Instead, I suggest that there may be a lack of clarity in tastes that limits complete accountings (sect. 7.7.2). And I suggest that a "completion effect" may interfere with the strength of any accounting seen (sect. 7.8, and the Appendix).

Di Lorenzo & Chen also cite the common view that the variety of words offered by the subjects in the experiment to describe the tastants (sect. 7.7.3) indicates that nongustatory inputs (thermal, tactile, etc.) give these tastants their distinguishing character; they are simply composites of the basics adulterated by nontaste inputs. It may be that this defense of the basic position is used more often than the missing facts might indicate, and should be examined in each case rather than assumed.

Logue suggests that the basic tastes idea is supported by the data because the basic taste stimuli (but not the basic words) are better than the nonbasic stimuli. But the definition of basic tastes (sect. R5.2) is that *they, and only they, totally account* for other stimuli. Then the model fails because (a) the accounting by the basics is not total; in fact, the basic words do rather poorly, and (b) the nonbasic stimuli are rather effective – they certainly do not lie along the baseline as good nonbasics should. Also, she points out a fault that the data were not treated statistically; but the definition of basics is absolute rather than statistical, as noted by **Hilbert**; what statistical tests would be appropriate?

Hilbert correctly points out that the protocol using words has no real control. However, the use of the basic words and stimuli as *equivalent* agents of the basic taste model permeates the literature, so they might well be compared as in this experiment. Still, I agree with his complaint, and hope the efficiency of a variety of words and stimuli to account for different tastes receives further study in unbiased, controlled settings.

R12. The "across-fiber pattern" term

Lemon uses the term "across-neuron pattern" and **Warren** uses "cross-fiber pattern," both evidently referring to the same idea as in "across-fiber pattern" – but I am not at all certain about this. And a number of other terms outside the field of taste are being used that probably have the same meaning as "across-fiber pattern," such as "combinatorial" coding in olfaction, and others (sect. 8.4.2). I suggest that to the extent that several terms refer to the same idea, it would be helpful to use the same term. This would also have the beneficial effect of requiring stringent definitions of each of these terms to determine if they do indeed refer to the same idea.

I would like to clarify my role in the across-fiber pattern model. **Logue** attributes the term "across-fiber pattern" to Pfaffmann (1941). Although he discussed the implications of patterns of activity in parallel neurons (1959), Pfaffmann did not claim that term. Throughout his career he was primarily concerned with the meaning of activity in broadly tuned "best stimulus" neuron types, which he considered to be labeled lines (Pfaffmann 1978; Pfaffmann et al. 1976; 1979). This idea was developed further by his student, Frank. My role was to realize the great strength and broad applicability of the across-fiber pattern idea, to realize that it had been discovered by many scientists in many or all neural systems since Young – and continues to be discovered, and advocated that it be given one name to the extent to which it is indeed one idea (Erickson 1963; 1968; 1974; 1978; 1982a; 1984b; 2001).

R13. Conclusion

The commentaries reinforce my view that we are indeed in the grip of the obscure and overshadowing idea of basic tastes; this gray eminence directs our research and thought whether we are aware of it or not. We clearly do not know what this core concept means, but we are so comfortable with it we do not want to raise any questions. We certainly have not tested it, even though testing of the core hypotheses – as distinct from data collection – is an absolutely essential part of science. But if someone thought to test it, how would they start? They would face the basic problems Hanig (sect. 3.1) and Henning (sect. R2; sects. 4.1.3 and 6.3) faced; what stimuli other than the basics could they use, and against what other hypothesis would they test it? "But what else could we do?" should not be a problem, but a realization of the necessity to search for a clear direction.

Such issues, which I have tried to emphasize for over 40 years, appear of little interest to researchers in taste; for example, although the across-fiber pattern theory is clear, no definitions for "basic tastes" have been forthcoming, or even concern shown. But if anyone is indeed concerned, I have a suggestion. Someone could start an on-line *Gustopedia*. Someone might offer a testable hypothesis, or a definition, or a statement of how one definition or level might relate to another. Another person could add their constructive comments. Studies from other areas of science could add perspective. The expression of differences would be most useful. Eventually some clarity could evolve to provide the firm basis required of any science.

References

Letters "a" and "r" appearing before authors' initials refer to target article and response, respectively.

Accolla, R., Bathellier, B., Petersen, C. C. & Carleton, A. (2007) Differential spatial representation of taste modalities in the rat gustatory cortex. *Journal of Neuroscience* 27(6):1396–1404. [EAF]

Adrian, E. D. (1955) The action of the mammalian olfactory organ. The Seman Lecture. *Journal of Laryngology and Otology* 70:1–14. [aRPE]

Aldenderfer, M. S. & Blashfield, R. K. (1984) *Cluster analysis: Quantitative applications in the social sciences*, ed. J. L. Sullivan & R. G. Niemi. Sage University Papers, Sage Publications. [aRPE]

Amoore, J. E., Johnston, J. W. & Rubin, M. (1964) The stereochemical theory of odor. *Scientific American* 210(2):42–49. [AWL]

Amrein, H. & Bray, S. (2003) Bitter-sweet solution in taste transduction. *Cell* 112:283–87. [aRPE]

Axel, R. (2005) Scents and sensibility: A molecular logic of olfactory perception (Nobel lecture). *Angewandte Chemie Internationale* 44(38):6110–27. [VR]

Balleine, B. W., Espinet, A. & González, F. (2005) Perceptual learning enhances retrospective revaluation of conditioned flavor preferences in rats. *Journal of Experimental Psychology. Animal and Behavioral Processes* 31(3):341–50. [MG]

Barlow, H. B. (2001) Redundancy reduction revisited. *Network: Computation in neural systems* 12:241–53. [SH]

Bartoshuk, L. M. (1988) Taste. In: *Stevens' handbook of experimental psychology, vol. 1*, 2nd edition, ed. R. C. Atkinson, R. J. Herrnstein, G. Lindzey & R. D. Luce, pp. 461–99. Wiley. [arRPE, AWL]

Bear, M. F., Connors, B. W. & Paradiso, M. A. (1996) *Neurosciences: Exploring the brain*. Williams and Wilkins. [aRPE]

Beidler, L. M. (1974) The chemical senses: Gustation and olfaction. In: *Medical physiology*, 13th edition, ed. V. B. Mountcastle, pp. 536–50. Mosby. [aRPE]

Belpaeme, T. & Bleys, J. (2005) Explaining universal colour categories through a constrained acquisition process. *Adaptive Behavior* 13(4):293–310. [TB]

Berlin, B. & Kay, P. (1969) *Basic color terms: Their universality and evolution*. University of California Press. [TB, JEC, AM]

Bernstein, D. A., Pener, L. A., Clarke-Stewart, A. & Roy, E. J. (2006) *Psychology*. Houghton Mifflin. [aRPE]

Birch, G. G. (1977) Taste properties of sugar molecules. In: *Proceedings of the Sixth International Symposium on Olfaction and Taste*, ed. J. Le Magnen & P. Mac Leod, pp. 27–33. Information Retrieval. [aRPE]

Booth, D. A. (1994) Recognition of objects by physical attributes. Continuing Commentary on: G. R. Lockhead, Psychophysical scaling: Judgments of attributes or objects? *Behavioral and Brain Sciences* 17:759–60. [DAB]

(1995) Cognitive processes in odorant mixture assessment. *Chemical Senses* 20:639–43. [DAB]

(2005) Perceiving the texture of a food: Biomechanical and cognitive mechanisms and their measurement. In: *Food colloids: Interactions, microstructure and processing*, ed. E. Dickinson, pp. 339–55. Royal Society of Chemistry, Cambridge. [DAB]

Booth, D. A. & Freeman, R. P.J. (1993) Discriminative measurement of feature integration in object recognition. *Acta Psychologica* 84:1–16. [DAB]

Booth, D. A., Freeman, R. P. J. & Kendal-Reed, M. S. (1995) Recognition of aromas by subconscious cognitive integration of receptor patterns. In: *Aroma: perception, formation, evaluation*, ed. M. Rothe & H.-P. Kruse, pp. 101–16. Deutsches Institut für Ernährungsforschung, Potsdam. [DAB]

Booth, D. A., Konle, M., Wainwright, C. J. & Sharpe, O. (submitted). Umami (savory) taste does not need a 5th type of gustatory receptor on the human tongue. [DAB]

Booth, D. A., Mobini, S., Earl, T. & Wainwright, C. J. (2003) Consumer-specified instrumental quality of short-dough cookie texture using penetrometry and break force. *Journal of Food Science: Sensory and Nutritive Qualities of Food* 68(1):382–87. [DAB]

Boring, E. G. (1942) *Sensation and perception in the history of experimental psychology.* Appleton-Century-Crofts. [aRPE]

Boughter, Jr., J. T., & Smith, D. V. (1998) Amiloride blocks acid responses in NaCl-best gustatory neurons of the hamster solitary nucleus. *Journal of Neurophysiogy* 80:1362–72. [aRPE]

Boughter, Jr., J. T., St. John, S. J. & Smith, D. V. (1999) Neural representation of the taste of NaCl and KCl in gustatory neurons of the hamster solitary nucleus. *Journal of Neurophysiology* 81:2636–46. [aRPE]

Boyle, R. (1663/1999) Some considerations touching the usefulness of experimental natural philosophy: The first part. In: *The works of Robert Boyle, vol. 3*, ed. M. Hunter & E. B. Davis, pp. 189–290. Pickering and Chatto. [JEC]

Brasser, S. M, Mozhui, K. & Smith, D. V. (2005) Differential covariation in taste responsiveness to bitter stimuli in rats. *Chemical Senses* 30:793–99. [aRPE]

Breslin, P. A. S., Beauchamp, G. K. & Pugh, E. N. (1996) Monogeusia for fructose, glucose, sucrose and maltose. *Perception and Psychophysics* 58:327–41. [DAB]

Brillat-Savarin, J. A. (1886/1971) *The physiology of taste*, p. 38. North Point Press. Translated by M. F. K. Fisher, The Heritage Press (1949). [aRPE]

Buck, L. B. (2004) Olfactory receptors and odor coding in mammals. *Nutrition Review* 62:S184–88; S224–41. [aRPE]

Buhusi, C. V. (2000) The across-fiber pattern theory and fuzzy logic: A matter of taste. *Physiology and Behavior* 69:97–106. [aRPE]

Caicedo, A., Kim, K.-N. & Roper, S. D. (2002) Individual mouse taste cells respond to multiple chemical stimuli. *Journal of Physiology* 544:501–09. [aRPE]

Caicedo, A. & Roper, S. D. (2001) Taste receptor cells that discriminate between bitter stimuli. *Science* 291:1557–60. [aRPE]

Calder, A. J., Lawrence, A. D. & Young, A. W. (2001) Neuropsychology of fear and loathing. *Nature Reviews Neuroscience* 2:352–63. [DS]

Caprio, J. (1978) Olfaction and taste in the channel catfish: An electrophysiological study of the responses to amino acids and derivatives. *Journal of Comparative Physiology, A* 123:375–81. [aRPE]

Chale-Rush, A., Burgess, J. R. & Mattes, R. D. (2007) Evidence for human orosensory (taste?) sensitivity to free fatty acids. *Chemical Senses* 10:1093. [aRPE]

Chamberlain, A. F. (1903) Primitive taste words. *American Journal of Psychology* 14:146–53. [AM]

Chandrashekar, J., Hoon, M. A., Ryba, J. P. & Zucker, C. S. (2006) The receptors and cells for mammalian taste. *Nature* 444:288–94. [aRPE, EAF, LMK]

Chang, F. C. & Scott, T. R. (1984) Conditioned taste aversions modify neural responses in the rat nucleus tractus solitarius. *Journal of Neuroscience* 4(7):1850–62. Available at: http://www.jneurosci.org/cgi/reprint/4/7/1850 [EAF, TRS]

Covey, E. (2000) Neural population coding and auditory temporal pattern analysis. *Physiology and Behavior* 69:211–20. [aRPE]

Critchtey, H. D. & Rolls, E. T. (1996) Responses of primate taste cortex neurons to the astringent tastant tannic acid. *Chemical Senses* 21:135–45. [aRPE]

Dahl, M., Erickson, R. P. & Simon, S. A. (1997) Neural responses to bitter compounds in rats. *Brain Research* 756:22–34. [aRPE]

Damak, S., Rong, M., Yasumatsu, K., Kokrashvili, Z., Varadarajan, V., Zou, S., Jiang, P., Ninomiya, Y. & Margolskee, R. F. (2003) Detection of sweet and umami taste in the absence of taste receptor T1r3. *Science* 301(5634):850–53. . Epub 2003 Jul 2017 available at: http://www.sciencemag.org/cgi/content/full/301/5634/850. [EAF]

Danilova, V., Danilov, Y., Roberts, T., Tinti, J. M., Nofre, C. & Hellekant, G. (2002) Sense of taste in a new world monkey, the common marmoset: Recordings from the chorda tympani and glossopharyngeal nerves. *Journal of Neurophysiology* 88(2):579–94. Available at: http://jn.physiology.org/cgi/content/full/88/2/579. [EAF]

Darwin, C. (1872) *The expression of emotions in man and animals*. Murray. [DS]

Dawkins, R. (1976) Preface to 1989 edition. In: *The selfish gene*, 2nd edition, pp. viii–xi. Oxford University Press. [EAF]

De Valois, R. & De Valois, K. K. (1988) *Spatial vision*. Oxford University Press. [SH]

De Valois, R. L. (1960) Color vision mechanisms in the monkey. *Journal of General Physiology* 43:115–28. [rRPE]

De Valois, R. L., Abramov, I. & Jacobs, G. H. (1966) Analysis of response patterns of LGN cells. *Journal of the Optical Society of America* 56(7):966–77. [TB]

DeFazio, R. A., Dvoryanichikov, G., Maruyama, Y., Kim, J. W., Pereira, E., Roper, S. D. & Chaudhari, N. (2006) Separate populations of receptor cells and presynaptic cells in mouse taste buds. *Journal of Neuroscience* 26:3971–80. [LMK]

Delwiche, J. (2004) The impact of perceptual interactions on perceived flavor. *Food Quality and Preference* 15(2):137–46. [VR]

Descartes, R. (1998) *Les passions de l'âme*. Flammarion. Originally published in 1649 [DS]

Dethier, V. G. (1974) The specificity of the labellar chemoreceptors of the blowfly and the response to natural foods. *Journal of Insect Physiology* 20:1859–69. [LMK]

(1976) The hungry fly: A physiological study of the behaviour associated with feeding. Harvard University Press. [LMK]

Di Lorenzo, P. M. (1986) Neural and behavioral responsivity to ethyl alcohol as a tastant. *Alcohol* 3:55–61. [aRPE]

Di Lorenzo, P. M. & Victor, J. D. (2003) Taste response variability and temporal coding in the nucleus of the solitary tract of the rat. *Journal of Neurophysiology* 90:1418–31. [PMDL, CHL]

(2007) Neural coding mechanisms for flow rate in taste-responsive cells in the nucleus of the solitary tract of the rat. *Journal of Neurophysiology* 97(2):1857–61. [PMDL]

Doetsch, G. S. & Erickson, R. P. (1970) Synaptic processing of taste-quality information in the nucleus solitarius of the rat. *Journal of Neurophysiology* 33:490–507. [aRPE]

Dowman, M. (2006) Explaining color term typology with an evolutionary model. *Cognitive Science* 31(1):99–132. [TB]

Dravnieks, A., Bock, F. C., Powers, J. J., Tibbetts, M. & Ford, M. (1978) Comparison of odors directly and through profiling. *Chemical Senses* 3(2):191–225. [VR]

Drivonikou, G. V., Kay, P., Regier, T., Ivry, R. B., Gilbert, A. L., Franklin, A. & Davies, I. R. L. (2007) Further evidence that Whorfian effects are stronger in the right visual field than the left. *Proceedings of the National Academy of Sciences of the United States of America* 104(3):1097–02. [TB]

Duchamp-Viret, P., Duchamp, A. & Chaput, M. A. (2000) Peripheral odor coding in the rat and frog: Quality and intensity specification. *Journal of Neuroscience* 20(6):2383–90. [VR]

(2003) Single olfactory sensory neurons simultaneously integrate the components of an odour mixture. *European Journal of Neuroscience* 18(10):2690–96. [VR]

Eggers, S. C., Acree, T. E. & Shallenberger, R. S. (2000) Sweetness chemoreception theory and sweetness transduction. *Food Chemistry* 68:45–49. [aRPE]

Ekman, P. (1992) An argument for basic emotions. *Cognition and Emotion* 6:169–200. [DS]

(1999) Basic emotions. In: *Handbook of cognition and emotion*, ed. T. Dalgleish & M. Power, pp. 45–60. Wiley. [DS]

Ellsworth, P. C. & Scherer, K. R. (2003) Appraisal processes in emotion. In: *Handbook of the affective sciences*, ed. R. J. Davidson, H. Goldsmith & K. R. Scherer, pp. 572–95. Oxford University Press. [DS]

Erickson, R. P. (1963) Sensory neural patterns and gustation. In: *Olfaction and taste, vol. I*, ed. Y. Zotterman, pp. 205–13. Pergamon. [arRPE]

(1967) Neural coding of taste quality. In: *The chemical senses and nutrition*, ed. M. Kare & O. Maller, pp. 313–27. Johns Hopkins Press. [arRPE]

(1968) Stimulus coding in topographic and nontopographic afferent modalities: On the significance of the activity of individual sensory neurons. *Psychology Review* 75:447–65. [arRPE]

(1974) Parallel "population" neural coding in feature extraction. In: *The neurosciences: Third study program Cambridge*, ed. F. O. Schmitt & F. G. Worden, pp. 155–69. MIT Press. [arRPE]

(1977) The role of "primaries" in taste research. In: *Olfaction and taste, vol. 6*, ed. J. Le Magnen & P. MacLeod, pp. 369–76. Information Retrieval. [arRPE, JAS]

(1978) Common properties of sensory systems. In: *Handbook of behavioral neurobiology, vol. 1*, ed. R. B. Masterton. Plenum. [arRPE]

(1982a) Studies on the perception of taste: Do primaries exist? *Physiology and Behavior* 28:57–62. [aRPE]

(1982b) The "across-fiber pattern" theory: An organizing principle for molar neural function. In: *Contributions to sensory physiology*, *vol.* 7, ed. W. D. Neff, pp. 79–110. Academic Press. [arRPE]

(1984a) Ohrwall, Henning and von Skramlik: The foundations of the four primary positions in taste. *Neuroscience and Biobehavioral Reviews* 8:233–41. [arRPE]

(1984b) On the neural bases of behavior. *American Scientist* 233–41. [aRPE]

(1985a) Definitions: A matter of taste. In: *Taste, olfaction and the central nervous system*, ed. D. Pfaff, pp. 129–50. Rockefeller University Press. [aRPE]

(1985b) Grouping in the chemical senses. *Chemical Senses* 10:333–40. [aRPE]

(1986) A neural metric. *Neuroscience and Biobehavioral Reviews* 10:377–86. [aRPE]

(2000) The evolution of neural coding ideas in the chemical senses. *Physiology and Behavior* 69:3–13. [arRPE]

(2001) The evolution and implications of population and modular neural coding ideas. *Progress in Brain Research* 130:9–29. [arRPE]

Erickson, R. P. & Covey, E. (1980) On the singularity of taste sensations: What is a taste primary? *Physiology and Behavior* 25:527–33. [aRPE]

Erickson, R. P., Covey, E. & Doetsch, G. S. (1980) Neuron and stimulus typologies in the rat gustatory system. *Brain Research* 196:513–19. [aRPE]

Erickson, R. P., Di Lorenzo, P. M. & Woodbury, M. A. (1994) Classification of taste responses in brain stem: Membership in fuzzy sets. *Journal of Neurophysiology* 71:2139–50. [aRPE]

Erickson, R. P., Doetsch, G. S. & Marshall, D. A. (1965) The gustatory neural response function. *Journal of General Physiology* 49:247–63. [aRPE]

Erickson, R. P., Priolo, C. V., Warwick, Z. S. & Schiffman, S. S. (1990) Synthesis of tastes other than the 'primaries': Implications for neural coding theories and the concept of 'suppression.' *Chemical Senses* 15:495–504. [aRPE]

Erickson, R. P., Rodgers, J. L. & Sarle, W. S. (1993) Statistical analysis of neural organization. *Journal of Neurophysiology* 70:2289–2300. [aRPE]

Erickson, R. P. & Schiffman, S. S. (1975) The chemical senses: A systematic approach. In: *Handbook of psychobiology*, ed. M. S. Gazzaniga & C. Blakemore, pp. 393–426. Academic Press. [aRPE]

Erickson, R. P., Schiffman, S. S., Doetsch, G. S., Di Lorenzo, P. M. & Woodbury, M. A. (1995) A fuzzy set approach to the organization of the gustatory system. *Primary Sensory Neuron* 1:65–80. [aRPE]

Erickson, R. P., Woodbury, M. A. & Doetsch, G. S. (1996) Distributed neural coding based on fuzzy logic. *Information Sciences* 95:103–12. [aRPE]

Fairchild, M. D. (1998) *Color appearance models*. Addison-Wesley. [TB]

Frank, M. A. (1974) The classification of mammalian afferent taste nerve fibers. *Chemical. Senses and Flavor* 1:53–60. [aRPE]

(2000) Neuron types, receptors, behavior, and taste quality. *Physiology and Behavior* 69:53–62. [aRPE]

Freeman, R. P. J., Richardson, N. J., Kendal-Reed, M. S. & Booth, D. A. (1993) Bases of a cognitive technology for food quality. *British Food Journal* 95(9):37–44. [DAB]

Galindo-Cuspinera, V., Winning, M., Bufe, B., Meyerhof, W. & Breslin, P. A. (2006) TAS1R receptor-based explanation of sweet 'water-taste'. *Nature* 441:354–57. [LMK]

Gallo, M., Ballesteros, M. A., Molero, A. & Moron, I. (1999) Taste aversion learning as a tool for the study of hippocampal and non-hippocampal brain memory circuits regulating diet selection. *Nutritional Neuroscience* 2:277–302. [MG]

Ganchrow, J. R. & Erickson, R. P. (1970) Neural correlates of gustatory intensity and quality. *Journal of Neurophysiology* 33:768–83. [aRPE]

Gegenfurtner, K. R. & Sharpe, L. T. (1999) *Color vision: From genes to perception*. Cambridge University Press. [TB]

Geldard, F. A. (1964) The sense of taste. In: *The human senses*, pp. 295–323. Wiley. [aRPE]

Geran, L. C. & Travers, S. P. (2006) Single neurons in the nucleus of the solitary tract respond selectively to bitter taste stimuli. *Journal of Neurophysiology* 96:2513–27. [aRPE]

Gibson, J. J. (1979) *An ecological approach to visual perception*. Houghton Mifflin. [DAB]

Gilbert, A., Regier, T., Kay, P. & Ivry, R. (2006). Whorf hypothesis is supported in the right visual field but not the left. *Proceedings of the National Academy of Sciences* 103(2):489–94. [TB]

Gilbertson, T. A. (1998) Gustatory mechanisms for the detection of fat. *Current Biology* 8:447–52. [AM]

(2002) Hypoosmotic stimuli activate a chloride conductance in rat taste cells. *Chemical Senses* 27:383–94. [aRPE]

Gilbertson, T. A., Boughter, J. D., Zhang, H. & Smith, D. V. (2001) Distribution of gustatory sensitivities in rat taste cells: Whole-cell responses to apical chemical stimulation. *Journal of Neuroscience* 21:4931–41. [PMDL, aRPE, EAF]

Gilbertson, T. A., Fontenot, D. T., Liu, L., Zhang, H. & Monroe, W. T. (1997) Fatty acid modulation of K+ channels in taste receptor cells: Gustatory cues for dietary fat. *American Journal of Cell Physiology* 272:C1203–10. [aRPE]

Giza, B. K. & Scott, T. R. (1987a) Blood glucose level affects perceived sweetness intensity in rats. *Physiology & Behavior* 41(5):459–64. [EAF]

(1987b) Intravenous insulin infusions in rats decrease gustatory-evoked responses to sugars. *American Journal of Physiology* 252(5, Pt 2): R994–1002. Available at: http://ajpregu.physiology.org/cgi/reprint/252/5/R994 [EAF]

Giza, B. K. & Scott, T. R. & Vanderweele D. A. (1992) Administration of satiety factors and gustatory responsiveness in the nucleus tractus solitarius of the rat. *Brain Research Bulletin* 28(4):637–39. [CHL]

Gleason, H. A. (1961) *An introduction to descriptive linguistics*. Holt, Rinehart and Winston. [TB]

Glenn, J. F. & Erickson, R. P. (1976) Gastric modulation of gustatory afferent activity. *Physiology and Behavior* 16:561–68. [rRPE]

Gould, S. J. (1994) The persistently flat earth. *Natural History* 3:12–19. [aRPE]

Graham, R. B. (1990) *Physiological psychology*. Wadsworth. [aRPE]

Grandjean, D., Sander, D. & Scherer, K. R. (in press) Conscious emotional experience emerges as a function of multilevel, appraisal-driven response synchronization. *Consciousness and Cognition*. [DS]

Grobe, C. L. & Spector, A. C. (2006) A new method of assessing taste quality generalization in rats. *Chemical Senses* 31(5):A124. [CHL]

Hadley, K., Orlandi, R. R. & Fong, K. J. (2004) Basic anatomy and physiology of olfaction and taste. *Otolaryngologic Clinics of North America* 37(6):1115–26. [VR]

Hajnal, A., Takanouchi, K. & Norgren, R. (1999) Effect of intradoudenal lipid on parabrachial gustatory coding in awake rats. *Journal of Neuroscience* 19:7182–90. [TRS]

Halpern, B. P. (2002a) Taste. In: *Stevens' handbook of experimental psychology, vol. 1: Sensation and perception*, 3rd edition, ed. H. Pashler & S. Yantis, pp. 653–90. Wiley. [arRPE]

(2002b) What's in a name? Are MSG and umami the same? *Chemical Senses* 27:845–46. [aRPE]

Halpern, B. P. & Tapper, D. N. (1971) Taste stimuli: Quality coding time. *Science* 171:1256–58. [CHL]

Hamlyn, D. W. (1957) *The psychology of perception*. Routledge & Kegan Paul. [DAB]

Handel, S. (2006) *Perceptual coherence: Hearing and seeing*. Oxford University Press. [SH]

Hanig, D. P. (1901) Zur psychophysik des geschmackssinnes. *Philosophische Studien* 17:576–623. [aRPE, VR]

Hardin, C. L. & Maffi, L. (1997) *Color categories in thought and language*. Cambridge University Press. [TB]

Harrer, M. I. & Travers, S. P. (1996) Topographic organization of Fos-like immunoreactivity in the rostral nucleus of the solitary tract evoked by gustatory stimulation with sucrose and quinine. *Brain Research* 711(1–2):125–37. [EAF]

Hastie, T., Tibshirani, R. & Friedman, J. (2001) *The elements of statistical learning, data mining, inference, and prediction*. Springer. [ML]

Hellekant, G., Ninomiya, Y. & Danilova, V. (1998) Taste in chimpanzees. III: Labeled-line coding in sweet taste. *Physiology & Behavior* 65(2):191–200. [EAF]

Henning, H. (1916) Die qualitatenreihe des geschmacks (The quality series of taste). *Zeitschrift Psychologie* 74:203–19. (See Erickson 1984a for a translation.) [arRPE]

Hering, E. (1964) *Outlines of a theory of the light sense*. Harvard University Press. [TB]

Herness, S. (2000) Coding in taste receptor cells: The early years of intracellular recordings. *Physiology and Behavior* 69:17–27. [aRPE, LMK]

Herrnstein, R. J. & Boring, E. G. (1965) *A source book in the history of psychology*. Harvard University Press. [JEC]

Huang, A. L., Chen, X., Hoon, M. A., Chandrashekar, J., Guo, W., Trankner, D., Ryba, N. J. & Zuker, C. S. (2006) The cells and logic for mammalian sour taste detection. *Nature* 442(7105):934–38. [EAF]

Ikdea, K. (1909/2002) New seasonings. *Chemical Senses* 27:847–49. [AM]

Ishii, R. & O'Mahoney, M. (1987) Taste sorting and naming: Can taste concepts be misrepresented by traditional psychophysical labelling systems? *Chemical Senses* 12:37–51. [aRPE]

Izard, C. E. (2007) Basic emotions, natural kinds, emotion schemas, and a new paradigm. *Perspectives on Psychological Science* 2:260–80. [DS]

Jacobs, K. M., Mark, G. P. & Scott, T. R. (1988) Taste responses in the nucleus tractus solitarius of sodium-deprived rats. *Journal of Physiology* 406:393–410. [EAF, TRS]

James, W. (1890) *Principles of psychology, vol. I: The sources of error in psychology*, p. 194. Henry Holt. [aRPE]

Jameson, K. & D'Andrade, R. (1997) It's not really red, green, yellow, blue: An inquiry into perceptual color space. In: *Color categories in thought and language*, ed. C. L. Hardin & L. Maffi, pp. 295–319. Cambridge University Press. [TB]

Jameson, K. A. (2007) What is the role of computer modeling and evolutionary game theory in cross-cultural color categorisation research? Paper presented at the The Biennial Meeting of the Society for Psychological Anthropology, Manhattan Beach, CA., U.S.A., 2007. [TB]

Jiang, P., Cui, M., Snyder, L. A., Benard, L. M., Osman R., Max, M. & Margolskee, R. F. (2005) Identification of the cyclamate interaction site within the transmembrane domain of the human sweet taste receptor subunit T1R3. *Journal of Biological Chemistry* 280:34296–305. [LMK]

Jiang, P., Ji, Q., Liu, Z., Snyder, L. A., Benard, L. M., Margolskee, R. F. & Max, M. (2004) The cysteine-rich region of T1R3 determines responses to intensely sweet proteins. *Journal of Biochemistry* 270:45068–75. [LMK]

Judd, D. B., MacAdam, D. L. & Wyszecki, G. (1964) Spectral distribution of typical daylight as a function of correlated color temperature. *Journal of the Optical Society of America* 54:1031–40. [SH]

Kaiser, P. K. & Boynton, R. M. (1996) *Human color vision*. Optical Society of America. [DRH]

Kandel, E. R., Schwartz, J. H. & Jessell, T. M. (1991) Smell and taste: The chemical senses. In: *Principles of neural science*, 3rd edition, ed. J. Dodd & V. F. Castellucci, pp. 512–29. Elsevier/North-Holland. [aRPE]

Katz, D. B., Nicolelis, M. A. & Simon, S. A. (2002) Gustatory processing is dynamic and distributed. *Current Opinions in Neurobiology* 12(4):448–54. [PMDL]

Katz, D. B., Simon, S. A. & Nicolelis, M. A. (2001) Dynamic and multimodal responses of gustatory cortical neurons in awake rats. *Journal of Neuroscience* 21(12):4478–89. [PMDL, CHL]

Kay, P. & Regier, T. (2003) Resolving the question of color naming universals. *Proceedings of the National Academy of Sciences* 100(15):9085–89. [TB]

Kimble, G. A. (1996) *Psychology: The hope of a science*, p. 137. MIT Press. [aRPE]

Kruskal, J. B. & Wish, M. (1978) *Cluster analysis: Quantitative applications in the social sciences*, ed. E. M. Uslander. Sage University Papers, Sage Publications. [aRPE]

Kurlansky, M. (2002) *Salt: A world history.* Walker & Company. [JEC]

Lammens, J. M. G. (1994) A computational model of color perception and color naming. Unpublished doctoral dissertation, State University of New York at Buffalo. [TB]

Lashley, K. S. (1931) Mass action in cerebral function. *Science* 73:245–54. [aRPE]

Lawless, H. T., Stevens, D. A., Chapman, K. W. & Kurtz, A. (2005) Metallic taste from electrical and chemical stimulation. *Chemical Senses* 30:185–94. [aRPE]

Lemon, C. H. & Smith, D. V. (2005) Neural representation of bitter taste in the nucleus of the solitary tract. *Journal of Neurophysiology* 94(6):3719–29. [aRPE, CHL]

(2006) Influence of response variability on the coding performance of central gustatory neurons. *Journal of Neuroscience* 26:7433–43. [DAB, aRPE]

Lewicki, M. S. (2002) Efficient coding of natural sounds. *Nature Neuroscience* 5:356–63. [SH]

Li, W., Staszewski, L., Xu, H., Durick, K., Zoller, M. & Adler, E. (2002) Human receptors for sweet and umami taste. *Proceedings of the National Academy of Sciences* 99:4692–96. [LMK]

Lindemann, B., Ogiwara, Y. & Ninomiya, Y. (2002) The discovery of umami. *Chemical Senses* 27:843–44. [AM]

Lindsey, D. T. & Brown, A. M. (2006) Universality of color names. *Proceedings of the National Academy of Sciences of the United States of America* 103(44):16608–13. [TB]

Logue, A. W. (2004) *The psychology of eating and drinking*, 3rd edition. Brunner-Routledge. [AWL]

Mackintosh, N. J., Kaye, H. & Bennett, C. H. (1991) Perceptual learning in flavour aversion conditioning. *Quarterly Journal of Experimental Psychology B* 43(3):297–322. [MG]

Malnic, B., Hirono, J., Sato, T. & Buck, L. B. (1999) Combinatorial receptor codes for odors. *Cell* 96:713–23. [aRPE]

Mattes, R. D. (2005) Fat taste and lipid metabolism in humans. *Physiology and Behavior* 86:691–97. [aRPE]

McBurney, D. H. (1974) Are there primary tastes for man? *Chemical Senses and Flavor* 1:17–28. [aRPE]

McBurney, D. H. (1978) Psychophysical dimensions and perceptual analyses of taste. In: *Handbook of perception, vol.* VIA, ed. E. C. Carterette, & M. P. Friedman. Academic Press. [aRPE]

McBurney, D. H. & Gent, J. F. (1979) On the nature of taste qualities. *Psychology Bulletin* 86:151–67. [aRPE]

McCaughey, S. A. & Scott, T. R. (2000) Rapid induction of sodium appetite modifies taste-evoked activity in the rat nucleus of the solitary tract. *American Journal of Physiology* 279(3):R1121–31. Available at: http://ajpregu.physiology.org/cgi/content/full/279/3/R1121 [EAF, TRS]

McCormack, D. N., Clyburn, V. L. & Pittman, D. W. (2006) Detection of free fatty acids following a conditioned taste aversion in rats. *Physiology and Behavior* 87:582–94. [aRPE]

Miller, G. A. (1956) The magical number seven, plus or minus two: Some limits on our capacity for processing information. *The Psychological Review* 63:81–97. [aRPE]

Mineka, S. & Öhman, A. (2002) Phobias and preparedness: The selective, automatic, and encapsulated nature of fear. *Biological Psychiatry* 52(10):927–37. [DS]

Mintz, S. W. (1985) *Sweetness and power: The place of sugar in modern history.* Penguin. [JEC]

Mojet, J., Koster, E. P. & Prinz, J. F. (2005) Do tastants have a smell? 30(1):9–21. [VR]

Moncrieff, R. W. (1956) *The chemical senses*. Wiley. [aRPE]

Morini, G., Bassoli, A. & Temussi, P. A. (2005) From small sweeteners to sweet proteins: Anatomy of the binding sites of the human T1R2/T1R3 receptor. *Journal of Medicinal Chemistry* 48:5520–29. [LMK]

Mueller, K. L., Hoon, M. A., Erlenbach, I., Chandrashekar, J., Zuker, C. S. & Ryba, N. J. (2005) The receptors and coding logic for bitter taste. *Nature* 434(7030):225–29. Available at: http://www.nature.com/nature/journal/v434/n7030/abs/nature03352.html [PMDL, aRPE, EAF]

Mullen, K. T. & Kingdom, F. A. A. (2002) Differential distributions of red-green and blue-yellow cone opponency across the visual field. *Visual Neuroscience* 19:109–18. [JAS]

Myers, C. S. (1904) The taste-names of primitive peoples. *British Journal of Psychology* 1:117–26. [AM]

Nowlis, G. H., Frank, M. E. & Pfaffmann, C. (1980) Specificity of acquired aversions to taste qualities in hamsters and rats. *Journal of Comparative & Physiological Psychology* 94(5):932–42. [EAF]

O'Mahony, M., Atassi-Sheldon, S., Rothman, L. & Murphy-Ellison, T. (1983) Relative singularity/mixedness judgements for selected taste stimuli. *Physiology and Behavior* 31:749–55. [aRPE]

O'Mahony, M., Goldenberg, M., Stedmon, J. & Alford, J. (1979) Confusion in the use of the taste adjectives 'sour' and 'bitter'. *Chemical Senses* 4:301–18. [AM]

O'Mahony, M. & Ishii, R. (1987) The umami taste concept: Implications for the dogma of four basic tastes. In: *Umami: A basic taste*, ed. Y. Kawamura & M. R. Kare, pp. 75–93. Marcel Dekker. [aRPE]

Ortony, A. & Turner, T. J. (1990) What's basic about basic emotions? *Psychological Review* 97:315–31. [DS]

Osgood, C. E. (1956) *Method and theory in experimental psychology.* Oxford University Press. [aRPE]

Pfaffmann, C. (1941) Gustatory afferent impulses. *Journal of Cellular and Comparative Physiology* 17:243–58. [JEC, arRPE, AWL]

(1951) Taste and smell. In: *Handbook of experimental psychology*, ed. S. S. Stevens, pp. 1143–71. Wiley. [aRPE]

(1954) The chemical senses. In: *Experimental psychology*, ed. R. S. Woodworth & H. Schlosberg, pp. 297–322. H. Holt. [aRPE]

(1955) Gustatory nerve impulses in rat, cat and rabbit. *Journal of Neurophysiology* 18:429–40. [aRPE]

(1959) The afferent code for sensory quality. *American Psychologist* 14:226–32. [rRPE]

(1978) The vertebrate phylogeny, neural code, and integrative processes of taste. In: *Handbook of perception, vol. VIA: Tasting and smelling*, ed. E. C. Carterette & M. P. Friedman, pp. 51–123. Academic Press. [rRPE]

Pfaffmann, C., Frank, M., Bartoshuk, L. M. & Snell, T. C. (1976) Coding gustatory information in the squirrel monkey chorda tympani. In: *Progress in psychobiology and physiological psychology, vol. 6*, ed. J. M. Sprague & A. N. Epstein, pp. 1–27. Academic Press. [rRPE]

Pfaffmann, C., Frank, M. & Norgren, R. (1979) Neural mechanisms and behavioral aspects of taste. *Annual Review of Psychology* 30:283–325. [rRPE, AWL]

Pittman, D. W., Labban, C. E, Anderson, A. A. & O'Connor, H. E. (2006) Linoleic and oleic acids alter the licking responses to sweet, salt, sour, and bitter tastants in rats. *Chemical Senses* 31:835–43. [aRPE]

Poincaré, H. (1952) Hypotheses in physics. In: *Science and hypotheses.* Dover. [aRPE]

Popper, K. R. (1963) Conjectures and refutations, pp. 33–39. Routledge & Kegan. From T. Schiek, ed. (2000) *Readings in the philosophy of science*, pp. 9–13. Mayfield Publishing. [aRPE]

Puglisi, A., Baronchelli, A. & Loreto, V. (2007) Cultural route to the emergence of linguistic categories. Available at: http://arxiv.org/e-print/physics/0703164. [TB]

Purves, D., Augustine, G. J., Firzpatrick, D., Katz, L. C., La Mantia, A.-S., McNamara, J. O. & Williams, S. M., eds. (2001) The chemical senses. In: *Neuroscience*, pp. 317–44. Sinauer. [aRPE]

Regier, T., Kay, P. & Cook, R. S. (2005) Focal colors are universal after all. *Proceedings of the National Academy of Science* 102(23):8386–91. [TB, AM]

Regier, T., Kay, P. & Khetarpal, N. (2007) Color naming reflects optimal partitions of color space. *Proceedings of the National Academy of Sciences* 104:1436–41. [AM]

Richardson-Harman, N. J. & Booth, D. A. (2006) Do you like the sight or the feel of milk in coffee? Ecology and effortful attention in differential acuity and preference for sensed effects of milk substitute in vended coffee. *Appetite* 46:130–36. [DAB]

Roberson, D. & Hanley, J. R. (2007) Color vision: Color categories vary with language after all. *Current Biology* 17(15):605–07. [TB]

Robin, O., Rousmans, S., Dittmar, A. & Vernet-Maury, E. (2003) Gender influence on emotional responses to primary tastes. *Physiology & Behavior* 78(3):385–93. [DS]

Rolls, E. T. (2005). Taste and related systems in primates including humans. *Chemical Senses* 30, Suppl. 1, i76–i77. [aRPE]

Roussin, A. T., Victor, J. D., Chen, J.-Y. & Di Lorenzo, P. M. (2008) Variability in responses and temporal coding of tastants of similar quality in the nucleus of the solitary tract of the rat. *Journal of Neurophysiology* 99(2):644–55. [PMDL]

Ruderman, D. L., Cronin, T. W. & Chiao, C.-C. (1998) Statistics of cone responses to natural images: Implications for visual coding. *Journal of the Optical Society of America, A* 15:2036–45. [SH] 1649

Russell, J. A., Bachorowski. J. A. & Fernandez-Dols, J. M. (2003) Facial and vocal expressions of emotion. *Annual Review of Psychology* 54:329–49. [DS]

Sander, D., Grafman, J. & Zalla, T. (2003) The human amygdala: An evolved system for relevance detection. *Reviews in the Neurosciences* 14(4):303–16. [DS]

Sander, D., Grandjean, D. & Scherer, K.R. (2005) A systems approach to appraisal mechanisms in emotion. *Neural Networks* 18:317–52. [DS]

Sarle, W. (1987) Introduction to clustering procedures. In: *SAS/STAT guide for personal computers*, version 6, ed. R. D. Luginbuhl, S. D. Schlotzhauer & J. C. Parker. SAS Institute. [aRPE]

Scherer, K. R. (2001) Appraisal considered as a process of multi-level sequential checking. In: *Appraisal processes in emotion: Theory, methods, research*, ed. K. R. Scherer, A. Schorr & T. Johnstone, pp. 92–120. Oxford University Press. [DS]

Schiffman, S. S. & Dakis, C. (1975) Taste of nutrients: Amino acids, vitamins, and fatty acids. *Perception and Psychophysics* 17:140–46. [aRPE]

Schiffman, S. S. & Erickson, R. P. (1971) A psychophysical model for gustatory quality. *Physiology and Behavior* 7:617–33. [aRPE]

(1980) The issue of primary tastes versus a taste continuum. *Neuroscience and Biobehavioral Reviews* 4:109–17. [aRPE]

(1993) Psychophysics: Insights into transduction mechanisms and neural coding. In: *Mechanisms of taste transduction*, ed. S. A. Simon & S. D. Roper, pp. 395–424. CRC Press. [aRPE]

Schiffman, S. S., Orlandi, M. & Erickson, R. P. (1979) Changes in taste and smell with age: Biological aspects. In: *Sensory systems and communication in the elderly*, ed. J. M. Ordy & K. Brizzee, pp. 247–68. Raven Press. [aRPE]

Schivelbusch, W. (1992) *Tastes of paradise: A social history of spices, stimulants, and intoxicants.* Vintage. [JEC]

Sclafani, A. (2004) The sixth taste? *Appetite* 43:1–3. [AWL]

Scott, K. (2004) The sweet and the bitter of mammalian taste. *Current Opinion in Neurobiology* 14:423–427. [aRPE]

Scott, T. R. & Erickson, R. P. (1971) Synaptic processing of taste-quality information in thalamus of the rat. *Journal of Neurophysiology* 33:490–507. [aRPE]

Scott, T. R. & Giza, B. K. (1990) Coding channels in the taste system of the rat. *Science* 249(4976):1585–87. [EAF, TRS]

(2000) Issues of gustatory neural coding: Where they stand today. *Physiology & Behavior* 69(1–2):65–76. [aRPE, EAF]

Scott, T. R., Giza, B. K. & Yan, J. (1998) Electrophysiological responses to bitter stimuli in primate cortex. In: *Olfaction and taste XII: An international symposium*, ed. C. Murphy, pp. 498–501. New York Academy of Sciences. [AWL]

Scott, T. R. & Plata-Salaman, C. R. (1991) Coding of taste quality. In: *Smell and taste in health and disease*, ed. T. V. Getchell, L. M. Bartoshuk, R. L. Doty & J. B. Snow, pp. 345–68. Raven Press. [AWL]

(1999) Taste in the monkey cortex. *Physiology & Behavior* 67(4):489–511. [EAF]

Shallenberger, R. S. & Acree, T. E. (1967) Molecular theory of sweet taste. *Nature* 216:480–82. [aRPE]

(1971) Chemical structure of compounds and their sweet and bitter taste. In: *Handbook of neurophysiology, vol. IV: Chemical senses, Part 2, Taste*, ed. L. M. Beidler, pp. 221–78. Springer. [aRPE]

Shema, R., Sacktor, T. C. & Dudai, Y. (2007) Rapid erasure of long-term memory associations in the cortex by an inhibitor of PKM zeta. *Science* 317(5840):951–53. [MG]

Shepherd, G. M. (1994) Chemical senses. In: *Neurobiology*, 3rd edition. pp. 247–66. Oxford University Press. [aRPE]

Simon, S. S., de Araujo, I. E., Gutierrez, R. & Nicolelis, M. A. L. (2006) The neural mechanisms of gustation: A distributed code. *Nature Reviews: Neuroscience* 7:8–19. [aRPE]

Small, D. M. & Prescott, J. (2005) Odor/taste integration and the perception of flavor. *Experimental Brain Research* 166(3–4):345–57. [VR]

Smith, D. V. & Davis, B. J. (2000) Neural representation of taste. *The neurobiology of taste and smell*, 2nd edition, ed. T. E. Finger, W. L. Silver & D. Restrepo, pp. 353–94. Wiley/Liss. [aRPE]

Smith, D. V. & Li, C.-S. (1998) Tonic GABAergic inhibition of taste-responsive neurons in the nucleus of the solitary tract. *Chemical Senses* 23:159–69. [aRPE]

(2000) GABA-mediated corticofugal inhibition of taste-responsive neurons in the nucleus of the solitary tract. *Brain Research* 858:408–15. [aRPE]

Smith, D. V. & Margolskee, R. F. (2001) Making sense of taste. *Scientific American* 284:32–39. [aRPE, AWL]

Smith, D. V. & Scott, T. R. (2001) Gustatory neural coding. In: *Handbook of olfaction and gustation*, 2nd edition. Marcel Dekker. [aRPE]

Smith, D. V. & St. John, S. J. (1999) Neural coding of gustatory information. *Current Opinion in Neurobiology* 9:427–35. [aRPE]

Smith, D. V., St. John, S. J. & Boughter, Jr., J. D. (2000) Neuronal cell types and taste quality coding. *Physiology & Behavior* 69:77–85. [aRPE, CHL]

Smith, D. V., Van Buskirk, R. L., Travers, J. B. & Bieber, S. L. (1983) Coding of taste stimuli by hamster brain stem neurons. *Journal of Neurophysiology* 50(2):541–58. [PMDL]

Smith, D. V. & Vogt, M. B. (1997) The neural code and integrative processes of taste. In: *Tasting and smelling*, pp. 25–76. Academic Press. [aRPE]

Sokal, R. & Sneath, P. (1963) *Principles of numerical taxonomy.* Freeman. [aRPE]

Stapelton, J. R., Lavine, M. L., Wolpert, R. L., Nicolelis, M. A. L. & Simon, S. A. (2006) Rapid taste responses in the gustatory cortex during licking. *Journal of Neuroscience* 26:4126–38. [aRPE]

Steels, L. & Belpaeme, T. (2005) Coordinating perceptually grounded categories through language: A case study for colour. *Behavioral and Brain Sciences* 24(8):469–529. [TB]

Sternheim, C. E. & Boynton, R. M. (1966) Uniqueness of perceived hues investigated with a continuous judgmental technique. *Journal of Experimental Psychology* 72(5):770–76. [DRH]

Steward, O. (2000) *Functional neuroscience*, pp. 425–36. Springer. [aRPE]

Stillman, J. A. (2002) Gustation: Inter-sensory experience par excellence. *Perception* 31:1491–1500. [JAS]

St. John, S. J. & Smith, D. V. (1999) Salt taste discrimination by rats depends upon differential responses across gustatory neuron types. *Chemical Senses* 24:547–48. [aRPE]

Sugita, M. (2006) Taste perception and coding in the periphery. *Cellular and Molecular Life Sciences* 63:2000–15. [LMK]

Sugita, M. & Shiba, Y. (2005) Genetic tracing shows segregation of taste neuronal circuitries for bitter and sweet. *Science* 309:781–85. Available at: http://www.sciencemag.org/cgi/content/full/309/5735/781 [aRPE, EAF]

Tateda, H. (1965) Sugar receptor and α-amino acid in the rat. In: *Olfaction and taste, vol. II*, ed. T. Hayashi, pp. 383–97. Pergamon. [aRPE]

Tepper, B. J. & Nurse, R. J. (1997) Fat perception is related to PROP taster status. *Physiology & Behavior* 61:949–54. [AM]

Tomchik, S. M., Berg, S., Kim, J. W., Chaudhari, N. & Roper, S. D. (2007) Breadth of tuning and taste coding in mammalian taste buds. *Journal of Neuroscience* 27:10840–48. [rRPE, EAF, LMK]

Tomkins, S. S. (1963) *Affect, imagery, consciousness, vol. 2: The negative affects*. New York. [DS]

Travers, S. P. (2002) Quinine and citric acid elicit distinctive Fos-like immunoreactivity in the rat nucleus of the solitary tract. *American Journal of Physiology* 282(6):R1798–1810. [EAF]

Unschuld, P. U. (1993) *Huang di nei jing su wen: Nature, knowledge, imagery in an ancient Chinese medical text.* University of California Press. [aRPE]

Van Buskirk, R. L. & Erickson, R. P. (1977a) Odorant responses in taste neurons of the rat NTS. *Brain Research* 135:287–303. [rRPE]

(1977b) Responses in the rostral medulla to electrical stimulation of an intranasal trigeminal nerve: Convergence of oral and nasal inputs. *Neuroscience Letters* 5:321–26. [rRPE]

Verhagen, J. V., Giza, B. K. & Scott, T. R. (2005) Effect of amiloride on gustatory responses in the ventroposteromedial nucleus of the thalamus in rats. *Journal of Neurophysiology* 93(1):157–66. Available at: http://jn.physiology.org/cgi/content/full/93/1/157 [EAF]

von Helmholtz, H. (1924) *Physiological optics*, trans. J. P. C. Southall. Optical Society of America. [aRPE]

Wandell, B. (1995) *Foundations of vision*. Sinauer. [SH]

Warren, R. M. (1953) *Taste perception – Literature survey*. Reproduced by General Foods Corporation. [RMW]

Wilson, R. I. (2007) Neural circuits underlying chemical perception. *Science* 318:584–85. [SH]

Woolston, D. C. & Erickson, R. P. (1979) Concept of neuron types in gustation in the rat. *Journal of Neurophysiology* 42:1390–1409. [aRPE]

Xu, H., Staszewski, L., Tang, H., Adler, E., Zoller, M. & Li, X. (2004) Different functional roles of T1R subunits in the heteromeric taste receptors. *Proceedings of the National Academy of Sciences* 101:14258–63. [LMK]

Xu, P., Atkinson, R., Jones, D. N. M. & Smith, D. P. (2005) Drosophila OBP LUSH is required for activity of pheromone-sensitive neurons. *Neuron* 45:193–200. [SH]

Yamamoto, T. (2003) Brain mechanisms of sweetness and palatability of sugars. *Nutrition Reviews* 61(5 pt. 2):S5–S9. [MG]

Yamamoto, T. & Yasoshima, Y. (2007) Electrophysiological representation of taste memory. In: *Neural plasticity and memory: From genes to brain imaging*, ed. F. Bermúdez-Rattoni. CRC Press. [MG]

Young, T. (1802) On the theory of light and colours. *Philosophical Transactions, Royal Society of London* 92:12–48. [aRPE, EAF, SH]

(1807/1961) On physical optics. A course of lectures on natural philosophy and the mechanical arts, I. In: *Color vision*, ed. R. C. Teevan & R. C. Birney. Van Nostrand. [aRPE, EAF]

Zaidi, F. N. & Whitehead, M. C. (2006) Discrete innervation of murine taste buds by peripheral taste neurons. *Journal of Neuroscience* 26(32):8243–53. Available at: http://www.jneurosci.org/cgi/content/full/26/32/8243 [EAF]

Zarzo, M. & Stanton, D. T. (2006) Identification of latent variables in a semantic odor profile database using principal component analysis. *Chemical Senses* 31(8):713–24. [VR]

Zhang, Y., Hoon, M. A., Chandrashekar, J., Mueller, K. L., Cook, B., Wu, D., Zuker, C. S. & Ryba, J. P. (2003) Coding of sweet, bitter, and umami tastes: Different receptor cells sharing similar signaling pathways. *Cell* 112:293–301. [aRPE, LMK, AWL]

Zhao, G. Q., Zhang, Y. F., Hoon, M. A., Chandrashekar, J., Erlenbach, I., Ryba, N. J. P. & Zuker, C. S. (2003) The receptors for mammalian sweet and umami taste. *Cell* 115:255–66. [aRPE, EAF, LMK]