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 NH₄Cl. 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

doi: 10.1017/S0140525X08003373

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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.

Commentary/Erickson: A study of the science of taste

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 \neq 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

doi: 10.1017/S0140525X08003385

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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-basic 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