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Taste as a basis for body wisdom

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ABSTRACT

The sense of taste uses a variety of discrete receptor mechanisms to identify nutrients and toxins. Information from receptors is arrayed along a dimension of physiological welfare, which serves as the organizing principle of the taste system. This, in turn, drives central physiological and neurochemical processes that underlie hedonics: nutrients elicit reward; toxins, aversion. The sensitivity of the taste system, and so the placement of chemical stimuli along the welfare dimension, is modifiable based on level of satiety, experience, or physiological need. These modifications may be sufficient to guide the animal's food choices according to those that satisfy its needs at the moment. Thus, judicious changes in taste sensitivity of the rodent may underlie the demonstrated behavior of body wisdom.

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1. Meeting Bart Hoebel

My first image of Bart Hoebel was through a lab door as he hovered well above a rat which was pressing a bar feverishly for lateral hypothalamic stimulation. It was October 1964, and I was leaving Green Hall on the campus of Princeton University following a class in behavioral psychology. I entered Bart's lab that afternoon out of curiosity, and have not strayed far in the decades since from the topics he revealed to me that day. He captured me with this combination of physics, chemistry, biology and behavior in a field not yet named neuroscience.

I performed my senior thesis under Bart's direction, investigating whether lateral hypothalamic self-stimulation rates would fluctuate as a function of a female rat's estrous cycle, as Bart had shown they do with level of food deprivation [1]. We measured degree of sexual receptivity, food intake, impedance of brain tissue, and rate of self-stimulation under three conditions: (1) as rats proceeded spontaneously through their four-day estrous cycles, (2) when estrous was induced through a regimen of estrogen and progesterone injections, and (3) when an implanted bolus of estradiol induced chronic estrous.

Feeding reached a peak one day prior to estrous, while sexual receptivity and LH self-stimulation were at their maxima during estrous, as brain impedance declined (Fig. 1). I stayed on in Bart's lab through the summer of 1966 confirming these results and preparing them for presentation [2].

2. The organizing principle of taste

Then we parted for 15 years. I took my doctorate at Duke with Robert Erickson studying neural coding in taste, then continued with studies of gustatory coding of quality and intensity at various synaptic levels as a faculty member at the University of Delaware. A decade later, I finally addressed what I considered the fundamental issue in taste: whether it is a series of four or so independent modalities, evolved for distinct purposes and using discrete sets of pathways and central neurons to code for those modalities—analogous to the skin senses—or an integrated system encompassing multiple components, yet with a common theme that bound those components together, as in color vision. The sodium ion has a great deal to do with salty taste, but little influence over sour; the hydrogen ion, the opposite. A unifying dimension to taste, as wavelength is to color, proved elusive.

At the receptor level, taste is more like the skin senses. The transduction mechanisms for sodium salts [3] and acids [4] appear to involve an increase (salts) or decrease (acids) in ionic conductance through membrane channels, resulting in direct depolarization of receptor cells. Sugars [5], bitter stimuli [6], and monosodium glutamate [7] require specialized receptors and second messenger systems. But unlike the skin senses, taste does have one overarching mission: to guard the chemical welfare of the body through the acquisition of nutrients and avoidance of toxins. The common element that serves this mission was implicated by Schiffman and Erickson [8] in a psychophysical study in which they reported that pH, molecular weight, and palatability were three stimulus characteristics that served to organize the responses human subjects gave to a range of tastants. Of greatest importance and interest was the third, for palatability represents an interaction between the stimulus and subject, a subjective measure not previously considered.

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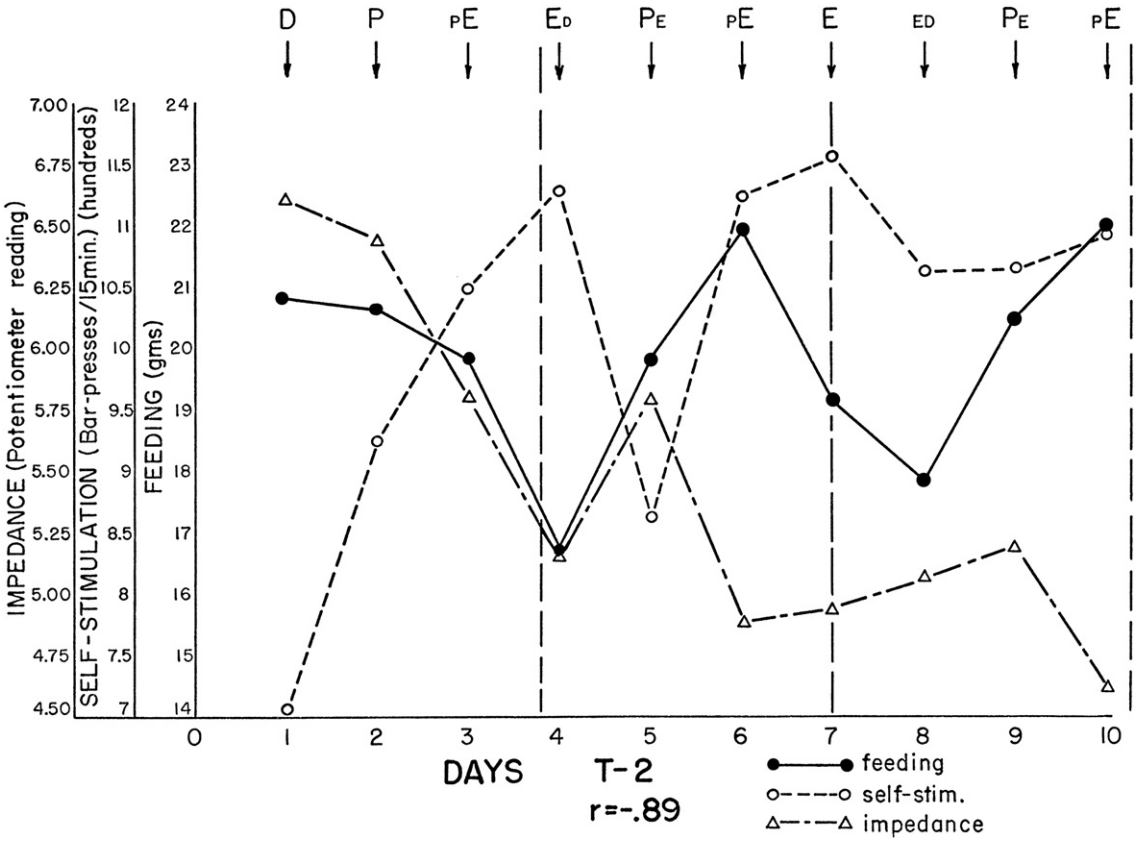

Fig. 1. Food intake, rate of lateral hypothalamic self-stimulation, and impedance of brain tissue as a function of a female rat's estrous cycle. Self-stimulation rate peaked during estrous, while food intake and brain impedance declined. D—diestrous; P—proestrous; E—estrous.
After Scott and Hoebel, 1966 [2].

We pursued this line of reasoning at behavioral and electrophysiological levels in rats. To find an objective measure of palatability we noted that in humans it correlates −0.86 with stimulus toxicity [8], encouraging us to use oral LD_{50} as a reasonable representation of palatability in rats.

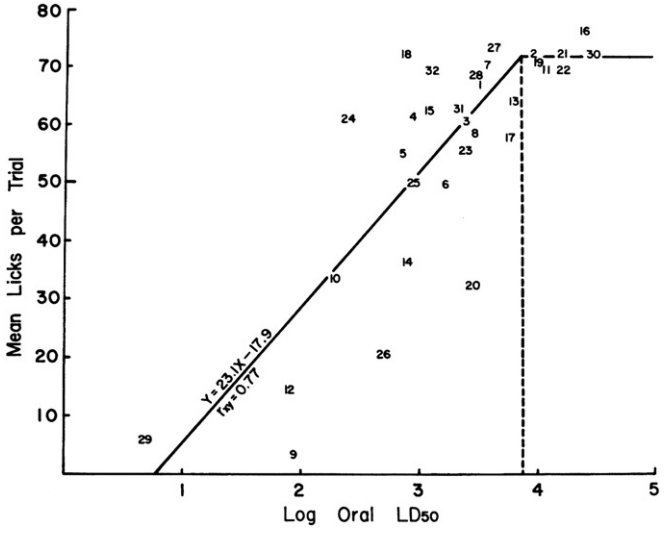

Fig. 2. Mean licks per 15-s trial as a function of stimulus toxicity. Naïve rats reject novel-tasting chemicals according to their level of toxicity (oral LD_{50}). Numbers refer to the stimuli in Table 1.
From Scott and Giza, 2000 [32].

Table 1
Chemicals used in a behavioral study of acceptance versus stimulus toxicity (Fig. 2).

No.	Chemical	Concentration (mM)	Rat oral LD_{50} (mg/kg)	Log LD_{50}
1	Acetic acid	10	3310	3.52
2	Acetone	2000	9750	3.99
3	Acetylcholine	3	2500	3.40
4	Acetylsalicylic acid	10	891	2.95
5	Adenine	3	745	2.87
6	Ammonium chloride	100	1650	3.22
7	Benzene	50	3800	3.58
8	Butyric acid	10	2940	3.47
9	Cadmium chloride	300	88	1.94
10	Caffeine	100	192	2.28
11	Citric acid	10	11,700	4.07
12	Cobalt chloride	100	80	1.90
13	Ethanol	1000	6300	3.80
14	Formaldehyde	300	800	2.90
15	Formic acid	10	1210	3.08
16	Glucose	500	25,800	4.41
17	Isopropanol	1000	5840	3.77
18	Lithium chloride	100	757	2.88
19	Lysine hydrochloride	30	10,000	4.00
20	Magnesium chloride	100	2800	3.45
21	Mannitol	500	17,000	4.23
22	Monosodium glutamate	100	17,000	4.23
23	Potassium chloride	300	2430	3.39
24	Potassium fluoride	300	243	2.39
25	Pyridine	100	891	2.95
26	Quinine hydrochloride	10	500	2.70
27	Sodium bicarbonate	100	4220	3.63
28	Sodium chloride	100	3000	3.48
29	Strychnine sulfate	3	5	0.70
30	Sucrose	500	29,700	4.47
31	Sulfuric acid	10	2140	3.33
32	Tartaric acid	10	1290	3.11

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