subtle differences between the variability in the ON responses to the annulus (circles) and the variability of the firing rates in the dark.

We have shown that ON response mechanisms have variability (noise) that is not shared by other mechanisms; our data also show that this noise is not simply an uncorrelated component that is added to the variability present in the dark. If an uncorrelated variance were added to an existing variance, the variance of the sum would be larger than either alone. In all the cells we have investigated, we have observed no systematic tendencies for the variance to go either up or down during the stimuli (in Table 1, for example, the variance happens to drop during the stimulus). Among the number of mathematically indistinguishable ways that this may be accomplished are the following. (i) A noise component may be introduced with the stimulus and added to the noise in the dark; however, to maintain a relatively constant variance in both conditions, the two components must be negatively correlated. (ii) If the noise that is added during the stimulus is not correlated with the noise in the dark, then the noise in the dark must be attenuated during the stimulus (*8*). The independence indicated by the different appearances of the autocorrelation functions leads us to prefer the second hypothesis (*9*).

In summary, we propose that ON and OFF information is generated in the retina by independent mechanisms, each of which contains its own source of variability. General theories of receptive field organization must account for this duplicity of ganglion cell operation. In addition, our method of analysis should be useful for investigating the relations between different receptor systems or different spatial components of the receptive field.

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References and Notes

1. We use the terms ON response to refer to the number of spikes that are produced during illumination, and OFF response to refer to the number of spikes that are produced during the second after offset of the stimulus. By maintained discharge we mean firing in the periods that precede the stimulus.
2. R. Granit, *Receptors and Sensory Perception* (Yale Univ. Press, New Haven, Conn., 1955).
3. H. K. Hartline, *Am. J. Physiol.* **121**, 400 (1938); S. W. Kuffler, *J. Neurophysiol.* **16**, 37 (1953); C. Enroth-Cugell and L. H. Pinto, *J. Physiol. (Lond.)* **220**, 441 (1972); M. L. Wolbarsht, H. G. Wagner, E. F. MacNichol, Jr., in *The Visual System: Neurophysiology and Psychophysics*, R. Jung and H. Kornhuber, Eds. (Springer-Verlag, Berlin, 1961).
4. This may be an explicit averaging, as in J. Stone and M. Fabian, *Vision Res.* **8**, 1023 (1968); H. Ikeda and M. J. Wright, *ibid.* **12**, 1465 (1972); more often there is a comparison of ON responses with OFF responses [for example, I. Abramov and M. W. Levine, *ibid.* **15**, 791 (1975); N. W. Daw, *J. Physiol. (Lond.)* **197**, 567 (1968); P. Gouras, *Science* **168**, 489 (1970); T. N. Wiesel and D. H. Hubel, *J. Neurophysiol.* **29**, 1115 (1966)]. It is also inherent in any method in which sinusoidal modulation of the stimuli is used.
5. Our methods are virtually identical to those described in M. W. Levine and I. Abramov, *Vision Res.* **15**, 777 (1975).
6. We classify the response type according to whether the excitatory response (increased firing rate relative to the maintained discharge) occurs at ON or OFF. Thus, an off-center unit is one that is inhibited during stimulation by a small, centered spot of light and fires at OFF; an on-center unit is the opposite.
7. An autocorrelation is the correlation of a signal at every time within some interval with the same signal delayed by some fixed amount. The autocorrelation function is the autocorrelation as a function of this delay time.
8. One might wish to consider the possibility of two or more components present in the dark, one of which is suppressed by the stimulus. All of the above arguments are valid, with the simple substitution of the word OFF for ON. In fact, this is equivalent to adding a negatively correlated component at ON.
9. This is most similar to the speculations of Granit (*2*).

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Cross-Cultural Differences in Simple Taste Preferences

Abstract. *A population of Indian laborers who show high preferences for sour and bitter tastes has been studied. Their judgments of taste intensity and pleasantness of sweet and salty stimuli are in accord with European population estimates, which suggests that dietary history may alter preferences for simple taste stimuli without affecting the gustatory system.*

It has been assumed that our pattern of taste preferences is part of our genetic composition. Sweetness is a pleasant taste, saltiness may be pleasant at low levels but unpleasant at higher ones, and sourness and bitterness become increasingly unpleasant as the concentrations increase. These taste preferences have been studied only with model aqueous systems, and generalizations to food preferences should be made with caution. The complexities and nuances of foods, and one's expectations about taste qualities, preclude any such simple classification once cognitive factors are taken into account. Evidence for the dichotomy of taste preferences for aqueous solutions derives from a long history of psychophysical studies, in which the subject is asked to judge either whether the taste is pleasant, neutral, or unpleasant (*1*), or the degree of such pleasantness and unpleasantness (*2–4*), or to rank tastes in order of pleasantness (*5*). The results of the studies obtained with Western populations agree with each other and confirm the striking division of the taste world into two categories with *sweet* referring to a pleasing aspect, and *bitter* and *sour* referring to a displeasing one.

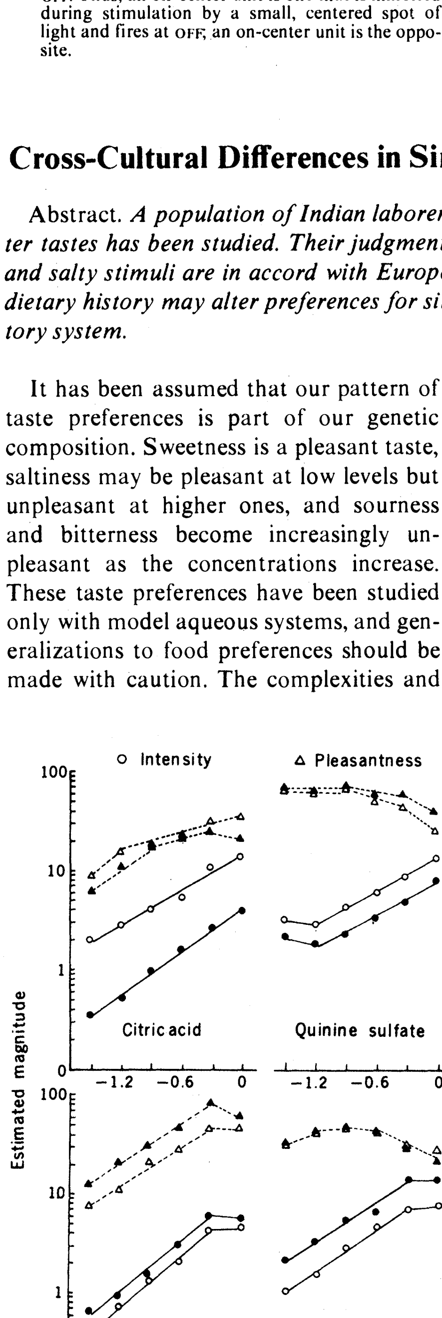

Fig. 1. Rated taste intensity and taste pleasantness for four compounds. The coordinates are log-log. The data, obtained by the method of line matching, are from a group of laborers from the Karnataka region of India. Solid markers are of judgments made after lunch and open markers are of judgments made after fasting.

Studies with Indian medical students from St. John's Medical College, Bangalore, India (*6*), which we conducted by standard psychophysical techniques confirmed that the sweet taste is pleasant, that salty is both pleasant and unpleasant, whereas sour and bitter are primarily unpleasant. In fact, the curve relating taste pleasantness of glucose solution exhibited the same maximum preference level (1.0*M* glucose) as did studies with U.S. testers in various other experiments (*3, 7*).

We find different preferences among illiterate Indian laborers from the Karnataka region in India. These laborers subsist on a sparse diet (1200 to 1500 calories) that contains many sour foods. The tamarind fruit, which tastes extremely sour and slightly sweet, is chewed as a confection, and another major dish, lentil soup, is flavored with tamarind fruit to produce a fairly sour dish. As a general rule their diet more strongly emphasizes sour tastes than do Western diets.

Because many of the individuals in this group of laborers were illiterate, we tested their subjective judgments of taste by having them draw lines to reflect the strength and the pleasantness of a taste (*8*). We tested ten individuals twice, once after a 14-hour fast (just before breakfast) and next, just after lunch (*9*). The taste stimuli were six concentrations each of glucose, NaCl, citric acid, and quinine sulfate (*10*). Three confirmatory replicate judgments were obtained for each quality (sweet, salty, sour, bitter), each concentration, each attribute (intensity, pleasantness), and each condition (fasting, after eating) (*9*). Small paper cups holding about 10 ml of solution were presented in a random order of concentration at room temperature. The subject was required to rinse his mouth with water between samples.

Subjects rated the more concentrated solutions as tasting stronger (Fig. 1). Since many of the functions appear to have long linear segments in log-log coordinates, the middle range of concentrations seems to produce power functions relating subjective taste intensity to physical molarity (*11*). In contrast, the ratings of preference are more curvilinear (*12*). The preferences for sour and bitter are anomalous. Whereas Western populations find the taste of citric acid and quinine to be unpleasant, the Karnataka laborers reported that citric acid became increasingly pleasant as the concentration was increased, and that quinine sulfate was exceptionally pleasant at low concentrations and became less pleasant only with large increases of concentration. We found no significant differences between ratings of pleasantness made under the two hunger conditions, in contrast to the hypothesis of alliesthesia (*13*), which predicts that satiety reduces the pleasantness of the sweet taste (*13, 14*).

Our findings bear upon two major issues in responses to simple sensory stimuli: (i) the influence of dietary (or genetic) factors and (ii) the influence of body state (hunger or satiety). The anomalously high pleasantness ratings for citric acid and quinine sulfate differ from the ratings for similar compounds made by Western subjects (*1*), and of Indian medical students tested in the same locale by similar procedures (*15*). The Karnataka group scored intensity and pleasantness of glucose and NaCl in a manner similar to that of Western populations, so that the anomaly is not due to the method of measurement. Dietary history recommends itself as a partial explanation. The tamarind fruit chewed by these laborers is slightly sweet but exceptionally sour. It seems reasonable to assume that these subjects were able to distinguish between the samples (aqueous solutions of test substances) and real foods, so that the high preference ratings given to citric acid probably reflect an actual preference for sourness. Another possibility is that genetic inbreeding of these laborers may yield a population which finds sourness acceptable; that hypothesis requires extensive further investigation.

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4. The method of magnitude estimation provides ratios of pleasantness, and category scaling provides intervals of pleasantness.
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8. This type of scoring or scaling, known as cross-modality matching, is a standard procedure in psychophysical measurement; the subject adjusts stimuli from one continuum (for example, numbers, the intensity of a tone, or the length of a line) until its perceived intensity matches that produced by a criterion stimulus (for example, perceived taste intensity). Ratios between line lengths are assumed to reflect ratios of perceived taste intensity or taste pleasantness. Line matching has been used by Jones, Moskowitz, Butters, and Glosser (*Neuropsychologia*, in press) to assess the perceived odor intensity of *n*-butanol by Korsakoff syndrome patients. The concept of "magnitude" is brought out clearly with the procedure, even for subjects with no concept of number or of the rules of arithmetic.
9. Lunch included rotti (bread), chappaties (whole wheat breads), and dahl (sour lentil soup). Most subjects were not vegetarians.
10. The initial concentrations were glucose, 2.0*M*; NaCl, 1.0*M*; citric acid, 0.06*M*; and quinine sulfate, 0.00075*M*. These concentrations were successively diluted (with an equal volume) five times to yield a 32 : 1 range of molarities for each compound.
11. These power functions are expressed by the equation $S = kC^n$, where S is sensory intensity and C is molarity. The lines in Fig. 1 are drawn without least squares procedures and are meant simply to show the trend of the data. Least squares estimates of the exponents, n, fitted to all of the data suggest that the rank order of power function exponents replicate the usual rank order but are lower in absolute magnitude [H. L. Meiselman, *Crit. Rev. Food Technol.* **3**, 89 (1972)].
12. Linear and quadratic trends of all the pleasantness ratings (regressed against concentration—cross-sectional data) and for the geometric mean rating of each concentration (across observers and replicates) were evaluated for significance. All trends showed significant ($P < .05$) linear components, with the exception of NaCl fasting (cross-sectional and mean data) and quinine sulfate nonfasting conditions (cross-sectional and mean data). The following conditions showed significant ($P < .05$) quadratic trends: NaCl fasting (cross-sectional and mean data), NaCl nonfasting (cross-sectional and mean data), citric acid nonfasting (mean data), quinine sulfate fasting (cross-sectional and mean data), and nonfasting (mean data).
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14. ______ and R. Duclaux, *Nature (London)* **227**, 966 (1970).
15. H. R. Moskowitz *et al.*, *Physiol. Behav.*, in press. Four groups of Indian medical students at St. John's Medical College, Bangalore, India, were tested after fasting, after breakfast, after lunch, and after ingesting a 20 percent (weight to volume) glucose solution (1.5 g per kilogram of body weight). Concentrations of the four taste substances were similar to those evaluated here.
16. We thank Dr. B. Halpern for helpful discussions on the manuscript and on the interpretations of preference measures.
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Cochlear Tuning Properties: Concurrent Basilar Membrane and Single Nerve Fiber Measurements

Abstract. *Removal of perilymph from the cochlea has been reported to destroy the sharp tuning of cochlear neurons. That these changes are mechanical in origin is refuted by the concurrent recording of sharp neural tuning with broad basilar membrane responses from the same region of the partially drained cat cochlea. A second cochlear filter is therefore necessary.*

There is still controversy concerning the origin of the sharply tuned characteristics exhibited by the single cochlear nerve fibers of all mammalian species so far investigated. Comparisons of the filtering characteristics observed in measurements of the amplitude of basilar membrane vibration with those of frequency threshold curves (FTC's or tuning curves) of single cochlear fibers in the same species show evidence of a substantial discrepancy [guinea pig (*1–4*); squirrel monkey (*5*)]. On this, and on a number of other grounds, it has been suggested that cochlear filtering is a two-stage process: the first filter (that of the basilar membrane) being followed by a physiologically vulnerable second filter (*1–3; 6*). The validity of these comparisons between basilar membrane and cochlear nerve measurements, however, has recently been questioned by Robertson (*7*), who demonstrated that drainage of the scala tympani, as is required for some of the mechanical measurements in the