DETECTING FLAVORANTS: MULTISENSORY PROCESSES IN CHEMOSENSATION

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Abstract

Flavors of foods and beverages taken into the mouth reflect a congeries of multisensory inputs: gustatory, olfactory, and somatosensory. One simple model hypothesizes that chemosensory inputs operate as independent channels whose outputs combine linearly. At suprathreshold levels, the model implies linear additivity of gustatory and olfactory contributions to perceived intensity of flavor mixtures. In the region of threshold, our version of the model assumes independent sources of noise in the gustatory and olfactory channels prior to summation. Data on the detection of the gustatory flavorant sucrose, the olfactory flavorant vanillin, and flavor mixtures of sucrose plus vanillin are consistent with this independent-channel model – although it is not yet possible to eliminate other plausible accounts of the detection of complex flavorants.

The perception of flavor of foods and beverages provides a clear-cut example of multisensory processing, for flavors depends only in small measure on contributions of taste proper (gustation), much more on olfaction (activated retronasally when stimuli are taken into the mouth), and commonly too on somatosensation (trigeminal responses mediating pungency, burning, and temperature). A fundamental question in the perception of flavors is: How do the stimulus components that activate different sensory modalities combine their effects in producing the qualities and intensities of flavor percepts? Do the components add their effects linearly? Or do they interact, perhaps in a complex manner?

Most foods and beverages contain an enormous number of distinct stimulus components, which separately and together typically activate several modalities. To simplify the problem, many investigators ask how people respond to mixtures containing just two stimulus components, one gustatory and the other olfactory. Several studies of perceived intensity of gustatory-olfactory mixtures suggest, perhaps surprisingly, that there is close to simple perceptual additivity of the components (Murphy, Cain, & Bartoshuk, 1977; Murphy & Cain, 1980; but see Hornung & Enns, 1986, for evidence suggesting less than complete additivity). Using magnitude estimation, the studies of Murphy et al. and of Murphy and Cain showed that the overall judged intensity of a mixture comprising a gustatory and an olfactory flavorant approximated the sum of the judged intensities of the components presented alone. To the extent that judgments of mixtures deviated slightly from additivity, the deviations might be chalked up to a small nonlinear response bias.

This interpretation assumes, however, that the overt numerical responses do closely parallel, in a quantitative way, the underlying sensory magnitues. This is to say, it is always possible, if not plausible, that a nonlinear process N characterizes the integration of gustatory and olfactory signals in flavor perception, but this nonlinearity its ’canceled out’ by a nonlinear relation N* betweeen the subjects’ numerical responses and the underlying perceptual magnitudes that is effectively the inverse of N, the nonlinear integration process.

Nevertheless, taking the suprathreshold data of Murphy et al. (1977) and Murphy and Cain (1980) at face value, those data suggest the following hypothesis: Under conditions in which subjects ’taste’ the stimuli, akin to taking foods and beverages into the mouth, the gustatory and olfactory systems act as independent channels whose outputs sum more or less linearly. At suprathreshold levels, this hypothesis is consistent with linear additivity of sensory intensity.

Detection of Gustatory-Olfactory Mixtures: Independent Channels

If gustatory and olfactory components of flavor combine linearly in perceived intensity at suprathreshold levels, then it is likely that the outputs of these flavor channels also combine linearly in mediating responses in the vicinity of absolute threshold. At threshold levels, however, the prediction of a model of independent channels is somewhat more complicated than it is at suprathreshold levels. The detectability of weak stimuli is ultimately limited by the noise in the sensory system – the principle underlying signal detection theory (Green & Swets, 1966). As in other modalities, so in taste (Linker, Moore, & Galanter, 1964) and olfaction (Semb, 1968), the receiver operating characteristic (ROC), which relates correct detections to false positive responses as criterion varies, is concave, and concave ROCs characterize noise-limited processes of detection and discrimination. The detection of gustatory-olfactory mixtures likewise is limited by the noise present in the two modalities. According to a model in which the outputs of two sensory channels add linearly, the detection of the mixture will be limited by the total noise in the two channels. As Green and Swets first showed, with independent channels (independent sources of noise), the hypothesis predicts:

$$d'_{mix} = (d'^{\,2}_{gust} + d'^{\,2}_{olf})^{1/2} \tag{1}$$

The term d'_{mix} gives sensitivity to the flavor mixture and d'_{gust} and d'_{olf} give sensitivities to the gustatory and olfactory components, respectively. If $d'_{gust} = d'_{olf}$, then Equation 1 predicts that d’ for the mixture will be about 1.4 times as great as d’ for either component; that is, adding a second component increases sensitivity by $2^{1/2}$. This model has been applied successfully, for example, to the ‘summation’ observed in the detection of simultaneously presented visual and auditory stimuli (Fidell, 1970).

The model characterized by Equation 1 assumes that all of the noise resides in the two independent channels themselves (peripheral noise), with (essentially) none in the more central integrator. At the other extreme, most of the noise that limits detection might reside centrally, in the integrator that receives both gustatory and olfactory inputs (central noise), with (essentially) no noise in the two peripheral channels. In this case, the prediction becomes:

$$d'_{mix} = d'_{gust} + d'_{olf} \tag{2}$$

Detection of Gustatory-Olfactory Mixtures: Probability Summation

Finally, consider another kind of model that also assumes that gustation and olfaction operate as independent channels – this a model that arose prior to the advent of signal detection theory. In the alternate model, p_i is defined as the probability of detecting a stimulus in channel i, and p_j is the (independent) probability of detecting a stimulus in channel j. Then, according to a model of *probability summation*, when the two stimuli are presented together, the subject essentially has ‘two shots’ at detecting something, and the resulting probability of detecting the mixture, p_{mix}, is

$$p_{mix} = p_i + p_j - p_i \times p_j \qquad (3)$$

Equation 3 gives the prediction derived by applying probability summation to a high-threshold model of detection. Unfortunately, Equation 3 applies only to the detection of signals that arise in channels without noise (or with noise that lies well below the detection thresholds). With noisy sensory systems, the model of probability summation (in, for example, a paradigm of two-alternative forced-choice, 2AFC) has to be characterized rather differently, as follows: A subject in 2AFC is presented on each trial with two possible stimulus intervals or events, one containing noise alone (e.g., just water) and the other containing a signal (water with either a single stimulus component or a mixture of two components). According to the probability-summation model, in each test interval or event, the subject monitors the levels of the outputs in the two channels, corresponding to the two possible components, and chooses the larger of the two values. The subject then compares the magnitude of the larger value in the first interval to the magnitude of the larger value in the second interval and chooses the interval in which the value is greater. That is, the model assumes no summation of neural outputs from the two channels (and no noise), only a decision based on the largest signal values observed across channels and across stimulus intervals or events. Tyler and Chen (2000) have worked out the quantitative features of this model, showing that the magnitude of probability summation, when computed in terms of d', is even smaller than the magnitude predicted by the model of independent channels and peripheral noise (Equation 1). With two equally detectable components, the detectability of the mixtures, d'_{mix}, should be about 1.2 times as great as the d' for either component alone – an increase in sensitivity of about $2^{0.25}$.

Detection of Flavor Mixtures: Ashkenazi and Marks (2004)

Ashkenazi and Marks (2004) reported results of a series of experiments that sought to compare the role of voluntary (endogenous) attention in the detection of gustatory and olfactory components of flavor mixtures. Although that study did not concern itself with the issue of mixture detection *per se*, the results of that study apply directly to the issue at hand. In different conditions of that study, Ashkenazi and Marks measured the detectability of weak levels of the gustatory flavorant sucrose, the olfactory flavorant vanillin (both dissolved in water and taken in the mouth), and sucrose-vanillin mixtures. Care was taken to ensure that subjects did not 'smell' the vanillin before 'tasting' any of the stimuli: Subjects pinched their nose until they had taken each solution into their mouth. From psychometric functions obtained for sucrose and vanillin in each subject, determined by a 2AFC method, it was possible to select concentrations of the two substances that gave six pairs of matched levels of detectability, d', in order to use those values in a subsequent mixture-detection experiment.

Figure 1 shows the results: the detecability (d') of each of the six mixtures, plotted against the detectability (d') of the corresponding unmixed, single component. For comparison are the predictions of three models of mixture detection. The heavy solid line shows the prediction made by the assumption of a central integrator receiving additive inputs from independent channels containing stochastically independent sources of peripheral noise, and it provides a good fit to the results. By way of contrast, the lighter solid line shows the prediction of a model of probability summation. Clearly, this model seriously underestimates sensitivity to the mixtures. Finally, the dashed line shows the prediction made by the assumption of a central integrator receiving additive inputs from independent channels, under the assumption of central noise (noise at the integrator). Clearly, the model hypothesizing a single source of central noise seriously overestimates sensitivity to the mixtures.

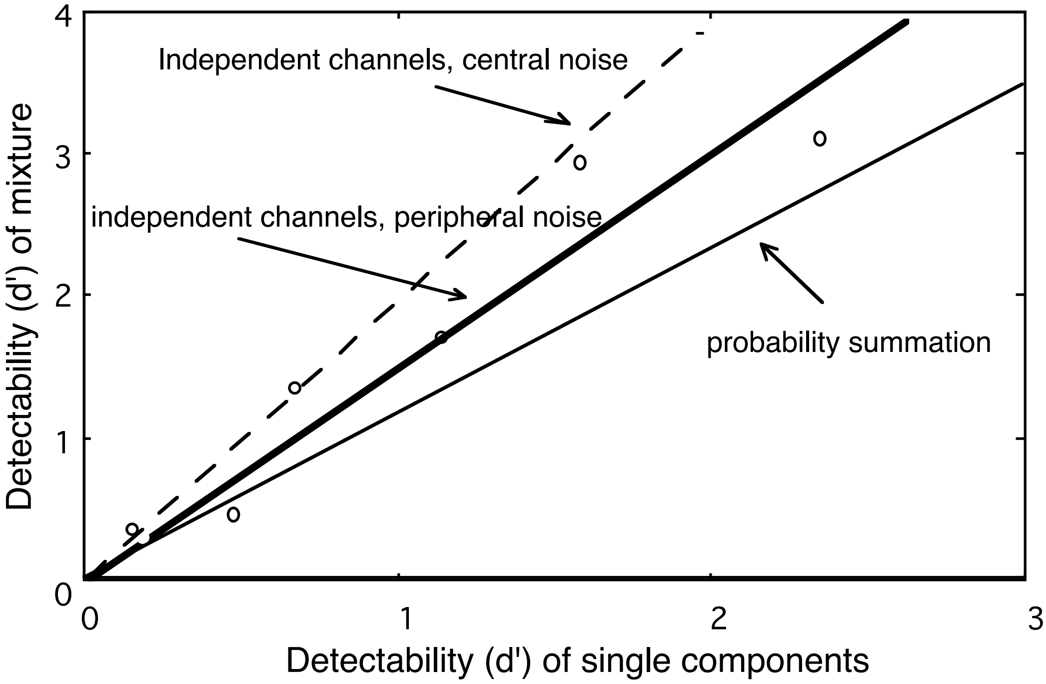

Fig. 1. Detectability, d', of mixtures of vanillin and sucrose, as a function of the corresponding values of d' for single, isolated components. Compared are the predictions of three models: (1) The heavy solid line shows the prediction from a model hypothesizing integration of outputs from independent channels with peripheral noise. (2) The dashed line shows the prediction from a model hypothesizing integration of outputs from independent channels with central (or correlated) noise. (3) The light line shows the prediction from a model hypothesizing probability summation. Data of Ashkenazi and Marks (2004).

Detection of Flavor Mixtures: Elgart and Marks (unpublished)

In most studies of flavor-mixture detection, such as the one just described, measures of detectability, or measures of absolute threshold, are determined over a restricted set of stimuli – typically, just for unmixed components plus a single mixture in which the two components are set nominally at equally detectable levels. A more thorough approach, albeit much more time-consuming, is to measure the detectability of all of the stimulus mixtures produced by pairing each of several concentrations of one component with each of several concentrations of another (factorial design). Just this approach was taken in a recent, preliminary study by Elgart and Marks (unpublished), who measured, in eight subjects, the detectability of various mixtures of near-threshold sucrose and vanillin. Extensive testing on each subject was needed, as it was first necessary to construct psychometric functions for both sucrose and vanillin, next to confirm the appropriate selection of concentrations of each flavorant to be combined in the mixtures within the factorial design of the main experiment, and, finally, to collect substantial amounts of data from each subject in the main experiment, over several sessions.

Figure 2 shows results, averaged over the eight subjects, for the nine mixtures formed by combining each of three concentrations of sucrose with each of three concentrations of vanillin. Low, medium, and high concentration levels corresponded to forced-choice detection probabilities of about 0.65, 0.75, and 0.85. Detectability in the 2AFC is a joint function of the concentrations of the gustatory and olfactory components. The overall magnitude of summation is modest, consistent with both the peripheral noise and central noise models (although the model postulating peripheral noise provides a slightly better account description the data).

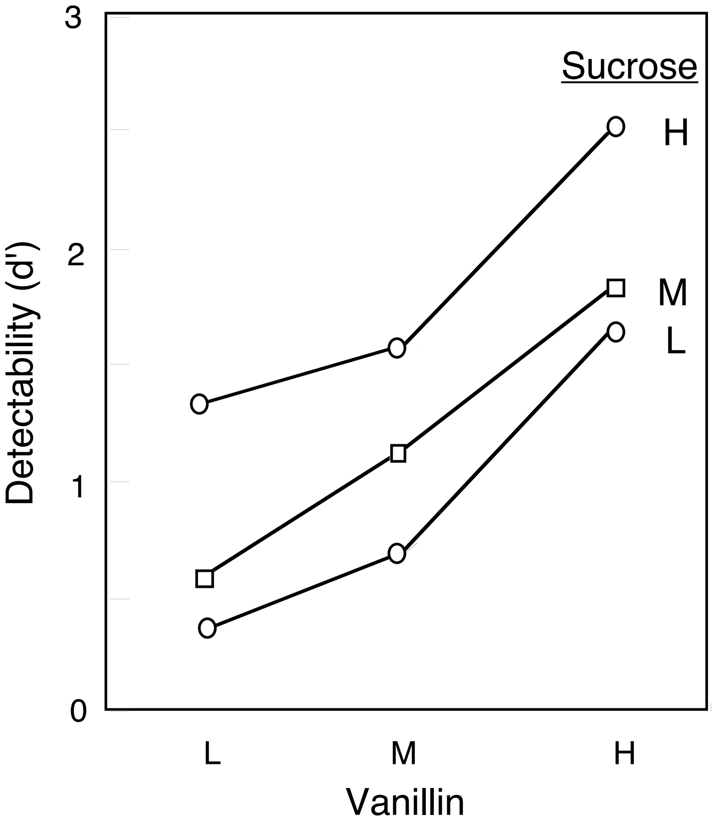

Fig. 2. Detectability (d') of nine gustatory-olfactory flavor mixtures created by combining each of three concentrations of sucrose (low, medium, high) with each of three concentrations of vanillin (low, medium, high). Data of Elgart and Marks (unpublished).

Perception and Detection of Flavor Mixtures: Other Findings

Both of the experiments described here used the same pair of flavorants, sucrose and vanillin. These two flavorants are typically described as 'congruent' or 'harmonious.' Often paired in real-world foods and beverages, sucrose and vanillin tend to 'go together.' Does the multisensory processing of flavor stimuli differ when the components are incongruent or inharmonious, rather than congruent or harmonious? Murphy and Cain (1980) reported similar, near-perfect additivity in suprathreshold intensity when the sweet-lemony olfactory flavorant citral was combined either with sucrose (congruent/harmonious) or with sodium chloride (incongruent/inharmonious).

More pertinent to the experiments described here, Delwiche and Heffelfinger (2005) found similar degrees of summation at threshold when a pineapple olfactory flavorant was paired either congruently with a mixture of aspartame/acesulfame potassium or incongruently with monosodium glutamate (MSG). In both cases, combining half-threshold amounts of the olfactory and gustatory stimuli produced new mixtures that were themselves about as detectable as each original full-strength component. Unfortunately, without complete psychometric functions for all of these stimuli, it is not possible to determine how well any of signal-detection based models might account for Delwiche and Heffelfinger's results. Those authors did ask how well a model of probability summation, based on a high-threshold mechanism of detection, might account for their results (not very well), but did not try to assess the results in terms of a probability-summation model grounded in signal-detection theory, like the model of Tyler and Chen (2000).

As Delwiche and Heffelfinger (2005) pointed out, the conclusion that both they and Murphy and Cain (1980) drew is at odds with that of Dalton, Doolittle, Nagata, and Breslin (2000), who found considerable summation at threshold between a congruent combination of the almond flavorant benzaldehyde and the sweet gustatory flavorant saccharin but virtually none between an incongruent combination of benzaldehyde and MSG. While the discrepant outcomes might conceivably reflect differences in neural processing of different flavorants *per se*, it is also possible, as Delwiche and Heffelfinger noted, that the discrepant outcomes reflect a fundamental difference between the kinds of multisensory processes activated by Dalton et al. and by other investigators. Instead of 'tasting' solutions containing olfactory and gustatory flavorants dissolved in aqueous solutions, the subjects in Dalton et al's experiment sipped the gustatory stimulus while sniffing the olfactory one. Thus while Dalton et al. did study a variant of multisensory integration of olfaction and taste, they did not study multisensory integration of flavor *per se*.

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References

Ashkenazi, A., & Marks, L.E. (2004). Effect of endogenous attention on detection of weak gustatory and olfactory flavors. *Perception & Psychophysics, 66,* 596-608.

Delwiche, J.F., & Heffelfinger, A.L. (2005). Cross-modal additivity of taste and smell. *Journal of Sensory Studies, 20*, 512-525.

Fidell, S. (1970). Sensory function in multimodal signal detection. *Journal of the Acoustical Society of America, 47,* 1009-1015.

Green, D.M., & Swets, J.A. (1966). *Signal Detection Theory and Psychophysics*. New York: Wiley.

Hornung, D.E., & Enns, M.P. (1986). The contributions of smell and taste to overall intensity: A model. *Perception & Psychophysics, 39,* 385-391.

Linker, E., Moore, M.E., & Galanter, E. (1964). Taste thresholds, detection models, and disparate results. *Journal of Experimental Psychology, 67,* 59-66.

Murphy, C., & Cain, W.S. (1980). Taste and olfaction: Independence vs. interaction. *Physiology & Behavior, 24,* 601-605.

Murphy, C., Cain, W.S., & Bartoshuk, L.M. (1977). Mutual action of taste and olfaction. *Sensory Processes, 1,* 204-211.

Semb, G. (1968). The detectability of the odor of butanol. *Perception & Psychophysics, 4,* 335-340.

Tyler, C.W., & Chen, C.-C. (2000). Signal detection theory in the 2AFC paradigm: Attention, channel uncertainty and probability summation. *Vision Research, 40,* 3121-3144.