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Attention and the Detectability of Weak Taste Stimuli

Lawrence E. Marks[1,2] and Mary E. Wheeler[1,3]

[1]John B. Pierce Laboratory, New Haven, CT, [2]Department of Epidemiology and Public Health and Department of Psychology, Yale University, New Haven, CT and [3]Yale College, New Haven, CT, USA

Correspondence to be sent to: Lawrence E. Marks, John B. Pierce Laboratory, 290 Congress Avenue, New Haven, CT 06519, USA

Abstract

Subjects detected weak solutions of sucrose or citric acid under conditions in which attention was directed toward one of the tastants or the other. Detection thresholds were measured using an adaptive, forced-choice procedure, with a three-down one-up rule, which computer simulations suggest should be more reliable than the popular two-down one-up rule. The thresholds were modestly but systematically lower for attended tastants than for unattended ones. Similar results have been reported in other sense modalities, including vision (greater sensitivity to stimuli presented to attended versus unattended spatial locations) and hearing (greater sensitivity to stimuli presented at attended versus unattended sound frequencies). Taken together, the findings are consistent with a general hypothesis regarding attention in sensory systems: gains or losses in detectability occur when a central attentional mechanism (or, conceivably, a preattentive mechanism) selectively and preferentially monitors signals arising from particular subsets of peripheral neural inputs.

Introduction

Does the ability to detect a particular tastant (e.g. sucrose) depend on whether one is expecting (attending to) that stimulus rather than another stimulus (e.g. citric acid)? The present paper serves as a first step toward elucidating such a role of attention in taste perception. Evidence recounted below has shown that attention can selectively modulate the detectability of weak stimuli in other sensory modalities, including vision, hearing and touch. Perhaps attention also modifies detectability in taste.

The detection or perception of a taste stimulus, or indeed any other sensory stimulus, invariably involves an amalgamation of low-level sensory processes and higher-level decisional and cognitive ones. A high-level process well-known to influence sensory detection and perception is attention, especially 'focused attention', in which subjects are disposed to expect certain classes of stimuli to the exclusion of others. Although most research on attention has been devoted to its role in vision (e.g. Kinchla, 1992), where studies have shown that attention can modify many aspects of visual performance, including the rate of acquisition of information (e.g. Treisman and Gormican, 1988; Wolfe *et al.*, 1989), the speed of response (e.g. Ericksen and Yeh, 1985) and the detectability or discriminability of stimuli (e.g. Gallant, 1989; Luck *et al.*, 1994), attention also influences the processing of signals in other modalities, including hearing (e.g. Mondor and Bregman, 1994; Spence and Driver, 1994; Ward and Mori, 1996) and touch (e.g. Posner, 1978; Butter *et al.*, 1989; Driver and Grossenbacher, 1996).

Most of the studies mentioned above measured attention in terms of changes in response time; that is, changes in the speed of responses made to relatively strong stimulation. There are advantages, however, to measuring attention instead in terms of changes in the detectability of weak stimuli. In particular, by measuring detectability using appropriate psychophysical methods, it is possible to isolate the effects of attention on the sensitivity of a perceptual system independent of any effects on response criteria. Further, research in other sensory modalities indicates that stimulus detection, as well as response time, can reveal selective effects of attention. Much of this research has been conducted in the realm of audition, where there is considerable evidence for the existence of 'attention bands' of sensitivity (Greenberg and Larkin, 1968; Scharf *et al.*, 1987; Dai *et al.*, 1991; Schlauch and Hafter, 1991; Botte, 1995).

Consider, for example, the following experiment: on a given trial, a subject expects (attends to) a signal of a particular sound frequency, say 1000 Hz; attention may be induced by presenting a weak 1000 Hz cue stimulus a few seconds before the test trial. The trial itself consists of two consecutive stimulus intervals, one containing a tonal signal and the other lacking the signal. The subject's task is to decide which interval had the signal. This two-interval forced choice controls effectively for response criterion. The measurement of attentional selection is made possible by varying the frequency of the signal on a fraction of trials. On most trials, the cue is valid, in that the signal has the same frequency as the cue (1000 Hz in the present example); but on a few trials, the signal actually takes on a somewhat lower or higher frequency. Results show clearly that sensitivity falls off as the frequency of the test stimulus deviates from that of the cue (Scharf *et al.*, 1987; Dai *et al.*, 1991; Botte, 1995). Of special theoretical interest is the finding that the shape of the sensitivity curve (the attentional band) bears a striking resemblance to the critical band for hearing, and critical bands seem to be related to the tuning characteristics of peripheral auditory nerve fibers (see Moore, 1989).

This outcome suggests that attention may involve the selective monitoring, presumably by a central neural mechanism, of a relatively small number of neural inputs arising from the periphery, and in particular, selective monitoring of those neurons most sensitive to the stimulus being attended. One analog of auditory attention to sound frequency is visual attention to spatial location: attending to particular locations in the visual field increases the detectability or discriminability of stimuli presented to that location relative to other locations (Gallant, 1989; Luck *et al.*, 1994). Further, unpublished results obtained in the first author's laboratory suggest that a similar principle may underlie selective attention to brief vibrotactile stimuli presented to the skin. The ability to detect one kind of stimulus (e.g. 250 Hz vibration, tailored to activate the Pacinian-corpuscle system) was greater when subjects expected (attended to) that stimulus rather than another (e.g. 20 Hz vibration, which activates the rapidly adapting Meissner system). Thus, it is possible that a general principle governs the processes of focal attention in signal detection. One caveat is in order. It is possible that some examples of selectivity could involve preattentive rather than attentive mechanisms. That is, selective effects could reflect some kind of automatic, preferential processing of stimulus information rather than controlled, attentive processing. In hearing, selectivity occurs even when the cues are 'symbolic' [e.g. visual stimuli representing the sound frequencies (Hafter *et al.*, 1993)] or even at a systematically different frequency, making it is unlikely that the results can be attributed to preattentive 'priming' of individual frequency channels. But preattentive processes might operate in other modalities.

The present study sought to show that the ability to detect weak solutions of sucrose and citric acid can depend on focal attention (or preattentive processing). In a given experimental session, we cued the subject to attend to one or the other of two tastants, within a two-interval forced-choice paradigm. On most of the trials, the test stimulus was the same as the cue stimulus, e.g. sucrose when sucrose was cued, but on the remaining trials the test stimulus differed from the cue, e.g. citric acid when sucrose was cued. If attention (or perhaps preattentive processing) selectively affects stimulus detection, then the threshold for attended stimuli should be lower than the threshold for unattended stimuli. To measure how threshold varies as a function of attention, we used a three-down one-up adaptive psychophysical method (Wetherill and Levitt, 1965). Also reported are the results of computer simulations, which suggest that use of a three-down one-up rule may prove more reliable than the more popular two-down one-up rule.

Materials and methods

From a methodological perspective, uncovering evidence for selective effects of attention (or preattentive processing) on taste detection is difficult. Initial attempts in this laboratory to find such evidence, pursued several years ago, were hampered in large measure by the substantial variability over time in taste sensitivity, a problem that is compounded by the need to collect substantial amounts of data in sessions run with the same subjects on different days. Those initial studies followed the procedure that has been used in analogous research on auditory detection: first, for each subject, the experimenter found a single stimulus concentration solution that was moderately well detected (~75–80% correct in two-interval forced choice), then measured how the detectability of that single stimulus varied as a function of attention. Unfortunately, fluctuations in the subjects' overall sensitivity—a given concentration originally detected 75% of the time might be detected the next day at chance frequency (50%) or perfectly (100%)—precluded the possibility of consistently discerning any effect of attention.

As a result, the study reported here switched to an adaptive procedure that tracks the threshold over time: the 'up–down transformed' or staircase method. In this procedure, stimulus concentration increases on trials following erroneous responses and decreases on trials following a fixed number of successive correct responses (we used a 'three-down one-up rule,' for reasons described below). This method ensures that the stimuli presented are always in the vicinity of the threshold. By randomly interleaving staircases containing the attended and unattended tastants within a given test session, it is possible to discern effects of attention even in the face of substantial fluctuations in sensitivity.

A pilot study using this procedure was encouraging. In the pilot study, each of five nonsmoking subjects (two women and three men, 18–26 years old) served in four sessions, alternating between a session in which sucrose was attended and citric acid was unattended and one in which citric acid was attended and sucrose was unattended. Attending selectively had no effect on either threshold of one subject, but produced slightly lower thresholds in both tastants in a second subject and clearly lower thresholds in both in the remaining three subjects. Pooled over subjects, thresholds for citric acid were lower by 0.21 log concentration units and thresholds for sucrose were lower by 0.16 units when the respective stimuli were attended rather than unattended. In addition to the generally positive outcome, the pilot study suggested two possible improvements in procedure that we incorporated into the main experiment. First, to help overcome variability, subjects seemed to need initial practice at the task; consequently, in the main experiment, an entire practice session was run with each subject before the main data were collected. Second, in the pilot study we sought to obtain baseline threshold measures for both citric acid and sucrose at the very start of each session, but this procedure seemed to make it harder for the subject to attend selectively to just one stimulus later in the session; consequently, the main experiment omitted these baseline measurements.

Stimuli

Tastants were sucrose and citric acid, two substances that are highly discriminable in quality at suprathreshold concentrations and are likely to be transduced and processed with considerable independence. At the receptor level, for instance, responses to sweet stimuli appear to require specific receptor molecules, whereas responses to acids involve direct interaction of hydrogen ions with apical ion channels (Kinnamon and Cummings, 1992).

The stimuli were dissolved in deionized water to create two concentration series. The sucrose series comprised 11 concentrations from 0.00032 to 0.1 M in steps of 0.25 log concentration units; the citric acid series comprised 11 concentrations from 0.0000018 to 0.00056 M, also in steps of 0.25 log units. The highest concentration in each series was used as the 'cue' stimulus to direct and maintain attention within the main part of each session.

Fresh batches of the stimuli were prepared every few days and stored under refrigeration, but brought to room temperature (~21°C) before each experimental session. Stimuli on each trial consisted of 5 ml of the dissolved test stimulus and 5 ml of deionized water, each of which was presented in a 30 ml plastic cup.

Subjects

Subjects, all non-smokers, were four women (19–23 years old) and two men (20 and 24 years old). Each subject served in five sessions, the first of which was considered practice and not included in the analysis. Subjects were paid $7.00 per hour to participate.

Procedure

Transformed up–down method

To ensure that most of the stimulus concentrations presented fell in the vicinity of the forced-choice threshold, we used Wetherill and Levitt's (1965) transformed up–down method (TUDM). On each trial the subject was given two stimuli to sample in succession, one containing sucrose or citric acid and the other containing water; the subject responded by indicating which stimulus, the first or the second, contained a solute. Subjects rinsed thoroughly with deionized water before sipping each stimulus. In the TUDM, the concentration of a stimulus is increased on the trial following a single incorrect response and decreased on the trial following n successive correct responses at a given concentration. This method is commonly used in psychophysical research, especially in taste, typically with a two-down one-up rule; that is, where $n = 2$ (e.g. Bartoshuk *et al.*, 1986; Stevens, 1996). Averaging the concentrations at the transition points, where the direction of stimulus concentration changes, yields a threshold defined as follows: the threshold concentration has probability P of being correctly detected in a two-alternative forced choice. In the TUDM, the probability of responding correctly on n consecutive trials equals the probability of responding incorrectly on one trial; both probabilities equal 0.5. Thus $P^n = 0.5$. When $n = 2$, the value of P equals 0.71. In the present study, however, n was 3, which corresponds to a threshold with a probability P of 0.79 correct detection in a two-alternative forced choice.

We selected the three-down one-up rule rather than the two-down one-up rule in the expectation that doing so would increase the reliability of the threshold measures. Green (1990) has argued, from both empirical data (auditory detection) and computer simulations, that the efficiency of adaptive procedures such as the TUDM is maximized when the stimulus-selection rule (e.g. value of n) places the threshold at a point on the psychometric function where the standard deviation in responding is smallest [a value that has been called the 'sweetpoint' of the function (Laming and Marsh, 1988)]; Green found that this entails using a rather large value of n, equal to 4 or 5. Unfortunately, the larger the value of n, the greater the number of trials required to provide a given number of transition points in the run. In many studies of taste, such as the present one, it is important to limit the number of trials in order to prevent fatigue in the subjects. Nevertheless, results of an empirical and simulation study by Kollmeier *et al.* (1988) suggest that a three-down one-up rule may be superior to a two-down one-up rule even when the number of trials is relatively small. Thus, we chose the former rule. In addition, we ran a number of Monte Carlo simulations, using two different up–down rules ($n = 2$ or 3), different psychometric functions and different starting locations on the psychometric function, and producing various numbers of transitions (4–100). Results of these simulations, described below, supported our decision to use a three-down one-up rule.

Manipulation of attention

To manipulate the subject's attention (or perhaps preattentive processing), a given test session contained a predominance of trials of a given type. Either 75% of the stimuli in the session were citric acid and the remaining 25% were sucrose or 75% were sucrose and 25% were citric acid, and subjects were told at the beginning of the session to expect one tastant or the other. Further, at the start of the test run (after the 20 practice trials) and every eight trials thereafter, the subject was given a sample of the cue stimulus (the highest concentration of the 11-stimulus series). Consequently, a given test run produced two tracks, one for the attended (75% probable, cued) stimulus and one for the unattended (25% probable, uncued) stimulus. On each trial, one of the two tracks was chosen at random (with probability 0.75 that it would be the attended stimulus), and the stimulus concentration was determined according to the subject's performance on that stimulus track. Subjects were instructed to choose the stimulus on each trial that contained a solute. That is, the subjects were instructed to respond not just to the attended stimulus, but to any taste stimulus that was not water. There is a small risk that instructing the subject in this way will induce them to share attention to all possible signals, and therefore not reveal any differential effect of selective attention; nevertheless, the instruction is necessary to prevent subjects from failing to report the detection of the unattended stimulus.

Experimental sessions

The experiment consisted of a practice session and four test sessions, all run on each of the six subjects. Every session began with a fixed number of practice trials (20), all of which contained the stimulus to be attended in that session. This procedure was chosen in order to help direct the subject's attention to the attended stimulus right from the start of the session. Immediately following the practice trials and without any interruption in the sequence of trials, the main part of the session began. Thresholds for sucrose and citric acid were measured in interleaved tracks while attention was directed toward one tastant or the other throughout the remainder of the session. The starting concentration for both the attended and unattended stimuli was always the seventh level in the series (0.1 M for sucrose and 0.00056 M for citric acid).

The main constraint on the number of trials required in each session was the number of transitions obtained with the unattended stimulus, since that stimulus was presented only 25% of the time. Each session continued until seven transitions had been obtained with the unattended stimulus, at which point the session ended. The last six of these seven transition values were averaged to give the threshold. For the attended stimulus, where many more transitions were generally obtained by the end of the session, we also omitted the very first transition point, calculating the threshold by averaging all of the other transitions if they were even in number and averaging all save the last one if they were odd in number [in the up–down procedure, it is important to average even numbers of transitions (see Wetherill and Levitt, 1965)]. The attended stimulus alternated between sucrose and citric acid from session to session; three subjects attended to sucrose in the first session after practice and three attended to citric acid.

Results

Table 1 gives the average log threshold concentrations for each subject in each session, the taste stimulus to which attention was directed and the number of transitions averaged to give the threshold for each stimulus. Average thresholds, pooled over subjects and sessions, appear at the bottom of the table. Note that there are (at least) two possible ways of calculating these averages. One way is to compute unweighted averages; that is, simply to average the concentrations for each subject in each session as they are listed in the table. The problem with this approach is that it weights all values equally, even though thresholds obtained from larger numbers of transitions are more reliable than thresholds obtained from smaller numbers of transitions. An alternative approach first weights the contribution of each subject's threshold by the number of transitions used to compute it before pooling across subjects. This second measure weights the measures more appropriately, but is more sensitive to session-to-session fluctuations in overall sensitivity. Overall, the second weighted method seems more appropriate. Fortunately, the two computations gave roughly comparable outcomes.

The results followed our expectations. Regardless of which method was used to average the results, mean threshold was generally lower when the taste stimulus was attended than when it was not attended, and this was true both when the subjects attended to sucrose and when they attended to citric acid. The difference in the case of the weighted averages was 0.20 log concentration units for citric acid and 0.18 log units for sucrose (0.26 and 0.17 log units, respectively, in the unweighted averages). Results of analysis of variance showed that citric acid thresholds were reliably smaller than sucrose thresholds [$F(1,5) = 25.76$, $P < 0.0001$]. More important, thresholds for attended stimuli were reliably smaller than thresholds for unattended stimuli [$F(1,5) = 23.27$, $P = 0.005$]. There was no interaction between attention and tastant [$F(1,5) = 0.002$, $P = 0.90$], consistent with the evidence that the effect of attention was more or less equivalent for the two tastants.

Computer simulations

Following Kollmeier *et al.* (1988), we simulated threshold runs using the transformed up–down method in a two-alternative forced choice, with either a two-down one-up or three-down one-up rule, varying the slope of the psychometric function (which is equivalent to varying the size of the stimulus steps) and the location on the psychometric function of the stimulus concentration presented on the first trial. As dependent measures we examined (i) the number of trials required to produce a fixed number of transitions and (ii) the variability in the average threshold for a given number of transitions (or trials).

Computer simulation makes it possible to produce an

Table 1 Forced-choice thresholds for citric acid and sucrose as a function of attention

	Threshold (log molarity)		Stimulus attended	Number of transitions	
	Citric acid	Sucrose		Citric acid	Sucrose
Subject 1					
Session 1	–4.75	–2.04	citric acid	6	6
Session 2	–3.42	–1.89	sucrose	6	30
Session 3 ·	–3.76	–1.63	citric acid	26	6
Session 4	–3.88	–1.92	sucrose	6	12
Subject 2					
Session 1	–4.10	–1.33	citric acid	20	6
Session 2	–4.08	–1.82	sucrose	6	30
Session 3	–4.16	–1.42	citric acid	24	6
Session 4	–4.13	–1.80	sucrose	6	14
Subject 3					
Session 1	–4.30	–2.42	citric acid	14	6
Session 2	–3.79	–1.82	sucrose	6	18
Session 3	–4.40	–2.04	citric acid	26	6
Session 4	–3.75	–1.57	sucrose	6	14
Subject 4					
Session 1	–3.17	–1.52	sucrose	6	12
Session 2	–3.20	–1.00	citric acid	18	6
Session 3	–3.50	–1.67	sucrose	6	36
Session 4	–3.55	–0.96	citric acid	22	6
Subject 5					
Session 1	–3.71	–1.87	sucrose	6	24
Session 2	–3.91	–1.42	citric acid	20	6
Session 3	–3.75	–1.76	sucrose	6	24
Session 4	–3.72	–1.63	citric acid	16	6
Subject 6					
Session 1	–3.42	–1.92	sucrose	6	18
Session 2	–3.38	–1.83	citric acid	28	6
Session 3	–3.29	–1.70	sucrose	6	10
Session 4	–3.78	–1.50	citric acid	28	6
Mean attended (unweighted)	–3.92	–1.77			
Mean unattended (unweighted)	–3.66	–1.60			
Mean attended (weighted)	–3.83	–1.79			
Mean unattended (weighted)	–3.66	–1.60			

indefinitely large number of results. In order to select conditions relevant to those of the present study, we relied on a simple measure that could be derived from the empirical data obtained in the main experiment, namely, the relation between the number of transitions obtained in a given run and the number of trials needed to produce that number of transitions.

The number of trials is plotted against the number of transitions in Figure 1, separately for sucrose and citric acid for each subject. Two aspects of this figure are notable. First, there is a roughly linear relation between trials and transitions, an outcome that is to be expected as long as the subjects are reasonably uniform in their sensitivity and maintain roughly constant psychometric functions across different runs. And second, the relation between trials and transitions is similar for both citric acid and sucrose. This implies that the size of the concentration steps was scaled comparably for the two substances relative to their underlying psychometric functions. Clearly, if the concentration steps were made very large or very small, the number of trials required to produce a given number of transitions could be concomitantly smaller or greater. Given these two properties, a single function characterizes the relation between trials and transitions for each tastant and for all six subjects reasonably well.

Given the empirical data of Figure 1, in the simulations we systematically varied the slope of the psychometric function until we obtained a comparable trial-versus-transition function. As a psychometric relation, we chose a logistic function, which closely approximates a cumulative

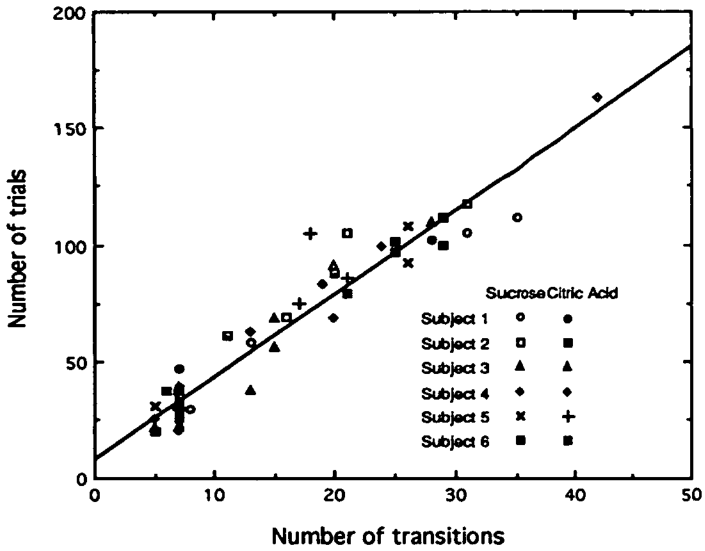

Figure 1 Number of trials versus number of transitions obtained in threshold runs for sucrose and citric acid using the transformed up–down procedure with a three-down one-up rule in a two-alternative forced choice. Each subject's data were obtained in five experimental sessions (one practice session plus four main sessions). The line represents the prediction obtained by computer simulation, given the psychometric function shown in Figure 2.

normal distribution and has been favored on theoretical grounds by some investigators to describe sensory discrimination (e.g. Link, 1992). For the present purposes, we defined the logistic function with regard to log stimulus concentration (C) using the equation:

$$P = 0.5\left(1 + \frac{1}{1 + e^{-a\log C + b}}\right) \tag{1}$$

Note that the multiplicative constant a determines the slope of the psychometric function, whereas the additive constant b depends largely on the choice of units for stimulus concentration; in fact, if we define the units of concentration such that $P = 0.75$ when $\log C = 0$, then $b = 0$ and equation (1) can be rewritten as

$$P = 0.5\,[1 + (1 + C^{-k})^{-1}] \tag{2}$$

where $k = a \cdot \log e$.

The function defined by equations (1) and (2) provided a satisfactory fit to the data of Figure 1 when $a = 10$, as shown by the straight line representing the results of the simulation; the logistic function that we used is shown in Figure 2. The equation of the straight line in Figure 1, determined by regressing the number of trials (Ti) against the number of transitions (Tr), is:

$$Ti = 3.543Tr + 8.394 \tag{3}$$

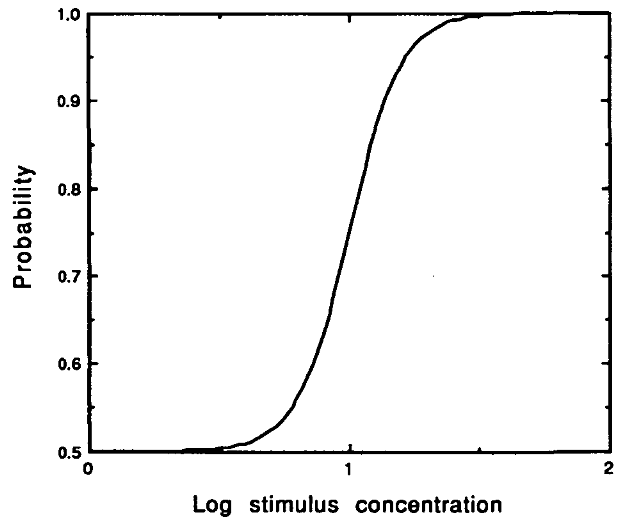

Figure 2 The logistic psychometric function for a two-alternative forced choice assumed in the computer simulations.

By way of comparison, the corresponding regression equations for the empirical results obtained with sucrose and citric acid, respectively, are:

$$Ti = 3.525Tr + 8.090 \tag{4}$$

$$Ti = 3.579Tr + 8.645 \tag{5}$$

Thus, for both tastants ~3.5 additional trials were needed to produce each additional transition point, or ~7 additional trials to produce each additional pair of transitions. Given that we used a three-down one-up rule, an additional four trials would be needed at the very least, even if the size of the stimulus step were extremely large. On the other hand, were the size of the stimulus step extremely small, many more than seven additional trials would be needed to produce each additional pair of transitions. Under such conditions, the stimulus would slowly move toward the level giving a probability of 0.79, then enter a 'random walk' that, according to our simulations, would average five trials per transition (10 trials per pair of transitions).

The psychometric function of Figure 2 effectively spans a little more than one logarithmic unit of stimulus concentration. Presumably, our subjects' psychometric functions were all at least roughly similar to this in shape. However, it is conceivable that the psychometric function operating at any given point in time was actually even steeper than the function in Figure 2, but sensitivity shifted over time during the course of a test run, thereby causing the function measured over longer periods of time to flatten. Such shifts have been suggested in the past in auditory detection (e.g. Hall, 1983; Taylor *et al.*, 1983; Kollmeier *et al.*, 1988).

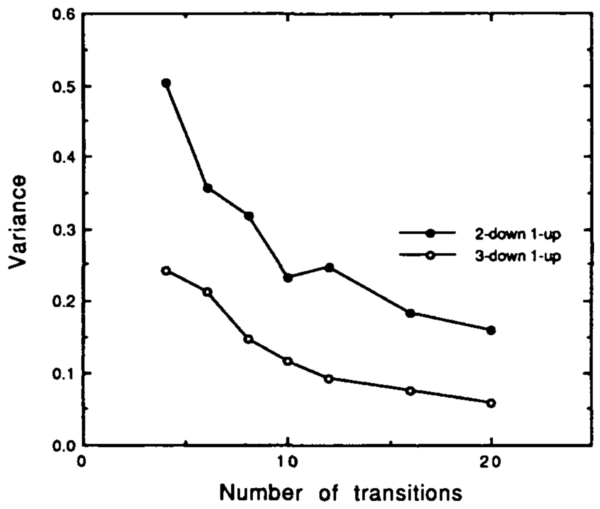

Figure 3 The variance in the simulated threshold measurements, plotted against the corresponding mean number of transitions used to determine the threshold, with two-down one-up and three-down one-up rules. Each units of variance corresponds to a single step of stimulus concentration, equivalent to 0.25 log concentration units.

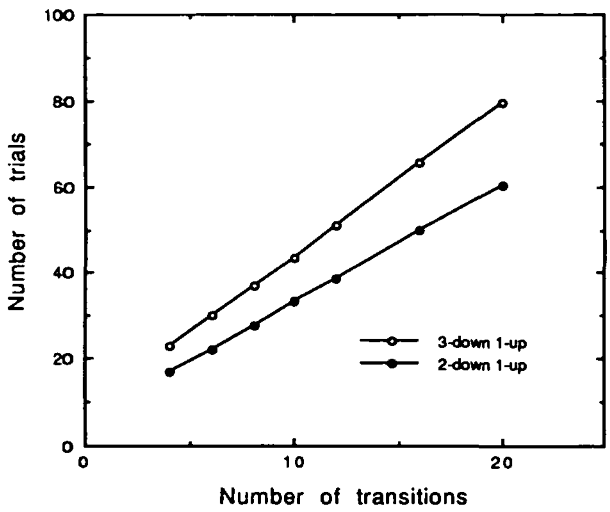

Figure 4 The mean number of trials in the simulated threshold measurements, plotted against the corresponding mean number of transitions, with two-down one-up and three-down one-up rules.

Following the lead of Kollmeier *et al.* (1988), we compared the results of simulating threshold runs using the psychometric function of Figure 2 with a two-down one-up rule as well as a three-down one-up rule. Two dependent measures were of special interest: (i) the number of trials needed to produce a given number of transitions and (ii) the variance of the simulated thresholds. A priori, one would expect that it would take more trials to produce a given number of transitions when three rather than two consecutive correct responses are needed before lowering stimulus concentration. But for a given number of transitions, requiring three rather than two correct responses should provide greater reliability. What was not clear was which rule, two-down one-up or three-down one-up, would give greater reliability (smaller overall variability) when the number of trials was held constant.

To answer this question, we simulated 1000 threshold runs with both two-down and three-down rules, fixing the number of transitions in both cases at several values from four to 20. Figure 3 shows how the variance of the simulated thresholds (in these computations, 1 unit of variance corresponds to a single concentration step, equivalent to 0.25 log concentration units) depends on the number of transitions. Clearly, for a fixed number of transitions the variability is substantially smaller with a three-down one-up rule than with a two-down one-up rule. The ratio of variances is ~1:2. As Figure 4 shows, the number of trials required to produce a fixed number of transitions is substantially greater (~30% greater) with the three-down rule (the straight line for the three-down rule is the same as the one plotted in Figure 1). Nevertheless, the cost in terms of additional trials is more than offset by the corresponding gain in reliability, as is evident in Figure 5, which plots variance against number of trials.

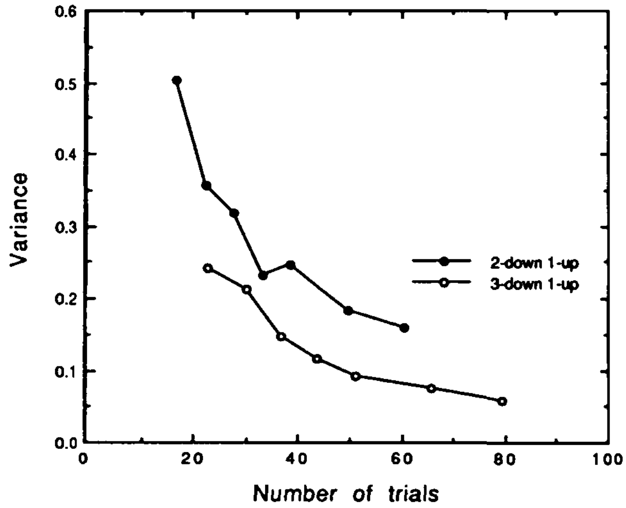

Figure 5 The variance in the simulated threshold measurements from Figure 3, plotted against the corresponding mean number of trials from Figure 4, with two-down one-up and three-down one-up rules.

Discussion

The present results gave evidence for the existence of selective, stimulus-specific effects of attention (or perhaps preattentive processes) in taste. The detection threshold for a given taste substance, sucrose or citric acid, was lower when the subjects were expecting that substance. Thus these results provide initial evidence for the role of attention in taste detection, using a psychophysical method that controls response criterion.

In order to find evidence for attentional (or preattentive) selectivity, two conditions must be met: the perceptual system must permit attentional selection and the psychophysical method must be sufficient to measure the attentional effects. Regarding the method, in chemosensory studies a limiting factor is often the number of trials that may be feasibly given within a given session. If the aim is to reduce variability due to sampling from the stochastic psychometric function, then our computer simulations suggest that, for a fixed number of trials, it is clearly preferable to use a three-down one-up rule rather than the popular two-down one-up rule, as Kollmeier *et al.* (1988) and Green (1990) have suggested. Further, this conclusion appears to have considerable generality: the only way we were able to make the variability associated with the two- down one-up rule as small or smaller than the variability associated with the three-down one-up rule was to choose a starting stimulus concentration that fell at or near 0.71 correct, that is, at or near the threshold as defined for the two-down one-up rule [it is possible that other approaches, e.g. maximum-likelihood adaptive procedures, may ultimately prove even better (Linschoten *et al.*, 1996)].

In order for attentional selectivity to take place, it is necessary for the perceptual system itself to satisfy two main constraints. First, neural elements in the perceptual system must respond differentially to different gustatory inputs; and second, a central attentional mechanism must be capable of capitalizing on these differential inputs. The panels of Figure 6 broadly characterize four models, two of which (A and B) do not permit selective attention (or preattention) and two of which (C and D) do. Each panel shows the same set of hypothetical sensitivity functions, which may be thought as characterizing the inverse of stimulus thresholds of peripheral nerve fibers (analogous to tuning curves in hearing). Although each of these hypothesized fiber types is relatively broadly tuned, being responsive to many tastants, each is characterized by greatest sensitivity to a particular tastant.

In the 'convergence model' of panel A, the responses from these (peripheral) neural units converge onto a single detector, which might itself be located either peripherally or centrally but in either case does not distinguish among the inputs; consequently, while attentional processes could modulate overall sensitivity to all taste stimuli, attention in this model could not affect sensitivity to particular tastants differentially. One might expect a model of this sort to apply to visual stimuli varying in wavelength, under conditions in which detection is mediated by a single 'luminosity' channel that pools the inputs from two or three cone receptors (see e.g. DeValois *et al.*, 1966). In the 'shared attention model' of panel B, the inputs arising from different classes of peripheral neurons do not converge, but the attentional system always monitors fully the activity in all of these detectors; that is, attention may be present but is *not*

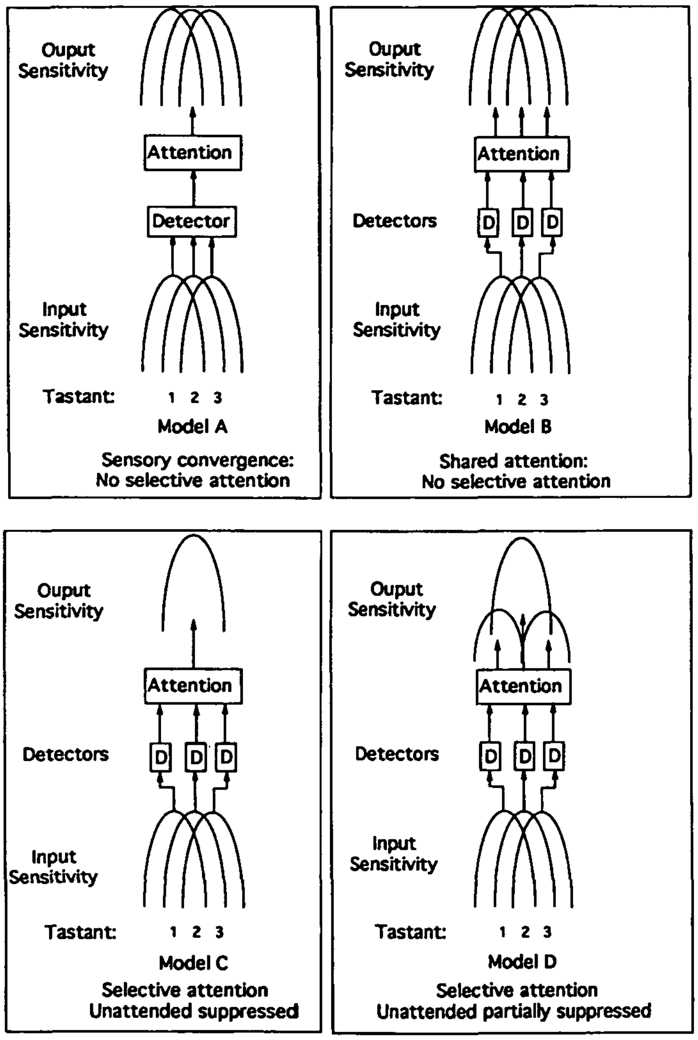

Figure 6 Four models. Models A and B do not permit selective attention (in A the neural inputs are pooled, and in B attention is nonselective), whereas models C and D do permit selective attention (selectivity being greater in C than in D).

selective. Functionally, the outcome is just like that of panel A. Response-time data obtained by Driver and Grossenbacher (1996) (and unpublished results in the present first author's laboratory measuring detection thresholds) suggest that such a model may apply to tactile spatial attention, under conditions where visual and proprioceptive attention are eliminated.

In fact, it is conceivable that some sharing of attention even took place in the present experiments. By its very nature, the so-called sip-and-spit method allows the subjects several seconds of time to sample each stimulus, making it possible to shift attention during the course of the trial. Such shifts in attention would serve to diminish the magnitude of the selective effects. Thus, the evidence found here for selective attention implies that the subjects did not fully avail themselves of the opportunity to share attention between citric acid and sucrose within test trials.

Models C and D both permit selective attention or preattentive processing. In both, the neural inputs permit differential responses across stimuli, and the central attentional monitor is capable of selectivity. Models of these kinds characterize visual attention to spatial locations, auditory attention to sound frequency, and, according to the present results, gustatory attention to at least some different tastants. The main difference between these models C and D stems from their degree of selectivity. Where selectivity is very great, as in panel C of Figure 6, detection of all stimuli is mediated by whichever detector (or detector system) has its outputs monitored by attention. This model may characterize auditory attention, at least over a modest range of sound frequencies. When subjects attend to a 1000 Hz tone, the detection of a 1000 Hz tone is mediated by that subset of neurons tuned to frequencies around 1000 Hz (call these '1000 Hz neurons'). When subjects attend to 950 Hz, then detection of a 950 Hz tone is mediated by neurons tuned to 950 Hz ('950 Hz neurons'). When subjects attend to 1000 Hz but are presented with a signal at 950 Hz, however, then (according to the model) the signal will be detected by neurons tuned to 1000 Hz. Detectability is reduced under these circumstances because 1000 Hz neurons are not as sensitive as 950 Hz neurons to 950 Hz signals.

Model D simply assumes somewhat smaller attentional selectivity. Selectivity is imperfect. In this case, to continue the auditory example, when subjects attend to 1000 Hz, the detection of a 950 Hz signal will now be mediated by 950 Hz neurons instead of 1000 Hz neurons. But, according to this model, attention has served to reduce the sensitivity of the 950 Hz neurons. Note that both model C and model D could also characterize the operation of preattentive selective processing. Thus, for example, what we have termed attention, implying voluntary control, might represent automatic preferential processing stimuli that are cued or presented most frequently, independent of the subjects' voluntary deployment of attention. Preattentive processing might even occur if presenting stimulus A more often than stimulus B preferentially sensitized or 'primed' the peripheral neural channel associated with A (although it should be pointed out that adaptation seems at least as likely as priming). Although studies of selective attending in hearing provide evidence against preattentive processing (Hafter *et al.*, 1993), the present study does not distinguish between possible preattentive and attentive mechanisms in taste, to which both model C and model D could apply. Thus allusions to attention include the possibility of preattentive mechanisms.

Which model, C or D, characterizes attention in taste? When subjects attended to sucrose, did they detect citric acid by means of their sucrose-detection system, which is less sensitive to citric acid than is the citric-acid-detection system? Or did they detect citric acid by the (attenuated) citric-acid-detection system? The relatively small amount of selective attention that turned up in the present studies, amounting to only ~0.2 log concentration units in sensitivity, suggests to us the latter. The matter may hinge on the form of the 'tuning curves' for different detectors in the taste system.

At the peripheral level, it is clear that different neural mechanisms serve to transduce different tastants. Individual peripheral nerve fibers in the chorda tympani and glossopharyngeal nerves show at least modest selectivity in their responsiveness (e.g. Frank, 1973; Frank *et al.*, 1988; Hanamori *et al.*, 1988), as do neurons in the central nervous system (e.g. Travers and Smith, 1979; see also Scott and Giza, 1990). But while many studies have reported response profiles in single taste units, relatively few studies actually measure threshold sensitivity to different tastants. A few studies have reported results obtained when stimulus concentration was varied (e.g. Travers and Smith, 1979) and these data suggest that individual units do vary in their sensitivity profiles, consistent with the general model in Figure 6, but it is difficult to assess the sharpness of the sensitivity profiles. Moreover, it would be critical to identify these profiles within the populations of neurons, presumably located in the central nervous system, that are directly responsible for detecting taste stimuli, and about which it is possible right now only to speculate.

Finally, it is worth pointing out that the present study focused on one of many potential psychophysical measures of attention. Much, perhaps most, research on the role of attention in perception has relied on response times, which provide robust and sensitive measures of performance. Nevertheless, measures of stimulus detection are especially useful for evaluating the underlying mechanisms. For example, Butter *et al.* (1989), working in the visual and tactile senses, found that subjects were quicker to identify an attended stimulus than an unattended one. Unfortunately, it is difficult to interpret the results of this and similar studies that use response-time paradigms, for it is not easy to decide whether shifts in performance reflect changes in sensitivity of the perceptual system (e.g. greater or lesser strength or clarity of the percept) or merely changes in response criteria. Current models of stimulus identification or choice, for instance, assume that subjects await the cumulation of evidence until the level of evidence for a particular response surpasses a decisional criterion (LaBerge, 1962; Vickers; 1970; Ben-Artzi and Marks, 1995). For example, if a person must decide whether the stimulus on a given trial is sucrose or citric acid, the person is hypothesized to respond as soon as the neural signals specifying either sucrose or citric acid reach a predetermined criterial level. Such criteria are readily modified, in that changes in instruction or pay-off can induce the subject to respond more quickly or more slowly to a particular stimulus; the gain or loss of speed is associated with a corresponding decrease or increase in accuracy (speed–accuracy tradeoff). Similarly, shifts in attention can modify performance by inducing the subject to shift the criteria for responding. Lowering the criterion to respond to an attended stimulus will reduce the response time but increase the likelihood of an erroneous response. Kuznicki and Turner (1986) noted that cognitive factors influenced the response times that they measured to tastants. To determine experimentally whether shifts in attention affect the strength or 'quality' of sensory information as well as the response criteria generally requires collecting data across sufficiently large numbers of trials to assess accurately the error rates, which tend to be low. Although measures of detectability are considerably more time-consuming than are measures of response times, they can provide invaluable data for probing the mechan- isms that underlie attention.

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References

Bartoshuk, L.M., Rifkin, B., Marks, L.E. and **Bars, P.** (1986) *Taste and aging*. J. Gerontol., 41, 51–57.

Ben-Artzi, E. and **Marks, L.E.** (1995) *Congruence effects in classifying auditory stimuli: a review and a model*. In Scharf, B. and Possamaï, C.-A. (eds), Fechner Day 95: Proceedings of the Eleventh Annual Meeting of the International Society for Psychophysics. ISP, Vancouver, pp. 145–150.

Botte, M.-C. (1995) *Auditory attentional bandwidth: effect of level and frequency range*. J. Acoust. Soc. Am., 98, 2475–2485.

Butter, C.M., Buchtel, H.A. and **Santucci, R.** (1989) *Spatial attentional shifts: further evidence for the role of polysensory mechanisms using visual and tactile stimuli*. Neuropsychologia, 27, 1231–1240.

Dai, H., Scharf, B. and **Buus, S.** (1991) *Effective attenuation of signals in noise under focused attention*. J. Acoust. Soc. Am., 89, 2839–2842.

DeValois, R.L., Abramov, I. and **Jacobs, G.H.** (1966) *Analysis of response patterns of LGN cells*. J. Opt. Soc. Am., 56, 966–977.

Driver, J. and **Grossenbacher, P.G.** (1996) *Multimodal spatial constraints on tactile selective attention*. In Inui, T. and McClelland, J.L. (eds), Attention and Performance XVI. MIT Press, Cambridge, MA, pp. 209–235.

Ericksen, C.W. and **Yeh, Y.** (1985) *Allocation of attention in the visual field*. Percept. Psychophys., 11, 583–597.

Frank, M. (1973) *An analysis of hamster taste nerve response functions*. J. Gen. Physiol., 61, 588–618.

Frank, M.E., Bieber, S.L. and **Smith, D.V.** (1988) *The organization of taste sensibilities in hamster chorda tympani nerve fibers*. J. Gen. Physiol., 91, 861–896.

Gallant, J.L. (1989) Mechanisms of Spatial Selective Attention. Doctoral dissertation, Department of Psychology, Yale University.

Green, D.M. (1990) *Stimulus selection in adaptive psychophysical procedures*. J. Acoust. Soc. Am., 87, 2662–2674.

Greenberg, G.Z. and **Larkin, W.D.** (1968) *Frequency–response characteristics of auditory observers detecting signals of a single frequency in noise: the probe–signal technique*. J. Acoust. Soc. Am., 44, 1513–1523.

Hafter, E.R., Schlauch, R.S. and **Tang, J.** (1993) *Attending to auditory filters that were not stimulated directly*. J. Acoust. Soc. Am., 94, 743–747.

Hall, J.L. (1983) *A procedure for detecting variability of psychometric functions*. J. Acoust. Soc. Am., 73, 663–667.

Hanamori, T., Miller, I.J., Jr and **Smith, D.V.** (1988) *Gustatory responsiveness of fibers in the hamster glossopharyngeal nerve*. J. Neurophysiol., 60, 478–498.

Kinchla, R.A. (1992) *Attention*. Annu. Rev. Psychol., l43, 711–742.

Kinnamon, S.C. and **Cummings, T.A.** (1992) *Chemosensory transduction mechanisms in taste*. Annu. Rev. Physiol., 54, 715–731.

Kollmeier, B., Gilkey, R.H. and **Sieben, U.K.** (1988) *Adaptive staircase techniques in psychoacoustics: a comparison of human data and a mathematical model*. J. Acoust. Soc. Am., 83, 1252–1262.

Kuznicki, J.T. and **Turner, L.S.** (1986) *Reaction time in the perceptual processing of taste quality*. Chem. Senses, 11, 183–201.

LaBerge, D.A. (1962) *A recruitment theory of simple behavior*. Psychometrika, 27, 375–396.

Laming, D. and **Marsh, D.** (1988) *Some performance tests of QUEST on measurements of vibrotactile thresholds*. Percept. Psychophys., 44, 99–107.

Link, S.W. (1992). The Wave Theory of Difference and Similarity. Lawrence Erlbaum Associates, Hillsdale, NJ.

Linschoten, M.R., Harvey, L.O., Jr, Eller, P.M. and **Jafek, B.W.** (1996) *Rapid and accurate measurement of taste and smell thresholds using an adaptive maximum-likelihood staircase procedure*. Poster presented at the Eighteenth Annual Meeting of the Association for Chemoreception Sciences, Sarasota, FL.

Luck, S.J., Hillyard, S.A., Mouloua, M., Woldorff, M.G., Clark, V.P. and **Hawkins, H.L.** (1994) *Effects of spatial cuing on luminance detectability: psychophysical and electrophysiological evidence for early selection*. J. Exp. Psychol.: Hum. Percept. Perform., 20, 887–904.

Mondor, T.A. and **Bregman, A.S.** (1994) *Allocating attention to frequency regions*. Percept. Psychophys., 56, 268–276.

Moore, B.C.J. (1989) An Introduction to the Psychology of Hearing, 3rd edn. Academic Press, New York.

Posner, M. (1978) Chronometric Explorations of Mind. Lawrence Erlbaum Associates, Hillsdale, NJ.

Scharf, B., Quigley, S., Aoki, C., Peachey, N. and **Reeves, A.** (1987) *Focused auditory attention and frequency selectivity*. Percept. Psychophys., 42, 215–223.

Schlauch, R.S. and **Hafter, E.R.** (1991) *Listening bandwidths and frequency uncertainty in pure-tone signal detection*. J. Acoust. Soc. Am., 90, 1332–1339.

Scott, T.R. and **Giza, B.K.** (1990) *Coding channels in the taste system of the rat*. Science, 249, 1585–1587.

Spence, C.J. and **Driver, J.** (1994) *Covert spatial orienting in audition: exogenous and endogenous mechanisms*. J. Exp. Psychol.: Hum. Percept. Perform., 20, 555–574.

Stevens, J.C. (1996) *Detection of tastes in mixtures with other tastes: issues of masking and aging*. Chem. Senses, 21, 211–221.

Taylor, M.M., Forbes, S.M. and **Creelman, C.D.** (1983) *PEST reduces bias in forced choice psychophysics*. J. Acoust. Soc. Am., 74, 1367–1374.

Travers, J.B. and **Smith, D.V.** (1979) *Gustatory sensitivities in neurons of the hamster nucleus tractus solitarius*. Sens. Proc., 3, 1–26.

Treisman, A. and **Gormican, S.** (1988) *Feature analysis in early vision: evidence from search asymmetries*. Psychol. Rev., 95, 15–48.

Vickers, D. (1970) *Evidence for an accumulator model of psychophysical discrimination*. Ergonomics, 13, 37–58.

Ward, L.M. and **Mori, S.** (1996) *Attention cueing aids auditory intensity resolution*. J. Acoust. Soc. Am., 100, 1702–1707.

Wetherill, G.B. and **Levitt, H.** (1965) *Sequential estimation of points on a psychometric function*. Br. J. Math. Stat. Psychol., 18, 1–10.

Wolfe, J.M., Cave, K.R. and **Franzel, S.L.** (1989) *Guided search: an alternative to the modified feature integration model for visual search*. J. Exp. Psychol.: Hum. Percept. Perform., 15, 419–433.

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