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Alternating Ingestive and Aversive Consummatory Responses Suggest a Two-Dimensional Analysis of Palatability in Rats

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The hedonic response to a taste is typically regarded to be the product of a central integration of gustatory afferent information, which ends in a single decision about the nature and intensity of the response to be given. This hedonic response is often characterized as a point lying along a single dimension of palatability, stretching from strongly positive to strongly negative. The present analysis of species-specific consummatory responses suggests that the final response is not made on the basis of a single central analysis of taste information but rather is the result of a competition between two separate systems that are activated by tastes. A single oral infusion of a taste solution may elicit rapid alternation between ingestive and aversive consummatory responses. Such alternation is better interpreted as due to a simultaneous activation of two palatability dimensions than as a reflection of neutral palatability. When increases in the magnitude of aversive responses are produced by taste mixtures, there is not necessarily a reciprocal decrease in ingestive responses. This asymmetry supports the hypothesis of independent palatability dimensions.

Palatability is a complex central evaluation which, in combination with other factors, determines the response that will be elicited by food. Palatability should not be confused with taste quality or intensity, although both of these contribute to the analysis of palatability. Human verbal reports show that the palatability of an unchanging sweet stimulus varies as a function of satiety (Cabanac, 1971). For other species, a variety of behavioral evidence indicates that palatability is separable from taste quality and intensity. Rats show a growing preference for sodium chloride as it increases in concentration until a certain point is reached. As concentration increases beyond that point, preference falls off even when postingestional consequences are eliminated by an esophageal fistula (Stellar, Hyman, & Samet, 1954). Since sodium chloride concentration and the discharge intensity of taste sensory nerves (e.g., VII and IX) are positively correlated, the correlation between sensory intensity and ingestion obviously changes from positive to negative at the point of preference reversal, assuming that sensory intensity and afferent nerve discharge rate are roughly identical (Pfaffmann, 1960). In a similar vein, preferred sweet tastes that are paired with LiCl-induced illness are subsequently avoided (Garcia & Koelling, 1966; Rozin, 1967), and the pattern of species-specific consummatory responses elicited by oral infusions of these tastes switches from ingestive to aversive (Berridge, Grill, & Norgren, 1981; Grill, 1975). Taste quality or intensity alone, therefore, cannot directly drive or predict behavior. To account for these and similar phenomena requires the postulation of a central nervous palatability variable which, while influenced by taste intensity and quality, must also at least take into account the

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animal's internal state and its past experience with that taste.

We usually conceive of palatability as varying along a single continuum or dimension: from very positive, through neutrality, to very negative (Figure 1). According to this single-dimension view of palatability, a taste may be either positive, negative, or neutral, but it is never both positive and negative at the same time. A possible alternative to this view is that palatability does not reflect a single decision but rather two distinct analyses of the positive and negative aspects of the taste. This second view requires positing two separate dimensions of positive and negative palatability and would allow a taste to be simultaneously perceived as both positive and negative to varying extents.

The idea of palatability as a single dimension, stretching from a positive extreme through neutrality to a negative extreme, has succeeded because it is intuitively acceptable and is supported by measures such as intake tests, preference tests, operants, lick rate, and so on (e.g., Davis, 1973; Guttman, 1954; Richter, 1942). A potential problem with these measures, however, is that they all use responses that are themselves best described as varying along a single continuum, either from high to low or from positive to negative. This means that data collected from such measures would be likely to produce the impression that taste responses are organized along a single dimension, even if the brain actually generated responses using a different sort of mechanism. The present data, obtained by a noncontinuous measurement of responses to tastes, species-specific consummatory actions, suggest that the two-dimensional view of palatability processing may be more accurate and that palabability may actually comprise two separate dimensions of ingestion and aversion. These dimensions appear largely independent and at times can be simultaneously activated.

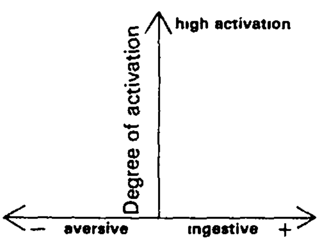

Figure 1 A single hedonic continuum model of palatability. (Modified from Young, 1977.)

Experiment 1

Taste-elicited consummatory responses provide a highly detailed and sensitive measure of the effects of different tastes. These consummatory responses are taste dependent and are easily classified as either ingestive (rhythmic mouth movements, tongue protrusions, and lateral tongue protrusions) or aversive (gapes, head shakes, chin rubs, paw wipes, and forelimb flailing; Figure 2). In addition, consummatory responses correlate well with other measures of taste palatability. Ingestive responses are elicited by sucrose infused into the mouth in a graded, concentration-dependent manner (Grill & Norgren, 1978a). Low concentrations elicit only mouth movements and tongue protrusions; lateral tongue protrusions increase with increasing sucrose concentrations. Aversive responses to quinine are also elicited in a concentration-dependent manner. Gapes and chin rubs are evoked by relatively low quinine concentrations; the other aversive components appear with higher concentrations.

Certain other tastes, such as .15 M NaCl or .3 M NH_4Cl, typically elicit a mixed response (Berridge et al., 1981). A close inspection of the data reveals that the midpoint between the two extremes, mixed responding, actually occurs in two very different ways. In one case, the portion of the stimulus that is not consumed is allowed to drip passively from the mouth as it is infused. In the other case, the nonconsumed portion is actively expelled from the mouth, although, at other moments within the same minute, the solution is consumed (Berridge & Grill, Note 1).

A mechanism that generated a response to a taste based on that taste's placement along a palatability continuum could be expected to produce a neutral response (i.e., a response that is neither truly ingestive nor truly aversive) when confronted with a taste that is perceived as neutral in palat-

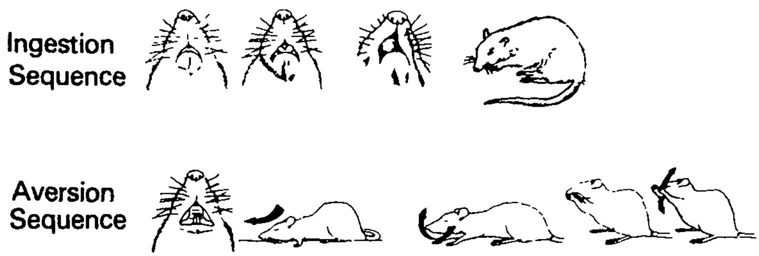

Figure 2 Taste-elicited consummatory responses. (Ingestive responses [top] are elicited by continuous oral infusions of glucose, sucrose, isotonic sodium chloride, and other palatable solutions and include rhythmic mouth movements, tongue protrusions, lateral tongue protrusions and paw licking Aversive responses [bottom] are elicited by infusions of quinine solutions and include gapes, chin rubs, head shakes, paw wipes, forelimb flailing, and locomotion [not shown]. Adapted by permission from "Relation of Consummatory Responses and Preabsorptive Insulin Release to Palatability and Learned Taste Aversions" by Kent Berridge, Harvey Grill, and Ralph Norgren, *Journal of Comparative and Physiological Psychology*, 1981, *95*, 363-382)

ability. The question is what constitutes a neutral response. Are both modes of mixed responding equally viable candidates for a neutral response? This experiment represents preliminary observations that arose out of a study involving presentation of a number of tastes of varying palatability. These preliminary observations of a pool of 50 mixed responses to various tastes suggest that, in fact, only instances in which the solution is passively allowed to drip from the mouth qualify as neutral responses to tastes. A mixed response that contains some active rejection, accompanied by partial ingestion, is better described as a simultaneous activation of ingestive and aversive response systems than as an activation of neither. This interpretation gives rise to a hypothesis that is tested in the second experiment.

Method

This analysis was performed as a part of a larger effort comparing consummatory responses and preabsorptive insulin responses to tastes. Male Sprague-Dawley rats (Charles River Laboratories), weighing between 300 and 400 g, were maintained on ad lib laboratory chow and water. Rats were run in groups of four or five, each group receiving four taste stimuli, and each experiment was conducted over 5 consecutive days. On the first day, each rat was surgically implanted with two chronic oral cannulas and with a chronic jugular cannula (all cannulas exited from the dorsal head and did not restrict movement) under barbituate anesthesia (Berridge et al., 1981). Testing began on the second day.

Testing procedure Rats were deprived of food beginning at 9:00 a.m. and were each tested 4 hr later. At this time, each rat's oral cannulas were connected to stimulus-delivery tubes. Each rat was allowed to habituate to the cylindrical, clear-plastic testing chamber for 10 min on each test day Then a 1-ml volume of the taste solution was infused into the mouth at a constant rate over 1 min, and the consummatory responses (see below) and time spent ingesting during the 1-min infusion were recorded.

Consummatory response criteria Each rat was scored for the occurrence of ingestive and aversive consummatory response components. Ingestive components (see Figure 2, top) are mouth movements—low-amplitude, rhythmic openings of the mandible (6.6 Hz); tongue protrusions—rhythmic protrusions of the tongue (8.8 Hz) on the midline, with the tongue covering the upper incisors; lateral tongue protrusions—nonrhythmic extensions of the tongue on either side of the mouth, with the tongue pushing the lip laterally as it moves forward, with duration of 85–215 msec, and paw licking—persistent direction of the ingestive response toward the rat's own forepaws, with the paws held close to the mouth and lapped for some seconds Aversive components (see Figure 2, bottom) are gaping—rapid large-amplitude opening of the mandible with concomitant retraction of the corners of the mouth to reveal the internal oral labia and retraction of the lower lip, lasting approximately 160 msec; chin rubbing—bringing the mouth in direct contact with a substrate (i.e., floor or wall) and projecting the body forward by flexion of the dorsal neck and by pectoral and forelimb musculature; head shaking—rapid side-to-side movements of the head at a rate faster than 60 Hz; forelimb flailing—rapidly shaking both forelimbs in the horizontal plane with a frequency of greater than 60 Hz; and paw wiping—the unilateral downward movement of either forepaw across the face. It can occur as a single movement or as a group of several wipes with the same paw.

If the solution was not entirely consumed, then the amount of time within the minute during which the stimulus was not ingested was recorded. In addition, instances of fluid ejection were classified as either passive drip or active rejection In passive drip, fluid simply accumulated along the tip of the lower mandible and dropped off. The rat might or might not simultaneously ingest part of the solution. In active rejection, the fluid was expelled with force, usually in conjunction with an aversive response component such as headshake, forelimb flailing, or chin rubbing.

Taste stimuli During a test week, each rat received four different taste stimuli, one on each day. The order of taste presentation was counterbalanced across each group. Taste stimuli were glucose (2.76 M), glucose, sucrose, maltose, galactose, and sorbitol (all .8 M), lactose (.5 M), HCl (.025 M), sodium saccharin (.15%), sunflower oil, mineral oil, leucine (.05 M), lysine (.05 M), argenine (.05 M), proline (.05 M), phenylalanine (.05 M), and tyrosine (.05 M).

Data analysis The purpose of the present analysis was to examine the pattern of consummatory responses that occurs when a taste is neither unequivocally ingested nor unequivocally rejected. For this reason, only trials in which the rat consumed more than 10% but less than 90% of the taste solution were selected for analysis. Such a response was considered to be active if, at any moment during the minute's infusion, fluid was either wiped away or expelled with force from the mouth. If all of the nonconsumed portion of the stimulus was, instead, allowed to simply drip from the mouth, then the trial was classified as passive rejection.

Trials that met this criterion were assigned to either a passive or an active rejection category. Consummatory responses within each category were then added over all taste groups and expressed as a percentage of all rats within the category. Seconds spent ingesting during the minute of presentation were also averaged for each category.

Results

Under these conditions, 50 rats consumed between 10% and 90% of the taste solution and so were selected for analysis. In this group of 50 rats, both passive and active rejection were observed, with the former predominating by 42 to 8. The amount of ingestion was equivalent for both active and passive rejection, in each of which the stimulus was consumed for approximately 30 sec of the 60-sec trial. There were marked differences between active and passive rejection, however, in the pattern of consummatory responses (Figure 3). Rats that actively rejected the stimulus showed significantly more ($p < .01$; all statistics by a two-tailed z test of proportions) chin rubs (13% active vs. 2% passive) and head shakes (75% vs. 10%).

Surprisingly, ingestive responses were seen more frequently in active rejectors than in passive rejectors. Lateral tongue protrusions occurred significantly more often (75% active vs. 12% passive; $p < .01$), and paw licks (25% vs. 14%) were also more frequently seen. One other difference between the two groups stands out. In 26% of the instances in which passive drip was observed, mouth movements were the only consummatory response component emitted. In no instance of active rejection were mouth movements observed alone, nor even (allowing for the fact that active rejection involves by definition some aversive response) in the absence of other ingestive components. Active rejection, in other words, was always accompanied by at least two ingestive components.

Discussion

It is not surprising that active rejection, when accompanied by partial consumption, occurs with a higher proportion of headshakes, chin rubs, and gapes. This follows from the definition of active rejection. It is surprising, however, that active rejection also entails a significantly higher incidence of ingestion, specifically, a higher proportion of the most strongly ingestive consummatory response (i.e., the response elicited by high but not by low glucose concentrations), lateral tongue protrusions. These data suggest that (a) active rejection of the taste stimulus can occur even in the presence of a highly activated ingestive response system and (b) passive drip characterizes a response to taste that is neither strongly ingestive nor strongly aversive (i.e., a neutral response).

Mouth movements were observed in virtually every case (100% active vs. 98% passive) and thus appear not to be strongly hedonically weighted toward either ingestion or aversion. Mouth movements may serve in part to assist in the evaluation of taste stimuli, by facilitating contact with the gustatory receptors. These responses should not be considered to be entirely evaluative (rather than hedonically expressive), however, because evaluation of a taste often occurs without the occurrence of mouth movements and because the proportion of mouth movements does appear to be directly related to the positive palatability of the taste (Berridge et al., 1981). Thus this component may be best described as a weakly ingestive component with possible

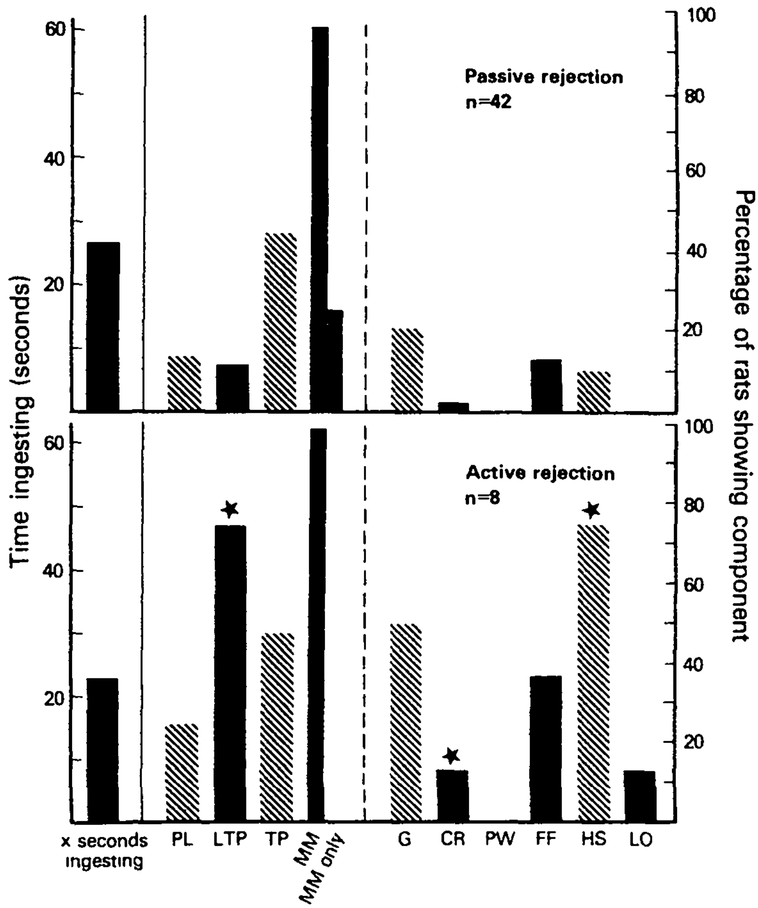

Figure 3. Active and passive responses across 17 taste stimuli. (Only responses in which more than 10% but less than 90% of the stimulus solution was consumed are depicted Rats that actively rejected any portion of the stimulus were classified as active rejectors; rats that allowed all of the nonconsumed portion of the stimulus to drip from the mouth were classified as passive rejectors. Stars denote significant differences, $p < .01$, between the two groups in the proportion of rats showing that consummatory response. Consummatory responses are paw licking [PL], lateral tongue protrusions [LTP], tongue protrusions [TP], and mouth movements [MM]. Aversive responses are gapes [G], chin rubs [CR], paw wipes [PW], forelimb flailing [FF], headshakes [HS], and locomotion [LO]. Ingesting time is the total seconds of stimulus consumption during a 1-min infusion.)

evaluative functions. If mouth movements are, indeed, a relatively unweighted response component, then the fact that passive drip is characterized in 26% of the cases by mouth movements in the absence of other consummatory responses supports our conclusion that passive drip represents a truly neutral consummatory response to taste. Mouth movements alone never occurred in instances of active rejection, which always contained other more strongly weighted ingestive as well as aversive components.

The presence of any intense consummatory response to taste implies the activation of a palatability response system. The additional presence of an opposing response implies, not neutrality, but the simultaneous activation of two extremes. We interpret our finding, that active rejection may be accompanied by stronger ingestion than was seen in passive rejection, to mean that consummatory responses to tastes may not be the result of a single analysis of a taste's palatability but instead may involve two separate analyses, which correspond re-

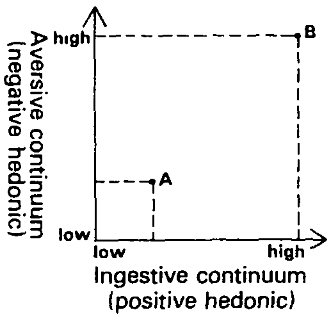

Figure 4 A two-dimensional model of palatability. (Point A represents a taste that weakly activates both ingestion and aversion and results in a passive response. Point B represents a taste that strongly activates both ingestion and aversion and results in active alternation of ingestive and aversive consummatory responses. The palatability of other tastes may be represented by points falling anywhere within the plane described by the axes of ingestion and aversion.)

spectively to dimensions of ingestion and aversion. Low activation of both dimensions (point A in Figure 4) results in a relatively neutral response, or passive drip. High activation of both (point B in Figure 4) results in the simultaneous expression of the two extremes, or the mixed pattern observed with active rejection. Such simultaneous elicitation of two extremes by the same taste might be expected to be an unusual event, and this is consistent with our observation that of 50 instances of partial consumption only 8 involved rejection.

The conclusion of simultaneous activation requires the demonstration that mixed consummatory responses, elicited over a minute's infusion, can in fact be elicited in rapid alternation and that a mixed response need not reflect, say, 30 sec of ingestion followed by 30 sec of rejection (a pattern we have also observed). A shift of this latter sort could be the result of a shift in perceived palatability resulting either from changes in internal factors (e.g., Cabanac, 1971) or from the inadvertent stimulation of different oral receptors during different portions of the minute (Craig, 1912). A brief examination of diverse kinds of mixed responses shows that one easily finds ingestive and aversive consummatory responses that rapidly alternate, rather than simply appear in different portions of the minute. Two such responses, which were videotaped and later scored, in one case to a novel presentation of .3 M NH_4Cl and in the other to a mixture of ammonium chloride, glucose, and quinine, are seen in Figure 5. Aversive and ingestive responses rapidly alternate over both minutes of infusion.

Rapid alternation between one behavior and its functional opposite has often been interpreted as revealing conflict between underlying mechanisms; such alternation has been termed "ambivalent behavior" (e.g., Tinbergen, 1952). The rapid alternation of ingestive and aversive response systems shown in Figure 5 implies a simultaneous activation of the two response systems and suggests that an actual conflict

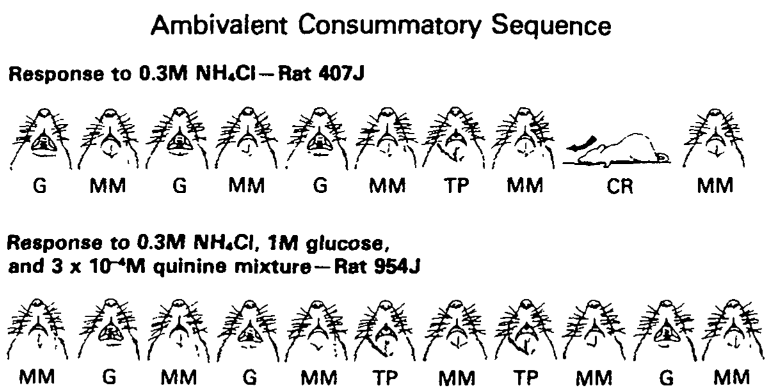

Figure 5 Rapid alternation of ingestive and aversive consummatory responses. (The pattern of responses given by a rat to a constant 1-min oral infusion of NH_4Cl [.3 M; top] and to a mixture [bottom] of NH_4Cl [.3 M], glucose [1 M], and quinine HCl [3×10^{-4} M], concentrations refer to the concentration of the final solution]. Consummatory responses are rhythmic mouth movements [MM], tongue protrusions [TP], gapes [G], and chin rubs [CR].)

exists between internal tendencies to emit two different types of responses. Such alternating sequences need not be the most commonly elicited response in order to be meaningful, and, in fact, we have observed other sequences as well. Alternation is seen with a frequency sufficient to leave no doubt as to its existence, however, and should be recognized for the potentially revealing phenomenon that it is. The fact that rhythmic mouth movements, a response component that we have classified as weakly ingestive, appear in every instance of mixed responding with partial consumption suggests that they may be a response that can express both simultaneously present tendencies, or what Andrew (1956) has called "compromise behavior."

Experiment 2

An implication of the hypothesis of two palatability dimensions is that the positive and negative aspects of a taste ought to be able to be manipulated independent of each other. It should be possible, for example, to increase the probability of showing aversive components without equally decreasing the probability of showing ingestive responses, and vice versa. This prediction might be tested by taking a taste whose palatability is perceived as being mixed, such as ammonium chloride, and simply adding other tastes to it. A single-continuum model of palatability would predict that any increase in either ingestive or aversive consummatory responses produced by such a manipulation is necessarily accompanied by a symmetrical decrease of the opposite consummatory response group. A two-dimensional model, on the other hand, would allow ingestive and aversive responses to be manipulated independently.

Method

Six male Sprague-Dawley rats, weighing 300–400 g, were implanted with chronic oral cannulas. Testing began 2 days after surgery. Stimulus presentation was performed according to the method used in Experiment 1 All behavior was videotaped for subsequent blind analysis. Each rat received one taste stimulus per day, and the order of stimulus presentation was counterbalanced over 4 days. The taste stimuli were .3 M ammonium chloride alone; a single solution that was both .3 M ammonium chloride and 1 M glucose; a single solution that was both .3 M ammonium chloride and 3×10^{-4} M quinine hydrochloride, and a single solution that was .3 M ammonium chloride, 1 M glucose, and 3×10^{-4} M quinine hydrochloride.

Results

Ammonium chloride alone elicited mixed consummatory responses, with ingestion predominating (Figure 6). Glucose combined with ammonium chloride produced no statistical change (eliciting both slightly fewer ingestive and slightly fewer aversive consummatory responses than ammonium chloride), which suggests that the palatability of these two tastes does not simply sum additively. Quinine and ammonium chloride elicited doubled aversive responding across each consummatory response, compared with ammonium chloride alone, and reduced ingestive responding by approximately 30%. What was most interesting was that ammonium chloride combined with both glucose and quinine elicited increased aversion, as reflected by a dramatic increase in the incidence of aversive gapes ($p < .02$, two-tailed z test of proportions), with no overall change in ingestive responses.

Discussion

The rationale for this experiment is based on the assumption that the palatability of two tastes will simply sum additively when combined. This assumption is often but not always true (Pfaffmann, Bartoshuk, & McBurney, 1971). In the case of the glucose and ammonium chloride mixture, the assumption is apparently false: Both ingestive and aversive responses declined relative to those from ammonium chloride alone. The other mixtures do largely support the summation assumption. Quinine mixed with ammonium chloride dramatically increased aversion while decreasing the probability of ingestive responses to a lesser extent. The interpretation of this effect is complicated by the fact that even if the systems responsible for palatability processing and for initiating consummatory responses are independent, the systems responsible for producing those

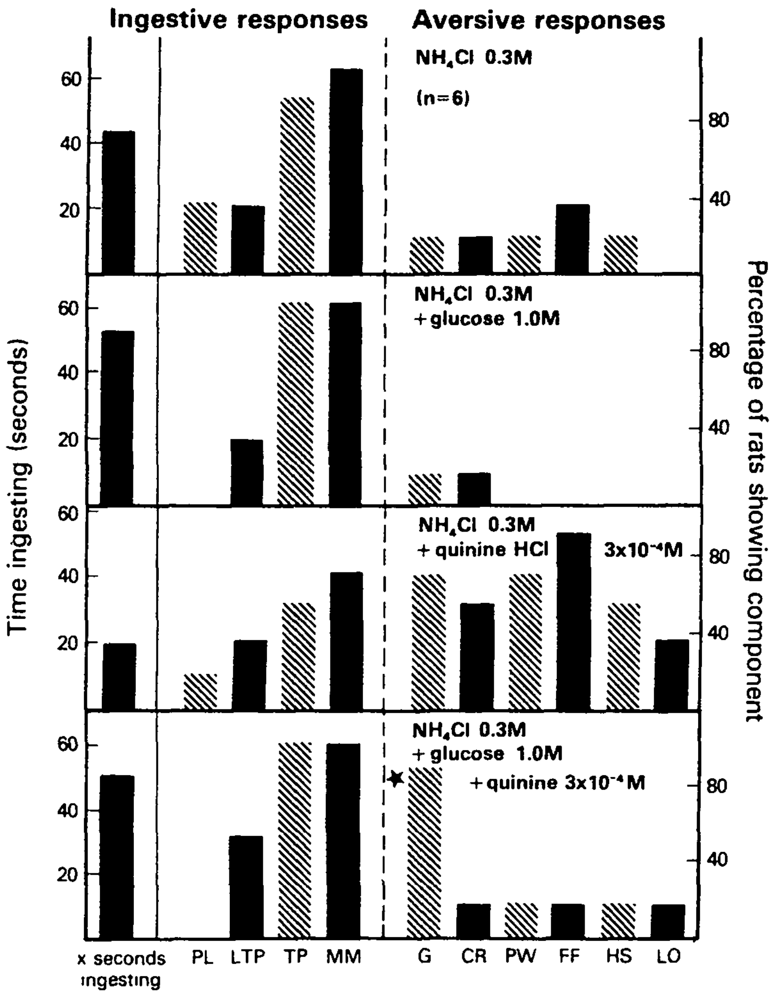

Figure 6 Consummatory response profiles to taste mixtures. (Changes in the pattern of responses of the same rats when NH_4Cl [.3 M] is combined with glucose [1 M], quinine HCl [3×10^{-4} M], or both [concentrations refer to the concentration of the final solution]. Star denotes significant difference from NH_4Cl alone, $p < .02$. Consummatory response symbols are as in Figure 3.)

responses are not. The rat can make only one response at a time, and competition for expression between two systems could possibly account for the 30% decrement in ingestive responses, even if the potential tendency to ingest remained constant. Fortunately, we escape this difficulty of interpretation in the ammonium chloride–glucose–quinine mixture. In this case a clear overall increase in aversive responses is seen, due to the statistically significant increase in gapes, and no overall change in ingestive responses. This is an asymmetrical change, and it is better accounted for by a two-dimensional model than by a single-continuum view.

General Discussion

The hedonic response to a taste is traditionally regarded as the product of a central integration of gustatory information, which ends in a single command or decision about the nature and intensity of the response to be given. This single decision is generally taken to be characterized by a point falling somewhere along a palatability continuum. Our present data suggest that a single palatability continuum may not be the best way to represent the processes involved in the production of species-typical consummatory responses. Pure ingestion and aversion do indeed exist in consummatory responses, but there is no single continuum to describe what lies between them, no smooth merging of the one into the other. Instead, tastes of ambiguous palatability may elicit two different types of responses. They may, on the one hand, elicit neither ingestive nor aversive responses and thus qualify as truly neutral in palatability. On the other hand, a taste may elicit both ingestive and aversive responses, in varying degrees of both and sometimes in alternation. By manipulating taste input, as we have done by additions of glucose or quinine to a test solution, the proportion of ingestion and aversion can be changed. These changes need not be symmetrical: Adding glucose and quinine to ammonium chloride statistically increased aversion while leaving ingestion unchanged.

The proportion of ingestive to aversive responses is not a constant, as might be the case if the difference between the two kinds of response patterns reflected merely differences in general arousal. Unpublished data (1981) from our laboratory show that as the concentration of a glucose solution descends from 2.53 M to .017 M, ingestion gradually gives way to a mixed response, with aversion beginning to rise before ingestive responses decline. Since a single palatability dimension, combined with an arousal continuum, could be expected to produce a mixed consummatory response at only one palatability point, namely, complete neutrality, the existence of gradual, asymmetrical shifts argues against a general arousal interpretation. This suggests that, even aside from the conceptual difficulties involved in positing a unitary continuum of arousal in explanations of animal behavior (see Andrew, 1974, for a critical review), adding an arousal postulate to a single palatability dimension will not account for the data.

As an alternative explanation, it might be suggested that our data reflect a single palatability evaluation which is translated into mixed consummatory responses by a rather complicated set of control rules (e.g., McFarland, 1974). These control rules would have to allow a single evaluation to elicit responses falling on either side of itself along the single dimension. Further, these opposite responses would have to be coordinated so to occasionally appear in alternation. Finally, these rules would have to specify that aversive responses have a higher trigger threshold than ingestive responses. This last clause is needed to account for the fact that aversive responses may be increased by taste manipulations that do not change ingestive responses (as seen in the second experiment). Such a model would predict that additional taste manipulations will continue to produce asymmetrical shifts only by changing aversive responses while ingestion remains constant. This can be examined in future research.

Even with these modifications, however, the single dimensional model still fails to account for the mutual existence of active mixed responding and passive nonresponding to tastes of "neutral" palatability. It appears that the best explanation of our data requires the positing of separate ingestive and aversive palatability processing systems which, under certain circumstances, can be separately activated. A given taste might elicit any combination of ingestive and aversive responses.

The hypothesis that palatability involves two separate evaluative analyses rather than one finds support from a number of other sources. Rat pups show ingestive consummatory responses at an earlier age than they do aversive responses: they detect and respond to sucrose by 1–3 days of age but do not respond to quinine until 9 days old (Grill & Norgren, 1978b; Hall & Bryan, 1981). From a variety of work, the "finickiness" of rats with ventromedial hypothalamic lesions (VMH) is well known (e.g., Teitelbaum, 1955). Recent work indicates that VMH finickiness is asymmetrical: VMH rats in sham-feeding analyses are hyperreactive to sweet but not to bitter foods. Sham-fed VMH rats overeat concentrated sucrose solutions, relative to weight-paired controls, but do not differ from controls in their intake of quinine-adulterated sucrose solution (Weingarten, 1982; Weingarten, Chang, & Jarvie, 1983).

Finally, when rats are divided into two groups based on their rates of intracranial self-stimulation, high self-stimulators are found to overrespond to saccharin solution but not to quinine solutions, compared with low self-stimulators (Ganchrow, Lieblich, & Cohen, 1981).

Rats that self-stimulate at high rates tend to overconsume saccharin solutions, compared with low self-stimulators, but consume comparable amounts of quinine solutions. This may imply common or overlapping neural systems mediating positive hedonic responses. These various observations support the notion that the positive and negative aspects of taste palatability may be separately processed. Of course, it is possible that these separate analyses, which may well be performed at or below the midbrain level, are themselves combined into a single decision at the forebrain level to drive appetitive behavior and subjective perceptions of palatability. Solutions of extreme palatability, such as sucrose or quinine, elicit appropriate consummatory responses in chronic decerebrate rats, which lack a functioning forebrain (Grill & Norgren, 1978b).

The data presented here tentatively suggest a two-dimensional model of palatability processing. However, much more remains to be done. It is important to expand our list of tastes and taste mixtures to establish the generality of these findings. Consummatory comparisons of isohedonic tastes (Young & Madsen, 1963) may help to elucidate the relation between consummatory and appetitive mechanisms. It is also important to improve the present behavioral analysis so as to be more sensitive to the sequence and patterning of the consummatory responses. These are the goals of future research.

Reference Note

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