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Effects of Selective Adaptation on Coding Sugar and Salt Tastes in Mixtures

Marion E. Frank, Holly F. Goyert, Bradley K. Formaker and Thomas P. Hettinger

Department of Oral Health and Diagnostic Sciences, Division of Periodontology, Center for Chemosensory Sciences, School of Dental Medicine, University of Connecticut Health Center, 263 Farmington Avenue, Farmington, CT 06030-1715, USA

Correspondence to be sent to: Marion E. Frank, Department of Oral Health and Diagnostic Sciences, Division of Periodontology, Center for Chemosensory Sciences, School of Dental Medicine, University of Connecticut Health Center, 263 Farmington Avenue, Farmington, CT 06030-1715, USA. e-mail: mfrank@neuron.uchc.edu

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Abstract

Little is known about coding of taste mixtures in complex dynamic stimulus environments. A protocol developed for odor stimuli was used to test whether rapid selective adaptation extracted sugar and salt component tastes from mixtures as it did component odors. Seventeen human subjects identified taste components of "salt + sugar" mixtures. In 4 sessions, 16 adapt–test stimulus pairs were presented as atomized, 150-μL "taste puffs" to the tongue tip to simulate odor sniffs. Stimuli were NaCl, sucrose, "NaCl + sucrose," and water. The sugar was 98% identified but the suppressed salt 65% identified in unadapted mixtures of 2 concentrations of NaCl, 0.1 or 0.05 M, and sucrose at 3 times those concentrations, 0.3 or 0.15 M. Rapid selective adaptation decreased identification of sugar and salt preadapted ambient components to 35%, well below the 74% self-adapted level, despite variation in stimulus concentration and adapting time (<5 or >10 s). The 96% identification of sugar and salt extra mixture components was as certain as identification of single compounds. The results revealed that salt–sugar mixture suppression, dependent on relative mixture-component concentration, was mutual. Furthermore, like odors, stronger and recent tastes are emphasized in dynamic experimental conditions replicating natural situations.

Key words: binary mixtures, dynamic taste coding, mixture suppression, selective adaptation

Introduction

Adaptation and mixture suppression influence identification of taste stimuli in the natural world, where mixtures prevail now as they did when the gustatory system evolved. These prominent processes weaken identification of taste stimuli with the passage of time and in the presence of other taste stimuli. Failure to resolve complex mixtures has been considered evidence for synthetic processing. However, we propose that human taste may follow basic rules established for simultaneous identification of components of olfactory mixtures (Laing and Wilcox 1983; Laing et al. 1984; Laing and Francis 1989). Preceded by rapid selective adaptation of ambient mixture components (Goyert et al. 2007; Frank et al. 2010), identification of the latest and strongest odors is promoted. In the current study, we test how selective preadaptation affects mixture-component identification in the sense of taste, with a handful of dedicated independent receptors (Yarmolinsky et al. 2009), compared to the sense of smell, with hundreds of receptors (Olender et al. 2008).

Adaptation to a single taste stimulus may enhance sensitivity near adapted levels to improve detection of abrupt changes in ambient stimulus concentration (McBurney and Balaban 2009). But, the weakening of ambient stimuli over time may itself serve a critical dynamic coding function. Self-adaptation of ambient stimuli may rapidly shift gustatory emphasis from the adapted stimulus to another distinct stimulus identity. Compounds that do not cross-adapt (Smith and van der Klaauw 1995) and activate independent taste receptors would become more salient and identifiable.

The tastes of equi-intense stimuli representing distinct taste qualities such as sucrose and sodium chloride are mutually suppressed in mixtures (Bartoshuk 1975), more so as the number of mixture components is increased. Potential mechanisms for the suppression have been explored (Lawless 1982; Kroeze 1989). Mutual suppression of independent mixture components occurs in gustatory, olfactory, and gustatory–olfactory mixtures (Laing et al. 1984; Livermore and Laing 1996; Laing et al. 2002). Yet, near-equal intensity binary mixtures of tastes are identified as one of the single taste components without prompting (Wang et al. 2009). Rather than a coding failure, we propose mixture suppression plays an important role in promotion of individual-component taste-stimulus identification.

Under stable controlled experimental conditions, the intensity of odor components and odor–mixture complexity (number of components) determine which dissimilar (independent) mixture components will be identified (Laing and Wilcox 1983; Laing et al. 1984; Laing and Francis 1989). Both components of binary mixtures can be identified more than half of the time (Goyert et al. 2007; Frank et al. 2010); but if a small difference in intensity is introduced, the stronger component will prevail, and when the difference is larger, only the stronger component is identified. In more complex mixtures of odors with equal salience, reliable simultaneous identification is limited to 3 or 4 components (Laing et al. 2002), and, if not matched, only the strongest component is identified.

Chemosensory coding strategies that combine rapid sensory adaptation and mixture suppression may explain our shifting ability to perceive characteristic qualities of mixture components (Frank 2008). This dynamic coding was tested with natural sniffing for olfaction. Goyert et al. (2007) used adapt–test stimulus pairs of 4 water-soluble compounds in which test stimuli contained 1 extra compound in addition to the adapted stimuli. Frank et al. (2010) used adapt–test stimulus pairs of 2 compounds shown to self-adapt but not cross-adapt. Adaptation of a single component of the mixture decreased preadapted (ambient) component odor identification below that expected for self-adaptation. Unadapted (extra) component identification of rose and vanilla odors increased to approach control identification of single compounds sniffed after water vapor. Here, we test dynamic coding of taste mixtures with taste puffs (150-μL atomized solution aliquots) of adapt–test pairs of sucrose and NaCl. Sucrose and NaCl activate different taste receptors (Yarmolinsky et al. 2009) and their distinct, readily identified tastes self adapt. We test the complex hypothesis that selective taste adaptation of one mixture component decreases ambient preadapted component identification more than self-adaptation and increases extra component identification to approach the identification of single compounds tasted after water.

Materials and methods

Subjects

Seventeen volunteers of mean age 25 years (standard deviation [SD] = 4), nonsmokers, healthy, and without known taste or smell disorders, were monetarily compensated for participation in as many as four 1-h testing sessions on separate days. Subjects were asked to neither eat nor drink anything besides water, nor use scented products such as perfume or cologne, immediately prior to an appointment. The research protocol was approved by the Institutional Review Board of the University of Connecticut Health Center.

Stimuli, labels, and stimulus delivery

Stimuli (labels, abbreviations) used were deionized water (water, ''0''), 100 mM NaCl (salt, ''N''), 300 mM sucrose (sugar, ''S''), and the binary salt–sugar mixture (''NS'') for Experiment 1. Lower concentrations (50 mM NaCl and 150 mM sucrose) that would decrease perceptual intensities (Haase et al. 2009) were used for Experiment 2. The high and low concentrations were 100% identifiable and approximated previously published sucrose–NaCl perceptual intensity matches (McBurney and Shick 1971; Helms et al. 1995; Breslin and Tharp 2001; Marshall et al. 2006; Haase et al. 2009; Green et al. 2010). Taste-quality identification approaches 100% at well below maximal ratings of taste intensity (Watson et al. 2001). Stimuli were diluted from stock solutions with deionized water so that corresponding concentrations of compounds were identical in single and mixture stimuli. Stimuli were delivered to the tongue tip with 2 or 4 oz. clear polyethylene bottles fitted with atomizing (mister) spray caps (Specialty Bottle LLC) and containing 50 or 100 mL of solution.

The mister was operated manually by thumb-press and sprayed straight down so as not to wet the subject's upper lip or chin. It delivered in 1 pulse (''puff''), a 45° conical mist with a volume of 150 μL that covered the surface of the extended tongue tip. Stimulation was limited to the portion of the tongue beyond the subject's lips that were clasped around the tongue to prevent stimulus access to the oral cavity. This method guaranteed that 2 puffs, an adapt–test pair, delivered <5 s apart for Experiment 1 and either <5 or >10 s apart for Experiment 2, stimulated the same area. The method of delivery was meant to duplicate as closely as possible odor delivery to the olfactory epithelium by natural sniffing used in Goyert et al. (2007) and Frank et al. (2010). The atomized microdroplets served to stabilize adaptation by minimizing recruitment of additional taste receptors and the involvement of general sensory receptors (Gent 1979). One set of taste stimuli was used and refreshed weekly, at which point the caps were rinsed with hot water and allowed to dry. Stock solutions were replaced every 3–4 weeks. Hidden solution labels were attached to each bottle and cap, and a blind was set up between the subject and the stimuli.

On each trial, duplicate bottles of 4 solutions (N, S, NS, and 0) were used. The duplicates allowed separation of the 4 adapting stimuli from the 4 identical test stimuli. The 8 stimulus bottles were used 4 times to present 16 adapt–test pairs of stimuli in a different random order to each subject on each trial (see Figure 1). Presentations of adapt–test pairs of stimuli were spaced at 1-min intervals, leaving ~40- to 45-s rest periods, during which subjects rinsed their mouths with deionized water from a cup.

Procedures

Training and testing took place in a relatively odor-free room equipped for clinical dentistry. Seated subjects comfortably

A BINARY TASTE MIXURES: 100 mM NaCl & 300 mM Sucrose											
	Stimulus		Total Identifications								
	Adapt time		<5 sec			<5 sec			Average %		
	Trial		1			2			Identification		
Item	Adapt	Test	[N]	[S]	[0]	[N]	[S]	[0]	[N]	[S]	[0]
1	0	0	0	0	10	0	0	10	0	0	100
2	N	0	0	0	10	0	1	9	0	5	95
3	N	N	9	2	0	7	1	3	80	15	15
4	0	N	10	1	0	7	2	1	85	15	5
5	S	N	9	1	0	10	1	0	95	10	0
6	NS	N	8	0	2	8	2	1	80	10	15
7	S	NS	10	2	0	10	4	0	100	30	0
8	0	NS	9	10	0	5	9	0	70	95	0
9	NS	NS	8	6	1	9	9	0	85	75	5
10	N	NS	3	10	0	2	10	0	25	100	0
11	NS	S	2	9	0	1	9	1	15	90	5
12	N	S	0	10	0	0	10	0	0	100	0
13	0	S	0	10	0	1	10	0	5	100	0
14	S	S	1	6	4	1	8	2	10	70	30
15	S	0	0	0	10	0	1	9	0	5	95
16	NS	0	0	2	8	1	2	8	5	20	80
Item	Adapt	Test	[N]	[S]	[0]	[N]	[S]	[0]	[N]	[S]	[0]

B BINARY TASTE MIXTURES: 50 mM NaCl & 150 mM Sucrose											
	Stimulus		Total Identifications								
	Adapt time		<5 sec			>10 sec			Average %		
	Trial		1			2			Identification		
Item	Adapt	Test	[N]	[S]	[0]	[N]	[S]	[0]	[N]	[S]	[0]
1	0	0	0	0	5	0	0	8	0	0	100
2	N	0	0	0	5	0	1	7	0	8	92
3	N	N	4	0	1	5	3	2	69	23	23
4	0	N	5	1	0	8	1	0	100	15	0
5	S	N	5	0	0	8	0	0	100	0	0
6	NS	N	4	1	0	5	1	3	69	15	23
7	S	NS	4	2	0	7	4	0	85	46	0
8	0	NS	2	5	0	6	8	0	62	100	0
9	NS	NS	3	5	0	4	6	1	54	85	8
10	N	NS	1	5	0	5	8	0	46	100	0
11	NS	S	2	4	0	2	5	1	31	69	8
12	N	S	1	5	0	1	7	0	15	92	0
13	0	S	1	5	0	1	8	0	15	100	0
14	S	S	1	5	0	1	4	4	15	69	31
15	S	0	0	0	5	0	0	8	0	0	100
16	NS	0	0	0	5	0	0	8	0	0	100
Item	Adapt	Test	[N]	[S]	[0]	[N]	[S]	[0]	[N]	[S]	[0]

Figure 1 Matrices for (**A)** Experiment 1—high concentrations (100 mM NaCl and 300 mM sucrose) and (**B**) Experiment 2—low concentrations (50 mM NaCl and 150 mM sucrose). Entries are "total identifications" and "average % identifications" for 2 trials. Sugar *([S])*, salt *([N])*, or water *([0])* tastes were identified with presentation of 16 test stimuli containing NaCl (N), sucrose (S), NaCl + sucrose (NS), or water (0). Gold shading highlights numbers of veridically correct responses. (A) Ten subjects identified tastes after sampling water or an adapt stimulus for <5 s adapt time in trials 1 and 2. (B) Five subjects identified tastes after sampling water or an adapt stimulus for <5 s adapt time in trial 1; 8 subjects identified tastes after sampling water or an adapt stimulus for >10 s adapt time in trial 2.

stabilized their heads on a chin rest (American Optical Company) and extended their tongues through the lips to receive the taste puffs. The experimenter (H.F.G.), who wore latex gloves, gave the following directions: "Each minute, I will ask you to place your head on the chin rest and extend your tongue, on which I will spray a mist from 2 bottles one after the other. When you identify what you taste in the second bottle only, please point to your response on the list, without moving your tongue. Then, you may retract your tongue, take a sip of water, swish the water around your mouth, and spit into the sink. Swish the water as often as you need before the next minute to rinse the previous taste out of your mouth. Let's practice this with water."

Next, subjects were trained to recognize water and each single taste by its name. The 2 single tastes (N and S) were introduced individually 1 min apart, with alternating order across subjects and sessions. Subjects were then trained with randomized stimulus pairs, consisting of water followed by either a single taste or water. They were required to accurately identify salt, sugar, and water twice in a row before proceeding to an experimental trial. Subjects received corrective feedback if wrong.

Experimental trials without feedback, during which subjects could refer to the list of taste choices at all times (salt, sugar, both, and water), began after giving the following instructions: "As in the training, I will present items to you in pairs. In addition to each single taste and water, you may or may not taste a combination of the two. In other words, respond to the best of your knowledge as to whether you taste salt, sugar, both, or water in the second bottle, by pointing to the list."

Experimental design

The testing trials of Experiment 1 and 2, randomized presentations of 16 adapt–test stimulus pairs to the tongue tip (adapt stimuli followed by test stimuli), are tabulated in Figure 1A and B. Item and adapt–test stimulus columns are color coded to signify experimental conditions. Blue shading means controls in which water [0] is the test stimulus. Yellow shading denotes single test stimuli, either NaCl or sucrose, which were tested for self-adaptation [X → X], no-adaptation [0 → X], cross-adaptation [Y → X], and mixture-adaptation [XY → X]. Pink shading highlights the key selectively adapted mixture (NaCl + sucrose), which is preadapted either by 1 or the other of the 2 mixture components [X → XY, Y → XY]. The adapted component is "ambient" when tested and the additional unadapted component "extra" as in Goyert et al. (2007) and Frank et al. (2010). Tan shading identifies cases in which the mixture test stimulus is preceded by water or the mixture itself [0 → XY, XY → XY]. Matrix entries are raw response data: the total salt [N], sugar [S], and water [0] identifications given by groups of subjects. The entries represent aggregate response frequencies from trials 1 and 2 run on separate days for each experiment. In order to track identification of individual stimuli for each item, a response of "both" was tallied as "sugar" and "salt." Thus, entries for total responses may exceed the number of subjects for a stimulus if at least 1 subject chose both. Calculation of both, salt, and sugar identification frequencies from the tabulated entries is described in Frank et al. (2010) under "data analysis." In "total identification" columns, gold shading highlights veridically correct responding, which is the identification of all compounds present in the test stimulus. Finally, "average % identification" entries are tabulated to show overall consistencies between the 2 experiments (3 columns to the right in A and B).

Data analysis

Critical results were evaluated using analysis of variance (ANOVA) of proportions of aggregate identifications; post hoc Newman–Keuls tests and *t*-tests were also used, $\alpha = 0.05$. Proportions were calculated by dividing aggregate identifications (total identifications entries in matrices) by the number of people in the group tested. With 2 trials in each experiment, there are 4 proportions for each condition. For example, for the "NaCl + sucrose" mixture (NS) preadapted by sucrose (S) (item 7 in Figure 1), 10 of 10 subjects chose salt [N] on trials 1 and 2 in Experiment 1 (A) and 4 of 5 subjects chose salt on trial 1 and 7 of 8 subjects chose salt on trial 2 in Experiment 2 (B). Dividing by appropriate subject numbers yields 4 proportions of subjects [1.0, 1.0, 0.8, 0.9] for identifying salt when presented with the sucrose–NaCl mixture after adapting to sucrose. Primary analyses were two 2-way ANOVAs for proportions so derived from entries in total identification matrices A and B (Figure 1) combined, with test stimulus compound and adapting condition as factors. In 1 ANOVA, the identified test stimulus was a single compound (either N or S), not-adapted (0 → N or 0 → S), cross-adapted (S → N or N → S), self-adapted (N → N or S → S), or mixture-adapted (NS → N or NS → S) (8 stimulus columns highlighted in yellow in Figure 1). In the second ANOVA, the identified test stimulus was a component (N or S) of the binary mixture (NS), not-adapted N or S (0 → NS), unadapted N (S → NS) or unadapted S (N → NS), adapted N (N → NS) or adapted S (S → NS), or mixture-adapted N or S (NS → NS), each containing identifications of the 2 individual components (4 stimulus columns highlighted in pink or tan in Figure 1). Within the test mixture, besides adaptation, the cross-adapted extra component and self-adapted ambient component are exposed to mixture interactions. Aggregate proportions derived from total identification matrices A and B for the 2 experiments have statistically equivalent average single-compound ($F_{1,22} = 0.01$, $P = 0.93$) and mixture-component ($F_{1,14} = 0.002$, $P = 0.96$) values, and there is no experiment by trial interactions. Combining the experiments provided additional overall statistical power, while tolerating experimental variation in concentration and adapting time within the data set (notable in Figure 1: average % identification).

Results

Sucrose and sodium chloride were used in 2 experiments on binary mixtures in which the sucrose concentration was 3 times as strong as the NaCl concentration. Aggregate proportions (total correct identifications ÷ number of subjects tested) in the 4 trials, 2 from each experiment, were used for statistical analysis of single-compound or mixture-component versus adaptation condition. Control water identification (after water, single compounds or the mixture) averaged 96 ± 2%. Thus, water was accurately identified under any adapting condition (Figure 1). To ascertain how mixtures are processed, identification of a compound as a component of a binary mixture was compared with its identification as a single compound under each adapting condition. Average percent correct responses (+ standard error of the mean) are given in Figure 2.

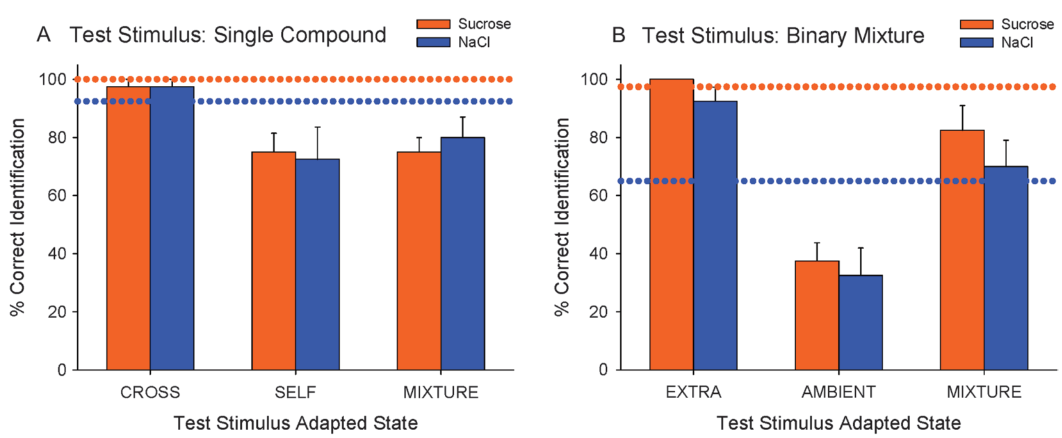

Figure 2 Averages for (**A**) identification of single compounds and (**B**) identification of components of binary mixtures. Results are derived from matrices A and B (Figure 1) combined. (A) Test stimuli were cross-adapted, self-adapted, or mixture-adapted single compounds. Characteristic tastes of sucrose (sugar) and NaCl (salt) were readily identified when preceded by water (dotted horizontal lines) or after cross-adaptation; but the tastes were equally less salient after self-adaptation or mixture-adaptation. (B) Test stimuli were extra-, ambient-, and mixture-adapted components of binary mixtures. The sugar taste component was identified more readily than the salt taste component when the mixture followed water (dotted horizontal lines). Extra component sugar taste after NaCl and salt taste after sucrose were as salient as single components after water (A). Component sugar and salt tastes after the mixture were as salient as single components following the mixture (A). The pre-adapted ambient-component sugar and salt tastes (B), exposed to self-adaptation and mixture suppression, were much less salient than the self-adapted single compounds (A).

Single-compound identification after adaptation

Figure 2A presents average single-compound sugar and salt identifications. The equally identifiable independent tastes of sucrose and NaCl rapidly self-adapted to a water-like taste.

The similar average correct identifications of single compounds after water, 96 ± 4% (dotted horizontal lines), and cross-adaptation, 98 ± 2% (first set of bars), were higher than the similar averages for self-adapted, 74 ± 6% (second set of bars), and mixture-adapted, 78 ± 4% (third set of bars), conditions ($F_{3,9}$ = 7.35, P = 0.009). Correspondingly, average misidentifications of salt and sugar as water after self-adaptation, 24 ± 6%, and after mixture-adaptation, 11 ± 5%, were higher than misidentifications of salt and sugar as water following not-adapted or cross-adapted, 1 ± 1%, conditions ($F_{3,9}$ = 10.5, P = 0.003) (Figure 1). Parallel effects of self- and mixture-adapting on single-compound perceptual intensities have been reported (Kroeze 1978; 1979).

Mixture-component identification after selective adaptation

Figure 2B presents average mixture-component sugar and salt identifications. The control mixture imbalance toward sucrose was augmented or offset by selective adaptation of the alternate components. Selective adaptation by NaCl augmented the imbalance to further reduce salt identification. Whereas, selective adaptation by sucrose reset the intensity imbalance toward the extra salt component. Afterward, salt identification approached perfection and suppressed the sugar taste in the mixture. When prior adaptation was not restricted to 1 of the 2 mixture components, identification was consistent with independent self-adaptation of each component.

Tested after water, control identification of salt and sugar components (dotted horizontal lines) differed significantly from one another ($F_{3,9}$ = 18.3, P = 0.0004). The 98 ± 2% identification of sugar, a value leaving no room for improvement, was greater than the 65 ± 1% for salt (P = 0.007). After selective adaptation by sucrose, identification of the unadapted extra salt component improved to 92 ± 5% (P = 0.01) and matched identification of the extra sugar (first set of bars). Combined sugar and salt identifications averaged 96 ± 3% for the 2 extra mixture components, much greater than the average 35 ± 5% for the 2 ambient components, P = 0.0005 (second set of bars). Thus the intensity dominance of the sugar was also lost for ambient components after selective adaptation. Average identification of mixture-adapted components, 76 ± 6% (third set of bars), for which salt and sugar identifications also did not differ significantly, was greater than for ambient components, P = 0.001, as well.

Mixture-component compared with single-compound identification

Salt identification was no longer suppressed by the weakened ambient-adapted sugar component. Ambient sugar or salt components were poorly identified, consistent with inferred decreases in intensity. Prior adaptation restricted to 1 of the 2 components was necessary for differential impact on binary mixture-component identification.

Identifications of unadapted single compounds (Figure 2A) and unadapted extra mixture components (Figure 2B) were an identical 96%. Whereas, the 74% identified self-adapted single compounds (Figure 2A) were more evident than the 35% identified ambient mixture components (Figure 2B) (t_7 = 4.3, P = 0.003). Identifications of self-adapted, 74%, and mixture-adapted, 78%, single compounds (Figure 2A) and mixture-adapted mixture components, 76% (Figure 2B), were essentially equal.

Thus, in temporally dynamic environments, selectively adapting components of taste mixtures leads to subsequent emergence of characteristic tastes of previously suppressed mixture components. These taste results are quite similar to our published results for vanilla and rose odors (Frank et al. 2010), as explained in the Discussion.

Discussion

Sixteen adapt–test pairs of 150-μL atomized "taste puffs," with 4 different correct responses (sugar, salt, both, and water) equally represented, were randomly presented in this first study on how rapid selective adaptation changes the ability to identify sugar and salt in a binary mixture in humans. No animal work on this topic is available. Adapting puffs to the tongue tip were followed in a few seconds by test puffs restricted to the same adapted region. Sucrose, NaCl, and "NaCl + sucrose" were used to directly compare with our previous work on the sniffing of water-soluble phenethyl alcohol (PEA), vanillin, and "PEA + vanillin" (Frank et al. 2010). The equally identifiable independent salt and sugar tastes, like vanilla and rose odors, did not cross-adapt but quickly self-adapted. After a 5- to 10-s adapting period, self-adapted tastes were confused with water 25% of the time, suggesting their tastes had faded. Control water was 96% accurately identified, suggesting correct guessing and carryover of adapting stimuli were as uncommon for taste puffs as for odor sniffs (95%; Frank et al. 2010). Anomalous sugar identifications of water (McBurney and Shick 1971; Bartoshuk et al. 1978) were not observed. Water was not confused with sugar after NaCl nor was weakened self-adapted NaCl mistaken for sugar. As hypothesized, characteristic qualities of tastes of recently introduced compounds were emphasized under experimental conditions that simulate natural situations, a result dependent on rapid effective self-adaptation.

Self-adaptation regulates identification of taste compounds in seconds

Taste puffs of individual compounds were identified an average 25% less frequently than controls after 5–10 s of self-adaptation. This allowed us to efficiently study taste identification under dynamic experimental stimulus conditions. Quantitative study of temporal limits of self-adaptation is needed. However, perhaps reflecting the interaction between stimulus intensity and adaptation (Szabo et al. 1997), increasing adapting time from 5 to 10 s appeared to reduce identification of the weaker stimuli in Experiment 2. Identification decreased by 20% with a 5-s but by 40% with a 10-s adapt time ($t_5 = 4.2$, $P = 0.009$) for single and mixture self-adapt cases (items 3, 9, and 14 in Figure 1). Our identifications of taste puffs compare to taste intensity ratings with regionally restricted solutions (Lawless 1982; Bujas et al. 1991b) and minimized tactile stimulation (Gent and McBurney 1978; Gent 1979). Under these conditions, self-adaptation reduced taste intensities to 50% in 30 s regardless of initial intensity or quality (ibid). Human peripheral neural responses and perceptual intensities of NaCl (McBurney and Pfaffmann 1963; Diamant et al. 1965; Bujas et al. 1991b) adapted completely within 1–2 min.

When salt was the unadapted extra taste in the mixture, it emerged from mixture suppression to approach 100% identification. After selective adaptation, ambient sucrose identification fell by 65%, a 40% selective- over self-adaptation advantage that compares to a smaller 15% advantage for rose and vanilla odors (Frank et al. 2010). The additional reduction may reflect asymmetric suppression of mixture components with unbalanced stimulus salience imposed by selective adaptation. The fading of 1 percept frees the other from mixture suppression. Although weakened, the average 35% identification of ambient mixture components likely is remaining detectability rather than chance performance, given the average 4% error rate in identifying NaCl or sucrose following water. Quantitative evaluation of limits of selective adaptation on identification requires further study; nonetheless, our identification results are consistent with adapted mixture component intensities dropping to near zero after 30 s (Lawless 1982). As in olfaction, the driving force behind taste mixture processing appears to be the manipulation of effective intensity by adaptation and suppression.

Mixture "intensity dominance" or "perceptual predominance?"

Coding of selectively adapted rose and vanilla odors (Frank et al. 2010) and sugar and salt tastes in mixtures are alike. Stimuli were as accurately identified by gustatory and olfactory systems operating at higher or lower levels of stimulation. Extra odors and tastes in mixtures were as identifiable as single compounds tested after sniffed water vapors at the olfactory epithelium or water aerosols at the tongue tip. One component dominated in the control binary mixture after water (sniff or puff). Rose odor was 20% more potent than vanilla odor and sugar taste was 33% more potent than salt taste. Although more likely examples of dominance of perceptually more intense mixture components (Laing and Wilcox 1983; Laing et al. 1984; Laing and Francis 1989) than rose odor and sweet taste predominance (Green et al. 2010), systematic variation in concentration has not been done. Sucrose (150 and 300 mM) and NaCl (50 and 150 mM) were tested but with sucrose–NaCl pairs at a 3:1 concentration ratio.

Mutual mixture suppression among independent components of mixtures in animals, as well as humans (Kroeze 1989), is most likely generated in the central nervous system by separate (Chen et al. 2011) antagonistic neural inputs. Sources of human quality-specific taste mixture suppression have been sought with inhibitor, preadaptation and "split tongue" experiments (Lawless 1979; Lawless 1982; Kroeze 1989). Suppression of mixtures of taste stimuli detected by animal peripheral nerves is typically unidirectional and may be due to taste receptor antagonism (Formaker et al. 2009, 2012) or taste bud circuitry (Chaudhari and Roper 2010). The hamster chorda tympani nerve does not detect sucrose suppression of NaCl responses (Formaker and Frank 1996); however, hamster behaviors toward binary mixture components are mutually suppressed (Frank et al. 2003).

Asymmetric perceptual suppression in mixtures for the human bitter taste by NaCl (Breslin and Beauchamp 1997) and salt taste by sucrose (Watson et al. 2001; Wang et al. 2009; Green et al. 2010) is documented. Neither asymmetric mixture suppression of the identity of vanilla odor by PEA (Frank et al. 2010) nor salt taste by sucrose in the present study obscured observation of selective adaptation. We chose 100% identifiable high and low concentration levels of sucrose and NaCl here or vanillin and PEA earlier (Frank et al. 2010) to test the generality of selective adaptation across well-identified concentration levels. Maximal intensity ratings occur well above 100% identifiable stimulus quality (Watson et al. 2001). If 2 concentrations differing by a factor of 3 were to elicit parallel "stimulus intensity versus response" plots for the 2 taste (or odor) compounds, the compound with higher response levels would dominate in the control mixture (presented after water) at both low and high intensities as observed. However, selective adaptation of the mixture, by reducing effective perceptual intensity of the adapted sugar (or rose) and, thereby, its ability to suppress the intensity of the unadapted extra salt (or vanilla), overcame dominance. This suggests that dominance may also be overcome by simply increasing the actual intensity of the dominated compound. Substantiation of an equivalence of selective adaptation (reduced mixture-component effective concentration by prior adaptation) and actual mixture-component intensity imbalance requires confirmation with psychometric functions for tastes elicited by atomized puffs (Haase et al. 2009).

Accentuating stronger and newer tastes as well as smells

There are many fewer taste than smell receptors and most, the 30 T2R variants, may be combined in a single dedicated pathway (Chandrashekar et al. 2006; Yarmolinsky et al. 2009;

Chen et al. 2011). In humans, 5 taste pathways compare with the 390 odor pathways associated with receptor variants expressed in dedicated sensory neurons (Buck and Axel 1991; Olender et al. 2008). We had speculated that olfactory coding, by adjusting effective stimulus intensity, would reduce many activated odor pathways to few (Goyert et al. 2007; Frank et al. 2010). Here, we suggest that activated taste pathways are similarly reduced when stimuli are regionally confined.

Olfactory stimuli are directed toward the olfactory epithelium and restricted to a few seconds by active sniffing (Laing 1983; Laing 1986; Goyert et al. 2007). Taste stimuli are progressively moved through the mouth to be rejected or ingested via sensorimotor reflexes (Beckman and Whitehead 1991; Travers and Travers 2005; Nasse et al. 2008). Like smells, tastes adapt quickly when the stimulated receptor set is stable, perhaps as in chewing and mixing food morsels with saliva. Saliva contains Na^+, K^+, and Cl^- (Chen et al. 2004; Mori et al. 2008), key ions of salt tastes that are self-adapted at ambient salivary concentrations (McBurney and Pfaffmann 1963; Bartoshuk 1974) but would recover (Bujas et al. 1991a; Szabo et al. 1997) between items with water rinsing as seen in our results for water controls.

Separate oral taste regions contain distinct receptor populations in rodents (Frank 1991; King et al. 2000; Geran and Travers 2006; Travers and Geran 2009), and parallel differences may hold for humans (Grover and Frank 2008). Yet, responses elicited in human fungiform, circumvallate, and palatal regions adapt at similar rates (Gent 1979), and taste mixture identification is mutually suppressed with restricted anterior tongue dorsal flow and whole-mouth "sip and spit" stimulation (Bartoshuk 1975; Laing et al. 2002; Wang et al. 2009). Interestingly, sugar "predominance" may prevail if subjects continue tasting "with normal mouth movements" that distribute taste solutions to all regions (Green et al. 2010). Perhaps stimuli moving through the mouth activate and quickly adapt receptor populations in sequence.

As long as stimuli are moving, tastes can control intake, initiate anticipatory cephalic-phase actions in the gut (Power and Schulkin 2008), and contribute to learned satiety and appetite (Sclafani 2006; Davis and Smith 2009). Ingestion or rejection of mixtures of positive and negative stimuli may simply depend on centrally assigned hedonic signs of momentarily strong stimuli (Hajnal et al. 2009). However, once stimuli stabilize, tastes fade and eating is managed by gastric sources, including secretions of enteroendocrine cells, internal partners of tasting activated by many of the same chemicals (Cummings and Overduin 2007; Sternini et al. 2008) involved in nutrient utilization and toxin control of ingested material (Peyrot des Gachons et al. 2011). Thus, a taste itself, and its influences on actions, may critically depend on changes in effective concentrations in dynamic natural situations.

Dynamic imbalances are necessary for chemosensory perception

Neither tastes nor smells are coded along a single dimension-like color. The visual system color codes electromagnetic wavelength with several broadly tuned chemical pigments. There may be as many chemosensory stimulus chemistries as there are chemosensory qualities (Frank 2008). Large numbers of smells require large numbers of odor receptors with individualistic chemistry that initiate separate paths to the brain (Axel 2005; Buck 2005). Smaller numbers of tastes require fewer receptors, stimulus chemistries (Chandrashekar et al. 2006; Yarmolinsky et al. 2009) and paths to the brain (Frank et al. 2008; Chen et al. 2011). Yet, both chemical senses may be neurobiologically organized for interpathway processing, which was short circuited in a mostly one receptor "monoclonal nose" (Fleischmann et al. 2008). As hypothesized, dynamic imbalances in perceptual intensities of stimulus compounds imposed by selective adaptation and mixture suppression may be strategies used to identify characteristic tastes, as well as odors, in complex chemical situations.

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