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Chemosensory Context Effects: Role of Perceived Similarity and Neural Commonality

Krystyna M. Rankin and Lawrence E. Marks[1,2]

Givaudan-Roure Corporation, Teaneck, NJ, [1]John B. Pierce Laboratory, New Haven, CT and [2]Yale University, New Haven, CT, USA

Correspondence to be be sent to: Lawrence E. Marks, John B. Pierce Laboratory, 290 Congress Avenue, New Haven, CT 06519, USA. e-mail: marks@jbpierce.org

Abstract

Seven experiments investigated how stimulus context affects judgements of the magnitude of chemosensory stimuli. In each experiment, subjects gave magnitude estimates of the intensity of several concentrations of two substances, with the contextual set of concentrations varying across experimental conditions. Different experiments used different pairs of substances, which could be tastants (sucrose or NaCl) that were sipped, odorants (orange or vanillin) that were sipped (i.e. presented retronasally) or the same odorants sniffed (i.e. presented orthonasally). Varying the stimulus context affected the judgements differentially when the two substances were compositionally different (sucrose and NaCl; sucrose and orange; sucrose and vanillin) but not when they were the same (vanillin or orange presented orally and nasally). Judgements of qualitative similarity of the same pairs of substances, obtained in a separate experiment, failed to predict accurately the pattern of differential context effects. Taken together, the results suggest that differential effects of context relate only indirectly to perceptual dissimilarity *per se* but may primarily reflect the result of stimulus-specific adaptation-like processes.

Introduction

Psychophysical judgements often depend crucially on stimulus context. Especially noteworthy are the contextual effects evident in the paradigm known as magnitude matching (Stevens and Marks, 1980), where subjects give magnitude estimates, on a common perceptual scale, of the intensity of qualitatively different stimuli taken from either the same modality or different ones. Using this paradigm, Marks and co-workers (Marks, 1988, 1994; Marks and Warner, 1991) showed that judgements of loudness depended systematically on two variables: the qualitative similarity between the stimuli and the contextual set of stimulus intensities. The magnitude estimates assigned to equally intense signals of different frequencies varied with the mean intensity levels of the two signals. For example, subjects judged a 70 dB tone at a low frequency (e.g. 500 Hz) to be louder than a 70 dB tone at a high frequency (e.g. 2500 Hz) when most of the low-frequency signals were weaker than most of the high-frequency signals; switching the contexts so most low-frequency signals were stronger than most high-frequency signals reversed the effect.

These shifts in relative judgement have been termed differential effects of context. Differential effects of context refer to shifts in the judgement of one kind of stimulus relative to another—in the example given above, to shifts in the relative loudnesses of 500 and 2500 Hz tones. No such shift in judgements occurred, however, when the tones were close in frequency (e.g. 1103 and 1134 Hz), that is, when the tones were qualitatively similar (Marks and Warner, 1991; Marks, 1994).

Differential context effects are not limited to judgements of loudness, or even to the auditory system, but have been demonstrated in judgements of the lengths of objects presented in different spatial orientations and gauged by proprioception (Marks and Armstrong, 1996) and by vision (Marks and Armstrong, 1996; Armstrong and Marks, 1997). Rankin and Marks (Rankin and Marks, 1991) reported analogous effects when subjects gave magnitude estimates of the taste intensity of sucrose and sodium chloride—compounds that are perceived as different in quality (as assessed independently, by direct ratings of similarity). On the other hand, when taste stimuli were judged to be qualitatively similar (e.g. NaCl and a mixture of sucrose and NaCl; or sucrose and saccharin), the differential effects of context diminished in size (Rankin and Marks, 1991) or disappeared altogether (Rankin and Marks, 1992).

Given that differential context effects have been reported in several perceptual modalities, it may be tempting to attribute these effects to cognitive processes of decision and judgement, for instance, to a 'relativity of judgement' that affects the ways in which subjects implicitly label sensory magnitudes or make overt responses (Stevens, 1958; Anderson, 1975). By this token, differential context effects could reflect a tendency for subjects to apply different response scales to perceptually different taste substances. In fact, Marks (Marks, 1988) originally suggested that differential context effects might reflect a tendency for subjects to give a relatively constant range of perceptual judgements to every qualitatively distinct sensory experience, even in the face of changes in the levels of the physical stimulus. Consider a study in which subjects give adjectival ratings to perceived taste intensities. The subjects might tend to judge the lowest and highest concentrations of sucrose as 'weak' and 'strong', respectively, and the lowest and highest concentrations of NaCl as 'weak' and 'strong', respectively, even when the concentration levels change differentially across conditions. If so, then the judgements will show differential context effects. According to this model, differential context effects represent a kind of general cognitive or judgemental 'bias'.

As appealing as this hypothesis may be, three kinds of evidence speak against it. First, differential context effects are far from universal. For example, judgements of loudness of tones at different frequencies show differential context effects but judgements of duration of tones of the same frequencies do not. Judgements of length of lines in different orientations show the effects but judgements of length of lines in different colors do not (Marks, 1992b). If differential context effects reflect general cognitive processes, then it is not clear why they should sometimes be absent. Second, differential context effects occur in forced-choice paradigms where subjects compare stimuli directly (Marks, 1992a, 1994; Mapes-Riordan and Yost, 1999). The effects therefore do not require overt ratings of sensory magnitude. Third, in a variant of the procedure, high contextual stimulus levels reduced judgements of magnitude but low levels failed to enhance judgements; indeed, they had no effect at all (Marks, 1993; Armstrong and Marks, 1997). Taken together, these findings are less compatible with a cognitive model than with a model hypothesizing some kind of level-dependent perceptual adaptation (a stimulus-induced change in sensitivity or responsiveness). Nevertheless, definitive evidence regarding the underlying mechanism is still lacking.

A cognitive model of differential context effects predicts a close connection between the magnitude of the contextual effects and the qualitative similarity between the stimuli: the more dissimilar the stimuli, the greater should be the tendency to use different response scales and thus the greater the differential context effect (Marks and Warner, 1991; Rankin and Marks, 1991, 1992). But is it qualitative similarity *per se* between stimuli that matters, or is dissimilarity only a surrogate for another, more pertinent variable? Neurons in the auditory system are selectively responsive to relatively narrow bands of sound frequency, thereby constituting an analytical system that presumably helps encode tones differing in quality (pitch). Several pieces of evidence, including evidence that differential context effects in hearing are induced primarily by intense rather than weak stimuli and that they transfer interaurally, led Marks (Marks, 1994, 1996) to argue that these effects represent the outcome of a frequency-specific, centrally based perceptual adaptation [see (Armstrong and Marks, 1997) for a related argument in vision]. According to this account, differential effects of context represent selective reductions in underlying perceptual magnitudes rather than a relativity of judgement (Algom and Marks, 1990; Schneider and Parker, 1990; Marks, 1994, 1996; Mapes-Riordan and Yost, 1999). Marks (Marks, 1994, 1996) speculated that differential effects of context arise when populations of neural elements that are selectively sensitive to different sound frequencies 'adapt' differentially.

The gustatory system does not appear to be nearly as analytical as the auditory system; nevertheless, the hypothesis of 'differential adaptation' might apply also to taste. Although there is substantial evidence suggesting that taste quality depends on the pattern of activity across gustatory neurons (Erickson, 1968), the taste system also reveals specificity, in that many peripheral and central taste neurons are primarily responsive to subsets of taste stimuli (Pfaffmann, 1974) [see also (Frank, 1973; Scott and Chang, 1984; Frank *et al.*, 1988; Hanamori *et al.*, 1988)]. Consequently, Rankin and Marks's (Rankin and Marks, 1991) findings, of significant differential context effects with sucrose and NaCl but not with sucrose and sucrose–NaCl mixtures, are readily explicable both in terms of relativity of judgement, related to qualitative dissimilarity, and in terms of differential 'adaptation'.

Do differential context effects depend on qualitative dissimilarity *per se*, or on activation of, and perhaps differential adaptation in, different populations of gustatory neurons (which also happen to correlate with different sensory qualities)? Rankin and Marks (Rankin and Marks, 1992) reported differential effects of context to be absent from judgements of sucrose and saccharin, a pair of taste substances perceived as qualitatively similar. These results too are compatible both with a cognitive model, in which differential context effects arise only when qualities differ perceptually, and with a perceptual-adaptation model, in which sucrose and saccharin activate a common 'adapting' channel. The perceptual-adaptation model could be viable even if the sweetness of sucrose and the sweetness of saccharin are mediated by different receptor sites on a given receptor cell or by different receptor cells (Faurion *et al.*, 1980; Schiffman *et al.*, 1981; Lindemann, 1996), as long as the information were fed to a more central, common site of 'adaptation'. Unfortunately, even if such a site exists, there is currently no direct evidence regarding its locus or properties.

With the aim of identifying the crucial variable underlying differential context effects, the present experiments sought to dissociate, at least in part, qualitative similarity from commonality in neural elements. To accomplish this, we included in the present experiments pairs of stimuli that are perceived to be moderately similar in quality but that selectively stimulate different peripheral afferents and central neurons. That is, we selected gustatory and olfactory stimuli such that, in some cases, a particular pair of gustatory and olfactory stimuli should be as similar or more similar than a particular pair of gustatory stimuli. To this end, we used (i) sucrose, NaCl, a sucrose–NaCl mixture and citric acid, four gustatory stimuli that cover a wide range of qualitative similarity; and (ii) vanillin and orange, two olfactory stimuli that should be perceived as qualitatively similar to sucrose. In experiment 1, subjects directly compared the qualitative similarity of this ensemble of stimuli.

Although stimuli that activate the same receptors, and thus activate the same populations of peripheral and central neurons, are likely to be perceived as qualitatively similar, the converse need not be true. That is, qualitative similarity need not rely exclusively on commonality in neural elements. For example, it has been our experience that the olfactory stimulus vanillin is perceived as qualitatively similar to the gustatory stimulus sucrose, even though vanillin and sucrose activate distinct peripheral afferents and central neural populations. Perhaps different populations of neurons can evoke similar perceptual qualities when the spatio-temporal patterns of activity in the populations are the same. Commonality in spatio-temporal patterning has been proposed as one mechanism for coding cross-modal similarity (Marks and Bornstein, 1987).

The present study reports the results of a similarity-scaling experiment, followed by a series of seven magnitude-estimation experiments. In experiment 1, subjects judged the qualitative similarity of pairs of stimuli taken from an ensemble that included the substances tested in the seven magnitude-estimation experiments (experiments 2–8). All of the magnitude-estimation experiments used a common paradigm in which subjects judged the perceived intensity of various concentrations of two chemosensory substances. In each of these experiments, the two substances were selected from the ensemble that included the tastants sucrose and NaCl, the olfactants vanillin and orange sipped (that is, presented intraorally, as flavorants, where they stimulate olfactory receptors retronasally) and the same olfactants vanillin and orange sniffed (where they stimulate olfactory receptors orthonasally). If differential context effects depend on the stimuli being perceived as qualitatively dissimilar, then, for example, the context effects should appear when the two stimuli are sucrose and NaCl (two taste stimuli perceived as qualitatively dissimilar) but not when the two stimuli are sucrose and vanillin (a taste stimulus and an olfactory stimulus perceived as qualitatively similar). If, however, differential context effects occur only when the two stimuli activate different neural channels, not when they activate common channels, then these context effects should also appear when the stimuli are sucrose and vanillin.

Experiment 1

The first experiment assessed the qualitative similarity among a set of eight stimuli: four tastants (sucrose, NaCl, a sucrose–NaCl mixture and citric acid) and two olfactory flavorants (vanillin and orange), each of the latter being presented both orthonasally (sniffed) and retronasally (sipped). We anticipated that the gustatory stimulus sucrose would be perceived as qualitatively more similar to the olfactory stimulus vanillin, and perhaps also to the olfactory orange, than to the gustatory stimuli NaCl and citric acid.

Materials and methods

Subjects

Subjects were paid, non-smoking volunteers from the Yale community, all under the age of 40 years. A total of 22 men and women participated in experiment 1.

Stimuli

The stimuli comprised two odorants/flavorants (vanillin and orange) and four tastants (sucrose, NaCl, a sucrose–NaCl mixture and citric acid) dissolved in deionized water. All stimuli were matched as far as possible for perceived intensity. Vanillin (3W3107-0) was obtained from Aldrich Chemical Company (Milwaukee, WI). Orange flavorant was obtained from International Flavors and Fragrances (IFF, Dayton, NJ) (for experiments 2–8, the flavorant was IFF no. 134-98295; however, because this flavorant was no longer available when we conducted the similarity scaling, which followed the magnitude-estimation experiments, experiment 1 used IFF no. 136-15313, which was generously prepared at IFF to match closely in quality and characteristics of no. 134-98295). Sucrose, NaCl and citric acid were 'Baker Analyzed' reagent grade.

Procedure

The subjects rated the qualitative similarity of pairs drawn from the ensemble of eight stimuli. Each of the $(8 \times 7)/2 = 28$ pairs (all possible combinations of different stimuli) was presented and judged once in the session by marking a 200 mm line, labeled 'same' on the left and 'different' on the right. A separate response sheet was provided for each judgement. Subjects were instructed explicitly to judge the degree of qualitative similarity/dissimilarity of each pair of stimuli. Each subject received a different random order of stimulus pairs.

Results

Each response was measured as the distance in millimeters to the mark from the left-hand end of the rating line; the greater the distance, the more dissimilar the pair. Ratings given to each pair of stimuli were then averaged arithmetically over all subjects.

Table 1 presents the means and standard deviations of the judgements given to the 28 pairs of stimuli. It is noteworthy that subjects found sucrose to be qualitatively more similar

Table 1 Means and standard deviations of the ratings of qualitative dissimilarity for each of the 28 pairs of stimuli from experiment 1

Stimuli	Mean	SD
Sucrose, NaCl	164.74	26.02
Sucrose, sucrose–NaCl	75.01	48.81
Sucrose, citric acid	172.41	29.05
Sucrose, orange sipped	122.79	43.42
Sucrose, vanillin sipped	126.80	53.20
Sucrose, orange sniffed	75.38	54.71
Sucrose, vanillin sniffed	64.38	44.63
NaCl, sucrose–NaCl	122.65	56.35
NaCl, citric acid	135.80	60.64
NaCl, orange sipped	131.83	51.44
NaCl, vanillin sipped	151.32	32.41
NaCl, orange sniffed	144.15	40.48
NaCl, vanillin sniffed	142.49	41.48
Sucrose–NaCl, citric acid	166.34	32.44
Sucrose–NaCl, orange sipped	119.28	52.96
Sucrose–NaCl, vanillin sipped	135.58	48.23
Sucrose–NaCl, orange sniffed	75.17	53.20
Sucrose–NaCl, vanillin sniffed	74.43	55.50
Citric acid, orange sipped	140.99	45.39
Citric acid, vanillin sipped	140.85	42.23
Citric acid, orange sniffed	138.59	49.57
Citric acid, vanillin sniffed	149.01	39.97
Orange sipped, vanillin sipped	56.65	46.65
Orange sipped, vanillin sniffed	93.91	52.37
Vanillin sipped, orange sniffed	123.66	40.93
Orange sniffed, vanillin sniffed	114.79	53.89
Orange sipped, orange sniffed	73.15	59.64
Vanillin sipped, vanillin sniffed	74.07	53.02

to both vanillin and orange than to NaCl, even though sucrose and NaCl (sucrose/NaCl dissimilarity = 165) are both tastants whereas vanillin and orange are odorants. Further, this was the case both when vanillin and orange were sipped (dissimilarities to sucrose = 127 and 123, respectively) and when vanillin and orange were sniffed (dissimilarities to sucrose = 64 and 75, respectively). For each odorant, the qualitative dissimilarity between sucrose and NaCl was statistically greater than that between sucrose and that odorant; for sucrose/NaCl versus sucrose/vanillin sipped, $t(21) = 5.89$, $P < 0.0001$; for sucrose/NaCl versus sucrose/orange sipped, $t(21) = 3.73$, $P < 0.0015$; for sucrose/NaCl versus sucrose/vanillin sniffed, $t(21) = 8.87$, $P < 0.0001$; and for sucrose/NaCl versus sucrose/orange sniffed, $t(21) = 6.82$, $P < 0.0001$. Indeed, sucrose was judged about as similar to sniffed vanillin and to sniffed orange as sipped vanillin was to sniffed vanillin (mean dissimilarity = 74) and as sipped orange was to sniffed orange (mean dissimilarity = 73).

A similar picture emerged when the ratings of dissimilarity were subjected to nonmetric multidimensional scaling (Shepard, 1963), as instantiated in SYSTAT 5.2. Multidimensional scaling has the virtue of using the entire matrix of dissimilarities to scale the differences between each pair

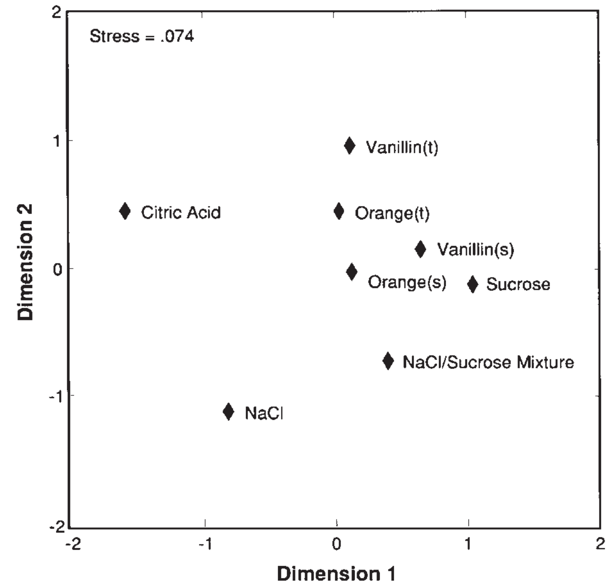

Figure 1 Nonmetric multidimensional scaling solution obtained in two dimensions for the mean ratings of dissimilarity given in Table 1.

of stimuli, although it lacks statistical tests of differences between scaled distances. Scalings were performed assuming dimensionalities of 1, 2 and 3, leading to values of stress (an indicant of 'badness of fit') equal to 0.216, 0.074 and 0.029, respectively. Because stress declined substantially when dimensionality increased from 1 to 2, whereas adding a third dimension had little overall effect on the results, we focused on the two-dimensional analysis.

Figure 1 plots the results. Consistent with the values listed in Table 1 and with the statistical analyses described above, in the similarity space sucrose is situated relatively distant from NaCl (and citric acid), but relatively close to sipped and sniffed orange and sipped vanillin (but, surprisingly, somewhat further from sipped vanillin). It is also useful to examine the relative locations of the stimuli on each of the two dimensions in Figure 1, lest only one of them reflect qualitative similarity *per se* (dimension 1 might, for instance, reflect hedonic value). In fact, the locations of the stimuli relative to one another on each of the component dimensions resemble their locations in the space as a whole. For example, sucrose lies further from NaCl than from sipped orange, sniffed orange and sniffed vanillin on both dimensions 1 and 2, and further from NaCl than from sipped vanillin on dimension 1 (and about as far on dimension 2). Thus, the results of experiment 1 fulfilled our main goal, which was to identify instances in which pairs of stimuli comprising two tastants are perceived as qualitatively more dissimilar than pairs comprising a tastant and an odorant.

Experiments 2–8

A series of seven experiments used the method of magnitude estimation to determine whether differential effects of stimulus context depend on qualitative similarity *per se* or on the commonality of the neural elements activated. If the presence of differential context effects requires that the stimuli be qualitatively dissimilar, then, on the basis of results of experiment 1, we would predict these effects to be absent or small when subjects judge sucrose and vanillin or sucrose and orange, as both of these flavorants were judged fairly similar to sucrose. Indeed, sucrose was judged as similar to sniffed vanillin and sniffed orange as sipped vanillin was to sniffed vanillin and as sipped orange was to sniffed orange. If qualitative similarity is critical, then differential context effects should be near-identical for sucrose versus vanillin, sipped vanillin versus sniffed vanillin, and sipped orange versus sniffed orange. If, on the other hand, differential context effects require activation of different neural populations, then the effects should be evident with sucrose versus vanillin but not with sniffed versus sipped vanillin or orange.

Materials and methods

Subjects

Subjects for experiments 2–8 were drawn, on the basis of availability, from a pool of 30 men and women, again paid non-smoking volunteers under the age of 40 years. Experiments 2–8 tested 21, 21, 17, 20, 16, 16 and 16 subjects, respectively, none of whom participated in experiment 1.

Stimuli

The stimuli in experiments 2–8 were identical to those in experiment 1, except that the orange flavorant was IFF no. 134-98295. Stimuli were adjusted to appropriate series of concentrations as described below.

Procedure

The varying-context paradigm, as applied to studies of taste, has been described elsewhere in detail (Rankin and Marks, 1991, 1992). Subjects were presented concentration series of two stimuli, judging their intensity on a single perceptual scale using the method of magnitude estimation. The concentrations of each set of stimuli differed in the two contextual conditions. In condition A, subjects received the seven strongest concentrations of stimulus 1, selected from a set of 10, and the seven weakest concentrations of stimulus 2, from another set of 10. In condition B these subsets were reversed. Consequently, the overall range of stimulus concentrations did not change over conditions, but the distribution of concentrations across the two stimuli did. Note further that four concentrations from each subset were common to the two contextual conditions.

In experiments 2–4, all of the stimuli were sipped. Experiment 2 used two tastants (sucrose and NaCl), while experiments 3 and 4 used a tastant (sucrose) and an odorant (vanillin in experiment 3 and orange in experiment 4). In experiments 5–8, one stimulus was sipped and the other was sniffed. Experiments 5 and 6 used the tastant sucrose and a sniffed odorant, either vanillin (experiment 5) or orange (experiment 6). Experiment 7 used vanillin sipped as one stimulus and vanillin sniffed as the other, and experiment 8 used orange sipped as one stimulus and orange sniffed as the other. The concentrations used in these experiments appear in Table 2. Note that the range of sucrose concentrations differed in the three experiments (resulting from our attempt in each experiment to match the overall subjective ranges of tastants and odorants).

Table 2 Molar and percentage stimulus concentrations used in experiments 2–8

Experiments 2, 4, 6 and 8			Experiments 3, 5 and 7	
[Sucrose] (M)	[NaCl] (M)	[Orange] (%)[1]	[Sucrose] (M)	[Vanillin] (M)
1.00	0.25	0.63	0.210	0.013
0.73	0.185	0.39	0.140	0.0089
0.54	0.136	0.25	0.097	0.0061
0.39	**0.10**	**0.16**	**0.066**	**0.0042**
0.29	**0.074**	**0.10**	**0.049**	**0.0028**
0.21	**0.054**	**0.063**	**0.031**	**0.0019**
0.15	**0.04**	**0.039**	**0.021**	**0.0013**
0.11	0.029	0.025	0.014	0.0009
0.08	0.022	0.010	0.0097	0.0006
0.06	0.016	0.0063	0.0066	0.0004

The four concentrations common to the two contextual conditions are given in bold type.

[1]1% orange = 10 ml of liquid flavorant dissolved in 1000 ml of deionized water.

For oral sampling of sucrose, NaCl, vanillin and orange, 5 ml of each stimulus was poured into an opaque, plastic medical cup and presented at room temperature. For sniffing vanillin and orange, 30 ml of each stimulus was placed in 250 ml squeezable, high-density polyethylene bottles with pop-up spouts (Cain *et al.*, 1988). In experiment 2, which used only tastants, the cups were uncovered. In experiments 3 and 4, where half of the stimuli were odorants, all of the cups were covered with laboratory film in order to prevent the subject from detecting any odor before sipping the stimulus. A small opening in the film was made just before 'tasting' the sample, and the subjects pinched their nose before and at the start of sipping. Once the sample was in the mouth, the subjects breathed normally. The same procedure was used for the sipped odorants in experiments 5–8. Subjects rinsed their mouths with deionized water before sipping each sample, whether odorant or tastant.

Subjects judged the perceived intensity of all stimuli by magnitude estimation, assigning whatever number seemed appropriate to represent the intensity of the first stimulus, and other numbers to subsequent stimuli in proportion to their perceived magnitude. Subjects were informed that there were no 'blanks' in the experiment. This was done to

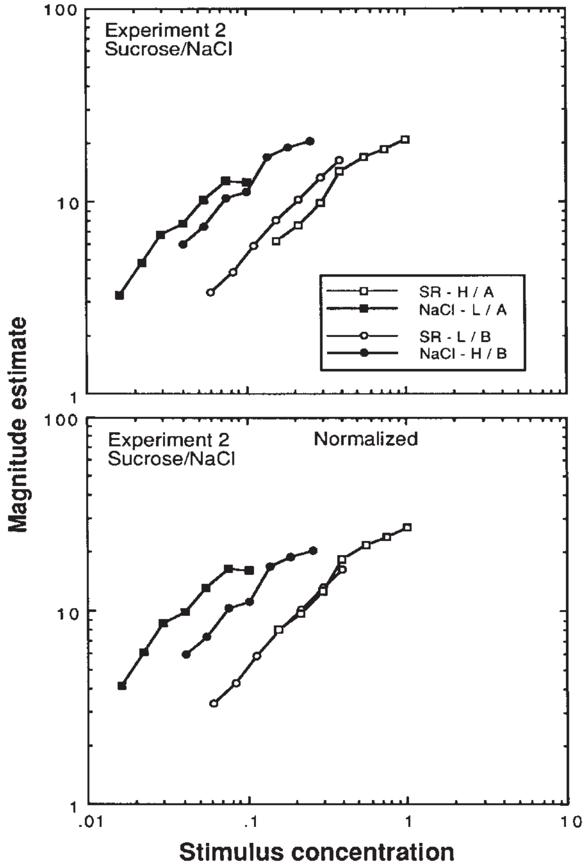

Figure 2 Geometric mean magnitude estimates of sucrose (SR, open symbols) and sodium chloride (NaCl, filled symbols), plotted against stimulus concentration, in two contextual conditions, where either concentrations of sucrose were high and those of NaCl were low (condition A, squares) or concentrations of sucrose were low and those of NaCl were high (condition B, circles). The upper panel shows the geometric means of the original data and the lower panel the geometric means after normalization to sucrose.

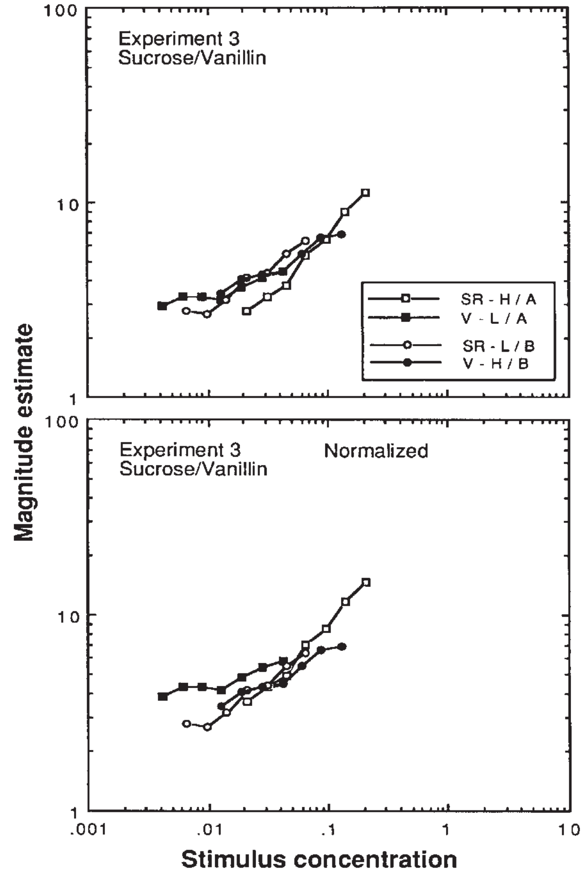

Figure 3 Geometric mean magnitude estimates of sucrose (SR, open symbols) and vanillin (V, filled symbols), plotted against stimulus concentration, in two contextual conditions, where either concentrations of sucrose were high and those of vanillin were low (condition A, squares) or concentrations of sucrose were low and those of vanillin were high (condition B, circles). All stimuli were sipped. For ease of display, concentrations of vanillin have been multiplied by 10. The upper panel shows the geometric means of the original data and the lower panel the geometric means after normalization to sucrose.

discourage subjects from using values of zero. In each condition of each experiment, the subjects judged 42 samples altogether: seven concentrations of stimulus 1 plus seven concentrations of stimulus 2, all 14 stimuli presented in three replicates. The order of presentation was randomized for each subject. The two contextual conditions, A and B, of each experiment were run on separate days within the same week. Half the subjects, or approximately half, in each experiment started with condition A and the others with condition B.

Results

The magnitude estimates given to each stimulus within each condition of each experiment were averaged arithmetically for every subject, then averaged geometrically across subjects. Figures 2–8 show the resulting psychophysical functions for experiments 2–8, respectively. In each case, the geometric means have been plotted against the concentrations of the two stimuli, separately for each contextual condition.

Note that each figure contains two panels. The upper panel of each figure shows the averages of the original data, whereas the lower panel of each figure, following Rankin and Marks (Rankin and Marks, 1991), shows the averages obtained after 'data normalization'. Normalization of the data entailed equating across the two contextual conditions the overall geometric average of responses to the four common concentrations of one of the stimuli, the 'normalizing stimulus' (sucrose in Figures 2–6, sipped vanillin in Figure 7 and sipped orange in Figure 8). Normalization was accomplished in each case by calculating the overall geometric average of responses to the four common concentrations of the normalizing stimulus in condition A, M(A), calculating the corresponding average in condition B, M(B), then multiplying all of the data obtained in condition A by M(B)/M(A). In graphical terms, this procedure corresponds

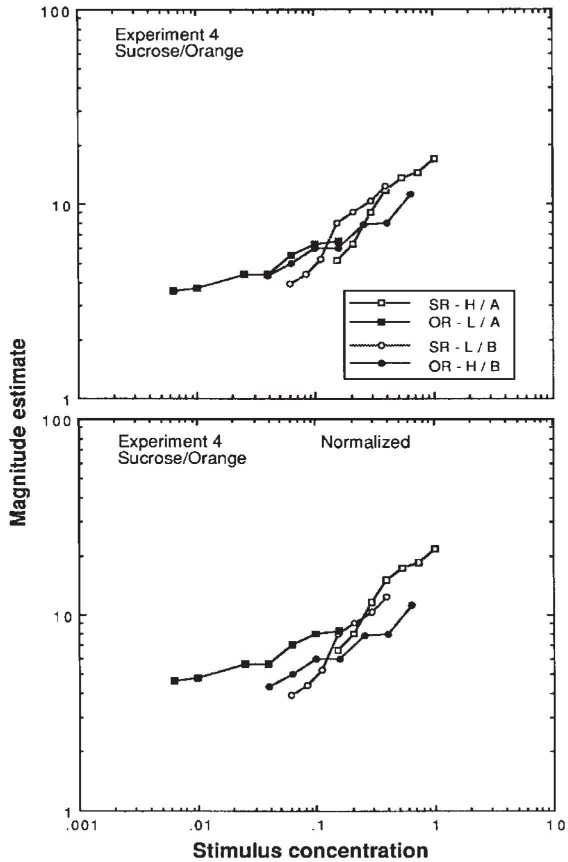

Figure 4 Magnitude estimates of sucrose (SR, open symbols) and orange (OR, filled symbols), plotted against stimulus concentration, in two contextual conditions, where either concentrations of sucrose were high and those of orange were low (condition A, squares) or concentrations of sucrose were low and those of orange were high (condition B, circles). All stimuli were sipped. The upper panel shows the geometric means of the original data and the lower panel the geometric means after normalization to sucrose.

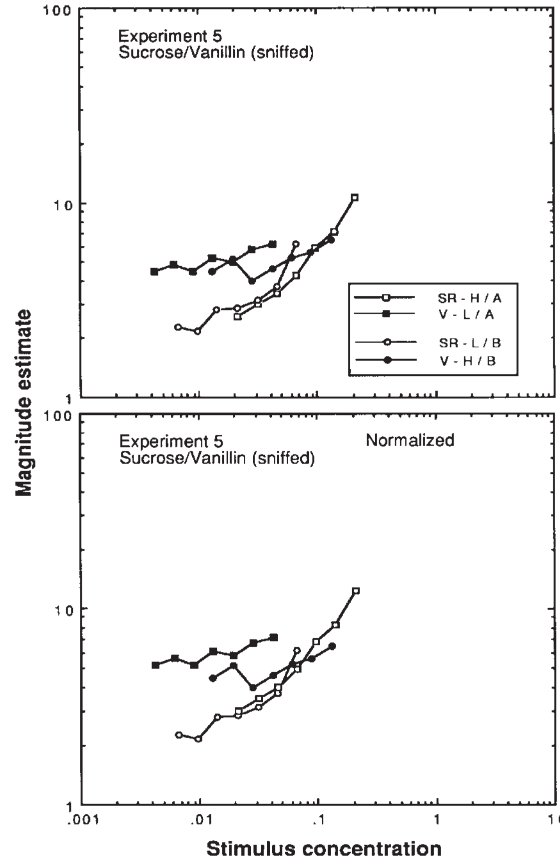

Figure 5 Magnitude estimates of sucrose (SR, open symbols) and vanillin sniffed (V, filled symbols), plotted against stimulus concentration, in two contextual conditions, where either concentrations of sucrose were high and those of vanillin were low (condition A, squares) or concentrations of sucrose were low and those of vanillin were high (condition B, circles). For ease of display, concentrations of vanillin have been multiplied by 10. The upper panel shows the geometric means of the original data and the lower panel the geometric means after normalization to sucrose.

to shifting the vertical positions of the plotted points in condition A while holding constant the positions of the points in condition B, such that the two sets of data for the normalizing stimulus overlap maximally. If context exerts no differential effect, then this normalization should simultaneously make the two sets of data for the other stimulus also overlap maximally. To the extent that context does exert a differential effect, however, normalization will produce a shift in the relative positions of the functions for the second stimulus in the two contextual conditions. For instance, in experiment 2, all of the data in condition A were multiplied by the constant that maximized the overlap between the functions obtained for sucrose in conditions A and B (Figure 2). The resulting displacement in the functions obtained for NaCl thereby reveals the overall magnitude of the differential context effect.

Experiment 2: sucrose and NaCl

As Figure 2 shows, changing the stimulus context produced substantial and consistent shifts in relative magnitude estimates of intensity of sucrose and NaCl: That is, the relative intercepts of the two functions changed from one condition to another, which in turn implies a change in the stimulus concentrations that match for perceived intensity. Thus, the results show differential context effects. The slopes of straight lines fitted to these log–log functions, corresponding to power-function exponents, remained reasonably stable, however, across conditions A and B (respectively, 0.69 and 0.86 for sucrose, and 0.75 and 0.70 for NaCl).

The four common concentrations of NaCl produced greater magnitude estimates in condition A, when they fell in the 'low' set (and the concentrations of sucrose were 'high'), as shown by the filled squares, than they did in condition B, when they fell in the 'high' set (and sucrose concentrations were 'low'), as shown by the filled circles. For example, in condition A, 0.04 M NaCl was judged stronger than 0.15 M sucrose, whereas, in condition B, 0.04 M NaCl was judged weaker than 0.15 M sucrose. Analysis of vari-

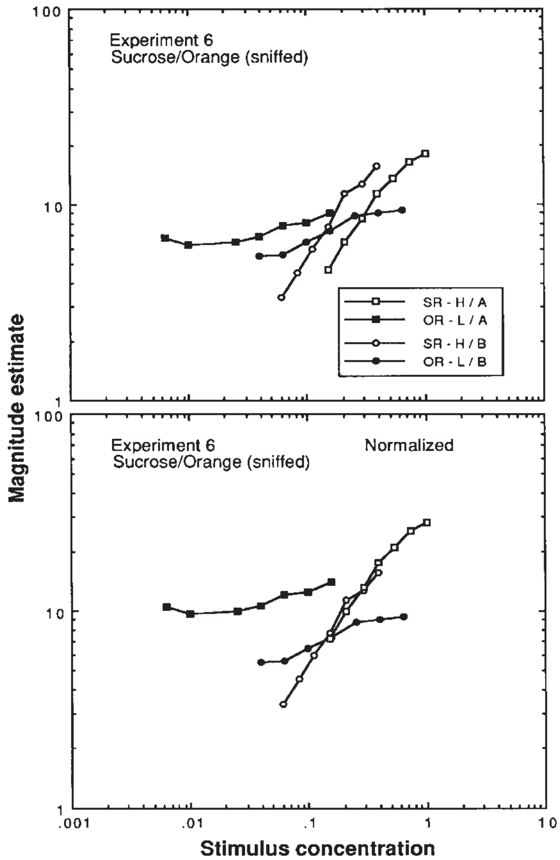

Figure 6 Magnitude estimates of sucrose (SR, open symbols) and orange sniffed (OR, filled symbols), plotted against stimulus concentration, in two contextual conditions, where either concentrations of sucrose were high and those of orange were low (condition A, squares) or concentrations of sucrose were low and those of orange were high (condition B, circles). The upper panel shows the geometric means of the original data and the lower panel the geometric means after normalization to sucrose.

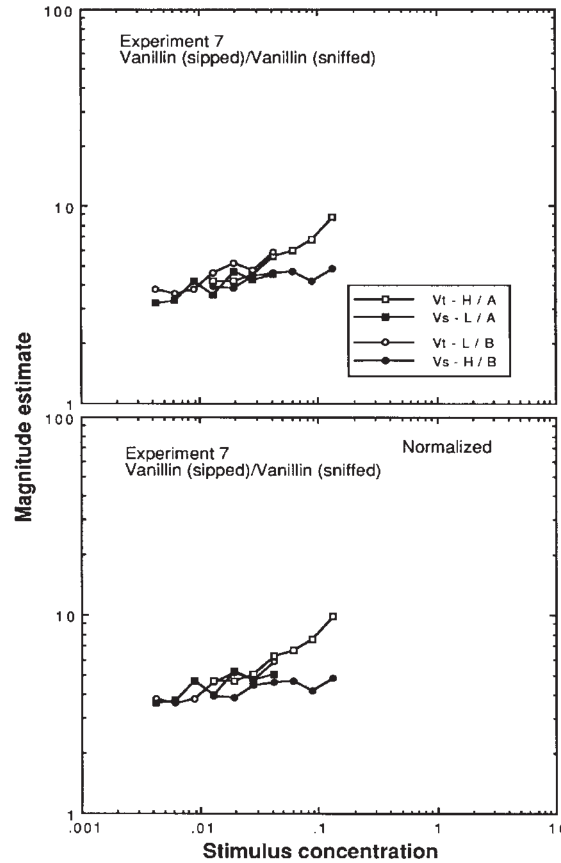

Figure 7 Magnitude estimates of vanillin sipped (Vt, open symbols) and vanillin sniffed (Vs, filled symbols), plotted against stimulus concentration, in two contextual conditions, where either concentrations of sipped vanillin were high and those of sniffed vanillin were low (condition A, squares) or concentrations of sipped vanillin were low and those of sniffed vanillin were high (condition B, circles). The upper panel shows the geometric means of the original data and the lower panel the geometric means after normalization to sipped vanillin.

ance (ANOVA) was calculated on the logarithms of the intensity judgements for the four common concentrations; it confirmed that the shift in judgements across contextual conditions (interaction of stimulus and condition) was reliable, $F(1,20) = 34.5$, $P < 0.0001$. On average, ratings of sucrose were 28% greater in condition B than in condition A, but ratings of NaCl were 19% smaller. The differential effect of context is clearly evident in the lower panel of Figure 2, which shows the displacement in the functions for NaCl in conditions A and B after normalizing the data across conditions with respect to sucrose.

Two other effects were statistically reliable: (i) the main effect of intensity, $F(3,60) = 64.7$, $P < 0.0001$ (the values of P, here and subsequently, are corrected for possible non-sphericity of repeated measures; see Huynh and Feldt, 1976), confirming that magnitude estimates increased with stimulus concentration; and (ii) the interaction of stimulus and intensity, $F(3,60) = 4.9$, $P = 0.004$, reflecting differences in the form (slope) of the intensity functions for NaCl and sucrose. The effect of condition was insignificant, $F(1,20) < 1$, indicating that, overall, the magnitude estimates did not vary reliably across the two conditions. In short, these results confirm those of experiment 2 in Rankin and Marks (Rankin and Marks, 1991): judgements of intensity of two qualitatively dissimilar taste stimuli revealed clear differential effects of context.

Experiment 3: sucrose and vanillin

Once more, the intensity functions for the two stimuli shifted across the two conditions (Figure 3). The four common concentrations of the flavorant vanillin produced greater magnitude estimates in condition A, when they fell in the 'low' set (and the concentrations of the tastant sucrose were 'high'), as shown by the filled squares, than they did in condition B, when they fell in the 'high' set (and the sucrose concentration was 'low'), as shown by the filled circles. Vanillin and sucrose behaved in experiment 3 much as NaCl and sucrose did in experiment 2.

The judgements given to sucrose and vanillin were both

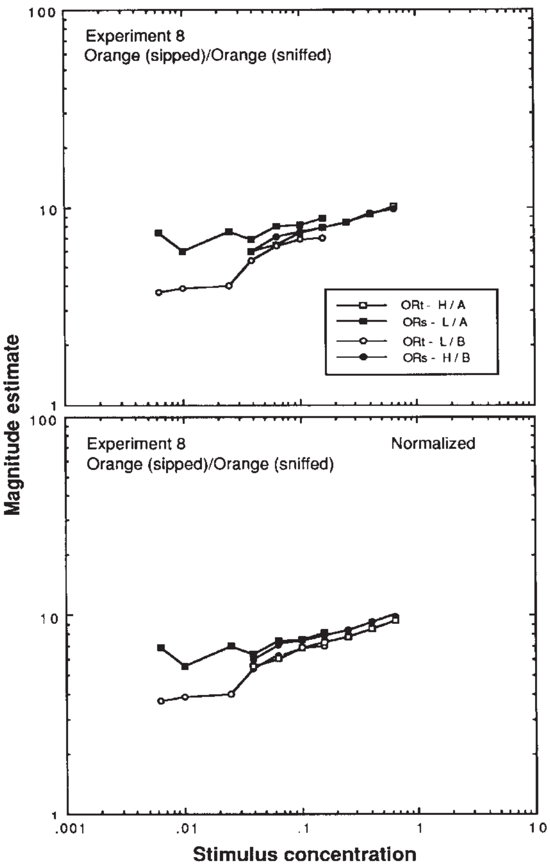

Figure 8 Magnitude estimates of orange sipped (ORt, open symbols) and orange sniffed (ORs, filled symbols), plotted against stimulus concentration, in two contextual conditions, where either concentrations of sipped orange were high and those of sniffed orange were low (condition A, squares) or concentrations of sipped orange were low and those of sniffed orange were high (condition B, circles). The upper panel shows the geometric means of the original data and the lower panel the geometric means after normalization to sipped orange.

greater in condition B than in condition A, sucrose by 37% and vanillin by 5%. This pattern, not evident in the other experiments, reflects the fact that the magnitude estimates were numerically greater overall in condition B (albeit not reliably so, as indicated below); this was probably the result of subjects changing their magnitude-estimation scales from day to day—one of the reasons underlying the data normalization, which obliterates such changes in scale; in any case, such changes in scale are statistically independent of *differential* changes, which constitute the main topic of interest.

Again, an ANOVA was applied to the results, this time showing one nonsignificant and three significant effects: (i) a small and not quite significant main effect of condition, $F(1,20) = 3.4$, $P = 0.08$; (ii) a main effect of intensity, $F(3,60) = 25.7$, $P < 0.0001$, showing that judgements increased with concentration; (iii) a small but significant interaction of stimulus and intensity, $F(3,60) = 3.8$, $P = 0.02$, reflecting slope differences between vanillin and sucrose; and, most relevant and important; and (iv) an interaction of stimulus and condition (context), $F(1,20) = 8.4$, $P = 0.009$, representing the differential effect of context.

Experiment 4: sucrose and orange

Judgements of sucrose and orange resembled those in experiment 3, as shown in Figure 4. Once more, changes in stimulus concentration differentially affected judgements of intensity of the two qualities. Switching from condition A to B led to an average increase of 30% in the estimates of sucrose and an average decrease of 6% in the estimates of orange. An ANOVA revealed one nonsignificant effect and four significant ones: (i) a small and not reliable main effect of condition, $F(1,16) = 3.2$, $P = 0.09$; (ii) a main effect of stimulus, $F(1,16) = 27.3$, $P = 0.0001$, representing the greater estimates given overall to sucrose; (iii) a main effect of intensity, $F(3,48) = 40.8$, $P < 0.0001$; (iv) an interaction of stimulus and intensity, $F(3,48) = 10.5$, $P = 0.0002$, reflecting the steeper slopes for sucrose; and, again most importantly, (v) a stimulus–condition (context) interaction, $F(1,16) = 10.7$, $P = 0.005$, showing, once more, the differential effect of context.

Summary of experiments 2–4

All three magnitude-estimation experiments showed reliable differential effects of context, both when the subjects judged the intensities of two tastants (sucrose and NaCl, experiment 2) and when the subjects judged the tastant sucrose and an odorant/flavorant (vanillin in experiment 3; orange in experiment 4). This occurred even though, as experiment 1 showed, sucrose is qualitatively more similar to orange and to vanillin than to NaCl. The present results by themselves are far from definitive, however. Further, it is conceivable, albeit unlikely, that the effects of context observed in experiments 3 and 4 owe in part to some gustatory component in the flavorants at higher concentrations. Experiments 5 and 6 address this issue by having subjects sniff the odorants and orally sample the tastants.

We expected, on the basis of earlier cross-modality comparisons of taste and smell (e.g. Marks *et al.*, 1988), that experiments 2–4 would show differential context effects. It is less clear, however, whether the mode of stimulus delivery should matter: does the size of the context effect depend on whether the odorants are sniffed (presented orthonasally) or 'tasted' (presented retronasally)? Whether the odorant is delivered through the nose or the mouth may make little difference to the differential effects of context if these depend purely on activation of different subsets of chemosensory neurons, but the mode of delivery may make a difference to differential context effects if these effects depend, even in part, on factors such as perceived similarity or site of localization. To test this possibility, the last two experiments had subjects judge the intensity of a given odorant/flavorant (vanillin in experiment 7 and orange in experiment 8) when different contextual sets of concentrations were presented to the nose (sniffed) and to the mouth (sipped).

Experiment 5: sucrose and vanillin (sniffed)

As Figure 5 shows, there was once more a small but reliable differential effect of context; for the stimulus–condition (context) interaction, $F(1,19) = 5.7$, $P = 0.03$, reflecting the shift in the relative intensity judgements of sucrose and vanillin across the two contextual conditions. Results of ANOVA showed four other significant effects: (i) a main effect of stimulus, $F(1,19) = 14.0$, $P = 0.0014$, confirming that on average vanillin was judged stronger than sucrose; (ii) a main effect of intensity, $F(3,57) = 20.6$, $P < 0.0001$; (iii) an interaction of stimulus and intensity, $F(3,57) = 14.6$, $P < 0.0001$, reflecting the difference in the form of the psychophysical functions for sucrose and vanillin; and (iv) an interaction of stimulus, condition and intensity, $F(3,57) = 5.4$, $P = 0.003$, reflecting changes in the relative form of the functions for sucrose and vanillin across contextual conditions (the meaning of which is unclear).

Despite the substantial difference in the slopes of the functions for vanillin and sucrose, the differential effects of context are clear. Over the common concentrations, the magnitude estimates given to sucrose were 17% greater in condition B than in condition A, whereas those given to vanillin were 17% smaller in condition B. Further, the shift was not constant across concentrations. For sucrose, it was greatest (43%) at the strongest of the common concentrations, compared with an average of ~7% over the other three concentrations. For vanillin, the decrease was greatest at the two highest concentrations (25 and 31%), but at the next concentration down there was almost no change.

Again, as in earlier experiments, the psychophysical functions for the odorant had much smaller log–log slopes than those for the tastant. The power-function exponent for vanillin was 0.14 in both conditions A and B, whereas the corresponding values for sucrose were 0.61 and 0.38. The difference in the sucrose exponents between conditions A and B might be the result of nonlinearity in the log–log functions for sucrose over the range tested. Sucrose exponents in experiment 3 [sucrose and vanillin (sipped)] showed an almost identical pattern, 0.69 and 0.39 for conditions A and B, respectively. The characteristic U-shaped curve at the lowest concentrations of both sucrose functions in condition B suggests that those concentrations were near threshold. No such large difference in the size of exponent was found in either experiment 2 or 4, where sucrose concentrations were higher and the log–log functions much more linear.

Experiment 6: sucrose and orange (sniffed)

At the common concentrations, orange was judged stronger than sucrose in condition A, but weaker than sucrose in condition B (Figure 6). Statistical analysis (ANOVA) confirmed that the interaction of stimulus and condition (context) was reliable, $F(1,15) = 37.5$, $P < 0.0001$. Only two other terms were reliable: (i) the interaction of stimulus and intensity, $F(3,45) = 15.0$, $P < 0.0001$, once again reflecting the greater slope of the function for sucrose; and (ii) the main effect of intensity, $F(3,45) = 37.5$, $P < 0.0001$. Judgements of sucrose shifted twice as much as did judgements of orange, the former being 58% greater and the latter 22% smaller in condition B than in condition A, implying that the subjects used slightly different response scales in the two conditions. However, the main effect of condition was not significant, $F(1,15) = 2.5$, $P = 0.14$.

Experiment 7: vanillin sipped and vanillin sniffed

There was very little if any differential effect of context on the judgements of vanillin at the four common concentrations when this same substance was either sipped (Vt) or sniffed (Vs) (Figure 7). Statistically, the interaction between stimulus (delivery) and condition was not significant, $F(1,15) = 1.4$, $P = 0.25$. The residual effect, though not statistically significant, might reflect a slight bitter aftertaste of vanillin. Nevertheless, the failure to uncover significant effects of context again is consistent with the notion that differential effects depend largely on basic mechanisms involved in processing of sensory information, that is, the activation of different sets of neural elements.

The only statistically reliable effect in experiment 7 was that of intensity, $F(3,45) = 10.5$, $P = 0.0003$. Note, however, that all of the functions are fairly flat. The exponents were slightly greater when vanillin was sipped (0.32 and 0.20 for conditions A and B, respectively) rather than sniffed (0.16 and 0.08). Although the change in exponent with mode of delivery conforms to the change observed in experiments 3 and 5, the present differences were not reliable: for the interaction of stimulus (delivery) and intensity, $F(3,45) = 1.1$, $P = 0.48$.

Experiment 8: orange sipped and orange sniffed

As with vanillin, judgements of sipped and sniffed orange revealed no differential effect of context (Figure 8), the interaction of stimulus (delivery) and condition being nonsignificant, $F(1,15) < 1$. The only statistically reliable effect was that of intensity, $F(3,45) = 32.9$, $P < 0.0001$. Like the intensity functions for vanillin, the intensity functions for orange were rather flat in slope. Although the average exponent for orange was a little greater when the odorant was sipped rather than sniffed (0.34 versus 0.14 in condition A and 0.27 versus 0.29 in condition B), consistent with results of experiments 3 and 5, the stimulus (delivery)–intensity interaction again was unreliable, $F(3,45) < 1$.

Discussion

Differential effects of context

Earlier studies (Rankin and Marks, 1991, 1992) showed that the presence (or magnitude) of differential context effects in judgements of taste intensity was closely related to the degree of qualitative similarity between the stimuli. When stimuli were qualitatively dissimilar, differential effects were substantial. When stimuli were similar, differential effects were small or absent. However, if qualitative differences in taste perception themselves depend at least in part on the activation of different subsets of neural elements, then the presence of differential context effects may reflect the degree of this underlying neural commonality rather than perceived similarity itself. The present experiments sought to answer the question: will two stimuli that are perceived as qualitatively similar but mediated by different sensory systems (e.g. different receptors and central neural pathways) show differential context effects? To answer this question, we measured differential effects of context on judgements of intensity using gustatory and olfactory stimuli that varied in their degree of perceived similarity, both when the stimuli activated the same and different sensory modalities.

Taken together, the results support the hypothesis that differential context effects arise not just when the stimuli are perceived to be qualitatively different but, more critically, when they activate different sensory pathways. Thus, significant differential effects of context emerged when subjects judged the tastant sucrose and an odorant, either vanillin or orange, and it hardly mattered whether the odorant was delivered orthonasally (sniffed) or retronasally (sipped). No evidence at all of differential context effects emerged when subjects judged the same olfactory stimulus, vanillin or orange, delivered retronasally and orthonasally. The simple relation between presence or absence of differential context effects and modality of stimulation (effects being large when the modalities differed and small when the modalities were the same) contrasts sharply with the judgements of qualitative similarity. Here, stimuli from different modalities (sucrose and sniffed vanillin or orange) could be judged as similar as stimuli from the same modality (sniffed and sipped vanillin or orange). The upshot is that modality was a better predictor of differential context effects than was qualitative similarity. Nevertheless, perceived similarity *per se* may be a relevant, albeit second-order, factor.

Rankin and Marks (Rankin and Marks, 1992) considered the possible relation between qualitative similarity and differential context effects in taste. Earlier, Marks and Warner (Marks and Warner, 1991) had considered this possibility when they investigated the effects of context on loudness judgements of tones varying in frequency. They found that the magnitude of the context effect was directly related to the frequency difference separating the tones: the greater the separation, the greater the effect. Taste perception shows similar variations in the magnitude of the context effect. When subjects judged the intensity of pure NaCl and sucrose–NaCl mixtures (Rankin and Marks, 1991) or sucrose and saccharin (Rankin and Marks, 1992), differential effects of context were small (and not reliable) in the former case and absent in the second.

Although we had anticipated that the differential effects of context on judgements of a tastant and an odorant might be greater when the odorant was sniffed rather than sipped (the tastant being sipped in both cases), the data provided only a little support for this expectation. With sucrose and vanillin, differential effects were comparable in size in experiments 3 (vanillin sipped) and 5 (vanillin sniffed). A within-subjects ANOVA revealed the interaction of experiment, stimulus and condition to be trivial, $F(1,19) < 1$. On the other hand, with sucrose and orange, the differential effects were smaller when the orange was sipped (experiment 4) than when it was sniffed (experiment 6), and a between-subjects ANOVA (necessary because most of the subjects differed) revealed a highly reliable interaction of experiment, stimulus and condition, $F(1,31) = 6.9$, $P = 0.01$. Thus, it appears that the manner of delivery—through the mouth or nose—may modulate whatever process underlies differential context effects.

Perception with orthonasal and retronasal delivery of odorants

Whether the odor percept is aroused via the mouth or nose, presumably the same receptor cells in the olfactory epithelium are stimulated. Nevertheless some researchers have suggested that olfactory stimulation via the mouth and that via the nose provide qualitatively different perceptual experiences (Rozin, 1982). The present experiment 1 addresses this issue: the ratings of similarity indicate that sipping and sniffing an olfactant, vanillin or orange, produced perceptual experiences that were judged to be as different, qualitatively, as those produced by sipping the tastant sucrose and sniffing either olfactant.

The present results also address the functional equivalence of oral and nasal perception. As discussed earlier, the exponents of the magnitude-estimation functions for both vanillin and orange were generally greater when these odorants were sipped rather than sniffed. So in this functional sense, the perception of intensity of the odorants may differ slightly depending on whether the stimuli are delivered retronasally or orthonasally. In addition, the relation between nominal stimulus concentrations reported here and the effective concentrations at the olfactory receptors could differ depending on mode of delivery. Consequently, comparisons of exponents obtained with different modes of delivery must be interpreted cautiously. Note, however, that there is one further indication of a possible functional difference between nasal and oral delivery of odorants: differential context effects were greater with sucrose and orange when the orange was sniffed (experiment 6) rather than sipped (experiment 4).

What mechanism underlies differential effects of context?

Earlier studies (Rankin and Marks, 1991, 1992) explored the possibility that differential effects of context vary in size in direct relation to the perceived dissimilarity of the stimuli:

the more dissimilar the stimuli, the greater the differential context effects. Results of the present experiments imply that these context effects do not rely as directly on perceived dissimilarity *per se* as on the stimulation of different neural elements (not only receptors but, undoubtedly, higher-level neurons). Marks (Marks, 1994) suggested that differential context effects in hearing (which he called 'recalibration') may represent the results of a stimulus-specific, adaptation-like process (Schneider and Parker, 1990; Parker and Schneider, 1994; Mapes-Riordan and Yost, 1999). Such an interpretation is compatible with the present results, given the reasonable assumption that this 'adaptation' would reflect changes in supraliminal responsiveness in the stimulus-specific subset of neurons.

We should, however, qualify these inferences. Often, the differential effects of context were greater when subjects judged two tastants (sucrose and NaCl) than when subjects judged a tastant (sucrose) and an odorant (vanillin or orange), so we should not dismiss the hypothesis that perceived dissimilarity and consequent cognitive processes may, under some circumstances, modulate differential context effects.

If differential context effects reflect the outcome of an adaptation-like process, it is important to determine just where in the nervous system this adaptation takes place. It seems unlikely that the adaptation occurs peripherally. Thus, two stimuli may activate different subsets of receptors, whose outputs converge more centrally, after which contextual effects could arise. If so, then differential context effects would be absent with stimuli that produce similar taste qualities, even if they activate different receptors or receptor cells. This speculation is compatible with data suggesting more than one type of receptor for sweet (Bartoshuk, 1987) as well as bitter (Hall *et al.*, 1975). Bitter substances do not show complete cross-adaptation (McBurney, 1972; McBurney and Bartoshuk, 1973), nor do sweet substances (McBurney *et al.*, 1972; Schiffman *et al.*, 1981; Lawless and Stevens, 1983). Yet despite the multiplicity of receptor mechanisms, one entire class of substances can basically give rise to a common perceptual experience of sweetness, and another class to a common experience of bitterness.

We suspect that differential effects of context arise at a central neural level, although we acknowledge that the present findings by themselves are equally consistent with the hypothesis that the locus is more peripheral. Regardless of the locus, the main finding of this study is that a tastant and an odorant judged qualitatively similar (e.g. sucrose and vanillin) nonetheless can display clear differential context effects, whereas the same odorant (vanillin) judged just as similar when delivered retronasally and orthonasally displays no differential effect of context at all. One intriguing question raised by these findings concerns the relation between perceived qualitative similarity and neural commonality. Whereas commonality may entail qualitative similarity, the converse need not be true, which is to say that similarity may have several sources. It is conceivable, for example, that sucrose and vanillin are similar not because they activate a common set of neurons but because they produce similar or identical spatio-temporal patterns of response in different sets of neurons, within which adaptation-like processes may nonetheless engender differential effects of context. An explanation of this sort has been proffered to account for the cross-modal similarity between brightness of visual stimuli and the pitch and loudness of auditory stimuli (Marks and Bornstein, 1987).

It is important to recognize, however, that the similarity between sucrose and both vanillin and orange may depend substantially on learning and experience. Perhaps all three stimuli are perceived as 'sweet' by dint of their common presence in various foods and beverages. Presumably, the neural processes underlying the formation of such taste–flavor associations occur relatively late in stimulus processing—and, we suspect, reside in a neural locus beyond the site of generation of differential context effects.

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