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Hedonic and Sensory Characteristics of Odors Conditioned by Pairing With Tastants in Humans

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Animals readily acquire positive odor–taste hedonic associations, but evidence for this in humans remains weak and was explored further. Retronasal pairing of odors with sucrose or salty stimuli (Experiment 1) increased the rated sweetness of sucrose-paired odors without altering liking, although changes in odor pleasantness correlated with sucrose liking. Experience of odors with sucrose or quinine by sweet likers (Experiment 2) found increased pleasantness and sweetness for sucrose-paired odors, whereas quinine-paired odors became less liked and more bitter. Odor–sucrose pairings in sweet likers and dislikers (Experiment 3) found increased sweetness in both groups but increased odor liking only in likers. These data suggest that evaluative and sensory learning are dissociable and that evaluative changes are sensitive to individual differences in sweet liking.

Keywords: olfaction, taste, flavor, evaluative conditioning, hedonics

Flavor–flavor conditioning refers to a situation in which repeated pairings of a neutral flavor (conditioned stimulus; CS) with a second flavor that already has motivational significance (unconditioned stimulus; US) leads to some form of change in responding to the CS alone. In animal studies, the most commonly used paradigm pairs a neutral flavor with a sweet US—most frequently, sucrose or saccharin (Capaldi et al., 1994; Fanselow & Birk, 1982; Harris et al., 2000; Holder, 1991; Holman, 1975; Myers & Hall, 1998; Warwick & Weingarten, 1996). The usual outcome of these studies is an increased preference for the sucrose-paired flavor relative to a water-paired control flavor. Thus, in animals, flavor–flavor conditioning with a sweet US produces robust changes in hedonic responding to the CS alone.

In human studies, flavor–flavor pairings can also result in hedonic changes. Thus, repeated pairings of a neutral-flavor CS with an aversive US (Tween) resulted in decreased liking for the CS alone (Baeyens et al., 1996, 1995; Baeyens et al., 1990). However, although repeated pairing of a CS with an aversive US results in reliable decreases in liking, the equivalent pairings of a neutral flavor CS with a positive US (sucrose) have been less consistent, with one study finding evidence of acquired flavor liking (Zellner et al., 1983) and a more recent study finding no significant effects of pairing with sucrose (Baeyens et al., 1990).

A recent variation of the flavor–flavor conditioning paradigm has been the specific association of novel odor CS with gustatory US, most commonly with the sweet taste of sucrose (Stevenson et al., 1995, 1998, 2000). In these studies, participants evaluated odors in terms of tastelike properties in an orthonasal (sniff) test, which was then followed by repeated experience of the same odor experienced retronasally in combination with a gustatory US during training sessions in which the test stimuli were experienced orally. The odor was subsequently reevaluated orthonasally at a postconditioning test. The most robust finding from these studies was that odors that had been paired repeatedly with the sweet taste of sucrose were now reliably rated as smelling sweeter (Stevenson et al., 1995, 1998, 2000). These findings extend the wider observation that sweetness is often attributed to odors and that odor sweetness interacts closely with sweetness generated by tastants, most notably when the presence of relevant food-related odors enhances the experience of sweetness generated by sweet tastants like sucrose (Frank & Byram, 1988; Frank et al., 1989). However, although repeated experience of odor and sweetness altered subsequent experience of odor sweetness, no overall increase in liking for the sucrose-paired odor has been reported. The only other gustatory US tested in this paradigm to date was the sour taste of citric acid, resulting in conditioned increases in the rated sourness of the paired flavor, but again, no overall change in hedonic evaluation of the trained odor (Stevenson et al., 1998, 1995).

A possible explanation for the lack of hedonic change to odors trained by pairing with gustatory US is that the tastants used to date are not sufficiently liked or disliked to be used as effective hedonic US. Because aversive US were the most effective stimuli in more general studies of flavor–flavor learning, the first objective of the studies reported here was to test whether pairing of an odor CS with an aversive US results in conditioned dislike for the trained odor. Previous flavor–flavor conditioning studies have used Tween 80 as the aversive US (Baeyens et al., 1990, 1995). However, Tween is not a simple gustatory stimulus, and its soapy flavor derives from a combination of olfactory, gustatory, and other oral (mouthfeel) components. To test olfactory conditioning

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with a purely gustatory US, in Experiment 1 we used a combination of NaCl and monosodium glutamate (SALT) that was rated as aversive in pilot studies. The specific prediction was that liking for an odor paired with the SALT US would result in an overall decrease in rated pleasantness of the SALT-paired odor.

The second objective of the present studies was to explore in more detail hedonic changes arising from pairings of an odor CS with a sweet US in the olfactory conditioning paradigm. Although only one of the two published studies of flavor–flavor learning with sucrose as US found significant increases in liking for the sweet-paired flavor (Zellner et al., 1983), it was noted that there was some evidence for enhanced liking in the second study but only in those participants who showed the strongest liking for the US (Baeyens et al., 1990). Previous studies using the olfactory conditioning paradigm have not included any hedonic evaluation of the training stimuli, thereby preventing any analysis of the relationship between liking for the training sucrose US and any change in liking for the CS. If there was significant variation between individuals in liking for the US, then individual changes in liking for the CS through association with the US may occur without resulting in any overall change in liking for the CS. This seems particularly possible in the case of liking for sweet tastes. First, for most consumers, the relationship between intensity and liking for sweet tastes follows an inverted-U pattern, with peak liking occurring at the optimal level of sweetness and liking decreasing progressively as sweetness deviates from this optimal point (Moskowitz et al., 1974; Riskey et al., 1979). If the same relationship was true for the rated sweetness of an odor, then theoretically increased sweetness need not result in increased liking if the change in sweetness was from a point below to one above the optimal level of sweetness. However, this suggestion relies on the inverted U-shape relationship between sweetness, pleasantness, and intensity applying to odors in the same way as it does to tastes, and the only study we are aware of suggests that this may not always be so (Doty, 1975). Second, the classic inverted-U pattern relating pleasantness to intensity for sweet taste is not observed with all consumers, with a significant minority showing an almost monotonic decrease in liking as sweetness increases (Looy et al., 1992; Looy & Weingarten, 1991). Because no measure of sweet liking was made in previous studies of olfactory conditioning with sweet tastes, individual variation in liking for the trained sweet stimuli could have resulted in a mixture of increases and decreases in conditioned odor pleasantness. Finally, liking for sweetness has been reported to vary as a function of current motivational state, with greater liking when hungry than when sated (Cabanac, 1971). All of these factors could potentially affect hedonic evaluation of a CS which has been paired with a sweet US. However, in all cases, the prediction would be that overall liking for a sweet-paired odor should be related to the actual liking for the trained level of sweetness. Thus, in Experiment 1, we tested whether changes in liking for odors paired with a sweet US varied depending on the hedonic evaluation of the US. The specific prediction was that changes in liking for the trained odor CS would be positively correlated with liking for the trained US, with a decrease in liking for those participants who rated the US as aversive, and an increase in odor pleasantness for those who liked the sweet US.

Experiment 1

Method

Design

In this study, we used a within-participants design to contrast changes in hedonic and sensory evaluations of three test odors experienced orthonasally as a consequence of retronasal experience of these odors paired with sucrose, SALT, or water in four disguised training trials (the exposure phase).

Participants

We recruited 36 participants (25 women, 11 men) from staff and students at the University of Sussex, using e-mail, personal communication, and poster advertisements. All volunteers were healthy, none of the participants smoked, and none had respiratory infections. They were informed that the study took about 2 hr to complete, and they were paid £10 on completion of the study, following debriefing. The protocol was approved by the University of Sussex Ethics Committee, and the study was conducted according to the ethical standards established in the Declaration of Helsinki, 1964.

Test Stimuli

To maximize the chance of an association between the test odor and both the sweet and savory tastants, we carefully selected odors to be stimuli that were not rated as sweet or savory in character but were considered to have the potential to be perceived as either sweet or savory. The three odors selected for the study were nominally called cream (Firmenich, U.K. Limited), beer (International Flavours and Fragrances Inc., United Kingdom), and tea (International Flavours and Fragrances Inc., United Kingdom). These odors were selected from pilot studies; they were chosen because they were rated ambiguously in terms of whether they were sweet or savory and were also rated near neutral in overall pleasantness. The odors were presented at concentrations in which the odor was clearly detectable but odor identification difficult, thus increasing the novelty and ambiguity of the target stimuli. Odor novelty was considered important in minimizing CS preexposure effects, particularly because flavor novelty correlated with the degree of conditioning seen in other studies with a flavor CS (Yeomans et al., 1998). The odor concentrations used, presented as a percentage of the full-strength extract, were as follows: 0.25% beer, 0.05% tea, and 0.10% cream. These odors were made up in water to give pure odor solutions and were also combined with the two conditioning tastants. The two taste solutions (US) used in conditioning were 10% sucrose and a combination of 0.16% monosodium glutamate and 0.2% NaCl (SALT). In addition, a solution of 3% lemon juice in water was used as a distracter during training.

All stimuli were presented as 10-ml servings in 50-ml flat-bottomed, stoppered glass tubes. In the orthonasal evaluations made pre- and posttest, participants were presented with 10 stimuli in random order (see Table 1). Four of these stimuli consisted of two test odors presented both in water alone and in the solution with which it would be experienced during training (sucrose or SALT) to ensure that there was no discernible confounding effect of dissolving the odor in either sucrose or SALT on odor quality. The third odor, which was paired with water during conditioning, was presented twice in water so that the three test odors were given equal exposure pre- and posttest. The remaining four pre- and posttest solutions were dilute lemon juice and three water-only controls, included purely as distracters. During the retronasal odor training phase, only five stimuli were presented, consisting of one odor paired with sucrose, one with SALT, and one with water (control), along with one lemon juice distracter and one water distracter. Counterbalancing of the three test odors and training conditions (sucrose, SALT, and water) generated six potential

Table 1
Summary of the Stimuli Used in the Three Stages of Experiment 1

Stage	Target stimuli	Distractors
Pretest	Odor A[a] in water	Water (presented three times)
	Odor A in 10% sucrose	Citric acid
	Odor B in water	
	Odor B in SALT	
	Odor C in water (presented twice)	
Training	Odor A in 10% sucrose	Water
	Odor B in SALT	Citric acid
	Odor C in water	
	Odor A in water	
	Odor A in 10% sucrose	
Posttest	Odor B in water	Water (presented three times)
	Odor B in SALT	Citric acid
	Odor C in water (presented twice)	

Note. SALT = a combination of monosodium glutamate and sodium chloride.
[a] The allocation of each of the three test odors (beer, tea, and cream) was counterbalanced across participants.

combinations of odor CS and tastant US (odor sets), with 6 participants assigned at random to each of these six odor sets.

Procedure

Participants reported to the laboratory between 10:00 a.m. and 12:30 p.m. and were tested in small, ventilated cubicles in the Ingestive Behavior Unit at the University of Sussex. They received instructions on what the procedure would involve, and they were given a rating sheet and instructed on how to use the rating scales. They were instructed to place each of the 10 test solutions roughly 2 cm below their nose and to inhale deeply. Participants were then allowed to smell each solution for as long as they liked, until they started to complete the ratings. For each odor, five evaluations were made on the rating sheets provided. The first rating was a hedonic measure, consisting of a 100-mm horizontal line end anchored with *Very unpleasant* and *Very pleasant*, with the label for the scale (Pleasant) above the scale. This was followed by four sensory ratings, each presented as a 100-mm horizontal line, ranging from *Not at all* (0) and *Extremely* (100) as end anchors, with the label for the dimension to be evaluated written above the center of each line. The four sensory evaluations were salty, sweet, meaty, and familiar in that order. We included the salty and meaty descriptors to try and capture the savory flavor characteristic of umami. Unlike the traditional tastes, there is no single accepted descriptor for monosodium glutamate, and meaty was used experimentally here in an attempt to characterize the umami taste and test whether odors paired with this taste developed umami-like qualities. Participants made these evaluations for all 10 odor pretest samples, in random order, and were allowed to work at their own pace. They then moved immediately into the conditioning phase. Here, they were instructed to empty the content of the relevant tube into their mouth, swill it around, and then expectorate into a container. To familiarize participants with this procedure, we gave them a practice water solution to start with, and the experimenter was present during this phase. They were then left alone to evaluate the five conditioning stimuli. As in the pretest, participants made specific evaluations for each of the conditioning stimuli, using exactly the same scales as during pretest. Once they had evaluated all 5 stimuli, they were free to leave the test cubicle and relax in an adjacent waiting room. After a 15-min interval, they returned to the test cubicle and completed the next training trial; this pattern continued until all four training trials had been completed. Thus in training, each participant experienced four trials in which one odor was paired with sucrose, four trials in which a second odor was paired with SALT, and four control trials in which the third odor was paired with water. Fifteen minutes after the final training trial, participants completed the posttest trial, which followed the procedure from pretest, with participants evaluating all 10 odor stimuli using the orthonasal procedure. Once this test was complete, participants underwent a structured debriefing, during which they were asked what they thought the purpose of the experiment was, before being given a detailed account of what the study was testing.

Data Analysis

The principal hypotheses tested here related to how the perception of the odors changed as a consequence of repeated pairing with sucrose, SALT, and water during training, with the prediction of increased sweetness and liking for the sucrose-paired odor and acquired saltiness/meatiness and dislike for the SALT-paired odor. To simplify data to allow focused analysis of these hypotheses, we used initial analyses to test whether having the US present when odors were evaluated orthonasally significantly affected odor evaluation. We conducted separate four-way analyses of variance (ANOVAs) on pleasant, sweet, salty, and meaty ratings for the odors paired with sucrose and SALT, with version (presented in water or US context), time of rating (pre- or posttest), odor set, and US (sucrose or SALT) as conditions. If context had affected these evaluations, then we would have expected a main effect or interaction of version; however, none of these effects were significant. Therefore pre- and posttest ratings data were averaged across the two contexts for SALT and sucrose conditions, and the two sets of ratings for the water-paired odor were averaged.

To test the main hypotheses, we calculated changes in evaluations of the trained odors by subtracting pretraining from posttraining ratings, and we conducted two-way ANOVAs on these change scores, with training condition (sucrose, SALT, or water) as within-subject factor, and odor set as an additional factor. Odor set was included because it was possible that the three target odors may have differed in the extent to which participants were willing to ascribe the rated properties to different odors and also in the degree to which the odor–US pairings were rated as pleasant. The main hypotheses predicted significant effects of training condition on changes in evaluation of pleasantness, sweetness, saltiness, and meatiness of the trained odors. To test for potential confounding effects of baseline evaluations, we conducted the same two-way ANOVAs on pretraining ratings only.

Finally, we used stepwise linear regression to assess the extent to which individual differences in pleasantness ratings for the odors paired with sucrose and SALT were a consequence of the rated hedonic and sensory properties of the training stimuli, with change in pleasantness as dependent variable and rated liking and sensory property (sweet for sucrose, salty for SALT) as factors. We conducted all analyses using SPSS 11.0 run on a Macintosh G4 computer.

Results

Changes in Orthonasal Odor Evaluations

The primary hypotheses tested here were that both the rated pleasantness and sensory characteristics of the test odors would change at posttest, relative to pretest, as a consequence of associations with the sucrose and SALT stimuli during training. Figure 1 shows the average (mean plus or minus standard error of the mean) changes in rated pleasantness, sweetness, saltiness, and meatiness of the test odors as a consequence of pairing with the sucrose, SALT, or the water control taste US. Preliminary analysis of pretraining data alone confirmed no effects of the training condition on any of the odor evaluations; thus, the reported

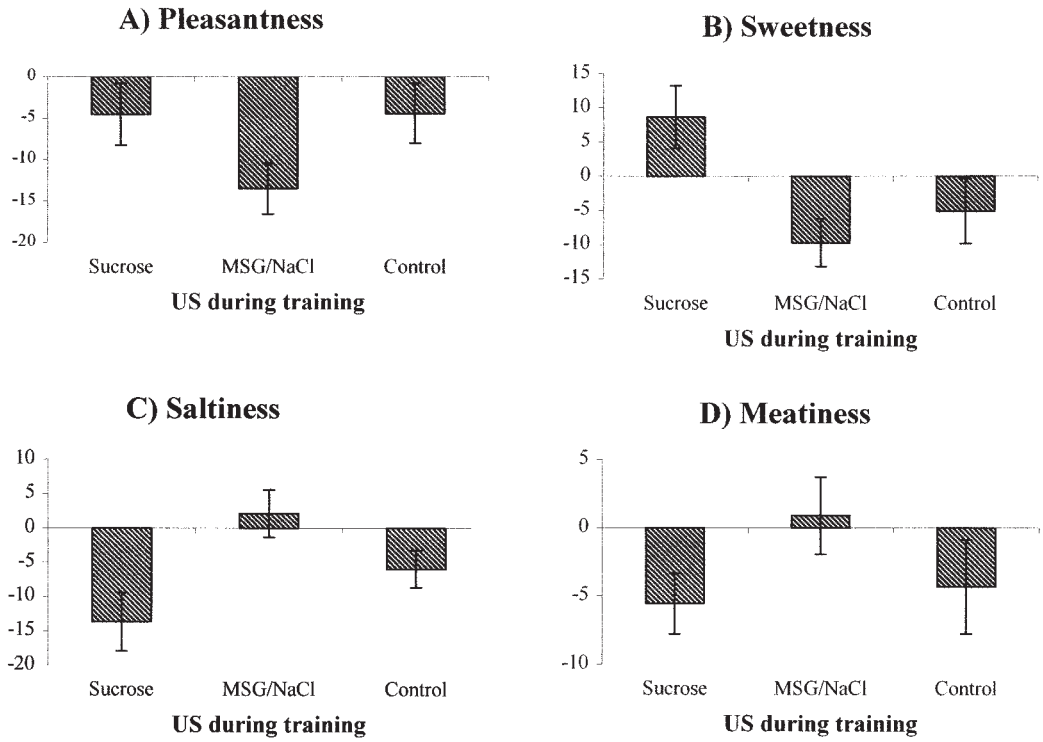

Figure 1. Changes in rated pleasantness (A), sweetness (B), saltiness (C), and meatiness (D) of odors paired previously with 10% sucrose, a combination of 0.16% monosodium glutamate and NaCl (MSG/NaCl), or a water control in Experiment 1. All values are means ± standard errors of the mean, $n = 36$. US = unconditioned stimulus.

changes in odor evaluation as a consequence of pairing with the taste US cannot be attributed to spurious differences of evaluations at baseline. Contrasts of pleasant, sweet, salty, and meaty ratings at pretraining for the three odors used confirmed that the odors were well matched, with no significant differences in baseline evaluations of the three odors used (see Table 2).

The rated pleasantness of odors experienced orthonasally (Figure 1A) varied depending on the training US, $F(2, 60) = 3.56$, $p < .05$. This change was independent of the odor set used (no main effect or interaction involving odor set). Pleasantness decreased significantly by 13.5 ± 3.0, relative to baseline in the SALT condition, $t(35) = 4.47$, $p < .001$, but did not change significantly from baseline in the sucrose or control condition. Protected pairwise comparisons of overall changes in pleasantness between conditions indicated that the decrease in the SALT condition was significantly greater than the changes in either the sucrose or water condition (both ps $< .01$).

Table 2
Sensory and Hedonic Evaluations of the Target Odors at Pretraining in Experiment 1

	M ± *SEM*			
Odor used	Pleasant	Sweet	Salty	Meaty
Beer	32.8 ± 3.8	27.3 ± 3.7	39.4 ± 4.2	16.6 ± 3.2
Cream	35.2 ± 3.8	28.1 ± 3.9	36.1 ± 3.7	12.7 ± 2.6
Tea	31.3 ± 3.3	36.6 ± 4.1	35.1 ± 4.3	17.5 ± 2.8

The rated sweetness of the odors experienced orthonasally (Figure 1B) also varied depending on the training US, $F(2, 60) = 7.22$, $p < .005$, regardless of the odor rated (no main effect or interaction involving odor set). As predicted, sweetness increased significantly by 8.7 ± 4.4, relative to baseline in the sucrose condition, $t(35) = 2.02$, $p < .05$, whereas sweetness decreased by 9.7 ± 3.5 from baseline in the SALT condition, $t(35) = 2.77$, $p < .01$, but did not change in the water condition. Pairwise comparisons confirmed that the change in sweetness ratings in the sucrose condition differed significantly from the equivalent changes in the SALT ($p < .001$) and water ($p < .02$) conditions. The effects of training on evaluations of saltiness and meatiness were less coherent. The saltiness of the test odor (Figure 1C) did vary between the test conditions, $F(2, 70) = 6.23$, $p < .005$; however, the only significant change was a decrease (of 13.7 ± 4.2) in the rated saltiness of the sucrose-paired odor. In contrasts between conditions, we found no difference in overall change in saltiness between the sucrose and control conditions, and important to note, there was no significant change in rated saltiness of the SALT-paired odor. Changes in meatiness of the test odor appeared similar to those for saltiness (Figure 1D), but the overall effect of training US was not significant, $F(2, 60) = 1.93$, *ns*. It was apparent during testing that meatiness was a more difficult evaluation for participants to make. Overall, the sensory data suggest that participants

found it easier to attribute sweetness than the more savory perceptual qualities to the odors.

Although previous flavor–flavor studies have generally failed to find evidence of hedonic change for odors or flavors paired with sucrose, it was noted previously that increased liking for a sweet-paired flavor was more evident in those participants who showed a distinct liking for the trained sweet taste (Baeyens et al., 1990). We thus predicted that, even if training with odor–sucrose pairings did not produce an absolute increase in the pleasantness of the odor evaluated alone, the degree of change in odor pleasantness might reflect actual pleasantness of the odor–sucrose stimuli during training. If so, then the change in odor pleasantness pre- to posttest and the rated pleasantness of the trained odor–sucrose stimuli (see Figure 2) should be positively correlated. The linear regression analysis confirmed this prediction. When change in pleasantness was regressed against pleasantness and sweetness of the training sucrose stimulus and change in sweetness of the odor, the overall regression model was significant, $F(3, 32) = 5.24$, $p < .005$: adjusted $r^2 = .27$, and a unique proportion of this variance was accounted for by the average rated pleasantness of the odor–sucrose combination during training (see Table 3). There was also some evidence that the change in sweetness for the sucrose-paired odor contributed to the change in pleasantness for that odor (see Table 3), with increased odor sweetness associated with higher rated pleasantness independent of the influence of the effect of sucrose pleasantness. Thus, this analysis suggests that the change in liking for the sucrose-paired odor was a consequence of at least two factors: the degree to which the sucrose stimulus was rated as pleasant and the acquired sweetness of the odor. When the analysis was repeated with the change in sweetness as dependent variable, with sweetness and liking for sucrose and change in liking for the sucrose-paired odor as predictors, the overall model was again significant, $F(3, 32) = 3.91$, $p < .05$; adjusted $r^2 = .20$. However, neither sweetness or liking for sucrose accounted for significant independent variance in this model, with the trend for a relationship between the change in odor pleasantness and change in odor sweetness (discussed earlier) the only factor to approach significance. Thus, although sucrose pleasantness uniquely predicted the change in odor pleasantness, neither sucrose pleasantness nor sweetness independently predicted the change in odor sweetness.

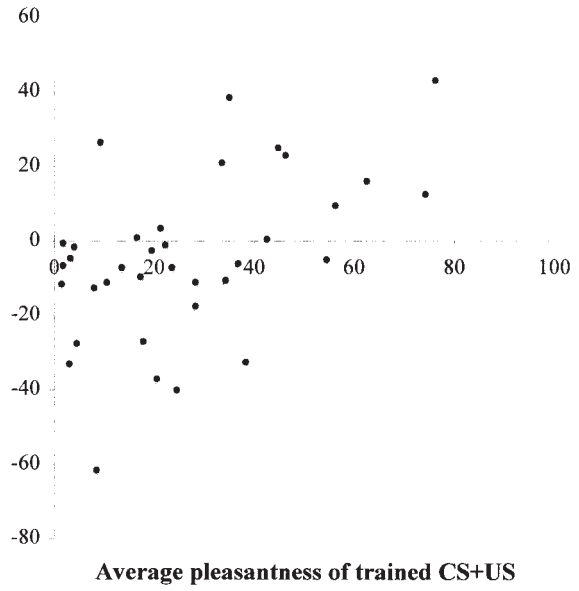

Figure 2. The relationship between the change in rated pleasantness of the sucrose-paired odor and the rated pleasantness of the odor/sucrose stimulus during training. CS = conditioned stimulus; US = unconditioned stimulus.

When the equivalent linear regression model was applied to the change in pleasantness of the SALT-paired odor, with pleasantness and saltiness of the SALT stimulus and the change in rated saltiness of the odor from pre- to posttest as factors, the overall regression model was not significant, $F(3, 32) = 0.88$, *ns*, and none of the three predictors accounted for unique variance in the model. Likewise, when change in saltiness of the SALT-paired odor was regressed against rated pleasantness and saltiness of SALT, and the concomitant change in pleasantness of the SALT-paired odor, this model was not significant overall, $F(3, 32) = 1.51$, *ns*. Thus, these analyses of changes in the SALT-paired odor did not bear out the findings for sucrose. However, this may reflect the restricted range of liking for the SALT US, as average liking for the SALT US was low (6.8 on the 100-point rating scale), and variability in liking for the SALT US was much less than for the sucrose US (Howell, 1992).

Evaluation of the Trained US

As with previous studies (Stevenson et al., 1995, 1998, 2000), the present study relied on the training US having the appropriate characteristics to facilitate conditioned changes in odor quality. The inclusion of ratings of the test stimuli during the training phase allowed us to explicitly test whether this was so. For pleasantness, the predicted main effect of training condition was significant, $F(2, 60) = 21.07$, $p < .001$, with no significant effects of training session or odor set. As predicted, the highest pleasantness rating was in the sucrose condition, which was significantly greater than in the other two conditions (SALT, $p < .001$; control, $p < .001$; see Table 4). Unsurprisingly, sweetness of the training CS–US stimuli also varied with condition, $F(2, 60) = 105.63$, $p < .001$, with the sucrose condition rated as highly sweet and SALT and control as similarly unsweet. Ratings of sweetness did not differ across the four training sessions or differ between the odor sets used (no main effect or interaction of training session or odor set). As expected, both saltiness, $F(2, 60) = 56.85$, $p < .001$, and meatiness, $F(2, 60) = 6.09$, $p < .005$, also varied with condition, but here saltiness differed significantly in the order of SALT > control > sucrose (see Table 4), whereas sucrose and control conditions were rated similar in meatiness. In both cases, there was no effect of training session or odor set on evaluation of these stimuli. Overall, these analyses confirm that the training US stimuli had the predicted characteristics, with the exception that the assumption that 10% sucrose is a universally liked stimulus was not upheld. These analyses also suggest that the three odors used in these tests did not differ systematically in the way they were evaluated. Thus, the effects on drink pleasantness of adding beer odor to sucrose did not differ systematically from that of adding cream or tea odor to sucrose.

Table 3
Regression Analysis With Change in Odor Pleasantness as the Dependent Variable for Experiment 1

Parameter assessed	Pearson *r*s			Model coefficients	
	Change in odor pleasantness	SUC pleasantness	SUC sweetness	*B*	*t*
SUC pleasantness	.49			0.40	2.40*
SUC sweetness	.04	.21		0.04	0.23
Change in odor sweetness	.45	.02	.19	0.26	1.96

Note. Variables in the model were sucrose (SUC) pleasantness and sweetness during the training phase and change in odor sweetness.
* $p < .05$.

Discussion

Experiment 1 provides the first direct evidence of hedonic changes in orthonasal evaluations of odors that had been paired retronasally with an hedonically significant gustatory US (SALT). The study also confirms the previous suggestion in the broader human flavor–flavor learning literature that acquired dislikes are more robust than acquired likes: Repeated retronasal pairing of odors with the disliked SALT stimulus reliably reduced odor pleasantness when assessed orthonasally, but pairing with sucrose did not result in an overall increase in odor pleasantness. However, regression analysis suggested that individual changes in odor pleasantness for the sweet-paired odor were positively correlated with the rated pleasantness of the odor–sucrose stimulus pairs used during training. Thus, as was previously suggested with more complex flavor stimuli (Baeyens et al., 1990), enhanced liking for odors may be seen in those participants who specifically like sweet tastes. The next two experiments were designed specifically to test this contention and to evaluate further the nature of acquired sensory and hedonic characteristics of odors.

The detailed analyses of changes in liking for sucrose-paired odors in Experiment 1 clearly showed that human participants vary considerably in the extent to which they express liking for 10% sucrose. As discussed earlier, this variation may have many causes, but it clearly acts as a confound in tests of the potential for enhanced liking for odors as a consequence of repeated association with a sweet taste. One potential method of removing this confound is to preselect participants on the basis of their evaluations of 10% sucrose and to explicitly exclude those who rate this stimulus as unpleasant; this was the approach adopted in Experiment 2. If no change in odor pleasantness was observed, a potential criticism would have been that the study lacked the power or sensitivity to pick up any hedonic changes. To control for this, we repeated the aversive conditioning procedure from Experiment 1, but we changed the aversive US from SALT, which clearly generated qualities that were hard to ascribe to odors, to quinine, which has an aversive bitter taste and so would be predicted to produce a reliable reduction in liking for paired odor stimuli. Inclusion of quinine also allowed us to evaluate further the generality of acquired sensory changes in olfactory conditioning by testing whether quinine-paired odors acquired bitter sensory characteristics.

In Experiment 1, participants evaluated the characteristics of the odor–taste pairs during training. This methodology allowed us to evaluate the potential relationship between the perceived characteristics of the US and any subsequent changes in CS quality. However, a potential criticism of this method is that it increases the possibility for demand characteristics to interfere with the study outcome, because participants are repeatedly being asked to make pleasantness judgments. Previous studies in olfactory conditioning avoided this problem by fully disguising the training session within a perceptual judgment task; the same method was adopted here.

Experiment 1 successfully replicated the main finding in previous olfactory conditioning studies using a sweet US, which was increased sweetness of the sucrose-paired odor. This effect has been described as a form of synesthesia (Stevenson et al., 1998) and has been interpreted in terms of integration in memory of incoming olfactory stimuli with a stored representation of the associated sweet taste (Stevenson & Boakes, 2004). Thus, in effect, the evaluation of sweetness for the sucrose-paired odor could be reinterpreted as a test of prospective memory for the likely taste of the solution being evaluated. If so, asking participants to evaluate how sweet the odor is or how sweet they expect the solution they are smelling to taste should generate the same response, as both should facilitate activation of the associated memory for sweetness. To test this, we asked one group of participants to rate the direct properties of the odor they were smelling and the second group to rate how they would expect the solution to taste on the basis of its smell alone.

Table 4
Average Evaluations of the Stimuli Used During the Four Training Trials From Experiment 1

Evaluation	*M* ± *SEM* for trained stimulus		
	Odor + sucrose	Odor + SALT	Odor + water
Pleasantness	25.6 ± 3.1	6.9 ± 1.4	9.1 ± 1.6
Sweetness	72.3 ± 3.1	17.5 ± 3.3	18.8 ± 3.1
Saltiness	16.9 ± 2.9	58.7 ± 4.0	29.7 ± 4.1
Meatiness	11.2 ± 2.6	23.5 ± 4.3	14.6 ± 3.0

Note. SALT = a combination of monosodium glutamate and sodium chloride.

Experiment 2

Method

Participants

The study was advertised to staff and students at the University of Sussex as a study of "the perceptual properties of common odours and tastes," and respondents were invited to attend a 10-min screening session. At the screening session, potential participants evaluated the taste of four test solutions, presented in random order. Participants were handed a written instruction sheet that briefly described how to taste the solutions and outlined the use of the rating scales. They were then required to taste and expectorate sample solutions of 10% sucrose, 0.01% quinine sulfate, 0.2% NaCl (saline), and water; then they evaluated each solution for pleasantness, sourness, sweetness, bitterness, and saltiness attributes using 100-mm line scales ranging from *Very unpleasant* to *Very pleasant* for the liking rating and from *Not at all* (0) to *Extremely* (100) for the other taste attribute ratings, as in Experiment 1. Solutions were presented as 20-ml servings in 50-ml glasses, and participants were required to rinse their mouths with water between tasting the solutions. The order in which samples were evaluated was counterbalanced with a Latin square design. To ensure that these stimuli would be effective US for these participants, we used as criteria the ratings of sweetness and pleasantness of sucrose in excess of 50 points on the 100-point rating scale and ratings of pleasantness of quinine less than 30 points and bitterness in excess of 50 points. Water and saline were included as distracters. The participants in the main study were the first 24 individuals who met these criteria, who did not smoke, and who were not suffering from colds or other respiratory infection while taking part in this study. Participants were divided at random into two groups: the olfactory group ($n = 12$, mean age = 23; 8 women, 4 men) and the taste expectancy group ($n = 12$, mean age = 23; 9 women, 3 men). The protocol was approved by the University of Sussex Ethics Committee, and the experiment was conducted according to the ethical standards laid down in the Declaration of Helsinki, 1964.

Stimuli

Orthonasal stimuli used at pre- and posttraining. Test odors (CS) for the conditioning study were selected from pilot studies with 20 untrained volunteers. The selected odors were 0.25% tea, 0.25% raisin (International Flavours and Fragrances Inc, United Kingdom), and 0.1% maracuja (Firmenich, U.K. Limited), made up in water to give pure odor solutions. Odors were different from those in Experiment 1 because, in that study, we deliberately selected odors with ambiguous sweet/savory elements to facilitate conditioning with SALT, but here we wanted to maximize the possibility of sweet and bitter associations. Of these three odors, tea and maracuja were used as target odors to mix with the sucrose and quinine tastants and raisin was used as a control odor. All three odors were rated as being neither particularly pleasant nor unpleasant, relatively novel, and neither strongly sweet nor bitter.

In addition to the test odors, other orthonasal distracter stimuli were 0.05% almond (Supercook, United Kingdom), 0.5% coconut (Supercook, United Kingdom), 0.05% star fruit (Firmenich, U.K. Limited), and 0.2% saline, all presented as a solution in water. In total, participants evaluated seven sample odor solutions at pre- and posttest sessions. These orthonasal stimuli were presented as 20-μl aliquot parts in a 50-μl glass covered by a lid and were presented in randomized order.

Stimuli during retronasal training trials. The two target taste solutions (US) used in conditioning (training) trials were 10% sucrose and 0.01% quinine sulfate. These stimuli were mixed with either the target 0.25% tea or 0.1% maracuja odor stimuli. A solution of 0.25% raisin odor in water was used as a control flavor. In addition, solutions of 0.5% coconut oil, 0.05% almond oil, and 0.2% saline, all in water, were used as distracters during training. All training stimuli were presented as 10-μl aliquot parts in a 50-μl glass covered by a lid. The pairing of the two target odors and taste stimuli (sucrose and quinine sulfate) was fully counterbalanced within each group.

Procedure

On the first test session, participants gave written consent and then completed the screening task (described earlier in detail in the *Participants* section of Experiment 2). Potential participants who failed to meet the study criteria ($n = 9$) were given a small payment once the screening results had been checked and took no further part in the study. The participants were the first 24 to pass the screening test, and they were given a short break following the screening taste tests; then they completed pretraining evaluations of the orthonasal stimuli. Participants in the olfactory group were asked to smell and then evaluate the smell of each sample ("How does it [the odorant] smell?"), but participants in the taste expectancy group were asked to smell and evaluate what they expected each stimulus to taste like ("How would it [the odorant] taste if you were to put it in your mouth?"). The descriptors evaluated were pleasant, sweet, bitter, sour, salty, strong, and familiar, with the same rating scales as those used Experiment 1. The order of odor presentation was randomized across the participants.

At least 24 hr after completing the pretest, participants returned for the first of three training sessions, with each session separated by a minimum of 24 hr. Unlike in Experiment 1, in which participants evaluated each training solution, here we used the triangle-test disguised-training method described previously (Stevenson et al., 1995). In each trial, participants were presented with three solutions, and their task was to identify the odd one out in terms of flavor. They were also told that some trials would be easy and some very difficult. There were seven trials in each training session, of which two were conditioning trials. One trial involved presentation of the control odor, and four were distracter trials. One conditioning trial consisted of one of the two target odors paired with sucrose, and in the second trial the other target odor paired with quinine. On the conditioning and control odor trials, the three solutions were identical (i.e., there was no odd one out), and this ruse ensured that participants paid close attention to the sensory characteristics while not explicitly evaluating liking. The remaining four distracter trials always contained one odd stimulus: almond, saline, saline; water, coconut, water; water, water, saline; saline, water, saline. Thus in total, participants tasted 21 solutions at each of the three training sessions, and they were instructed to rinse their mouth with mineral water between each solution.

At least 24 hr after completing the third training session, participants completed the posttraining orthonasal odor evaluations. The first part of this session was identical to pretraining, with orthonasal evaluations of the same seven odor solutions including the three test odors. To maintain the same rating context, we kept the order of presentation the same as in pretest for each participant. Following this, participants were asked about the purpose of the experiment and completed a contingency awareness test. In this test, they were presented with the two target odors along with the control odor (raisin) and were asked again to smell each one and recall, if they could, the taste of the solution it was previously presented with. They were then required to choose one of four boxes specified as sweet, bitter, salty, and neutral tastes for each odor and to rate how confident they were in their responses from 0 (*complete guess*) to 100 (*absolutely certain*). Participants were paid £15 on completion of the study, following debriefing.

Data Analysis

To confirm that the olfactory and expectancy groups did not differ in their evaluations of the US, we contrasted the pleasantness, sweetness, and bitterness ratings from the initial screening test between sucrose and quinine stimuli and the two groups, using a two-way ANOVA. As with

Experiment 1, because the principal interest was how the orthonasal hedonic and sensory evaluations of the target odors changed as a consequence of retronasal pairing of these odors with the sucrose and quinine US during training, we calculated change scores by subtracting pretraining pleasantness, sweetness, and bitterness odor evaluations from the posttraining ratings. Then we contrasted these change scores between training conditions (sucrose, quinine, or control) and group (olfactory or taste expectancy), using a three-way ANOVA, with the specific odor set used during training as a control factor to test for differential sensitivity to conditioning between the two main target odors. To ensure that change scores were not biased by spurious baseline differences, we used the same three-way ANOVAs to evaluate ratings at pretraining.

Results

Taste Screening

The rated pleasantness of sucrose was 65.7 ± 12.4 points, significantly greater than that of quinine (12.4 ± 2.1), $F(1, 22) = 284.44$, $p < .001$. There were no significant differences in these evaluations between olfactory and taste expectancy groups. The sucrose stimulus was rated as intensely sweet (87.9 ± 1.9), quinine was rated as bitter (86.6 ± 2.8), and again these ratings did not differ between groups.

Orthonasal Evaluations

Changes in the rated pleasantness of the target odors varied depending on the paired tastant (sucrose, quinine, or water), $F(2, 40) = 8.32$, $p < .001$ (see Figure 3A), and as predicted, the rated pleasantness of odors paired with sucrose increased significantly by 10.8 ± 4.7 from pre- to posttraining, $F(1, 20) = 5.05$, $p < .05$, whereas pleasantness decreased significantly by 15.9 ± 4.7 for odors paired with quinine, $F(1, 20) = 9.65$, $p < .01$. Pleasantness of the water-paired control odor did not change significantly, $F(1, 20) = 0.02$, *ns*. No effect of group was found (no significant main effect or interaction with group), with almost identical ratings in the olfactory and taste expectancy groups, and there was no effect of odor set. Pleasantness of odors at pretraining did not differ between conditions or groups, and these evaluations were unaffected by odor set.

Rated sweetness (Figure 3B) also varied depending on the associated US, $F(2, 40) = 15.15$, $p < .001$. Sweetness increased significantly by 31.0 ± 7.1 for odors paired with sucrose, $F(1, 22) = 18.45$, $p < .001$, whereas sweetness decreased significantly by 15.8 ± 5.4 for odors paired with quinine, $F(1, 22) = 8.35$, $p < .01$, but did not change significantly for the water-paired control odor, $F < 1$. Changes in sweetness ratings by the olfactory and taste expectancy groups did not differ significantly, and these changes were unaffected by odor set. Pretraining evaluations of sweetness did not vary between groups, training conditions, or odor set. Changes in rated bitterness (Figure 3C) also varied depending on the trained US, $F(2, 40) = 6.59$, $p < .005$, with no difference in evaluated bitterness of odors at pretraining. Odors paired with quinine were rated as more bitter (by 22.7 ± 6.5) at posttest, $F(1, 22) = 12.10$, $p < .005$, whereas bitterness ratings for odors paired with sucrose tended to decrease, $F(1, 22) = 3.62$, $p = .07$. Bitterness ratings did not change for the water-paired odor, and bitterness evaluations did not differ significantly between the olfactory and taste expectancy groups. Neither the change in rated bitterness after training nor the baseline evaluation of odor bitterness varied between the two odors used with sucrose and quinine.

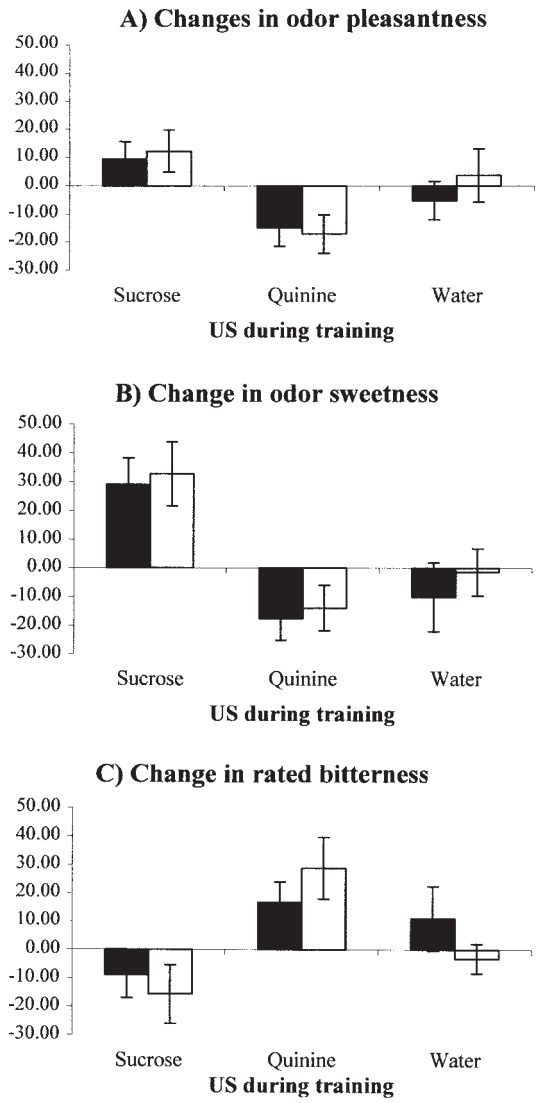

Figure 3. Mean (± *SEM*) changes in ratings of pleasantness (A), sweetness (B), and bitterness (C) for odors paired previously with 0.01% quinine solution, 10% sucrose solution, or water (control) for participants rating either the experienced odor quality (black bars, representing the olfactory group) or their expectations of how the solution would taste on the basis of its smell (white bars, representing the taste expectancy group). Data are from Experiment 2; $n = 12$ in each group. US = unconditioned stimulus.

As with Experiment 1, we used linear regression to explore whether changes in sweetness and pleasantness of the sucrose-paired odor were independent. Because no measure of pleasantness of the combined odor–taste stimuli used during training was taken, evaluation of the sucrose stimulus was determined with data from the screening test. In a test of whether the overall change in liking for sucrose was predicted by liking for sucrose, perceived sweetness of sucrose, or the overall change in odor sweetness, changes in pleasantness for the sucrose-paired odor were regressed against rated pleasantness and sweetness of sucrose at the screening test

and the overall change in sweetness of the sucrose-paired odor. Because earlier analyses found no difference between olfactory and taste expectancy groups, both sets of data were included to maximize power. The overall fit of this regression model was significant, $F(3, 20) = 3.34$, $p < .05$, adjusted $r^2 = .23$. As in Experiment 1, liking for the sucrose US (here based on ratings from the screening session) accounted for significant independent variance in the model, but in this case, changes in sweetness of the sucrose-paired odor was not a significant predictor of pleasantness change (see Table 5). A similar regression model of changes in sweetness using pleasantness and sweetness of sucrose at screening and change in odor pleasantness as factors did not produce a significant overall fit, $F(3, 20) = 1.51$, *ns*, in contrast to Experiment 1. Likewise, regression models of both change in pleasantness and bitterness of the quinine-paired odor, with rated pleasantness and bitterness and pleasantness of quinine at screening as factors, did not produce significant overall fits: pleasantness, $F(3, 20) = 1.79$, *ns*; bitterness, $F(3, 20) = 0.34$, *ns*.

Debriefing and Contingency Awareness

Although most participants believed that the experiment was related to taste and smell, no one explicitly mentioned liking change or any other phrase implying hedonic evaluation when asked the purpose of the study, and so the reported changes in pleasantness are unlikely to arise from demand effects. Sixteen of the 24 (67%) participants correctly recognized the odors paired with either sucrose or quinine, with a mean confidence rating of 85% for the bitter taste and 92% for the sweet taste, whereas only 4 (17%) participants correctly identified the associated tastants for all three odors. Reanalysis of changes in pleasantness, sweetness, and bitterness ratings, with awareness as an additional factor, did not alter the significant differences in changes in evaluations between conditions.

Discussion

The results from Experiment 2 clearly demonstrate hedonic changes within the olfactory conditioning paradigm, extending the outcome of Experiment 1. When the US was the aversive bitter stimulus quinine, rated pleasantness of the quinine-paired odor evaluated orthonasally decreased significantly, in line with the effects of training with the aversive SALT stimulus from Experiment 1. Thus, associations of odors and aversive tastes result in the development of a clear dislike for the associated smell. The regression model for bitterness, however, shed no light on whether the hedonic or the sensory qualities of quinine predicted the change in pleasantness of the quinine-paired odor. As with SALT in Experiment 1, it may be that restricted variance in scores for dislike of quinine limited the power of the regression analysis.

In Experiment 1, overall liking for odors paired with sucrose did not increase, but here preselection of participants (to ensure that they rated SUC as pleasant) resulted in clear increases in hedonic evaluation of the sucrose-paired odor. Thus, these data provide the first clear evidence for increased liking for orthonasal evaluation of odors in the olfactory conditioning paradigm. The only previous study to report changes in liking for flavor stimuli paired with sucrose (Zellner et al., 1983) assessed flavor for stimuli after a swill-and-spit test, and although the flavor stimuli used in that study (flavored teas) are likely to have had large olfactory components, the odor would have been experienced retronasally, along with any taste-related components. Thus, the present study is the first clear demonstration of hedonic change produced by association with sweetness for pure olfactory stimuli. The present data for sucrose also suggest that previous failures to find overall increases in pleasantness for flavors paired with sweetness in the flavor–flavor evaluative conditioning literature (Baeyens et al., 1990) may be attributed to individual differences in sweet liking between participants. The outcome of the regression analysis for changes in odor pleasantness in Experiment 2 confirmed the findings of Experiment 1, that pleasantness of the US is the major factor underlying change in odor pleasantness. Thus, despite restricting the variance in rated pleasantness of the sucrose stimulus used during training and basing the pleasantness evaluation on data collected for sucrose on its own prior to training, the change in pleasantness for the sucrose-paired odor correlated with sucrose pleasantness at screening, and this factor accounted for significant independent variance in the regression model. In contrast, change in sweetness of the sucrose-paired odor was only weakly correlated with pleasantness change and did not predict the change in odor pleasantness when overall sucrose pleasantness was in the regression model. Thus, as with Experiment 1, it appears that the change in liking for the sucrose-paired odor operated primarily through evaluative conditioning based on sucrose liking, rather than arising through the observed changes in odor sweetness.

Experiment 2 also confirms the robustness of acquired sweetness perception for sweet-paired odors but extends these findings

Table 5
Regression Analysis With Change in Odor Pleasantness as the Dependent Variable and Sucrose (SUC) Pleasantness and Sweetness During Screening and Change in Odor Sweetness Posttraining for Experiment 2

Variable	Pearson *r*s			Model coefficients	
	Change in odor pleasantness	SUC pleasantness	SUC sweetness	*B*	*t*
SUC pleasantness	0.49*			0.45	2.41*
SUC sweetness	−0.19	−0.04		−0.21	−1.12
Change in odor sweetness	0.29	0.13	0.13	0.26	1.41

* $p < .05$.

to suggest that odors may also acquire bitter characteristics when paired with a strong bitter taste, thus adding to previous findings of acquired sweetness and sourness.

The second aim of Experiment 2 was to contrast ratings of the actual experience of the odors with ratings of taste expectancy as a test of the theory that acquired odor characteristics are based on stimulation of odor memory by the sensed odor stimuli (Stevenson & Boakes, 2004). The similarity in ratings between the olfactory group (who rated the experience of the odor) and the taste expectancy group (who rated how they expected the solution to taste) was striking. Thus. these data are consistent with the idea that olfactory synesthesia is an example of multisensory integration resulting from activation of a previously encoded odor–taste percept. These results are also of interest because they suggest that participants may draw inferences about the type of taste with which the odor was previously paired from the purely sensory information available to them when the odor is sniffed.

Previously, it has been suggested that the acquired sweetness of a sucrose-paired odor could itself be explained as a quasi-hedonic evaluation rather than as a pure sensory evaluation (Stevenson & Boakes, 2004). In Experiment 1, the regression analyses suggested some independence between changes in liking and changes in sweetness, which further suggested that the two evaluations were, to some extent, independent of each other. In Experiment 2, increased sweetness was accompanied by increased pleasantness, and although the overall magnitude in sweetness change was much greater than the change in pleasantness, these data could be interpreted as evidence that changes in pleasantness and sweetness might both reflect hedonic change. To explore this idea further, in Experiment 3 we repeated the basic design of Experiment 2, but rather than explicitly excluding sweet dislikers, we used a taste screening test to define participants as either sweet likers or sweet dislikers prior to the onset of training. To simplify training, target odors were paired either with sucrose or water; otherwise, training and testing followed the same pattern as that in Experiment 2. The prediction was that both sweet likers and dislikers would report acquired sweetness for the sucrose-paired odor but that only the liker group would show concomitant increases in rated odor pleasantness.

Experiment 3

Method

Participants

A total of 24 nonsmoking volunteers were recruited from students and staff at the University of Sussex. As in Experiment 2, they were invited to take part in an initial screening test in which they had to taste and evaluate sucrose solution and water. Respondents who evaluated sucrose as low ($\leq$45) or high ($\geq$60) in pleasantness and who gave sucrose a high rating in sweetness ($\geq$60) on 100-mm line scales were selected to take part in the experiment. Thus, participants were assigned to one of two groups, the sweet liker group (n = 12, mean age = 22, 10 women, 2 men) or the sweet disliker group (n = 12, mean age = 22, 10 women, 2 men). None of the participants had colds or other respiratory infections during the experiment. The advertisement of the experiment and the approval of the study protocol were identical to those used for Experiment 2.

Stimuli

Taste screening. The taste stimuli were two identical samples of 10% sucrose and two samples of water, presented in an alternate order. Duplicate samples were used to ensure rater consistency. Samples were presented as 20-μl aliquot parts in a 50-μl glass.

Orthonasal evaluations. The three test odors were 0.25% raisin (International Flavours and Fragrances Inc, United Kingdom), 0.05% star fruit, and 0.1% lychee (control; Firmenich, U.K. Limited) made up in water to give pure odor solutions. Of these three odors, raisin and star fruit were used as target odors to mix with sucrose or water, and lychee was used as a control odor. These test odors were presented along with three other stimuli—0.05% almond (Supercook, United Kingdom), 0.5% coconut (Supercook, United Kingdom), and 0.2% saline—all in water as 20-μl aliquot parts in a 50-μl covered glass. The order of presentation was randomized across participants.

Conditioning flavors. Two target odors (raisin and starfruit: the CS) were mixed either with 10% sucrose (US) or water (control). A mixture of lychee in water was used as a control flavor. The concentrations of odors were identical to the orthonasal evaluation. In addition, solutions of 0.5% coconut oil, 0.05% almond oil, and 0.2% saline, all in water, were used as distracters during training. All stimuli were presented as 10-ml servings in a 50-ml glass covered by a lid, and the pairing of the two target odors with either sucrose or water was fully counterbalanced.

Procedure

In contrast to Experiment 2, here testing and training were completed in a single 3-hr session consisting of the screening test, pretest (orthonasal evaluation), four conditioning sessions, and a posttest session. Potential participants who did not meet the study criteria at screening were excluded (n = 13). The 24 participants completed the pretest shortly after the screening test. After this, they carried out the triangle test outlined in Experiment 2. Each conditioning session contained six trials, with three solutions presented on each trial (i.e., 18 solutions per session, in total). Of the six trials, one was a conditioning trial with a target odor paired with sucrose, one paired the second target odor with water, and one used the control odor (lychee) paired with water. Pairing of odors and sucrose was counterbalanced within each group. As in Experiment 2, the remaining three trials were masking trials and contained one odd stimulus: coconut, water, water; water, saline, water; water, water, almond. Each of the four conditioning sessions was separated by a 15-min period. The posttest orthonasal evaluation and contingency awareness test from Experiment 2 commenced 15 min after completion of the last conditioning session. Participants were paid £15 on completion of the study, after debriefing.

Data Analysis

To confirm that the liker and disliker groups differed in their hedonic evaluations of the sucrose US, and to test whether their sweetness evaluations also differed, we used a two-way ANOVA, with group and sample as factors, to contrast the sweetness and pleasantness of the two screening sucrose stimuli. As with previous experiments, because the principal interest was how orthonasal hedonic and sensory evaluations of the target odors changed as a consequence of retronasal pairing of these odors with sucrose or water (control) during training, we calculated change scores by subtracting pretraining pleasantness and sweetness odor evaluations from the posttraining ratings. Then we contrasted these change scores between training conditions (sucrose, water, or control) using a two-way ANOVA, with the specific odor set used during training as a control factor to test for differential sensitivity to conditioning between the two main target odors. A two-way ANOVA was also used to evaluate ratings at pretraining to test for spurious baseline differences.

Results

Taste Screening

Figure 4 shows the pleasantness and sweetness evaluations for the 10% sucrose screening solution in the two groups. As expected, rated pleasantness, $F(1, 22) = 116.6$, $p < .0001$, but not rated sweetness, $F < 1$, differed significantly between sweet liker and disliker groups.

Orthonasal Odor Evaluations

Baseline pleasantness ratings for the three trained odors did not differ between groups (there was no significant main effect or interaction involving group). Analysis of changes in pleasantness of odors revealed a significant Group × US interaction, $F(1, 20) = 4.37$, $p < .05$. The only significant change in pleasantness was an increase of 20.8 ± 7.9 in rated liking for the sucrose-paired odor in the sweet-liker group, $F(1, 20) = 4.07$, $p < .05$ (see Figure 5A). Change in liking for the sucrose-paired odor in the disliker group did not differ from zero or from the changes in liking for the odor paired with water in either group.

With sweetness, the change in rated sweetness of odors at posttest depended on the US during training, $F(1, 20) = 12.90$, $p < .005$; as expected, this was due to a large increase (30.3 ± 6.0) in rated sweetness of the sucrose-paired odor (see Figure 5B). The increase in sweetness did not differ between liker and disliker groups—a nonsignificant interaction of training US and group, $F(1, 20) = 0.57$—although the increase tended to be greater in the liker group. Rated sweetness of the two target odors at baseline did not differ significantly.

Debriefing

None of the participants precisely identified the main purpose of the experiment. Only 2 of 24 (8%) participants correctly identified which odor had been paired with sucrose.

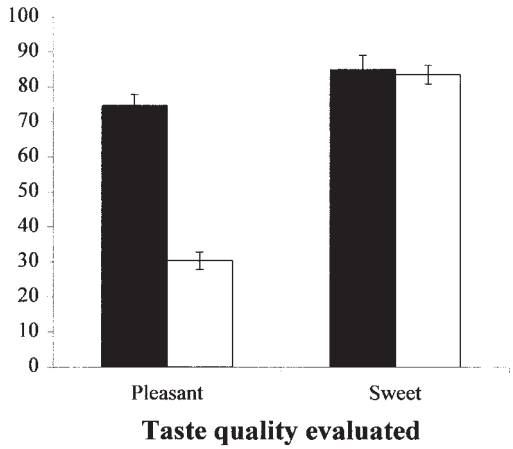

Figure 4. Mean (± *SEM*) ratings of the pleasantness and sweetness of 10% sucrose solution at the screening session for likers (black bars) and dislikers (white bars) in Experiment 3; $n = 12$ in each group.

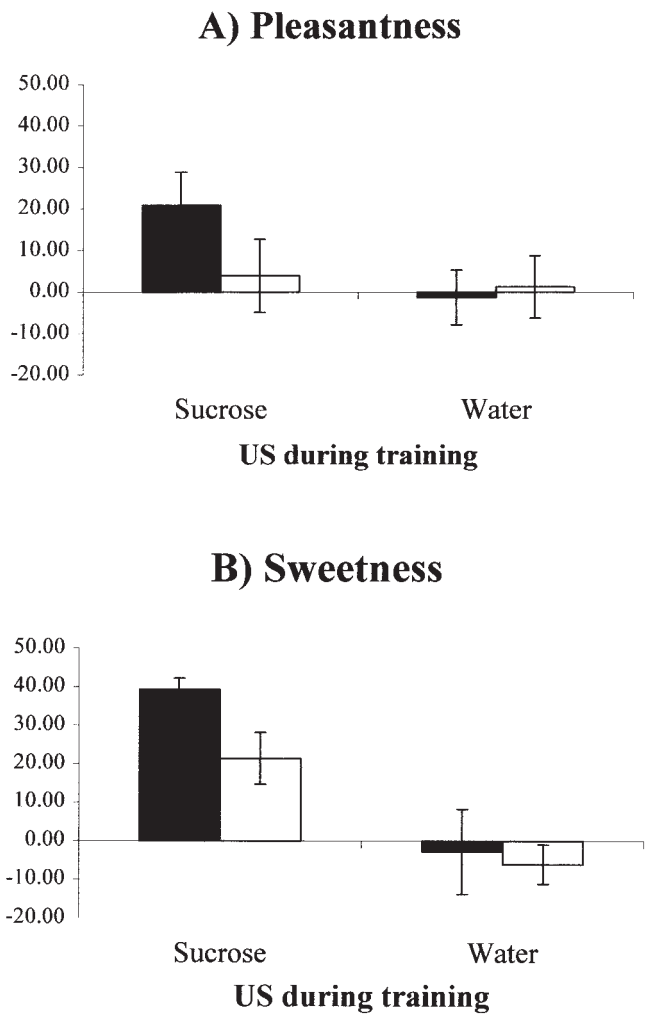

Figure 5. Mean (± *SEM*) changes in ratings of pleasantness (A) and sweetness (B) for odors paired previously with 10% sucrose solutions for participants in the sweet liker (black bars) and sweet disliker groups (white bars) in Experiment 3; $n = 12$ in each group.

General Discussion

In contrast to previous studies (Stevenson et al., 1995, 1998, 2000), the present series of experiments clearly establishes that repeated pairing of an odor with a tastant can result in altered liking for the taste-paired odor, with the direction of hedonic change determined by the hedonic tone of the tastant. Thus, pairing of an odor with the disliked taste of SALT in Experiment 1 and quinine in Experiment 2 resulted in a clear decrease in liking for the taste-paired odor when that odor was subsequently experienced orthonasally in the absence of the taste. Similarly, for sweet likers, repeated pairing of an odor with the liked taste of sucrose in Experiments 2 and 3 resulted in a clear increase in liking for the sucrose-paired odor experienced orthonasally posttraining.

The present results show similarity to those from studies using a more traditional flavor–flavor learning paradigm, in which the CS was a complex flavor experienced orally and therefore likely to consist of combined retronasal odor with taste elements (Baeyens,

Crombez et al., 1995, Baeyens, Eelens, et al., 1990; Zellner et al., 1983). The present series of studies offers some explanation for past inconsistency in the effectiveness of sucrose as a hedonic stimulus. In Experiment 1, although overall changes in rated pleasantness of the sucrose-paired odor were not significant, there was a positive correlation between the change in liking for the sucrose-paired odor and liking for the sucrose US during training. The implication that positive hedonic change was evident only in those participants who showed a clear liking for sucrose was confirmed in Experiments 2 and 3, in which liking for the sucrose-paired odor increased significantly in those participants identified as sweet likers prior to testing. Because no such preselection was used in previous odor-conditioning studies with sucrose (Stevenson et al., 1998, 2000; Stevenson et al., 1995) or in the flavor–flavor study that found ambiguous effects of sucrose (Baeyens et al., 1990), these previous failures to find positive hedonic change may be attributed to inconsistent hedonic responses to sucrose by participants in those studies.

The present experiments confirm and extend previous reports of changes in the sensory qualities of odors that had been paired with tastants (Stevenson et al., 1995, 1998, 2000), with the changes reflecting the specific sensory qualities of the tastant used as US. Thus, the present studies confirm the robustness of the increase in sweetness of odors paired with sucrose but extend these findings in Experiment 2 by showing clear increases in the rated bitterness of odors paired with the bitter taste of quinine. However, in Experiment 1, pairing of odors with the salty taste generated by the mixture of monosodium glutamate and NaCl failed to produce significant increases in saltlike evaluations of the odors posttraining. Whether this reflects a limit on the type of qualities that odors can acquire through this paradigm or poor choice of descriptors by which to classify the specific sensory qualities of SALT is unclear and warrants further investigation. It was clear, however, that participants found the "meaty" evaluation, in particular, difficult to make. It thus seems unlikely that the failure to find consistent SALT-like qualities in the SALT-paired odor is more likely to represent limitations in the ability of the present study to detect such changes rather than a fundamental difference in the way salty tastes associate with odors relative to sweet, bitter, or sour tastes.

Previously, it has been suggested that the use of "sweetness" as a descriptor of odors may confound sensory and hedonic evaluations, because sweetness can be used as an affective descriptor (Stevenson & Boakes, 2004). The sweetness data in Experiment 1, in line with previous studies (Stevenson et al., 1995, 1998, 2000), argue against this because the increase in rated sweetness of sucrose-paired odors was not accompanied by an equivalent change in the rated pleasantness of the sucrose-paired odor. Moreover, in Experiment 1, evaluations of the CS–US compound during the training phase also found evidence of a similar dissociation of pleasantness and sweetness evaluations: The training stimuli were, on average, rated as intensely sweet but not pleasant (see Table 4). Thus, the change in both the perceptual and hedonic qualities of the sucrose-paired odor matched well with the equivalent experience of the CS–US pairing during training. This is further supported by the analyses of factors that predicted the change in pleasantness of sucrose-paired odors: In both Experiment 1 and Experiment 2, pleasantness of either the US alone (Experiment 2) or the combined trained flavor (CS + US; Experiment 1) predicted the overall change in odor pleasantness and did so independently of changes in odor sweetness. In Experiment 3, the response of sweet dislikers also suggests dissociation of sensory and hedonic changes, as odors were rated as significantly sweeter in the absence of hedonic change. Thus, although an increase in sweetness can correspond with an increase in pleasantness (seen in terms of the overall changes with sweet likers in Experiments 2 and 3) and an increase in bitterness can correspond with a decrease in pleasantness (Experiment 2 with quinine as US), changes in sensory quality were not necessary for hedonic changes within this paradigm.

The contiguous experience of odor and taste in a food context is experienced as a single percept, the flavor of the food, rather than separate sensory experiences (Prescott, 2004). This has been taken to imply that the odor and taste components are stored as a single flavor representation (Prescott, 1999; Small & Prescott, 2005). If so, then olfactory conditioning may operate by odors triggering the representation of flavor, with the odor percept combining actual sensory information resulting from stimulation of neural pathways by the olfactory molecules and the excitation of the associated flavor representation. For this to be possible, the neural encoding of olfactory and gustatory information must overlap. Evidence from neuroimaging studies showing that independent presentations of an odorant or tastant produce overlapping activation in regions of the brain associated with perception of taste and or smell (e.g., the primary gustatory area, the insula cortex, [Gottfried et al., 2002; Poellinger et al., 2001; Small et al., 2003], and the orbitofrontal cortex, which is regarded as the secondary taste and smell region [de Araujo et al., 2003; Francis et al., 1999; O'Doherty et al., 2000; Small et al., 2003]) are thus consistent with the idea that odor presentation alone may trigger the experience of a tastelike quality. Experiment 2 lends further support to this idea; asking participants to rate how they experienced the odor or how they expected the relevant solution to taste produced identical results both in terms of changes in sensory evaluation of the odor and in the hedonic changes induced by conditioning.

In the present studies, we used individual hedonic evaluations of sucrose as an indicator of whether participants were sweet likers or dislikers, as the aim was specifically to assess liking for the trained US. Previous studies have tended to use more extensive tests, with multiple sweet stimuli, to achieve this distinction (e.g., Looy et al., 1992). Whether the simpler, single-solution test used here produces the same classification needs to be established in future studies. It is also possible that the evaluation of sweet taste may vary within an individual depending on when the evaluation is made, for example, in relation to current motivational state (Cabanac, 1971).

The conclusion from the present results are in line with substantial evidence of separate neural processes underlying sensory and hedonic aspects of taste in animals (Sewards, 2004), most notably, in terms of clear neuroanatomical divisions between areas of the brain that represent sensory aspects of taste and the equivalent hedonic evaluation of the same taste. Whether equivalent neural subdivisions are seen with olfactory stimuli is less clear in animals, although in humans the pleasantness of odors correlated with activity in a medial region of the rostral orbitofrontal cortex, unpleasantness correlated with activity in regions of the left and more lateral orbitofrontal cortex, and intensity judgments correlated with the signal in medial olfactory cortical areas including the pyriform and anterior entorhinal cortex (Rolls et al., 2003). The

present experiments facilitate future evaluations of neural encoding of olfactory stimuli as a consequence of conditioned associations with gustatory stimuli to determine whether the behavioral expression of changes in sensory and hedonic qualities of these odors is reflected in distinct neural response patterns.

Like all previous studies of changes in odor perception resulting from repeated pairing with tastants, the present series of experiments was based on the assumption that these taste molecules are not detected by the olfactory system. Intriguingly, recent evidence questions this assumption (Mojet et al., 2005). In Mojet et al.'s study, participants rated taste intensity of the primary tastants as less strong when olfaction was blocked during testing, and there was evidence of accurate identification if these tastants were experienced orthonasally. Likewise, another recent study reported that rats that were allowed to sniff but not taste a tastant that was subsequently paired with LiCl developed an aversion to that "taste" (Capaldi et al., 2004), consistent with the idea that the relevant percept is the integrated flavor rather than a simple gustatory representation. This raises two questions. First, could olfactory perception of the tastants used in the present studies have interfered with the effects of training? Second, do tastes paired with odors acquire odor-like qualities just as the odors paired with tastes acquired tastelike qualities? With regard to the first question, it is unlikely that any olfactory perception of the tastants used here invalidated the present findings. Thus, in Experiment 1, the rated qualities of the trained odors at baselines were the same regardless of whether they were experienced with or without the presence of the to-be-trained taste US. Moreover, the changes in odor perception were evident in the absence of the US in all three experiments. However, the recent finding that tastes can be perceived by smell could suggest that both the US and CS stimulated olfactory pathways during the training phase, further confirming the close interaction of taste and odor in flavor perception. The present studies do not allow any evaluation of the second question because we did not ask participants to make odorlike evaluations of the taste US, and future studies should look at this.

The overall conclusion from the present data is that hedonic and sensory changes to odors arising from repeated pairing with basic tastants reflects two different learning processes. The sensory changes appear to be a consequence of the fundamental manner in which flavor is encoded, with odor- and taste-based components of flavor stored together in the brain so that experience of an odor triggers off the representation of associated tastes. Hedonic changes, in contrast, appear best explained in terms of evaluative conditioning (De Houwer et al., 2001), with changes in liking for the taste-paired odor reflecting the hedonic evaluation of the taste US.

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