The Capacity of Humans to Identify Components in Complex Odor–taste Mixtures

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Abstract

Despite the fact that humans experience mixtures of odors and tastes each time they eat, little is known of their capacity to detect the individual components of foods. To investigate this capacity, 43 subjects were trained to identify three odors and three tastes and were required to indicate which of these could be identified in stimuli consisting of one to six components. Although the odor and taste components of most binary mixtures were identified, subjects encountered substantial difficulties with more complex mixtures with only two components being identified in the four- to six-component mixtures. In general, tastes were more easily identified than smells and were the only stimuli identified in the five- to six-component mixtures. Several mechanisms are proposed to account for the poor identification of components.

Key words: analytical capacity, humans, odor-taste mixtures

Introduction

When a food is masticated flavor components consisting of both odorants and tastants are released into the oral cavity in substantial numbers. How many of these are perceived is unknown, and there is little information on the factors that determine which components are perceived. Such factors are likely to include the rate of release from a food matrix (Baek et al., 1999), duration in the oral cavity, and the concentration and types of individual components (Laing et al., 1984). Relevant to the question of which components are perceived are recent studies which have shown that humans can identify up to three components in taste mixtures (Kroeze, 1990; Laing et al., 2002; Marshall et al., 2005) with a similar number reported for mixtures of odorants (Laing and Francis, 1989; Laing and Glenmarec, 1992; Livermore and Laing, 1996; Jinks and Laing, 1999a). With both types of mixtures, several mechanisms were proposed, including suppression of components and the limited capacity of working memory (Jinks and Laing, 1999b). As regards the analysis of odor-taste mixtures, there is no study that has been specifically designed to determine the capacity of humans to identify the components. Rather, they have focused on whether there are interactions between the two modalities. For example, no interaction between the modalities was reported in a study which investigated the intensity of both components in binary mixtures (Murphy et al., 1977; Murphy and Cain, 1980). In contrast, summation of perceived intensity was reported when an odorant and tastant were mixed at subthreshold levels (Dalton et al., 2000). Others found that an odorant's influence on taste is both odorant and tastant dependent (Frank and Byram, 1988), and in another study, odors were found to enhance or suppress tastants (Stevenson et al., 1999). In the study by Frank and Byram, interactions were most obvious when the odor and taste were congruent, for example, strawberry odor enhanced perception of sweettasting stimuli but not those tasting salty. Interactions between the two modalities also occurred in the only reported study of more complex odor-taste mixtures where it was found that identification of an odorant in mixtures with two tastants was very difficult (Laing et al., 2002). Since sweet, sour, and salty tastants suppressed perception of the only odorant octanol in the latter study and the odorant had little effect on the perception of the tastants, it was suggested that tastes may dominate odors in mixtures. Given that the latter proposal was based on mixtures containing

a single type of odorant, further research is needed to determine whether this finding generalizes to other odorants.

The present study, therefore, investigated the capacity of humans to identify the components of odor-taste mixtures containing up to three odorants and three tastants. In particular, it aimed to determine the number of components that can be identified in more complex mixtures than examined previously and whether one sense tends to dominate the other in mixtures.

Materials and methods

General

The subjects were 43 adults (24 females and 19 males) aged between 18 and 55 years (mean = 28.3 years, SD = 9.0), who were either students or staff from the University or residents from local suburbs. Many had previous experience in sensory studies, and all were paid \$15 per session. The study was approved by the University of Western Sydney Human Research Ethics Committee (approval no. 99.35), and subjects gave written consent.

The tastants were of analytical grade, and their names and sources were sucrose (sweet, Sigma, Castle Hill, Australia), sodium chloride (salty, British Drug House, Sydney, Australia), and citric acid (sour, British Drug House); the odorants were cinnamaldehyde (cinnamon, purity 99%), cis-3-hexen-1-ol (grassy, 98%), and 2-pentanone (like nail polish remover, 99%), and all were from Aldrich (Castle Hill, Australia). The particular olfactory stimuli were chosen because they had very different odor qualities and represented a diverse set of odorants, thus allowing a general conclusion to be reached as regards the outcomes of mixing odors and tastes. Each of the six stimuli was diluted with deionized water from a Milli-Ro-6 Plus System (conductivity 0.9 µS), and their concentrations (molar) and perceived intensities are given in Table 1. All the concentrations were determined in a pilot study where a separate group of 33 adults assessed the intensity of each stimulus using a nine-point category scale and where two sessions were used to obtain intensities that were moderate and approximately equal. Analysis of the intensity

Table 1 Characteristics of the components

Component	Perceived intensity	Concentration (M)
Sodium chloride	5.8	0.11
Citric acid	6.4 ^{ac}	0.0052
Sucrose	6.0 ^b	0.21
Cinnamaldehyde	4.6 ^{ab}	0.00032
Hexenol	5.4	0.0085
Pentanone	5.0 ^c	0.00065

Similar superscripts for two components indicate there was a significant difference between their perceived intensities.

data using a one-way repeated measures analysis of variance (ANOVA) indicated there was a difference between components (P < 0.001). Post hoc Bonferroni tests indicated there were differences between cinnamaldehyde and citric acid (P < 0.001), cinnamaldehyde and sucrose (P < 0.001), and pentanone and citric acid (P < 0.022), with no significant differences (P < 0.05) among the other six odor–taste comparisons or among the three tastes. The concentration of cinnamaldehyde was the maximum that could be achieved without producing a taste (Wilkes et al., 2003) and without separating from the water to form two immiscible phases in less than 24 h. Thus, solutions containing cinnamaldehyde and sucrose were used within 24 and 48 h of their preparation, respectively, and all solutions were stored at 4°C until shortly before use when they were equilibrated at room temperature (22–24°C). All stimuli were presented as ~15-ml samples in 30-ml clear plastic cups which had a lid and a straw protruding through a hole, and each was coded with a three-digit number. Subjects assessed a solution by sipping through the straw and swallowing. They were asked to swallow each sample to complete their assessment to enable the full retronasal sampling procedure to occur. The latter procedure ensured that the odorants released from the water solution in the mouth would proceed into the nasopharynx and nose in an identical manner to that which occurs during normal mouth sampling of a beverage. All testing was conducted in an air-conditioned room where each subject was sited in a small semiopen cubicle.

Training and test procedures

Subjects participated in two training sessions held on separate days followed a week later by two test sessions separated by 10 min. At the beginning of each training or test session, they were presented with a labeled sample of each of the six single stimuli at the concentration to be used in the test sessions. Each subject was asked to sample each of the stimuli through the straw and remember the sensation and label. In the training sessions, they then assessed a set of 18 samples consisting of the six single stimuli presented three times within a random series and were required to identify each stimulus. Subjects used a paper and pen method to record their responses, and the six common names for the stimuli were always on view as the choice. All subjects exceeded the criterion of 85% correct for selection in the test sessions during the second training session, with 36 identifying every sample and three and four subjects, respectively, obtaining 94% and 89% correct.

The 36 test stimuli (Figure 1) comprised six one-, two-, three-, four-, five-, and six-component stimuli. Within each type of stimulus, for example, five-component stimuli, all six mixtures were different, and there were no replications of any of these mixtures. The only exception was the six-component stimulus where the six mixtures were the same. During each of the two test sessions, subjects assessed the identity of the components of 18 of the stimuli using a paper and pen method similar to that described for the training sessions.

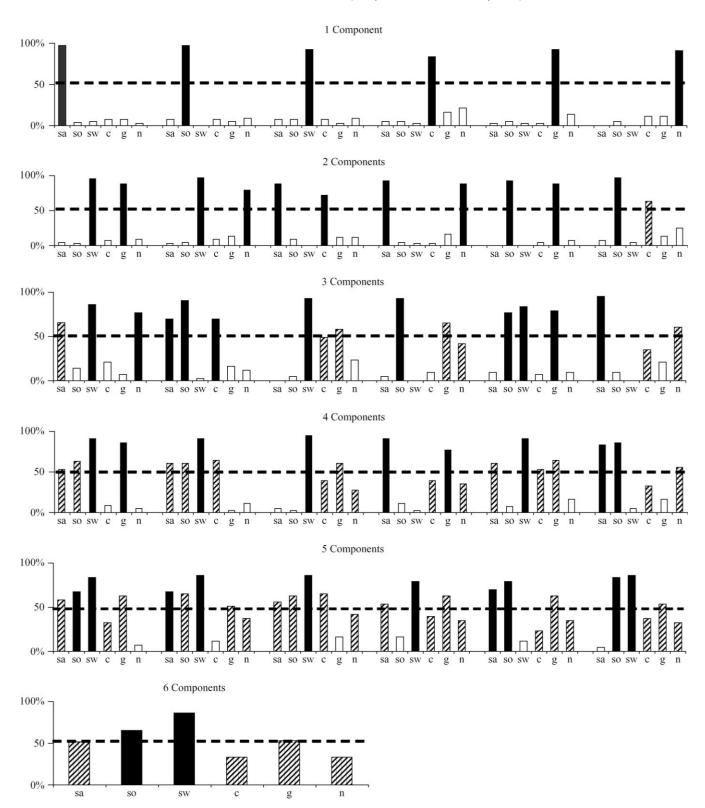


Figure 1 Identification of mixture components. The y-axis represents the percentage of subjects who identified a component, and the x-axis shows the names of the components. Filled bars represent above chance responses, hatched bars indicate a component was present but not identified above chance, and open bars indicate a component was not present in a particular mixture. The tastants are represented by sa, salty; so, sour; sw, sweet; the odorants are c, cinnamon; g, grassy; n, nail polish remover.

The 36 stimuli were presented in a different random sequence for each subject who was advised that each stimulus could contain between one and six components. In common with Laing et al. (2002), subjects were required to state whether each of the six components was present (yes) or absent (no) in each of the 36 single and mixture stimuli. This gave a total of 216 decisions for each subject. The six reference samples of the individual odorants and tastants were available at all times for a subject to refamiliarize himself/herself with a particular stimulus. There was no constraint on the number of times a subject could resample a test stimulus or on the time taken to assess a sample. During the training and test sessions, subjects cleansed their palate between each sample by sipping water, chewing a water cracker, and rinsing with water again.

Statistical analysis

A binomial test was used to determine whether a component was correctly identified above chance (50%, "yes/no") in the one- to five-component stimuli. For the six-component stimulus, the six replications were identical, the data were collapsed, and an identification score out of 6 derived for each component. A one-tailed t-test (Bonferroni corrected for familywise error) replaced the binomial test used with the one- to five-component stimuli. An additional oneway within-subjects ANOVA and post hoc paired comparison tests with Bonferroni corrections determined whether individual odors or tastes were identified more readily than others across all the stimuli, and a post hoc t-test was used to determine whether odorants as a group were identified better or worse than tastes across all 36 stimuli. Analyses were performed using SPSS version 11, with a criterion for statistical significance of P < 0.05 set for all tests.

Results

Figure 1 shows the levels of correct identification of components in the one- to six-component stimuli. A high level of identification of the single-component stimuli was achieved, with all being identified above the 90% level except cinnamon which was identified correctly on 84% of occasions. The binomial tests indicated that, in agreement with earlier studies (Murphy et al., 1977; Murphy and Cain, 1980), both components of the six two-component mixtures were identified above chance level except for cinnamon (63%) in a mixture with citric acid (P = 0.127). In contrast, only in two of the six three-component mixtures were all components identified. Thus, both odorants were not identified in the three mixtures where only one component, a tastant, was identified, whereas when a single odorant was present in a mixture with two tastants, it was identified. In addition, no odorant was identified less frequently than another, with each of the odorants being identified at chance level on two occasions and above chance once. As expected (Laing and Francis, 1989; Laing et al., 2002), with the four-component stimuli in no mixture were

all the components identified above chance. Thus, two components were identified in three of the mixtures and only one in the three others. When only one component was identified, it was always a tastant; where two components were identified, in two instances one was an odorant and in the other both were tastants. No odorant was identified above chance in any of the five-component mixtures. The maximum number of components identified was two which occurred on four occasions, with only one being identified in the other two mixtures. Similarly, no odorant was identified in the single six-component mixture, where only the sweet and sour tastants were identified above chance.

The poor performances of individual subjects shown in Figure 2 reinforce the findings from the group data of the limited capacity of humans to identify the components of the mixtures. The figure shows how many subjects successfully identified components with each of the six types of stimuli. Clearly, most subjects (31/43) correctly identified the single stimuli on all presentations; few made more than one error. However, only 10 subjects correctly identified the components of binary mixtures at every presentation, only four identified three components in ternary mixtures but only on four of the six trials, four and three subjects identified all the components in the four- and five-component mixtures on only two of the six trials, and only one subject correctly identified all six components on four of the six presentations. These results represent the responses of subjects who may also have selected other components incorrectly. When only absolutely correct responses were considered, that is, if two components were present and only these two were selected, the identification success fell dramatically.

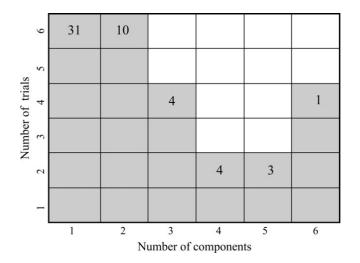


Figure 2 Identification of mixture components by individual subjects. Number of trials (*y*-axis) represents the number of presentations of a particular type of mixture, for example, the four-component mixture, with each presentation involving a different composition. The *x*-axis shows the number of components present in a stimulus. Numbers within the matrix indicate the number of subjects who correctly identified all the components present in a mixture, while the number of shaded boxes indicates the number of trials at which these particular subjects were successful.

Thus, no subject identified only the correct components in the three- to five-component mixtures at any of the six presentations. The maximum capacity of subjects in this study to analyze the mixtures into their components using the stricter criterion, therefore, was two.

The ANOVA indicated there was a significant difference between the identification scores for the six odor and taste components over all single- and multicomponent stimuli $(F_{5,210} = 40.285, P = 0.001)$. The most readily identified components in mixtures were the sweet (89.5%), sour (83.2%), and salt (78.3%) tastants (sweet-sour, $t_{42} = -2.71$, P =0.142), salt (sour-salt, $t_{42} = -2.15$, P = 0.551) (sweet-salt, $t_{42} = -4.803$, P = 0.001), followed by grass (72.2%) (salt– grass, $t_{42} = 2.53$, P = 0.015) and nail polish remover (63.1%) (grass–nail polish remover, $t_{42} = 4.14$, P = 0.001), and there was no difference between nail polish remover and cinnamon (60.9%) (nail polish remover–cinnamon, t_{42} = -0.78, P = 0.436). Further analysis indicated that across all stimuli, tastes (70.1%) were more frequently identified than odors (54.7%) ($t_{42} = -12.031$, P = 0.001).

Discussion

The main findings of the study were that 1) a maximum of only three components were identified in odor-taste mixtures which was reduced to two in mixtures containing four to six components, 2) only taste components were identified in the five- to six-component mixtures, and 3) taste appears to dominate smell as regards which components are identified in mixtures, particularly in complex mixtures.

The finding that a maximum of only three components in odor-taste mixtures could be identified is similar to the number identified in multicomponent odor mixtures (Laing and Francis, 1989; Laing and Glenmarec, 1992; Livermore and Laing, 1996) and taste mixtures (Kroeze, 1990; Laing et al., 2002). Several mechanisms have been proposed for the limited capacity of humans to analyze single-modality chemosensory mixtures, and these are likely to be relevant to the present findings. First, within each of the two modalities, suppression of a component may have occurred through competition for receptor sites in the olfactory epithelium or tongue or for odors through the well-established mechanism of lateral inhibition at the olfactory bulb or higher centers, with the higher intensity component generally being the suppressor (Laing et al., 1984; Bell et al., 1987). Examination of the present data provides some support for this intramodal mechanism. For example, in the threecomponent mixture of sweet and salt tastes and the nail polish remover odor, salt was suppressed, but it was not suppressed by the odorant in a binary mixture (Figure 1). This suggests that salt was suppressed by sweet in the three-component mixture. Similarly, the odors cinnamon and nail polish remover were perceived in binary mixtures with salt but not when all three were present in a threecomponent mixture. Suppression of cinnamon and nail polish

remover through intramodal suppression, therefore, appears to be the mechanism.

As regards the mechanism of intermodal suppression, it is unlikely that suppression of an odorant by a tastant or vice versa occurred because of receptor site competition: first, because at the concentrations used, the odors had no taste, and second, the tastants which are nonodorous could not reach the odor receptors in the nose. Intermodal suppression, if it occurred, may have proceeded via central mechanisms since the responses of bimodal neurons in the orbitofrontal cortex, for example, can be enhanced by a combination of an odor and a taste (Small et al., 2004). As yet, suppression of responses of these neurons by odor-taste mixtures has not been demonstrated when compared to unimodal stimulation. Whether intermodal interactions were the primary cause of identity loss in the present study cannot be resolved conclusively from the data. Only the binary mixture of sour taste and cinnamon odor in which the latter was suppressed provides a clear-cut example. Once three or more components are in a mixture, it becomes difficult to conclude the interactions have an intermodal basis.

The addition of just one more component to a binary mixture here was found to have substantive effects, with only two of the six three-component mixtures registering results that indicated all three components were identified (Figure 1). Increasing the number of components above three resulted in subjects having even greater difficulty in identifying components with only one or two being identified. Given the dramatic loss of information about the identity of components in mixtures with more than three components, another mechanism associated with the limited capacity of working memory which limits how much sensory information can be processed in a very short period of time (Baddeley, 1998) may become the critical determinant of successful identification. Evidence for this mechanism was provided in studies of the temporal processing of odors in the three-component mixtures (Laing et al., 1994; Jinks and Laing, 1999b) where loss of identity occurred when a critical difference in processing times of the three odorants was not exceeded. Similar temporal effects were observed with the three-component mixtures of tastants, although the outcomes were not as drastic as regards losing the identity of all components in ternary mixtures (Marshall et al., 2005). Although loss of identity of some tastants occurred in some mixtures, in others loss of order was not accompanied by loss of identity of any of the components. The results of the various temporal studies described above suggest that the greater the number of components a modality has to process and the more similar the processing times are for individual components, the greater the likelihood that identification of a component may not be achieved. The absence of knowledge of the location of olfactory and gustatory memory and how the mechanisms for processing of memory for odors could interfere with memory for tastes and vice versa does not allow any firm conclusion to be reached as regards

the role of working memory in the identification of components of odor—taste mixtures. Nevertheless, the dramatic loss of identity of components in mixtures containing three or more components, both here and in studies of odor mixtures and taste mixtures, suggests there is a critical cutoff point in the capacity of humans to analyze chemosensory mixtures which may be due to an overriding common factor. Working memory must surely be a strong candidate.

The failure of subjects to identify any of the odors in the five- and six-component mixtures was unexpected but could be related to the method of stimulation which involved both types of stimuli being presented via the mouth. For example, imaging studies have revealed that the simultaneous presentation of an odor via the orthonasal route and a taste via the mouth produced significant inhibition in cortical chemosensory areas (Small, 1997). In contrast, taste and orally delivered olfactory stimuli were reported to increase activation in cortical chemosensory areas (Voss et al., 2003). Unfortunately, neither study indicated whether subjects perceived one or both types of stimuli during inhibition or activation. Whether delivery of an odor via the mouth tends to activate centers containing bimodal neurons that are predominantly taste responsive is not known but could be the reason. Such neurons may be frequently activated in daily life by one of the four to five common tastes and their memory links reinforced to a much greater extent compared to the less frequent encounters with individual odors from the vast array of odor types that exist. Thus, for example, unlike sweet products one or more of which will be consumed each day, the odor of chocolate products, although highly liked, is not always experienced daily. Less commonly encountered odors but highly liked or disliked, such as mango or rotten egg, would be reinforced to an even lesser extent.

The latter explanation may be the underlying reason for the apparent domination of smell by taste in the present and earlier study (Laing et al., 2002). Examination of Figure 1 clearly shows that when two odorants were present in the threecomponent mixtures, on all three occasions, only the taste was identified. Similarly, in the four-component mixtures when three odors were present, the taste was always identified and at most only one odor was identified. The dominance of taste was overwhelmingly demonstrated in the five- and sixcomponent mixtures where with the former type of mixture no odor was identified above chance in stimuli containing three odors, and as mentioned above, no odor was identified in the latter type. Another factor which has the potential to influence the outcome of mixing odors and tastes and dominance of a modality is the congruency of the stimuli (Rozin, 1982). In the present study, the individual stimuli were not selected with this factor in mind, and as a result, there is little evidence in the data to suggest this was an issue in the study. Indeed, the incongruency of the mixture components appeared to assist the identification of components. For example, in binary mixture, identification of the odor and the taste occurred with five of the six pairs, success occurring with the incongruent pairs sweet–grass, sweet–nail polish remover, salt–cinnamon, salt–nail polish remover, and sour–grass.

Another possible reason for subjects having difficulty in identifying the individual components of mixtures is the formation or synthesis of new qualities. Loss of identity of tastants and odorants and the formation of new qualities, particularly in the more complex four- to six-component mixtures, could have occurred and not been detected since the psychophysical task did not require subjects to describe any of the qualities they perceived other than those of the six substances they had been advised could be present. Nevertheless, some analysis was possible in these more complex mixtures. With the four-component mixtures, either two tastants or a tastant and an odorant were identified by the group, while in the five- and six-component mixtures, at least one and sometimes two tastants were identified. A result that needs further investigation, which may provide an insight into the qualities that were present in these complex mixtures, is that although most components were not identified, those that were identified at chance or below chance levels were identified at levels which were almost always above those of components not in the mixture. Thus, a glance at Figure 1 shows that with mixtures containing more than two components, the hatched bars are clearly closer to the 50% chance line than the clear bars that represent components not in the particular mixtures. Subjects, therefore, seemed to be quite sure which components were not present but less so with many of the components that were present. The latter confusion could be evidence that not all the quality features of a component were lost, and at least some subjects were sufficiently convinced a component was present despite a full complement not being obvious. Data from a recent study of the qualities lost or retained during analysis of odor mixtures support this suggestion (Jinks and Laing, 2001).

In conclusion, the present study has shown that humans have great difficulty identifying the components of odortaste mixtures when more than two components are present. Several mechanisms are possible and several may contribute to the difficulty of the task. These include suppression via competition for receptor sites by components from within a modality, inhibition between the modalities at higher centers, temporal processing limitations and the low capacity of working memory, and changes to the major qualities of individual components. The finding that both components were usually identified with binary mixtures, but that there is a dramatic reduction in correct responses with more complex mixtures, suggests that as with single-modality chemosensory mixtures, the limited capacity of working memory may be the most significant factor affecting identification.

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References

- Baddeley, A. (1998) Working memory. C. R. Acad. Sci. Paris Life Sci., 321, 167-173.
- Baek, I., Linforth, R.S.T., Blake, A. and Taylor, A.J. (1999) Sensory perception is related to the rate of change of volatile concentration in-nose during eating of model gels. Chem. Senses, 24, 155-160.
- Bell, G.A., Laing, D.G. and Panhuber, H. (1987) Odour mixture suppression: evidence for a peripheral mechanism in human and rat. Brain Res., 426, 8-18.
- Dalton, P., Doolittle, N., Nagata, H. and Breslin, P.A.S. (2000) The merging of the senses: integration of subthreshold taste and smell. Nat. Neurosci., 3, 431-432.
- Frank, R.A. and Byram, J. (1988) Taste-smell interactions are tastant and odorant dependent. Chem. Senses, 13, 445-455.
- Jinks, A. and Laing, D.G. (1999a) A limit in the processing of components in odour mixtures. Perception, 28, 395-404.
- Jinks, A. and Laing, D.G. (1999b) Temporal processing reveals a mechanism for limiting the capacity of humans to analyze mixtures. Cogn. Brain Res., 8, 311-325.
- Jinks, A. and Laing, D.G. (2001) The analysis of odor mixtures by humans: evidence for a configurational process. Physiol. Behav., 72, 51-63.
- Kroeze, J.H.A. (1990) The perception of complex taste stimuli. In McBride, R.L. and MacFie, H.J.H. (eds), Psychological Basis of Sensory Evaluation. Elsevier Science, Essex, United Kingdom, pp. 41-68.
- Laing, D.G., Eddy, A., Francis, G.W. and Stephens, L. (1994) Evidence for the temporal coding of odor mixtures in humans. Brain Res., 651, 317–328.
- Laing, D.G. and Francis, G.W. (1989) The capacity of humans to identify odors in mixtures. Physiol. Behav., 46, 809-814.
- Laing, D.G. and Glenmarec, A. (1992) Selective attention and the perceptual analysis of odour mixtures. Physiol. Behav., 52, 1047–1053.

- Laing, D.G., Link, C., Jinks, A. and Hutchinson, I. (2002) The limited capacity of humans to identify the components of taste mixtures and taste-odor mixtures. Perception, 31, 617-635.
- Laing, D.G., Panhuber, H., Willcox, M.E. and Pittman, E.A. (1984) Quality and intensity of binary odor mixtures. Physiol. Behav., 33, 309-319.
- Livermore, B.A. and Laing, D.G. (1996) The influence of training and experience on the perception of multi-component mixtures. J. Exp. Psychol. Hum. Percept. Perform., 22, 267-277.
- Marshall, K., Laing, D.G., Jinks, A.L. and Hutchinson, I. (2005) Perception of temporal order and the identification of components in taste mixtures. Physiol. Behav., 83, 673-681.
- Murphy, C. and Cain, W.S. (1980) Taste and olfaction: independence vs interaction. Physiol. Behav., 24, 601-605.
- Murphy, C., Cain, W.S. and Bartoshuk, L.M. (1977) Mutual interaction of taste and olfaction. Sens. Process., 1, 204–211.
- **Rozin, P.** (1982) Taste-smell confusions and the duality of the olfactory sense. Percept. Psychophys., 31, 397–401.
- Small, D.M. (1997) Flavor processing: more than the sum of its parts. Neuroreport, 8, 3913-3917.
- Small, D.M., Voss, J., Mak, Y.E., Simmons, K.B. and Parrish, T.B. (2004) Experience- dependent neural integration of taste and smell in the human brain. J. Neurophysiol., 92, 1892–1903.
- Stevenson, R.J., Prescott, J. and Boakes, R.A. (1999) Confusing tastes and smells: how odours can influence the perception of sweet and sour tastes. Chem. Senses, 24, 627-635.
- Voss, J., Mak, E., Simmons, K., Parrish, T. and Small, D.M. (2003) Neural correlates of chemosensory integration in humans studied with fMRI. Chem. Senses, 28, 554.
- Wilkes, F., Laing, D.G., Jinks, A. and Hutchinson, I. (2003) The effect of learning modality on the retronasal identification of odors in odor-taste mixtures. In 25th Annual Meeting of the Association for Chemosensory Science, Sarasota, FL.

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