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Flavor Processing: Perceptual and Cognitive Factors in Multi-modal Integration

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The chemical senses may represent the most fundamental integrative sensory modalities. For example, flavor perception is widely considered to be an integrative process whereby two distinct neural systems (olfactory and gustatory) are activated peripherally to give rise to a unitary oral sensation of flavor. Benefits of multimodal sensory integration in other modalities include increased sensitivity and reaction times (Krushel and van der Kooy, 1988; Fowler and Dekle, 1991; Schifferstein and Verlegh, 1995). Investigations into the integration of multisensory information at a neural level in cats and primates have revealed that neurons of the superior colliculus are capable of integrating cues from three sensory modalities: vision, audition and somatosensation (Rolls and Baylis, 1994; Schul *et al.*, 1996; Whalen, 1998). The close relationship between smell and taste along with the evidence of the existence of neurons particularly sensitive to multimodal inputs, led us to hypothesize that neural inputs for odor and taste can be integrative and exhibit perceptual additivity at subthreshold intensities such as that seen previously only with mixtures within a single modality.

In the studies presented here, we evaluated the summation of odor and taste mixtures where each of the individual components were presented at sub-threshold levels. In the first study, multiple olfactory thresholds were measured within a group of 10 volunteers (five males and five females, ranging in age from 22 to 33 years) while holding an oral stimulus in the mouth (Dalton *et al.*, 2000).

One each day of testing, nasal detection thresholds for benzaldehyde and oral detection thresholds for saccharin were measured in counter-balanced order. A modified staircase method was employed for collecting detection thresholds using a five-reversal criterion. Subjects were given a 15 min break before a second nasal detection threshold for benzaldehyde was measured while holding a saccharin solution in the mouth. As single thresholds always preceded mixtures, a control procedure was incorporated where subjects were tested for single benzaldehyde thresholds followed by another single benzaldehyde threshold without taste stimuli.

While holding the oral saccharin solution, sensitivity to benzaldehyde increased by an average of 28% over benzaldehyde threshold taken alone. This increase in sensitivity was significant ($P = 0.01$) with 9 of 10 subjects showing marked differences between benzaldehyde thresholds alone and in the cross-modal mixture. The incorporation of the control trials ruled out any effect of repeated testing since these trials resulted in a nonsignificant ($P = 0.71$) decrease in sensitivity.

The effect did not appear to be due to concomitant somatosensory input from an oral stimulus or differences in breathing or airflow, as a second experiment found that filtered deionized water did not lower the threshold for benzaldehyde. However, there did appear to be an effect of stimulus congruency: when benzaldehyde was paired with an incongruent taste stimulus (L-glutamic acid monosodium salt or MSG) in the same protocol, thresholds for benzaldehyde were not significantly lower in the presence of MSG than when tested alone ($P = 0.57$).

The specificity of the benzaldehyde–saccharin pairing in enhancing sensitivity to benzaldehyde suggested that this phenomenon may not be evidence of a general integration of taste and olfaction but rather an interaction that may be specific to combinations of stimuli previously encountered. Accordingly, we evaluated the degree to which this integration was a product of prior experience by having eight new volunteers learn novel pairings of taste and smell stimuli (Belanger *et al.*, 2002). Flavorless gum base was infused with four incongruent flavor combinations: (i) phenylethyl alcohol (PEA) and citric acid, (ii) PEA and quinine, (iii) L-carvone and citric acid, or (iv) L-carvone and quinine (see Table 1). Each individual was given 3 weeks of daily exposure to one of the PEA or L-carvone gum flavor combinations while the other served as their control. At the beginning and end of this period, thresholds for the odor and taste were measured singly and in combination. After a 2 week break the procedure was repeated for each subject with the other odor–taste combination, such that each individual was exposed to only one of the PEA and L-carvone combinations. Assignment of flavor combination to exposure condition (learned versus novel) was counterbalanced across subjects. As predicted, sensitivity to the odorant (PEA or L-carvone) increased significantly more ($P = 0.0025$) when tested in combination with its exposure taste pairing ($M = 2.73$, SEM = 0.51) than when tested in combination with its control taste pairing ($M = 0.66$, SEM = 0.37).

Additive response to combinations of sensory stimuli have been demonstrated within and across many sensory modalities (Fowler and Dekle, 1991; Wallace *et al.*, 1996). For within-modality stimulation these summations are reminiscent of proximal or temporal additivity where the two stimuli are closely aligned in time or space and result in activation of a common perceptual channel. However, crossmodal summation should require the existence of a central point of integration sensitive to input from multiple perceptual channels. The work presented here presents evidence for such an integrative process and the forced-choice detection procedure

Table 1 Assignment of groups ($n = 4$/gp) to flavor learning condition

Flavor combos	Condition I		Condition II	
	PEA + quinine	L-carvone + quinine	PEA + citric acid	L-carvone + citric acid
Group 1	Exposure	Control	Exposure	Control
Group 2	Control	Exposure	Control	Exposure

Assignment to condition in the first or second phase was also counter-balanced across individuals within each group.

employed provides a control for attentional focus. The results provide additional support for, first, the functional significance of neural responses to combinations of odor and taste stimuli (Rolls and Baylis, 1994) and, second, the existence of central loci where neural inputs conveying olfactory and taste information from our everyday chemosensory experience are integrated, in essence, a 'flavor' substrate (Schul *et al.*, 1996). Integration appears to enhance the detectability of weak chemosensory signals and may yield novel sensations from the combined activation of sensory modalities receptive to chemical stimulation.

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