

Review Article

Tracking traumatic head injuries with the chemical senses

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Abstract Chemosensory disorders, primarily olfactory, have diagnostic significance for prevalent human illnesses, but the multitude of smells makes measuring function appear daunting. The olfactory system operates under dynamic natural sensing conditions in which many individual odor chemicals are waxing and waning. Yet, in experimentally controlled simulations, mixture-component selective adaptation shows individual or shared prominent characteristic odors are detected but molecular stimulus features are not. As in other biological signaling systems, including taste, odors activate dedicated receptors (OR). Given rapid OR adaptation with the passage of time, individual odor recognition is momentary. Receptive dendrites of the nearly 400 genetically variable human-OR in the olfactory epithelium critically project axons to the olfactory bulb through perforations in the cribriform plate of the skull. Analytic chemical-quality codes detect single odor-mixture components. However, identities of no more than 3 or 4 most salient odors are perceived due to central mixture-suppression, the mutual inhibition among diverse olfactory-bulb or cortical neurons. The componental codes allow olfaction to readily discern odor quality and valence of a wide range of unrelated chemicals, a few at a time. Head trauma may result in a partial or complete loss of smell and facial trauma a loss of taste-nerve function. Testing smell could plot the course of recovery from chronic traumatic encephalopathies that prevail in contact sports. Measuring brain function with olfaction would provide simpler and more direct monitoring of prognosis than biochemical sensors.

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Introduction

Chemosensory disorders have diagnostic significance for prevalent human illnesses. Primarily olfactory, they are frequently considered gustatory due to the oral retro-nasal origin of some odorous volatiles.¹ However, the multitude of possible smells, recently exaggerated from thousands to more than a trillion,² makes measuring individual odor sensing appear daunting.^{3,4} Furthermore, this conundrum has led to attempts to segregate roles of relevant functional groups,⁵ or use of crowd-sourcing methods,⁶ to count the number of recognizable multi-component odor objects that an individual can recognize.⁷

Odor component recognition

As in other biological chemical signaling systems, including taste-sensing^{8–10}; distinct odors likely activate dedicated receptors (OR).^{11,12} However, given the rapid odor adaptation with the passage of time, odor recognition is momentary.⁴ The ortho-nasal odor-stimulus is limited to the inhalation phase by the act of sniffing,¹³ and on the same time scale as sniffing, the odor rapidly adapts. To further complicate the stimulus situation, odor sensing occurs in dynamic natural sensing settings in which odors of many individual odor chemicals are simultaneously either waxing or waning. The olfactory system needs to be able to identify chemicals of harm or value under these conditions. Surprisingly, this may be accomplished by a combination of 'mixture suppression and selective adaptation.'

In experimentally controlled simulations, mixture-component selective adaptation shows individual or shared prominent characteristic odors ('odor notes') are detected by humans.⁴ However, individual molecular stimulus features are not. The perceptual saliencies of two individually presented components, A and B 'odor notes', are represented by bright colors in Fig. 1. The saliencies are reduced when both components are within a mixture (below), the feature known as 'mixture suppression' in olfaction,^{14–16} and taste.¹⁷ However, when component A alone is adapted for 10 s (center), its ambient salience in

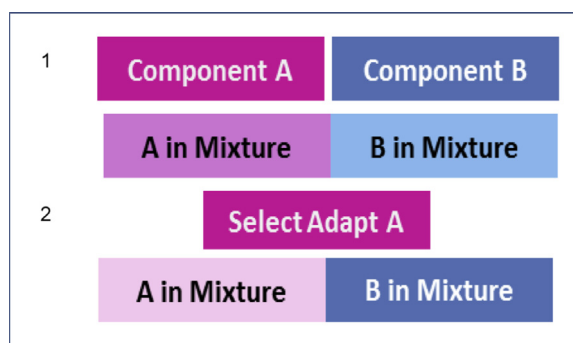


Fig. 1 (1) Mixture-component suppression is influenced by (2) selectively adapting a component odor. Odor intensity (color saturation) of a binary mixture component (rectangle) is either lowered (ambient A) or heightened (extra B) by 10-sec selective adaptation. Components may either be individual 'odor notes' or 'odor objects' having several notes.⁴

the following mixture (below) is further weakened but unadapted component B is 'released' from mixture inhibition. This startling outcome resulting by combining 'mixture suppression' and 'selective adaptation' of independent stimuli (defined as those that do not cross-adapt) explains how the olfactory system is able to identify individual mixture components in few-component mixtures.^{3,18,4} Thus, the odor mixtures are analyzed; they are not synthesized by a combinatorial process into a distinctly different quality. Gustatory mixtures of independent taste stimuli are also analyzed via the combination of 'mixture suppression' and 'selective adaptation'.¹⁹

An easy way to demonstrate selective adaptation is to use pieces of two kinds of chewing gum with independent odors (for example, juicy fruit and spearmint (@Wrigley's)). Three jars are set up with two having one or the other gum, and the third having both. Sniff for 10 s with a 10-sec inter-trial interval sniffing air. Test each type alone and mixed together. Then, test the mixture immediately after sniffing one kind of gum for 10 s. Repeat with the other kind. An efficient 'candy test' that uses retro-nasal smell,²⁰ has been described earlier.²¹

Limits to odor component detection

Although odor mixtures can have many more than a few components, identities of no more than 3 or 4 of the most salient odors are perceived simultaneously.^{16,22,23} The biological basis for this limitation resides in the olfactory pathway: (1) 400 human OR with dedicated olfactory sensory neurons (OSN) in the nasal epithelium, (2) inhibitory neuropil in the olfactory bulb, and (3) a predominantly inhibitory olfactory cortex.²¹ An odor stimulus activates OR located on OSN 'cilia' which excite neural action potentials in OSN axons. The axons must travel to the olfactory bulb on the under surface of the brain through perforations in the cribriform plate of the ethmoid bone of the skull, a site of OR vulnerability to head trauma shearing effects.²⁴ Bulbar glomeruli each process specific input from the many OSN carrying one OR type.^{5,12,25,26} When activated simultaneously, glomerular inhibitory interneurons dedicated to different OR types shut each other down,^{27–32} thus limiting the excitatory lateral olfactory tract input to the olfactory cortex to the most activated. Feedback inhibition from the cortex descends to the bulb.^{33–35} Consequently, although componental odor codes readily discern odor quality of a wide range of unrelated chemicals, only a few are perceived at one time in a mixture.

Head trauma and olfaction

Head trauma may result in partial or complete loss of smell,^{36,37} whereas, facial trauma may also reduce taste-nerve function.^{24,38} Post-traumatic smell loss is associated with structural damage to olfactory bulbs and tracts.³⁹

Testing smell could plot the course of recovery from chronic traumatic encephalopathies (CTE) that prevail in contact sports.^{39,40} The measuring of brain function with olfaction, an early indication of neurodegeneration, would provide simpler and more direct CTE monitoring of prognosis than biochemical sensors,⁴¹ and mouse models,⁴² that

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