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Odor Perception is Dynamic: Consequences for Interpretation of Odor Maps

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Introduction

The concept of odor maps in the olfactory system can imply a precise one-to-one mapping between the physicochemical stimulus, the central sensory representation of that stimulus, and the olfactory perception. However, in humans and animals, experience plays a major role in qualitative perception of odors. This suggests that either odor maps and coding in the olfactory bulb (OB) are highly dynamic and/or that odor perception is more closely linked to olfactory cortical ensemble processing where precise maps of odorant physicochemical features are less evident.

Hypothesis

Based on recent work in our laboratory comparing odor coding in the OB and piriform cortex (PCx), and neuroanatomical, computational and theoretical work from a number of other laboratories (e.g. Haberly, 2001), we hypothesize that most animals have dual olfactory systems within the main olfactory pathway. One system consists of a physicochemically driven, labeled-line system under strong evolutionary control and most generally used for perception of evolutionarily stable, adaptive stimuli such as pheromones, predator or host odors. In the labeled-line system, knowing what physicochemical stimulus is present and/or what specific central circuits (maps) are activated provides strong predictive power for determining the olfactory percept (maternal nipple, predator, etc.). While this system allows for accurate identification of specific odorants and reliable, rapid responses, it is necessarily limited in its tuning breadth to evolutionarily stable stimuli with predictable meanings.

The second olfactory system is a synthetic, memory-based system that rapidly learns to form perceptual odor objects from novel patterns of input. This system permits perceptual grouping of the complex, feature-rich input extracted by the highly analytical receptor sheet into discrete odor objects, distinct from other patterns of input and distinct from background. Most odors experienced by animals are complex mixtures of molecules, which themselves are composed of multiple submolecular features. Furthermore, very different odors can have extensively overlapping features, and it is generally the case that odors are experienced against an odorous background. The task of the memory-based olfactory system, then, is to learn which features should be grouped (associated) together to form a perceptual object. Once this associative learning has occurred and perceptual odor objects are formed, discrimination, recognition and figure-ground separation of those objects from other objects and background are enhanced. While the spatial similarity of central maps may place constraints on perceptual grouping and formation of distinct odor objects, knowledge of the physicochemical features or OB maps evoked by those features alone is insufficient to predict the ultimate olfactory percept. The strength of this system is that novel stimuli of varying complexity can come to acquire a unitary percept, vastly extending the tuning range of the olfactory system. It is this system that provides us with the unitary olfactory percept (odor object) of 'coffee', despite the fact that this odor is composed of hundreds of components.

Experience can shape odor coding in at least two ways. First, the encoding of odorant features may change with experience, such that familiar features are more precisely or fully encoded. We believe that OB circuits encode and enhance representation of odorant features, and thus predict that mitral cell encoding of familiar features will be modified compared to novel features. The second way that experience can shape odor coding is through synthesis of co-occurring features into odor objects. Simple convergence and coincidence detection of co-occurring features by cortical neurons is not sufficient to account for the complex nature of synthetic odor perception. Rather, we hypothesize that piriform cortical circuits learn which odorant features co-occur and, through associative synaptic plasticity, store a representation of that feature combination. Once this representation is stored it is more easily recognized from other, similar patterns of input and is robust in the face of partial degradation. This combination of characteristics makes familiar odor objects more distinct from other stimuli and also results in a break from strict reliance on OB maps of odorant features for a complete olfactory percept. The anatomy of the PCx, and the hypothesized reliance of the learning process on broadly projecting intracortical association fibers make it likely that odor object percepts are ultimately encoded by distributed ensembles of cortical neurons, without a precise organization or map of odor objects. This is similar to representation of visual objects in the inferotemporal cortex.

Supporting evidence

Under the conditions of a memory-based olfactory system, perceptual quality of physicochemical stimuli may not be constant but rather could be shaped by experience. Experience-induced enhancement of odor acuity (perceptual learning) and modification of perceptual quality have been demonstrated in both humans and rats. In rats, discrimination of molecularly similar odorants is enhanced by prior associative conditioning (Fletcher and Wilson, 2002). Importantly, blockade of cholinergic muscarinic receptors during the training prevents perceptual learning. As described below, acetylcholine modulates synaptic plasticity in the OB and PCx which provide a clue as to the underlying mechanisms of olfactory perceptual learning.

Associated with the experience-induced changes in behavioral perception are changes in both OB and PCx odorant response patterns. Associative conditioning modifies mitral cell responses to the learned odor, particularly cells near 2-deoxyglucose identified activated glomeruli (Wilson *et al.*, 1987). Furthermore, experience can shift mitral cell odorant receptive fields towards familiar odorants (Fletcher and Wilson, 2003). A shift such as this could increase the number of cells encoding familiar odorants, potentially increasing precision of encoding and acuity—similar to receptive field shifts in other sensory systems. It is hypothesized that mitral cell odorant receptive fields reflect both primary afferent input from a homogenous receptor population as well as lateral and feedback inhibitory circuitry particularly effective at modulating responses on the edge of the receptive field. Experience may modify these inhibi-

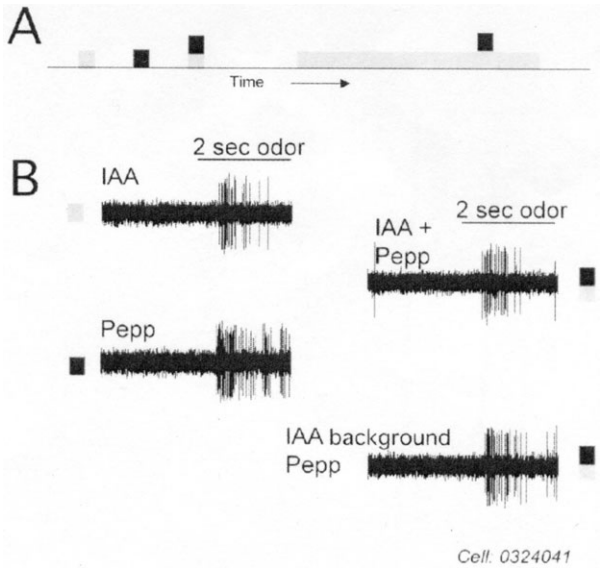

Figure 1 The PCx response to an odor is not determined solely by the physicochemical stimulus. **(A)** A schematic representation of the experimental design. Responses of single-units in the anterior PCx were determined for 2 s odorant stimuli both delivered alone (IAA = isoamyl acetate and Pepp = peppermint) and as binary mixtures. One of the odorants was then chosen to be the background and presented for 40 s before the 2 s binary mixture was again presented. The physicochemical stimuli during both IAA+Pepp and IAA background+Pepp are identical, yet the response of this cell and a significant subset of piriform neurons, is substantially different in the two conditions; the response to the latter being more similar to Pepp alone (M. Kadohisa and, D.A. Wilson, submitted for publication). See text for additional explanation.

tory circuits to allow limited experience-induced shifts in receptive fields towards familiar or meaningful odorant features.

The odorant features extracted and refined by receptors and OB circuitry converge on neurons in the anterior PCx to start the process of odor object synthesis (Zou *et al.*, 2001). However, simple anatomical convergence and coincidence detection do not appear sufficient to account for the enhanced odor discrimination ability of cortical neurons compared to their mitral cell afferents. Rather, the unique combination of multiple features within a complex odor appear to be learned by cortical circuits, such that after sufficient exposure, odor mixtures are treated as distinct from their components by cortical neurons, but not by mitral cells. With insufficient durations of exposure (Wilson, 2003) or with blockade of cortical muscarinic receptors (Wilson, 2001), piriform cortical neurons are no better at odor discrimination than mitral cells. Recall that muscarinic receptor activation is also required for behavioral odor perceptual learning. These results are consistent with the hypothesis that co-occurring odorant features are synthesized by cortical circuits into odor objects distinct from their components.

A hypothesized consequence of odor object synthesis and enhanced discriminability is recognition of odors against background. One characteristic of the PCx is rapid adaptation to repeated or prolonged stimuli (Wilson, 1998) which is mediated by pre-synaptic depression of mitral cell glutamate release (Best and Wilson, 2004). Prevention of this synaptic depression prevents cortical adaptation to odors, suggesting that adaptation to background odors is mediated centrally and not at the receptor or OB (Best and Wilson, 2004). As shown in Figure 1, the combination of rapid adaptation and excellent odor discrimination in the PCx may allow for figure-ground separation (M. Kadohisa and, D.A. Wilson, submitted for publication).

Summary

These results suggest that in order to understand odor coding, OB spatial maps are only the beginning. It is critical to understand how those maps are read, and how odorant features represented by those maps are synthesized into unique perceptual objects by cortical circuits. As shown here, both feature coding and feature synthesis are experience-dependent. The combination of hundreds of different olfactory receptors recognizing different odorant features and a memory-based central olfactory system allows perception and recognition of a nearly limitless variety of distinct odor objects.

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