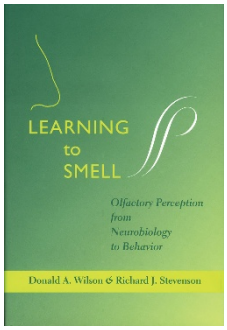
How the nose knows what it knows



Learning to Smell—Olfactory Perception from Neurobiology to Behavior

By Donald A Wilson and Richard J Stevenson

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Reviewed by Rehan M Khan and Noam Sobel

How can cartoonists use only a few lines and shades to depict a house or a car? They take advantage of the fact that our visual system encodes not lines or shades but visual objects, so that even a very impoverished rendition can still evoke the whole object. The first major theme in *Learning to Smell* is that, similarly, the olfactory system has not evolved to encode individual molecular features (as some researchers may contend), but rather to encode odor objects. Just as the cartoonist's sketch is perceived as an object, so too coffee is perceived as coffee, and not as the 800 or so different molecules that comprise it.

How does the olfactory system generate this odor-object percept? The receptor surface (epithelium) consists of hundreds of different types of receptors, each tuned to respond differentially to different types of molecules. Same-type receptors converge to common locations, termed glomeruli, on the surface of the olfactory bulb, where a spatiotemporal pattern of response is evident for each odor. The olfactory bulb projects to olfactory cortex, but how much of the bulbar spatiotemporal pattern is retained there remains unclear. With this organization in mind, olfaction research has been dominated by the 'bottom-up' or 'hardwired' approach. The extreme version of this approach holds that nothing but the identity of the activated receptors determines the olfactory percept.

In contrast to this view, the second major theme of the book is that olfactory percepts are not hardwired, but are largely plastic and depend on learning to constantly build and update representations of the olfactory world. For example, previous experience with an odor can change its hedonic representation, even though the repertoire of activated receptors presumably remains the same. Furthermore, the olfactory representation is highly susceptible to top-down influences. For example, the color of an odorant can significantly influence the identity of its perceived odor, as well as its hedonic tone. Finally, echoing the cartoonist's sketch, even a degraded portion of an odor, when encountered in the appropriate context, will be perceived as the complete odor, even though some of the odorant molecules normally present during that percept are absent or altered. The authors argue that to understand the olfactory system, it is insufficient to understand only the binding affinities and operation of the olfactory receptors or even olfactory wiring. Ivnstead, we must make a large and central allowance for the mechanisms of learning through experience.

These two themes—of object-based perception and of the primacy of experience and learning in sensory perception—may seem trivial to students of perception, but they have been sorely overlooked in the field of olfaction. In *Learning to Smell*, a psychologist (Stevenson) and a neurobiologist (Wilson) have joined forces to advocate a redirection in olfaction research, urging the field to seriously consider the importance of these influences in the formation of olfactory percepts. In this respect, this book is both timely and important.

Although Wilson and Stevenson argue their case forcefully and with much evidence, we think the authors have underemphasized some aspects of olfaction that cannot be adequately explained by experience alone. Whereas olfaction is inarguably object-based and learned, some olfactory objects are innate. A common example of innate chemical sensing, as Wilson and Stevenson acknowledge, is that of pheromonal communication. Many animals use conserved chemical signals to communicate information ranging from social status to reproductive state. As some of these signals are acted on by neonates, their perceptual meaning is assumed to be innate. Similarly, rodents display a fear response when presented with particular predator odors, but not other unfamiliar or noxious odors. This response remains strong despite generations of laboratory breeding with no exposure to predators. Although Wilson and Stevenson mention such data, it has only limited influence on their conclusions.

Furthermore, the authors' emphasis on learning may downplay the role of evolution in shaping olfactory perception. Sensory systems have evolved to encode objects in a world that is partly changing and partly constant. For example, in vision, photoreceptors exploit photon wavelength, which maps to the perception of color. Similarly, in audition, the arrangement of the sensory receptors and the shape of the cochlea reflect sound frequency, which is mapped onto perceived pitch. It is not unreasonable, therefore, to suppose that the olfactory system may reflect fundamental regularities within molecules themselves. Although a lawful mapping of odorant physicochemical structure to olfactory perception has yet to be identified, we think it is premature to conclude that it cannot exist.

These issues notwithstanding, *Learning to Smell* is an important contribution that deserves to be widely read. It is one of few attempts to generate a comprehensive perception-based framework for probing olfactory physiology. In this respect, it is a landmark that may reshape efforts in this field. In addition, it is also accessible to readers new to the field of olfaction. We strongly recommend it. ■

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