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Author
Cometto-Muniz, J. Enrique

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J. Enrique Cometto-Muñiz*

Chemosensory Perception Laboratory, Department of Surgery
(Otolaryngology), University of California, San Diego, CA, USA

* Correspondence to Dr. J. Enrique Cometto-Muñiz at: **ecometto@ucsd.edu**

Olfactory stimulus

In order for us to perceive something, there must be a source that triggers our perception. That source is called a stimulus. A stimulus is composed of some kind of energy that our senses are tuned to detect. For example, the visual system can detect electromagnetic energy, that is, light, and the auditory system can detect vibrational energy, that is, sounds. In turn, the sense of smell, called olfaction, is tuned to detect chemical energy stored in some particular compounds called odorants. The odorants constitute the olfactory stimuli.

Units of change of the olfactory stimulus

The discovery of the gene family of olfactory receptors in 1991 led to an accelerated and much better understanding of the olfactory sense. Among other issues, this progress clarified: a) the series of molecular events that take place within olfactory sensory neurons after the odorants bind to the olfactory receptors, and b) the organization of the anatomical connections through which the information is transmitted from the periphery to the olfactory bulb and higher levels of the olfactory system to produce an odor perception. The data supported the notion that, typically, each olfactory neuron uses one particular type of receptors, and each receptor type responds to more than one odorant. This lead to the conclusion that even a single kind of odorant molecule produces a neural message composed of the combined output (pattern) of many receptors with overlapping odorant specificity.

Despite these advances, little is known about the details of the interaction between an odorant and its receptors, or about the specific structure or molecular properties that make an odorant a strong olfactory stimulus, i.e., one with a low odor detection threshold, or a weak olfactory stimulus, i.e., one with a high odor detection threshold. For humans, and for terrestrial animals in general, odorants need to have, first of all, enough volatility to reach the olfactory receptors in the nose, since they enter as vapors carried by the air breathed. As discussed below, sniffing, the act of increasing the airflow through the nasal passages, is an important component of the olfactory process.

A problem encountered in trying to establish structure-activity relationships between odorants and olfactory outcomes such as odor detection thresholds, odor discrimination, and odor quality, is the lack of understanding of the “unit(s) of chemical change” that underlies the olfactory response. In olfaction, we lack the equivalent of the wavelength range of light in vision, or the vibrational range of sounds in hearing. One strategy employed to ameliorate this deficiency has been to test the olfactory outcome (e.g., threshold, discrimination, etc.) across homologous series of chemicals and across chemical functionalities. In this way, the number of carbon atoms in the chain, in the first approach, and the particular chemical functional group (e.g., alcohol, ester, ketone, etc.), in the second approach, become a parameter that partially reflects units of chemical change.

Studies of structure-activity relationships in olfaction have been more successful when limited to a particular type of odor, i.e., ambergris or musk, than when attempting to provide an explanation across the broad spectrum of odor qualities. There are odorants that despite having very different chemical structures still possess similar odors. For example, hydrogen cyanide and benzaldehyde are radically different molecules but they both smell like almonds to humans. Conversely, there are odorants very similar in structure but that evoke dissimilar odors. For example, D-carvone and L-carvone are practically identical molecules except that they cannot be superimposed since they are mirror images of each other (called enantiomers in chemistry). (To illustrate, the effect is similar to the way in which the left and right hands are also mirror images of each other and cannot be superimposed.) Still, D-carvone smells like peppermint and L-carvone smells like caraway, two similar but discriminable odors to humans. The bases for these contrasting effects regarding chemical structure similarity and odor quality are not completely understood.

Other investigations have focused on describing the physicochemical basis for odor detection, that is, odorant potency measured as thresholds, rather than for odor quality. This seems a productive initial approach since detection entails a simpler neural phenomenon than identification and probably rests on simpler general principles. In any case, whatever structure-odor relationships are deduced, there always seem to be exceptions. It is quite likely that the study and understanding of such exceptions will lead to a better knowledge of the topic.

Managing the olfactory stimulus

The lack of standardized equipment to handle the olfactory stimulus (i.e., the odorant vapor) and its inherent nature make its generation, control, delivery, and quantification more problematic than, for example, the visual stimulus, i.e., light, or the auditory stimulus, i.e., sound. The techniques used to handle and measure olfactory stimuli are called olfactometry, and the devices employed are called olfactometers. Some olfactory studies resort to nominal or indirect quantification of odorant vapors. For example, they might only measure the concentration of the liquid phase containing the odorant, but not that of the vapor phase that constitutes the actual stimulus. Thus, the vapor is either not quantified, or its concentration is theoretically calculated from values of vapor pressure that can vary widely among data sources, and that might be themselves the result of calculations. In other cases, quantification of the odorants take the form of percentages of dilution with air from a source that is assumed to have a certain concentration (e.g., vapor saturation at room temperature: ≈23°C), but that it is not experimentally measured, for example, by gas chromatography. Although the nature and scope of some investigations might not require an absolute and stringent chemical quantification of the odorant(s), progress in understanding many aspects of olfactory function rest on an accurate experimental measurement of the actual olfactory stimulus, i.e., the concentration of the odorant vapor. Although the human nose is often more sensitive and sophisticated than many apparatus for chemical measurement, the application of existing and emerging powerful chemical-analytical instruments to the management of the olfactory stimulus needs to be more common and widespread.

Very importantly, to achieve optimum olfactometric measurements, the quantification of the olfactory stimulus needs to be complemented with an appropriate availability of the stimulus to the tested subjects. It has been reported that an ‘average’ human sniff has an inhalation rate of 30 l/min, a volume of 200 ml, and a duration of 0.4 sec. If the olfactometer and technique employed for stimulus delivery does not meet the input required by the subject, the measurements obtained might not have full ecological relevance.

Complexity of the olfactory stimulus

Many studies of the sense of smell use a single type of odorant molecules as olfactory stimuli. The variability in structure and chemical functionality of individual odorants is enormous. Many odorants could be classified as volatile organic compounds but quite a few of them are semi-volatile (the border between volatile and semi-volatile is lax and fuzzy), and still others are small inorganic molecules, e.g., ammonia, hydrogen sulfide. Some investigations have used mixtures of two or more odorants to address the important issue of how olfaction process mixtures of odorants. In environmentally realistic situations, the olfactory stimulus is composed of dozens or even hundreds of individual odorants that are often perceived as a unity, for example the odor of coffee, chocolate, soap, tobacco, rubber, etc.

The rules of how mixtures of odorants are perceived as regards to odor detection, odor discrimination, and odor quality have not been clarified yet. Nevertheless some general principles have been suggested. At low levels of detection, individual odorants tend to add their individual detectabilities to generate the overall detection of the mixture to a larger degree than what they do at higher levels of individual detectability. Regarding odor discrimination, a number of studies found that humans could identify a maximum of 4 individual components in odor mixtures. This result did not seem to be altered with the training and experience of the subjects, the type of odorants mixed (i.e., good or bad “blenders”), or whether the individual “odors” where single chemicals or complex mixtures (e.g., cheese, honey). Regarding odor quality, mixtures of odorants can be perceived as different from the individual components or, in other cases, the components can retain their individual quality when mixed. Between these two extremes, a whole array of intermediate outcomes is also possible. Although the rules for the production of a particular result are not completely understood, the outcome has been shown to depend on chemical and perceptual similarity among components, on their relative concentration in the mixture, and on olfactory receptor overlap.

The sniff and the olfactory stimulus

Studies on the effect of sniff parameters on various olfactory outcomes indicated that the sniff plays an important role in odor detection, intensity, and identification. The parameters include sniff flowrate, volume, duration, interval, and number. The issue is important for olfactometry since any effort to standardize odorant delivery should make sure that instruments and methods provide the appropriate conditions for the particular olfactory task in the specific experimental context. Not surprisingly, natural sniffing produces optimum odor perception. It has been suggested that: a) sniffing influences olfactory neural activity in the olfactory bulb and cortex, b) there is a temporal synchrony between sniffing and the actual odorant-induced neural activity along various levels of the olfactory pathway, and c) there is a dedicated olfactomotor system, although little is known about the neural mechanisms that control it.

The importance of sniffing in olfaction rests in that the sniff determines the spatial and temporal distribution of the olfactory stimulus over the olfactory epithelium. Reciprocally, the olfactory stimulus has also been shown to alter sniffing behavior. For example, malodors produce a reflex-like reduction in sniffing, and stronger intensities of an odor induce lesser-volume sniffs. Within limits, odorant detection increases with sniff flowrate but does not change with sniff volume as long as a minimum 200 ml is sniffed. It has been suggested that the perceived intensity of a fixed odorant concentration remains constant despite varying sniff flowrate because the olfactory system produces a "correction" that accounts for perceived effort during the sniff. This model, however, might not generalize to all odorants or conditions.

Sniff flowrate can influence odor quality since, as odorant vapors travel above the olfactory mucosa, their deposition pattern will differ according to their tendency to dissolve, or sorb, in the mucosa. Low-sorption odorants will distribute uniformly across the mucosa at low rates, but unevenly (accumulating posteriorly) at high rates. In contrast, high-sorption odorants will distribute unevenly (accumulating anteriorly) at low rates, but uniformly at high rates.

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See also: Olfaction; Olfaction: Physiology; Olfactometry; Olfactory receptors and transduction; Olfactory cognition; Olfactory adaptation.

J. Enrique Cometto-Muñiz

Suggested further readings

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