Chapter Eight

ODOR PERCEPTION AND THE VARIABILITY IN NATURAL ODOR SCENES

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INTRODUCTION

Naturally occurring olfactory stimuli, such as floral perfumes or animal pheromones, are typically complex combinations of many chemical compounds.[1-3] Odor compounds emitted by a single odor source may have diverse chemical structures,[4] and each compound present may differ quantitatively from the others by several orders of magnitude in concentration. [1,5] Odors also vary spatially and temporally as a function of the turbulent nature of the air medium into which they disperse.[6,7] Most animals use odor signaling for several functions that are important to their fitness, including: attracting mates, identifying kin, finding food, and avoiding predators. Because many odors are ecologically important stimuli, the olfactory system must solve the problem of identifying odor stimuli and discriminating them from other odors, even when they vary significantly in concentration and precise composition from one odor-producing object to the next. How the olfactory system produces a reliable representation of odors is not yet entirely known.[2]

This review draws on other areas of sensory science to suggest how one might quantify the statistical structure of naturally occurring olfactory stimuli. We identify likely sources of variation in ecologically valid olfactory scenes, and we discuss how this variation might influence the way in which animals recognize and discriminate among salient odors. We focus mainly on odor signals that are learned rather than those that produce innate behaviors.

ODORS AS NATURAL STIMULI

Odorant molecules are typically small organic molecules with a molecular weight of 26-300.[8] An odor consists of millions of volatile molecules emitted into the fluid media of air or water. The vapor pressure of a compound is a measure that directly relates to its volatility; odorants with high vapor pressures in ambient conditions volatilize readily.[9,10] Inanimate odor sources passively emit odors; animate odor sources may passively or actively emit them. The intensity and chemical nature of both passive and active emission are a function of the properties of the compounds present, the temperature, and the atmospheric pressure. Examples of inanimate passive emission would include an inanimate object such as a glass of wine emitting hundreds of compounds from the fluid surface into the “headspace” in the immediately vicinity of the fluid.[11] Animate passive emission often occurs as a function of a metabolic process.[12] For example, the odors typically associated with rotting meat are produced and emitted by microbes as a byproduct of metabolism.[13] Mammals emit CO_2 and lactic acid as a byproduct of metabolism; CO_2 and lactic acid may be used by insects, such as mosquitos, to locate mammalian hosts.[14,15] In active emission, odors are synthesized and emitted by an animate signaler. Examples of this are: odor synthesis by flowers of plants; [4,16,17] pheromone production by animals for sexual or conspecific signaling; synomone production by plants that subsequently attracts parasitoids when a plant is attacked by insect herbivores.[3,18,19] In the case of flowers, odorant compounds are produced in the cells of petals or other floral parts [20-23] and released through epidermal cells or specialized glands.[3] Pheromones are often produced in specific glandular tissues specialized for their production,[24,25] but they may also arise from other scent sources such as body tissues.[26] Volatile compounds, such as ethylene and methyl jasmonate, are produced by plants during herbivorous attack and have been shown to act as signals to other plants for the up-regulation of the production of defensive compounds, and to act as cues for parasitoids that attack herbivores.[18,27]

Given the remarkable variety of both odor chemistry and olfactory contexts, it is reasonable to suggest that characterizing the statistical structure of an animal's olfactory environment would help us appreciate how animals encode and use olfactory signals efficiently. This is a relatively new departure for olfactory science, and we might borrow here from the other sensory sciences where attempts to characterize systematic characterization are becoming highly developed. Vision scientists have been the driving force behind much of this research: the philosophy of placing vision within a "natural" context grew out of work in the 1960s and 1970s by neuroscientists and psychologists such as Barlow (1961),[28,29] Gibson (1982),[30] and Mackay (1986).[31] A wealth of information about the statistics of natural visual scenes has appeared in the scientific literature. A good example is provided by Field's (1987) landmark study: "*Relations between the statistics of natural images and the response profiles of cortical cell*s."[32] This study showed that there are remarkable statistical regularities in ensembles of completely heterogeneous natural visual scenes. He also showed that the cellular physiology of the visual cortex is consistent with a coding system that takes advantage of these regularities to encode scenes efficiently. The notion of a match between the statistics of visual scenes and the processing in the human visual pathway has since been extended to include a wide variety of scene descriptors, such as orientation, color, spatial and temporal frequency.

For such studies to be possible, there must exist (i) a physical metrical space suitable for a general characterization of the physical relationships among different natural stimuli; (ii) measurable statistical regularities (non-randomness) in the stimuli when expressed in this metrical space; (iii) a perceptual metrical space suitable for a general characterization of the sensory discriminability of the natural stimuli. To take examples from vision, one might characterize the visual input physically by recording points of light as a function of time, wavelength, and space. Thus, a generalized, high-dimensional physical metrical space (a visual 'hypercube') exists for visual stimuli, though vision scientists work typically with down-projections from this space (*e.g.*, a static grayscale scene, which records only brightness as a function of space; or a color movie, which records only 3-dimensional colorimetric data as a function of space and time). Analyses of the statistics of natural visual scenes within these metrical subspaces have shown that, though remarkably heterogeneous visually, they are far from being statistically random. In fact, each natural visual stimulus is a sample drawn from a specific, highly complex distribution. If natural stimuli can be shown to have a definitive underlying distribution, one may start to make inferences about how these statistical regularities have influenced how the sensory system has evolved.[28,29,33,34] In addition, one can benchmark the sensory system by comparing its empirically observed performance with that of a so-called "ideal-observer model" (a theoretical model whose properties are optimized for the measured scene statistics): does the sensory system do as well as it could?

Following the above approach within the olfactory domain is likely to prove difficult. Taking the three requirements listed above, there are good reasons to expect that condition (ii) would be true in olfaction. A later section of this review will imply that there are probably a small, finite number of sources of variability in natural olfactory scenes, and it seems likely that the physical metrical space of olfactory stimuli would be just as structured (*i.e.*, nonrandom, with a characterizable statistical distribution) as that of visual or auditory stimuli. The key problems here are surely conditions (i) and (iii) above: providing definitive physical and perceptual characterizations of the olfactory scene. An important point here is that the scope of the physical metrical space must be at least as great, and preferably much greater, than that of the perceptual metrical space. In a sense, it is only by determining which physical characteristics our sensory systems *ignore* that we can answer those questions that help place perception in some sort of ecological context (*e.g.*, "why is human color vision merely three-dimensional when other animals have been shown to have many more color receptors?"[35]). In the olfactory domain, then, the physical metric space must encompass *at least* those properties of the stimulus known to be perceptually important. It is known, for example, that molecular shape is an important feature affecting odor perception.[36,37] Thus, an attempt to derive a chemical metric that could then be related to the perceptual qualities of odors must operate at least at the level of structural formulae. The difficulty in elaborating such a metric is clear, even for limited families of compounds; a completely general, structural-chemical metric would have to provide an index of similarity for diverse organic molecules. Indeed, the diversity and complexity of organic molecular structures makes it near-impossible to speculate even on how many *dimensions* such a metrical space should have.

Considering this, it should not be surprising that attempts to characterize the statistical features of naturally occurring odorants have been thus far limited to the detection and characterization of odor compounds and estimations of their relative concentrations. Further progress, however, can be made in spite of the difficulties outlined above — particularly the fact that we cannot determine the shape of the physical metrical space for characterizing odor chemistry — by considering the natural sources of variation in odor emission. Just as we can, in vision science, investigate the causes of surface color without concerning the dimensions or shape of the chromatic visual representation, we can look at the different types of variability (spatial, temporal, compositional, etc.) observed either across ensembles or within individual natural odor scenes and then use this natural variability to place odor scenes, and the recognition of odors in context. The next section discusses what these sources of variability might be.

PHYSICS OF ODOR PRODUCTION: SOURCES OF VARIATION

Spatiotemporal Plume Structure

Advances have been made in the last 20 years on characterizing the spatial distribution of odor plumes.[7,38-41] As odors are emitted in air, they disperse as complex, buoyant plumes.[42] The extent to which they disperse is a function of the momentum of the plume through the turbulent boundary layer of the fluid medium.[39] Dispersion produces a gradient of concentration that varies as a function of the distance from the source,[43] and depends on the prevailing environmental conditions such as the temperature and the air/wind speed.[42,44-46] Plumes of highly volatile compounds additionally have complex structures that arise from the distribution of the turbulent kinetic energy of the fluid medium in which they travel.[6,9,42,47] This structure is characterized by filamentous regions of odorant where the concentration varies dramatically within a local spatial region (Fig. 8.1).[7,37] Images taken of the spatial structure of odor plumes at specific time points during emission reveal that the structure of an odor plume changes as a function of the odor molecules' momentum when carried by a fluid medium such as air or water.[7,48] The contrast between odor concentrations in filaments tends to be greatest at the boundary of the odor plume than it is in the center of the plume near the source.[6]

Temporal Fluctuations in Active Emission

The temporal pattern of odor emission can also show marked periodicity on either a short timescale (milliseconds) or a longer one (hours or days). Scent production may occur on a short timescale such that odor quanta are produced and released discretely. For example, some species of female moths have been reported to produce odor "puffs" rather than steady odor production.[49] Odors used for defense, such as the spray secretions of skunks or bombardier beetles, may last only a few seconds.[50,51] On longer timescales, the scent emission of pheromones for some organisms may follow a temporal pattern that correlates with diurnal phases;[25,52-54] or with specific periods in the reproductive cycles of individuals.[55-58] Several studies of flowering plants have shown that floral scents are emitted for hours during those

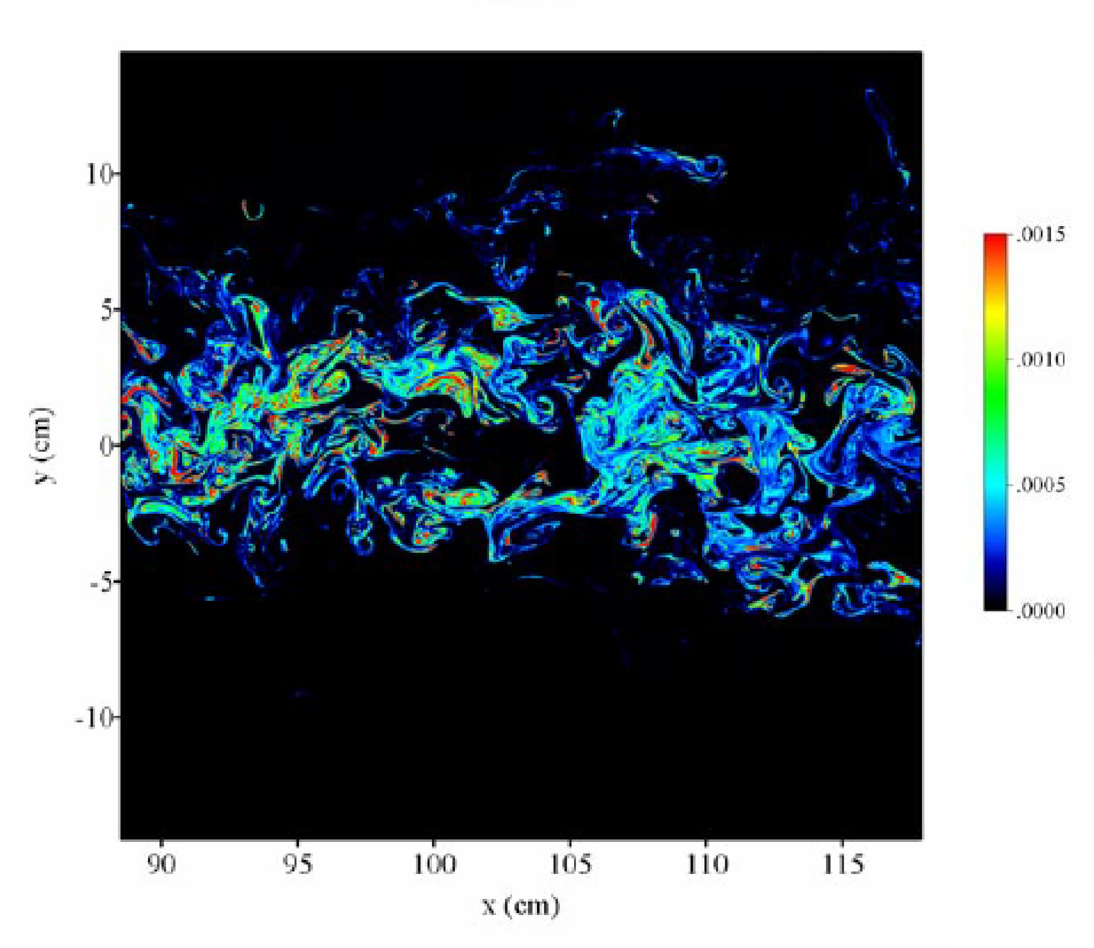


Fig. 8.1: An image of an odor plume taken using planar, laser-induced fluorescence. This image reveals the instantaneous scalar structure of the plume. The image was captured from the outer layer of the momentum boundary layer of the plume. It is a horizontal image spanning a lateral and streamwise range; it reveals the spatial patterns at a given vertical location. The color scale indicates the concentration of the odor in the plume; concentrations are normalized by the source concentration C_0 and color coded as shown in the legend. From Crimaldi et al., *J. Turbul*. 3: 1-24, 2002.[7] Reproduced with the permission of the authors and Institute of Physics Publishing.

epochs in a diurnal cycle that correlate with the appearance of their pollinators.[59-62] Raguso et al. (2003) showed that moth-pollinated plants show a 2-10 fold increase in scent production during the early nighttime hours when their pollinators fly.[62]

In situations where these temporal periodicities are constant, they could be studied using the standard statistical technique of power spectral analysis,[63] which would illustrate the variance in the rate of emission as a function of temporal frequency in cycles per time interval. Variation in such a diurnal cycle of emission can, however, occur when the environmental conditions change, since floral scent emission is also influenced by environmental factors such as light and temperature.[59] Statistically, such cases would be characterized by a change in the variance of the original periodicity due to the environmental factors, and techniques borrowed from higher-order statistical analysis would be appropriate here.[64]

Qualitative and Quantitative Variation in Odor Sources: Floral Scent as an Example

In addition to the spatial and temporal structure of odor emissions, another significant source of variability in a natural olfactory scene is likely to be composition of the volatile compounds across a population of odor sources.[65] Odors produced by similar sources (*e.g.,* flowers of the same species) may differ with respect to the number of compounds present, the types of compounds, the quantity of each compound, and the overall odor intensity (sum of the odors in the mixture, see below).[65,66] Each of these types of inter-odor differences may alter an odor's perceptual qualities, and, therefore, could also alter the way in which animals respond to them.

In the following subsections we will use flowers as an example of an odor source. Plants produce flowers with visual and olfactory displays that attract animal pollinators.[67] Floral signals both attract new pollinators and help them learn to associate the floral cues with reward so that they will visit other similar flowers and perform pollination. Odors are important signals used for identification and discrimination among flowers; insect pollinators, such as moths, will not feed from flowers unless they have the appropriate odor stimulus.[68] Floral signals may also advertise when flowers have been pollinated by changing their scent composition after pollination.[69,70] It has also been observed that specific suites of compounds may be more attractive to a particular "pollinator guild," such as moth pollinators,[71]and that natural selection by pollinators may select the production of odors these pollinators recognize.[1] The two subsections that follow describe some of the qualitative and quantitative inter-odor differences observed among volatile compounds found in flowers and discuss how to quantify these differences.

Qualitative Variation

Floral scents are often complex blends of several compounds.[1,4,65] These are mainly fatty-acid derivatives, benzenoids, phenylpropanoids, isoprenoids, nitrogen- and sulfur-containing compounds.[4] Knudsen et al.'s (1993) comprehensive review of floral odors reported floral scents with as few as three compounds and as many as several hundred.[4] A study of moth-pollinated flowers from the Nyctaginaceae reported as many as 77 compounds in floral scent and as few as one.[5] Studies that have focussed on identifying the site of volatile production in flowers report that they are produced mostly in the petals.[16] Volatiles are both synthesized and released by the epidermal cells or by special glandular trichomes on the petal surface.[72] Other studies have shown that the odor of pollen is also part of the odor signal.[21,73]

Variation in the emission of specific volatile compounds is likely to arise from differences in gene expression of enzymes that produce volatiles and their substrates.[74] Qualitative interspecific differences in the production of scent compounds are generally greater than intraspecific differences. [5,54,65,75,76] Natural selection may lead to differences in scent between species that are advantageous to the plant, as specific pollinators may be less likely to generalize to other plant species and, therefore, pollinate more efficiently. Grison et al. (1999) observed that most fig species produce 4-6 odorant compounds.[77] They observed that one species had 22 compounds; another had a completely different suite of compounds. Both of these traits, an increase in number and a suite of completely different compounds, would change the scent and make it less likely for fig wasps to confuse the scent with the scent of another fig tree. However, natural selection towards the production of volatiles preferred by particular pollinators could also lead to unrelated plant species producing the same suite of compounds.[4,67,78] In some environments, it may be to the plant's advantage to be indistinguishable from other species of plants, so that it increases its pollination rate by generalist pollinators when plants of the same species are less common.[79,80]

In general, examinations of intraspecific floral scent indicate considerable variability in scent composition. Most information about qualitative variation within species comes from studies of domestically cultivated flowering plants. For a given species, it is possible that all plants produce flowers that have the same number and type of compounds. This was shown to be the case for the scents of 4 snapdragon cultivars, in which 8 volatile compounds occurred in all cultivars.[81] A study by Kim et al. (2000) reported 41 compounds in the scent of roses including 8 different classes of compounds (alcohols, aldehydes, alkanes, monoterpenes, sesquiterpenes, ethers, esters, and ketones).[82] They examined 3 cultivars and found that each had approximately 30 compounds, but only 19 of those (63%) were found in all 3 cultivars. Another study of 4 cultivars of lavender by Kim and Lee (2002) reported that each produced approximately 28 compounds, with only 14 in common (50%) (Fig. 8.2 and 8.3).[83]

Variability in scent composition has been measured in some wild populations of flowering plants as well.[5,84-86] In a study of 20 species of moth pollinated flowers, Levin et al. (2001) found that variability in scent composition was different for each species.[5] They also noted that plants with more compounds in their scent may also have more variability in the types of scent compounds across the population.[5] Knudsen's (2002) study of 5 populations of *Geonoma macrostachys* from western Amazon reported that of 108 compounds found across all the samples, only 28 compounds were common to all; the remaining 70 were not consistently found in every sample.[85] The number of compounds found in the scent also varied among populations in a range from 39-95 compounds. Thus, even within a species, a substantial amount of qualitative variation may exist.

Quantitative Variation

Odor Intensity

The most variable aspect of odor is odor quantity. Even for individual flowers, the amount of scent produced can vary widely as a function of time of day, development stage, and environmental conditions.[16] The amount of scent produced by odor-emitting objects varies both in terms of the individual scent compounds and also in terms of the overall scent intensity. For our purposes, a rough measure of scent intensity is defined as the sum of the concentrations of each of the individual compounds. Considerations of the statistical features of naturally occurring odor objects and the way that animals perceive these objects should also include quantitative information. The overall intensity of floral odors has been reported to range over 4-5 orders of magnitude in concentration.[5,78,85] Differences in intensity may occur among species of plants; scent intensity is not dependent upon the number of compounds present in the odor, as complex scents may still have low intensities if all odor compounds are present at small concentrations. Scent intensity also varies for the same flower throughout its development,[87] and it may also vary as a function of the flower's diurnal cycle.[62] Raguso et al. (2003) reported up to a 10 fold increase in scent intensity over a diurnal cycle for moth pollinated flowers of *Nicotiana alata*.[62]

Correlations among Odorant Concentrations

Most naturally occurring odors are composed of several odorants; each compound is probably present at a different concentration (see Fig. 8.2). The concentration of individual odorants, in fact, can differ by orders of magnitude in concentration. Based on 6 studies of floral scent including the scents of 43 different

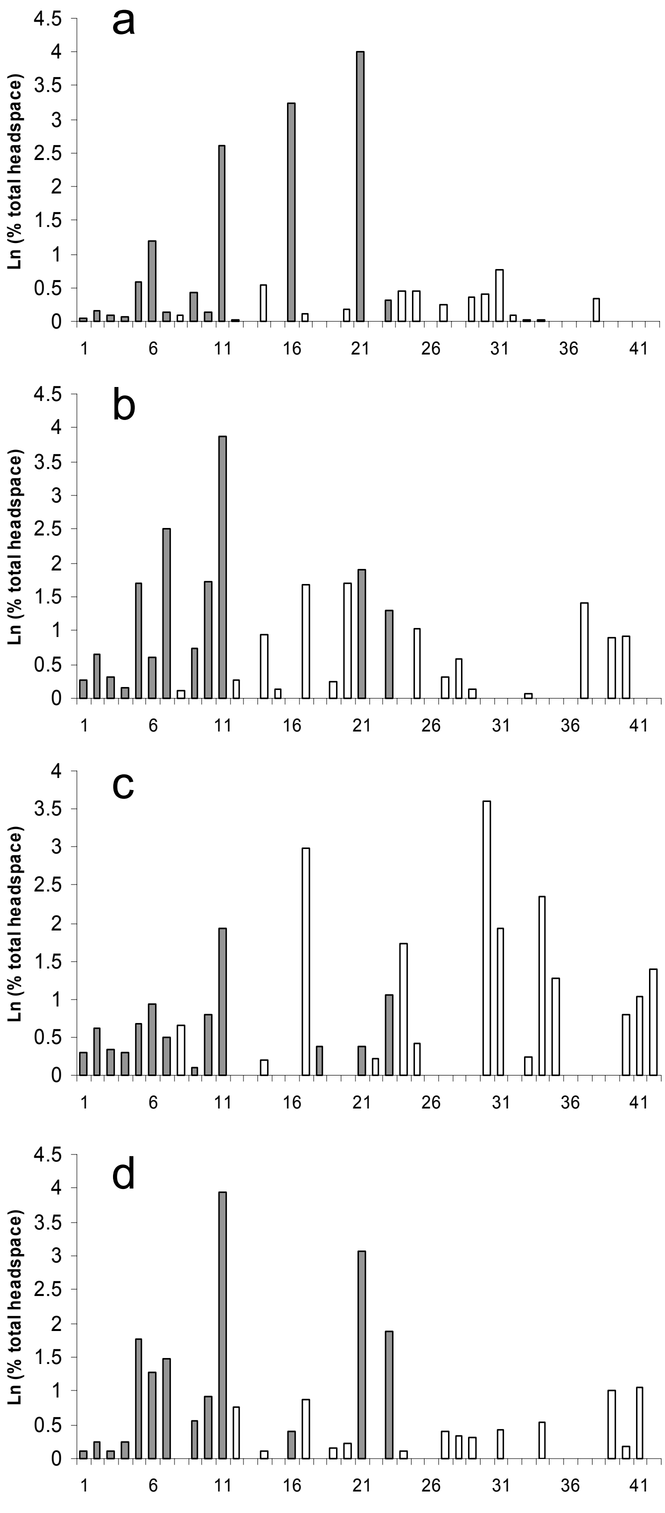
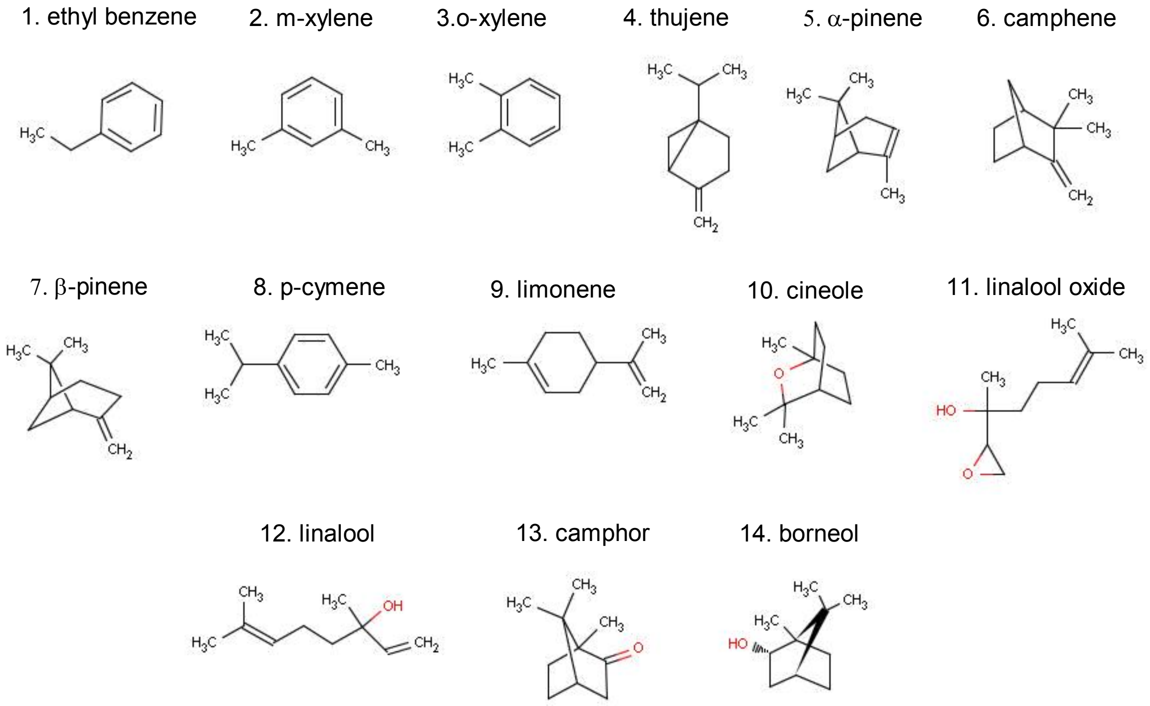

a
b
c
d
Ln (% total headspace)
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
1
6
11
16
21
26
31
36
41

Fig. 8.2: Lavender cultivars have only 14 volatile compounds in common out of 43 compounds detected by gas chromatography (dark bars; see Fig. 8.3 for structures of each compound). Y-axis represents the natural log transformed percentage of each volatile in the floral headspace. Four cultivars are represented a) French; b) Fringed; c) Hidcote; d) Sweet. Each bar represents a different odor. Kim and Lee., *J. Chrom. A* 982, 31-47, 2002.[82] Reproduced with the permission of the authors and Elsevier:

species, we estimated that the average floral scent has 31 compounds.[75,78,82,83,88,89] We also estimated the frequency of the compounds of different concentrations in the average floral scent. Approximately 17 compounds (54%) are present at low concentrations and are each less than 1% of the total scent output. Eight compounds (27%) each produce 1-5% of the total scent; 4 compounds (12%) each produce 5-20% of the total scent, and 2 of the compounds (6%) each produce over 20% of the scent. Analysis of correlations among compounds found in the scents of flowers of a population of plants can be accomplished by using statistical data-reduction techniques (*e.g.,* principal components analysis (PCA), characteristic vector analysis, factor analysis) designed to reduce many variables to a smaller subset of components, each of which represents linear correlations among the variables. A study by Ayasse et al. (2000) used PCA to examine correlations in 106 compounds extracted from the orchid, *Ophyrs sphegodes*.[90] They found that groups of compounds belonging to the same chemical class, such as n-alkenes, tended to be represented by the same principal component. Another study by Wright et al., (2005) showed that the first principal component computed from a dataset describing the volatile profile of the scents of snapdragon flowers arose largely as a result of a high, positive correlation between two compounds (*cis* and *trans*-methylcinnamate) produced by the same enzymatic pathway.[81]

Ratios of Odorant Concentrations

As a scent is composed of several compounds with different concentrations, the ratio of the concentrations may be a useful way of identifying the similarity of odor producing objects. These ratios are more likely to reflect the activity of the biosynthetic pathways producing odor than the differences in the vapor pressure of the compounds;[59,91] correlations among the presence and concentration of individual compounds could reflect common biosynthesis pathways.[27] For example, compounds produced by the same enzymatic pathway may be correlated.[54,62,81] Compounds



1. ethyl benzene
2. m-xylene
3.o-xylene
4. thujene
5. α-pinene
6. camphene
7. β-pinene
8. p-cymene
9. limonene
10. cineole
11. linalool oxide
12. linalool
13. camphor
14. borneol

Fig. 8.3: The 2-d structures of the 14 volatile compounds in common among lavender cultivars, reported by Kim and Lee (*J. Chrom. A* 982, 31-47, 2002).[83] The compounds are numbered in order according to their retention time on an SPB-5 column from a gas chromatograph. Structures were drawn using ChemIDPlus at the NIH website (http://chem.sis.nlm.nih.gov/chemidplus/).

produced from the same substrate could also be correlated,[74] as their appearance is dependent upon the amount of substrate available. When the substrate is present and plentiful, each compound may be present in high amounts; if it is limiting, then the concentrations of each may decrease.

As observed for the qualitative aspects of scent, the ratios of the concentration of compounds in scents may show greater inter-species than intra-species variation. This is true both for floral scents and for other, naturally occurring odors. The amount that scent production varies over a specific time interval may vary widely from one individual to the next.[53,92,93] Additionally, some odorants found in scents may simply be intrinsically less variable across a population than others.[53,81,92] This variability can be characterized by measuring the coefficient of variation for each compound in a complex scent across a sampled population of odor-emitting objects.[12,81,90] The coefficient of variation is simply the standard deviation expressed as a percentage of the mean.[94] It provides a standardized way of comparing variation among populations that may exhibit great differences in their ranges of measurement.[94] Interestingly, Ayasse et al. (2000) reported less variability in the concentrations of the "bioactive" compounds in a sexually deceptive orchid than in the concentrations of the orchid's nonactive compounds.[90] The bioactive compounds are similar to the sex pheromone produced by the wasps and attract male wasps. The male wasps attempt to copulate with the flower and pollinate the flower. It is possible in this case that selection pressure is greatest on the odors mimicking the pheromones of the pollinating wasps, specifically such that a lower variation in their production is selected for.

One means of examining differences in variability in ratios of odors is by using methods of classification such as discriminant analysis or cluster analysis. Discriminant analysis is used to identify the maximal co-linearity among a set of variables and then to produce a function representing these linear relationships that maximally separates pre-defined populations or categories.[95,96] If the pre-determined categories are not distinguishable using the entered variables, then the discriminant functions produced will not be statistically significant. Thus, by using discriminant analysis, it is possible to compare the ratios of odor compounds among different species or different subpopulations.[96] When the variation in the ratios within a species or subpopulation is smaller than between species, significant differences will be observed.

This was recently shown in a study of 4 cultivars of snapdragons where even subtle differences in scent were found to be significantly different by discriminant analysis.[81] The analysis by Wright et al. (2005) reported 3 discriminant functions that split the cultivars into 4 significantly different groups.[81] Standardized coefficients are reported in Table 8.1; the magnitude of these coefficients reflects the importance of a specific odorant to the classification of each cultivar by the discriminant functions in the presence of the other odorants.[96] Each discriminant function represents a split of one cultivar from the others. The sign of the unstandardized coefficient reflects which cultivar was split from the group. This type of analysis provides information both about differences in scent profiles of putatively different odor producing objects and about which aspects of the scent are used to differentiate them.

Table 8.1: Discriminant analysis of the volatile compounds of the scents of 4 snapdragon cultivars. The standardized coefficients in bold indicate the volatiles that contributed the most to classification of the snapdragon varieties by each of the functions. The sign and magnitude of the unstandardized coefficients (in bold) indicate which cultivar was best separated from the others by the function. The order of the functions indicates the distance in similarity between the snapdragon cultivars. (From Wright et al., 2005,[81] reproduced with permission of Springer)

	Discriminant Function		
	1	2	3
Volatile compound	**Standardized Coefficients**		
Myrcene	**0.976**	0.417	0.049
E-β-ocimene	-0.306	**-0.757**	-0.222
MethylBenzoate	-0.260	**-1.12**	0.473
Acetophenone	-0.308	0.486	**0.632**
Linalool	0.244	0.370	0.410
Dimethoxytoluene	0.101	0.663	**-0.867**
C-methylcinnamate	-0.098	-0.268	-0.313
T-methylcinnamate	-0.173	0.547	0.241
Cultivar	**Unstandardized coefficients**		
PH	**-2.94**	0.088	0.021
MTP	2.15	**-1.68**	0.045
PP	3.59	0.501	**-0.442**
PW	3.01	0.591	0.811

Temporal Fluctuations in Ratios

The ratios of odorants in scent, however, may also change throughout a diurnal cycle of emission, as the increase in scent production during specific time intervals may not be the same for all compounds. Individual compounds may not have the same coefficient of variation.[81,90] One study by Helsper et al. (1998) showed that diurnal emission rates were different for each compound in the scent of single rose flowers (Fig. 8.4a).[59] Differences in the temporal structure of the emission of individual compounds changed the ratios of the concentrations of each of the compounds such that a different odor "profile" was produced depending on the sampling point (Fig. 8.4b). Additionally, if the intensity of the scent is calculated for this same study, the overall scent production was at a maximum 6 h into the light half of the day cycle. Thus, in a diurnal cycle, the ratios of the concentrations of the compounds may vary dramatically. The extent to which differences in scent emission are observed, however, is likely to be a function of the duration of the time interval of odor sampling.

ODOR PERCEPTION AND THE OLFACTORY SYSTEM

The olfactory system must allow animals to detect and discriminate among a vast array of possible odors. Interestingly, the olfactory systems of diverse animals exhibit common features, such as first-order processing at receptor neurons in the olfactory epithelium, followed by second-order processing at the glomeruli in the olfactory bulb (mammals) or antennal lobe (insects). It is likely that these structural features have evolved independently. The morphological identity of these olfactory systems may thus be a result of common evolutionary constraints,[97,98] which might in turn reflect statistical consistencies among naturally occurring odors.[34] Sensory transduction of odors occurs when odorant molecules come into contact with G-protein-coupled receptors present in the dendrites of receptor neurons. These receptor neurons may be "tuned" to respond to a specific range of odorant molecules; the extent of tuning may be proportional to the binding affinity of odorant molecules with that odorant receptor.[99-102] Depending on the animal, receptor neurons express one to several odorant receptors.[97,102] The receptor neurons are bipolar with dendrites expressing G-proteins for odorant binding and with axons that converge in the antennal lobe or the olfactory bulb.[102] The antennal lobe and olfactory bulb are composed of highly interconnected circuits of excitatory and inhibitory neurons that form glomeruli.[2] For animals expressing only one odorant receptor, axons from receptor neurons that express the same odorant receptor converge onto the same glomerulus or onto a small set of neighboring glomeruli.[100,103] The neurons in the antennal lobe relay information about an odor's identity via the action potentials of projection neurons to the higher centers of the brain.[2] The higher centers of the brain integrate information from other sensory modalities to form associations between sensory representations.[104,105]

Learning, Generalization and Discrimination

Animals show both innate and learned responses to odors in their environment. Examples of innate responses include the anemotactic behavior of those male moths that fly upwind towards a pheromone-emitting female[106] or the defensive responses of honeybees to their alarm pheromone.[107] Many animals also *learn* to associate odor with important events such as the presence of food. The

a

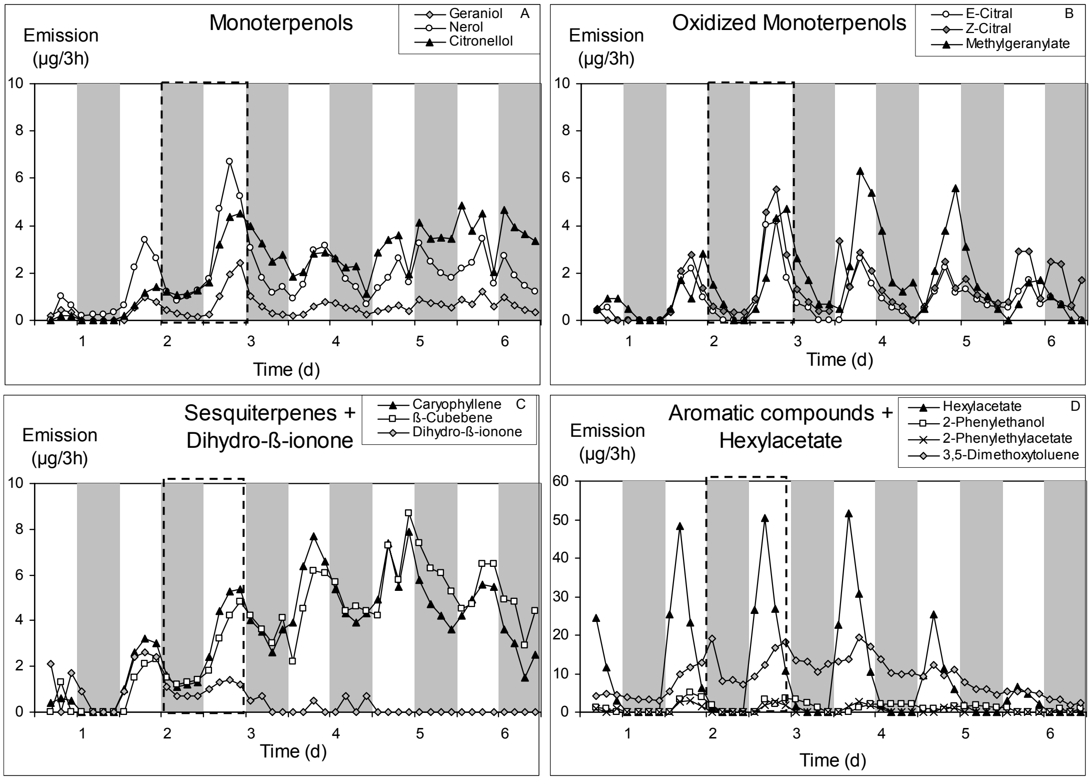
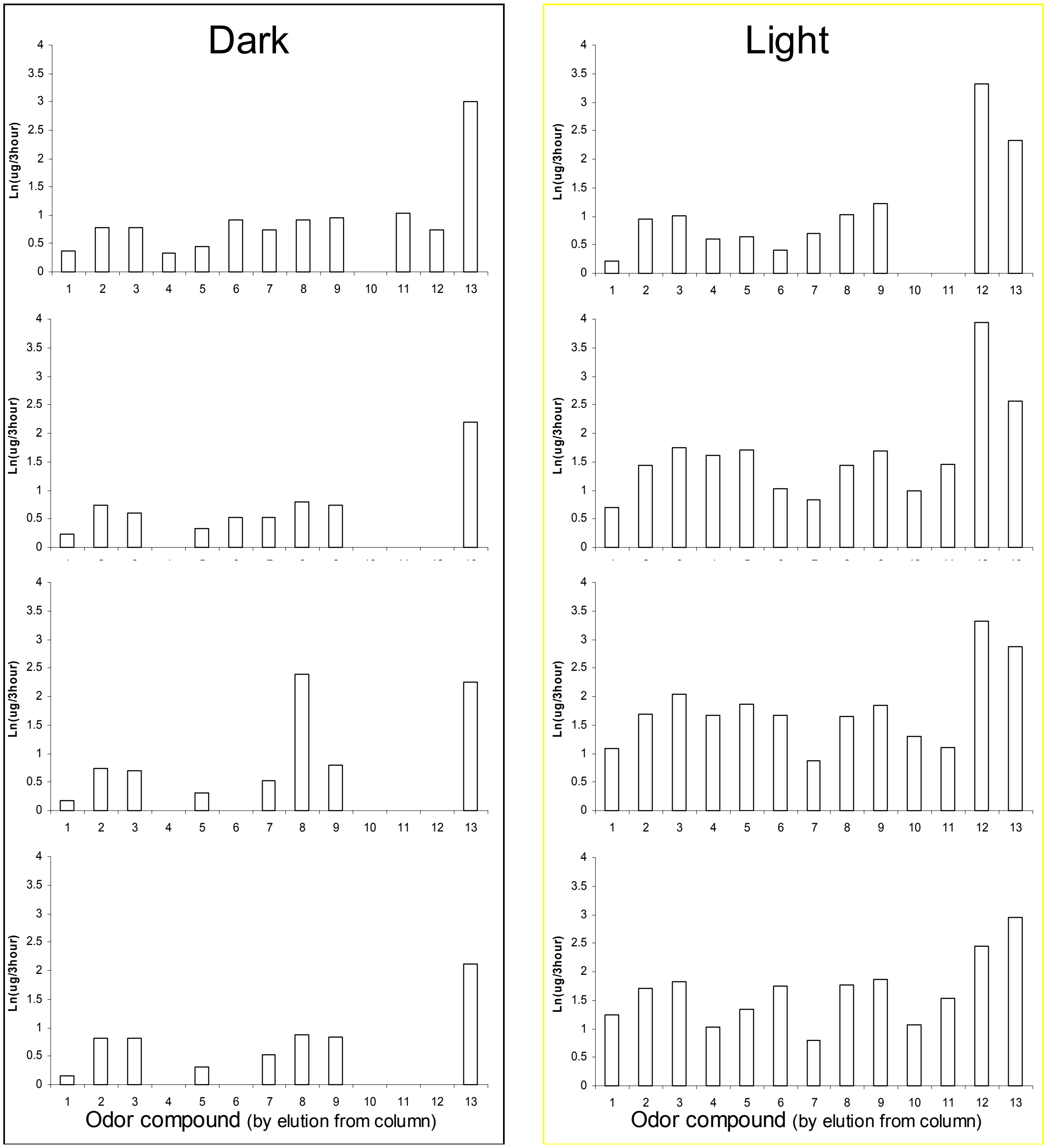


Fig. 8.4: The ratios of the concentrations of odor volatiles change as a function of the time period of sampling. a) Diurnal emission of individual odor volatiles by flowers of Rosa hybrida exposured to a 12-h photoperiod; shaded and non-shaded areas correspond to periods of darkness and light, from Helsper et al. (1998).[59] Each point represents the amount of a given volatile at a 3 h sampling period. b) Representation of the odor volatiles for each 3 h sampling period over a 24 h period (shown in a dotted box on (a)). The odors are represented on the x-axis as: 1=geraniol, 2=nerol, 3=citronellol, 4=e-citral, 5=z-citral, 6=methylgeranylate, 7=caryophyllene, 8=β-cubebene, 9=dihydro-B-ionone, 10=hexylacetate, 11=2-phenylethanol, 12=2-phenylethyl-acetate, 13=3,5 dimethyoxytoluene. Reproduced with the permission of the authors and Springer.

b


Dark
Light
Ln(ug/3hour)
0
0.5
1
1.5
2
2.5
3
3.5
4
1 2 3 4 5 6 7 8 9 10 11 12 13
Odor compound (by elution from column)
Odor compound (by elution from column)

following sections discuss how animals perceive odors and how the statistics of natural odors may affect what they perceive. We focus mainly on odor signals that are learned by animals.

Studies of learned behavior via associative conditioning with odors have shown that learning strongly influences the ability of animals to perceive and identify odors.[108] Animals learn by associating a “conditioning” stimulus or a context with an important event.[109] Learning is defined as an animal’s use of information about a conditioning stimulus to predict another stimulus or event.[110] By necessity, animals must take information about a conditioning stimulus from the first experience and generalize this information to the next experience because no conditioning stimulus is experienced in exactly the same way every time the animal encounters it.[109,111] Therefore, during learning, animals are forced also to generalize from one conditioning stimulus to the next. When perceiving a conditioning stimulus, an animal's responses are mediated by a comparison between previous experiences and the current stimulus. Generalization of a conditioned response, such as a learned association of an odor with food, occurs when animals perceive similarities among stimuli from one experience to the next.[110,111] Animals often face situations where they must generalize from an odor they have learned to another odor stimulus. One example of this is foraging by honeybees. Honeybees use pollen and nectar from flowers as their primary food source.[112] They use the odor of flowers to identify a good floral resource and forage on it exclusively to increase their foraging efficiency. When foraging, a honeybee learns the odor of a flower and compares its scent with the odors produced by new flowers to decide whether to forage on a new flower or not. It may use several features of the scent, including the types of compounds and their concentrations, to generalize what it learned to a new flower.[81,113]

In addition to generalizing from one odor experience to the next, animals must also discriminate among odors. Nursing lambs use the odor of their mother to identify her in a field of other ewes.[114,115] Honeybees also use the odors of flowers to discriminate rewarding flowers from unrewarding flowers; they may also place scent marks on flowers to discriminate a flower they just visited from a new flower of the same type.[116] The guard caste of honeybees patrols the entrance of the hive; they use the scent of entering workers to determine whether the worker is a hivemate or an intruder from another hive. In this case, a guard must generalize the scent of a nestmate to an entering worker that may have been exposed to other scents[117] yet discriminate nestmates from intruders attempting to rob the hive.[118,119]

Several variables influence both generalization and discrimination, including: the perceptual similarity of stimuli, the order of an animal’s experience with stimuli, the amount of experience it has had with the stimuli, and its motivational state to attend to differences in the stimuli. The specific features of stimuli used to generalize from one stimulus to another may be different from the features used to discriminate among stimuli. Generalization from one stimulus to the next may arise because an animal is unable to perceive differences among stimuli; it also arises when an animal uses features of stimuli to classify stimuli with similar meanings.[111] The ability to discriminate is related to an animal's ability to detect differences among scents (for example, differences among the types of compounds or their concentrations), but discriminative *behavior* is also strongly affected by motivational factors; for example, the cost of making a mistake when discriminating among stimuli.[110]

Perception of Odor Quality: Odor Similarity and Odor Space

One aim of studying olfaction has been to gain an understanding of how the physical features of odor molecules correlate with their perceptual qualities.[120] Unfortunately, the perceptual qualities do not often follow an easily ordered metric that can be simply related to molecular structures. We might, therefore, speak of a dual problem in attempting to relate odor perception to the features of the corresponding molecules: no obvious metric is available to describe either the space of odor perceptions or the space of odor chemistry.

Some studies have examined the ability of animals to discriminate among odor stimuli and have attempted to correlate failures of discrimination with structural similarity among odor molecules.[121] These studies may be used to form indices of the perceptual similarity of odors, and this may provide information about the way that a limited variety of chemical structures (*e.g.,* alcohol groups or double-bonded oxygen moieties (ketones)) are used as features by the olfactory system[120,122] Recent behavioral experiments using aliphatic alcohols, ketones, and aldehydes have shown that the perceptual qualities of odors are correlated with molecular features such as carbon-chain length.[121,123-125] For example, Daly et al. (2001) found that discrimination of aliphatic alcohols and ketones by the hawkmoth, *Manduca sexta*, was greatest for compounds of different functional groups (alcohol vs. ketone); moreover, among odorants that belonged to the same functional group, compounds with the greatest differences in carbon-chain length (*e.g.,* alcohols with different carbon backbones) were easiest for the hawkmoth to discriminate.[124] Thus, it is tempting to conclude that compounds closely related in respect of their chemical formulae may also be difficult to distinguish, whereas compounds with substantially different chemical formulae are likely to be easy to distinguish. As we have already discussed, however, counterexamples to such a hypothesis exist in the form of chiral enantiomers of odor molecules: enantiomers of the same molecule sometimes exhibit substantially different perceptual qualities.[36,37,122] Thus, an attempt to derive a chemical metric that could then be related to the perceptual qualities of odors must operate at least at the level of structural formulae, since chemical formulae do not take chirality into account. In view of the metrical problems outlined earlier, then, it seems that for the moment we will have to accept that attempts to relate odor chemistry to olfactory physiology must restrict themselves to piecewise analyses of small, isolated areas of the global psychophysical odor space.

The study of the perception of compounds present in odor mixtures is also fraught with the sorts of nonlinear "contextual effects" with which vision and auditory scientists are all too familiar. At present, most studies use human subjects to examine the way that odor compounds affect perception in complex mixtures; such studies show that perceived odor similarity between two complex blends is likely to be mediated both by the types of compounds found in the mixtures and the relative number of compounds that the two mixtures have in common.[126,127] Perception of similarity is also be affected by the presence of specific volatiles in common that overshadow other volatiles, either because their concentration is greater or they are easier to perceive;[126-128] this is similar to the "masking" effects seen in other sensory systems. A complex mixture may also produce a percept whose qualities are quite independent of the qualities of the individual compounds,[129,130] making it difficult to relate the sensory properties of a mixture back to each of the components, especially in mixtures containing several compounds.[126,127,131] Additionally, not all of the odorants in a mixture may contribute equally to a scent's perceptual qualities; some may not contribute at all.[128] Both types of complication could be interpreted as a violation of linearity (the response to A plus B is not the response to A plus the response to B) analogous to that which is seen in the later stages of processing in both auditory and visual systems.[132]

A final problem is the potential for confusing odor discriminability with the discriminability of odor categories. Some studies have addressed the problem of finding satisfactory metrics to express the relation between odor structure and the way that humans perceive them by using descriptive language to classify odors (for a review see: Wise et al. (2000[120])). For example, in the classification of Zwaardemaker (1925), odors considered to be "nutritive" were classified in some of the following categories: etherous, floral and balsamic, aromatic, and ambrosaic[133] (reported from Wise et al., 2000[120]). Returning once again to a color-vision analogy, being asked to visually discriminate two slightly different shades of red is clearly an entirely different task from being asked whether a given color is red or orange; the former is a perceptual discrimination, whereas the latter is a category discrimination. Imposing categories upon the psychological odor space may help produce a perceptual metric, but it is a metric of categories, not a metric of odors, and it is conceivable that the relationship between the two might turn out to be as complex as it is in color vision.

Odor Concentration and Odor Perception

As mentioned above, the concentration of an odor stimulus is a key physical feature of naturally occurring odors. The concentration of an odor may vary widely within an animal's experiences; between salient odor objects, concentration may be a defining feature used to identify important odors. The concentration may also convey information about an animal's distance from the source of emission. Odor learning and discrimination are affected by concentration. Odors of low concentration are more difficult to learn.[134-136] Discrimination among odors also increases as a function of odor concentration (Fig. 8.5).[136-139] This has been shown both for the discrimination of monomolecular compounds[136,138] and for discrimination among

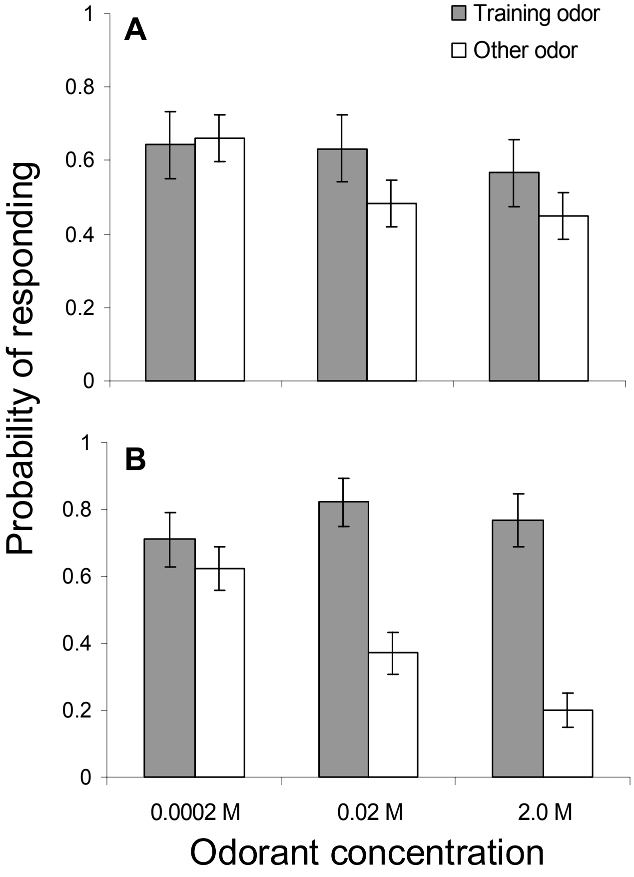


Fig. 8.5: Discrimination increases with concentration for dissimilar odors (b) but not for similar odors (a). Conditioning and testing were performed at the same concentration for the similar (**a**; n = 87 animals) or dissimilar (**b**; n = 88 animals) test odors. Generalization response levels to novel odors (open columns) are shown next to the response to the conditioned odor (shaded column) at a given training/testing concentration. Reproduced with permission of Oxford Univ. Press.

mixtures.[81,113] That odors are harder to discriminate at low concentrations suggests two possibilities: (i) as in other sensory systems, detectability is a function of the signal-to-noise ratio, such that a higher-strength signal is more reliably detected and thus easier to discriminate; (ii) that odors may not be perceptually invariant as a function of concentration. These two possibilities are not mutually exclusive, andindeed both may well turn out to be true. Variation in the perceptual qualities of odors as a function of concentration has been noted for many years[139-143] but is difficult to test exhaustively. Recent studies suggest that samples of the same odor at different concentrations are discriminated reliably by animals[134,144] and that odors may not be perceptually invariant as a function of concentration.[139] Additionally, for several insects with innate responses to odor, odor may be attractive at one concentration and repulsive at a higher concentration.[145,146] Erbilgin et al. (2003) recently showed that pine beetles (*Ips pini*) demonstrate an apparently highly nonlinear response to their aggregation pheromone, such that low concentrations of pheromone are not attractive, mid-range concentrations are highly attractive, and high concentrations are repulsive. [146] Dethier (1976) also showed a similar nonlinear response to odor in blowflies: he observed that blowflies were attracted to low concentrations of iso-valeraldehyde and repelled by high concentrations.[145]

Behavioral responses that vary as a function of concentration may indicate that the odor concentration is the feature that triggers the innate response for some animals. In other words, the animal may know something *a priori* about the statistics of the natural distribution of odorant concentration, and reject those concentrations that are in some sense ecologically valid. For this to be true, it must be the case that the odor in question simply does not remain perceptually invariant as a function of concentration: the animal perceives high-concentration odorant as a different substance altogether to low-concentration odorant. The existence of concentration-dependent variation in odor quality has profound implications for our understanding of olfactory coding and its relationship to the statistics of natural odor scenes. As thousands of different odor molecules exist, there may be evolutionary trade-offs between coding for a diverse set of odors and coding for an extensive range of odors. In particular, failure of invariance may suggest that the need to encode diverse odor molecules has exerted a greater pressure on the olfactory system than the need to identify a specific odor over a large range of concentrations. This may have arisen because the concentration range of naturally occurring odors is not large for a specific population of odor scenes. In this case, it may be important to maintain odor identity within the ecologically relevant range; if the animal is not likely to encounter an odor outside of this range, then the ability to render its perceptual qualities invariantly may be less important. Further research into the relationship between the concentration of natural odor scenes and the way that animals use odor scenes is necessary to test this hypothesis.

Odor Perception and Spatiotemporal Plume Structure

One additional aspect of odor concentration and its meaning to animals may be related to the spatial statistics of odor-concentration distribution. The concentration may convey information about the distance of the animal from the odor source.[40,41,106,147-151] In spite of studies that show that animals will perform upwind anemotaxis towards an odor source, it has yet to be shown definitively that behavior is simply concentration-driven: animals may not understand innately that low concentrations of an odor necessarily mean that they are far away from the source of emission.[152] Instead, other aspects of the signal, such as the frequency of encounter of (high-concentration) filaments of an odor plume or other —possibly higher-order — spatial statistics of the plume, may be the stimulus driving anemotaxis behavior.[40,41,150,151] The way that spatial statistics of odor plumes are used by animals may also depend on the animal and its environment.[44] A recent study by Keller and Weissburg (2004) showed that the chemosensation of the blue crab (*Callinectes sapidus*) used large-scale variation (pulses of 1-3 sec) in concentration in odor plumes to detect odor sources,[153] rather than using either fine-scale variation (less than 1 second) or acting as a flux detector.[154]

Perception of Ratios of Compounds in Complex Mixtures

In complex odor mixtures, the ratios of odorant concentrations may be important features that animals use to discriminate. This has been shown to be especially true of pheromone blends, where the ratio of the concentration of each pheromone compound in the blend may affect several behaviors, from anemotaxis to contact with the source of emission.[92,155] Variability of emission of the ratios of odorants in pheromone blends can occur within individuals[91] and across populations [92,156] or between species.[157,158] The strength of the effects of variation on behavior appears to be dependent upon the species involved, however.[92] In non-pheromonal odors, the ratios of odor compounds in scent may also be useful for discriminating among odor-emitting objects. Differences attributed to scent as a function of the ratios of odorant compounds may be more subtle than perceptual differences that occur from the subtraction or addition of different odorant compounds to an odor mixture. As these differences may be hard to detect, the extent to which animals use differences in the ratios of compounds may be governed by the cost of making a mistake between scents with different ratios.

Depending on the complexity of the blend, there may also be a limit to which these ratios actually affect the perceptual qualities of an odor. Other variables, such as intensity, may also change the effects of ratios on an odor's perceptual qualities.[126] There is evidence that both vertebrates and invertebrates can make fine discriminations based on the ratios of odorant concentrations. A study by Osada et al. (2003) showed that the ratios of the odor compounds in mouse urine changed as a function of age, and that mice could learn to discriminate among these ratios.[159] They found 38 odor compounds; eight were different between adult mice and aged mice. Five were greater in aged mice, and 3 were smaller in concentration. As the concentrations of all eight compounds were not greater in the aged mice, the mice were using the ratio rather than a change in the intensity of the scent. Honeybees are also able to use the ratios of compounds found in floral scents to make subtle discriminations. Wright et al. (2005) showed that honeybees could learn to discriminate the scents of 4 snapdragon cultivars.[81] Each cultivar had 8 compounds present; the cultivars were significantly different in the ratios of scent they emitted when classified by a discriminant analysis (see section above Table 8 1). The ability of honeybees to discriminate among the scents correlated with the differences in the ratios among the cultivars. Additionally, scent discrimination was also affected by scent intensity, such that discrimination using the ratios was more difficult when the scent was less intense.

Odor Perception and Temporal Variation

Animals experience odors sequentially. In particular, this is true of foraging animals that rely on scent for the identification of food items. For example, honeybees foraging on flowers go from one flower to the next; they may visit tens or hundreds of flowers on a single foraging trip.[160] Other animals, whether they are searching for mates using pheromones[92] or identifying nestmates,[118] are also likely to encounter variation among odor signals. Variability in the signal itself may, therefore, become an important feature that animals can use while learning to identify salient odors. As might be expected, the sequence of odor experience has been shown to affect which features an animal uses to identify a previously experienced scent.[108] Of particular importance is the presence of common features that occur from one olfactory stimulus to the next. Studies of the behavioral mechanism known as olfactory blocking have shown that an odorant that is common throughout conditioning will become a dominant perceptual feature of subsequently experienced binary mixtures.[161-164] In this case, the presence of an odorant that has the least variability throughout conditioning also acquires the most salience.

A recent study by Wright and Smith (2004a) showed that multiple features of odor mixtures influence which features are used by honeybees to identify previously experienced odors.[165] In particular, the study observed that both variation in the concentration of individual odorants in a mixture and the overall intensity of an odor mixture affected what honeybees learned about odors during conditioning. They conditioned honeybees with mixtures of odorants where the concentration of one odorant remained the same throughout conditioning and the concentration of the other odorants varied. Generalization was greatest from the conditioned mixture to the non-varying odorant. However, this occurred only for odors composed of structurally dissimilar odorants. Generalization was also affected both by the overall amount of variability from one conditioning trial to the next and the average odor intensity experienced during conditioning. Generalization increased when variability in the mixture increased (Fig. 8.6). Honeybees conditioned with mixtures with an average high concentration generalized less to low-concentration odorants. Thus, the second-order statistics of a population of natural odor scenes have been shown to be detectable features used by honeybees to identify salient odors.

Source-to-source odor variation in a population of odor-producing objects may be an important statistical feature affecting olfactory perception and behavior. Another recent study showed that variability in the major-histocompatability-complex (MHC) odor signal and the amount of scent marking by individuals affected scent use by female mice when they were selecting mates.[166] They showed that a

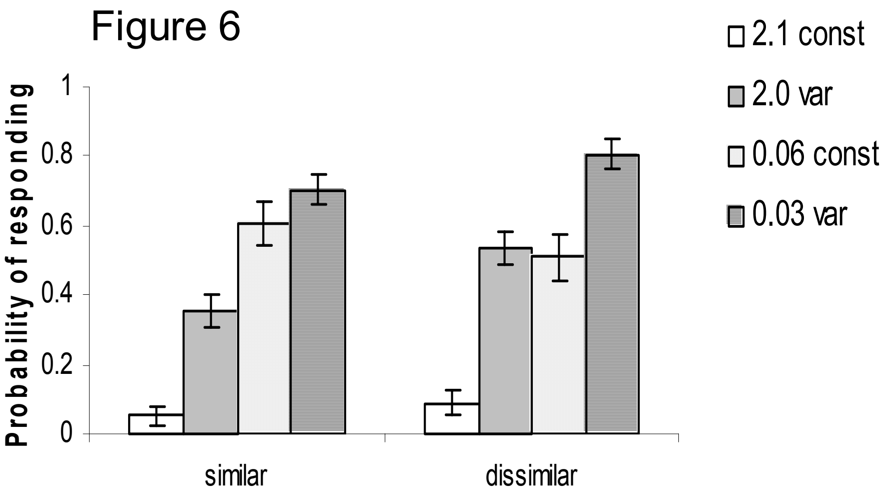


Fig. 8.6: Generalization from one odor stimulus to another increases as a function of variation in odors. Generalization to low concentration odorants is also affected by the intensity of the conditioning mixture. When honeybees were conditioned with high intensity mixtures (2.0 and 2.1 M) they responded less than honeybees conditioned with low intensity mixtures (0.03 and 0.06 M). Honeybees conditioned with highly variable mixtures (*var*) responded with a higher probability than honeybees conditioned with no variation present in the mixture (*const*). Reproduced with the permission of the Royal Society of London.

female mouse determined her genetic similarity to other mice through information about the variability in the MHC complexes and the marking rates of the males she encountered. Variability in the MHC was a function of the population of males she encountered. When variability in the MHC complex was small, a female would use marking rate as a means of choosing a male. In this case, variation in the MHC was used in a context-dependent manner. It is likely that as variation in natural odor scenes becomes easier to measure and more common to report that future studies will also observe that it affects feature recognition by other animals

CONCLUSIONS

The study of the statistics of naturally occurring odor scenes is likely to yield rich information about the way that organisms produce and use scent in their interactions. One approach to studying odor perception and recognition may be via detailed studies that examine both the statistics of natural odor scenes and the way in which animals use these features to generalize among odor scenes. Studies of this kind may show that in addition to second-order features (*i.e.*, variation), the higher-order features of odor scenes are also important features used for odor recognition. As has been shown in the visual and auditory sciences, relating olfactory physiology to the statistics of natural scenes may also lead to insight into the way in which odors are represented by the nervous system. This is true not just at the level of the olfactory periphery but also higher up in the nervous system. Studies of odor coding in the insect antennal lobe and the olfactory bulbs of fish and mammals indicate that higher-order coding at these levels contributes to the way that the brain organizes information about odors,[2] and this higher-order neural coding may provide a means of reliably producing a neural representation in the face of variation in natural stimuli. Future work that examines both the statistics of odors and the physiology of these higher-order odor representations may reveal that the overall morphology of the olfactory system is adapted for the detection and discrimination of specifically those odors that have ecological signification for a given animal.

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