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Theory and methods for odor evaluation

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Introduction

The typical study of the sense of smell is concerned with the effects of a single odor substance. Most of our knowledge therefore applies to pure substances and not complex gas mixtures[27,42,66]. In real life, however, most odors are complex mixtures of various components in rather low concentrations. Although much is still unknown about the functioning of the olfactory system, the knowledge available gives an impressive picture of its capacity[22]. For example, the ability to discriminate among odorous compounds is enormous even in the ever present odorous environment[28]. Further, the sense can handle a wide range of stimulus concentrations and can often detect odor substances at the ppb level[18]. On the other hand, the sense of smell is easily fatigued by continuous and constant odor exposure, though it recovers fast on the termination of exposure[38,42]. The development of optimal methods for sensory odor evaluation using human observers presents both a challenge and a promise, regardless of whether the odor system is used as a measurement tool or as an indicator of environmental pollution.
In the following, theories and methods for odor evaluation are discussed. Examples are given from laboratory as well as field research. Needless to say there is not much difference in the methodological requirements of basic and applied research.

Stimulus control

A large number of different devices for the sensory evaluation of odors have been constructed since the end of the 19th century when Zwaardemaker[104] introduced his classic olfactometer. For the most part the purpose of these devices has been to establish absolute odor thresholds, discrimination thresholds or odor intensity measures according to methods introduced by Gustav Fechner and S. S. Stevens. The measures may be obtained for various single substances or odor mixtures. Some of these devices have been used in clinical neurology in the diagnosis of disorders of the odor sense[45]. In recent decades field equipment has been described for the sensory evaluation of odorous air pollution in buildings, from industrial processes, ill-smelling bodies of water, and other sources.
In diluting odor substances two main principles have been used depending on whether the substance was in the gas or the liquid phases. Gases have been mixed in known proportions with nonodorous gases or mixtures, e.g., nitrogen or clean air. Most olfactometers described are of this type and several surveys have been published[36,61,70,71,98,101]. The other method involves the mixing of a substance in liquid form with a nonodorous solvent after which the mixture is vaporized[42,47,49].

Subjects may be exposed to the target (test) odors in various ways. In principle the exposure system may be static or dynamic. In static exposure the gas mixture is stationary, except for movements due to diffusion or to a subject's inhalation, and involves the use of closed vessels or containers of various types. Dynamic exposure on the other hand requires a continuous flow of gas and from a dosage viewpoint is often to be preferred since it facilitates rapid changes in concentration. Furthermore, the dangers of unintentional variation in odor concentration and composition due to adsorption, chemical decomposition, etc, are reduced. A disadvantage is that movements of the odorous gas may affect the subject's odor perception.
The most common procedure in sensory evaluation of simple odor substances has been to have the subject inhale from the opening of a small container or dosage system[84]. However, a disadvantage in this method is that extraneous elements in the surroundings such as other odors, variation in temperature and humidity, and possible unintentional dilution of the gas may affect the results. Some authors have avoided this by introducing the odorant directly into one or both nostrils[3,37,40,48,52,67]. Another advantage is achieved since pressure and flow volume can be controlled[79]. However, it would seem that this procedure may involve too much of a departure from normal inhalation. Comparative studies have shown that free respiratory conditions result in a significantly higher degree of sensitivity to odors[55].
Efforts have therefore been made to make the exposure to target odors as similar as possible to natural exposure. It has been found suitable to use limited volumes of gases, static or dynamic, in which the concentration of the odorant is stable, where the disturbing influence of other smells and differences in humidity and temperature can be avoided and, finally, in which normal inhalation may be used. These considerations have led many to the construction of odor chambers large enough to accommodate a test subject, sitting completely surrounded by the odorous gas[2,10,29,53,60,83]. However, these arrangements require space and extensive installations. Furthermore, the large volume of gas makes changes in concentration difficult.
Many investigators have chosen the odor hood as the most acceptable way to combine the advantages of the odor chamber with simplicity of construction and operation. In this case only the face or the head is exposed[23,29,61,75,84].
The experience from using different olfactometers may be summarized as follows:
1) To control subject performance as well as psychophysical method the dosage system should deliver reference odors produced in the system.

2) The dosage system should be able to handle test gases with minimal change in the composition of the odor samples and permit a controlled dilution of the samples.
3) Most sensory measurement methods demand that a fast stimulus change can be achieved by the exposure device.
4) The exposure situation should be free from non-target odors since they may create adaptation effects in the test subjects and distort their judgments.

Examples of contemporary olfactometers. In industrial contexts the ASTM method[3] has been widely used. Today, the method is avoided since comparative measurements have shown low reliability. The method may underestimate the odor intensity of a sample by 200–20000 times[86,100].

At present a frequently used, commercially available olfactometer is the Dynamic Triangle Olfactometer[37]. This olfactometer is fairly small and mobile and the test subjects are exposed to different odors at small sniff ports. To compensate for the unintentional dilution with room air during sniffing, it is recommended that the flow through the sniff ports be adjusted in pretests. Since the odor and air mixtures are presented along with samples of clean air, the hits and false alarm rates can be calculated.

A variant of this olfactometer is the dynamic dilution binary scale. By using equipment similar to the Dynamic Triangle Olfactometer a reference odor can be diluted and presented to the test subjects in different concentrations. A reference scale has been established in physical terms for a reference compound, usually n-butanol. By equal-odor intensity matching the subjects can match the intensity of the test odor to the reference concentrations[72,89].

Based on the functional demands described above, a series of mobile olfactometers have been constructed for environmental odor control[10,16,61,103]. These laboratories contain analytical equipment and systems for odorant dosage, an exposure chamber with exposure hoods, and a waiting room for the test subjects. The room for the test subjects is temperature controlled and ventilated with cleaned air. The performance and reliability of the equipment have been assessed in thorough tests[11,61]. The reference system of the olfactometer permits a presentation of many different concentrations of reference gases (hydrogen sulfide, pyridine, n-butanol, acetone, dimethyl monosulfide). The design of the equipment permits the use of a number of different sensory techniques for odor evaluation[16,17,89].

The effective odor stimulus. It is not fully understood to what extent odor perception is influenced by the sniffing behavior of the observer. The odor area of the nasal cavity is poorly ventilated and most of the inhaled air passes through the lower part of the cavity. Apparently the configuration of the nasal cavity creates turbulent air flows when sniffing and the air stream is directed upwards[77]. By increasing the flow rate of the inhaled air, the proportion reaching the olfactory mucosa may be increased from about 5 to 20%[99]. As a result, the number of molecules available to the olfactory receptors also increases with flow rate. Surprisingly, the perceived odor intensity does not always increase with flow rate. Teghtsoonian and associates[90,91] found that observer controlled flow rate does not alter odor intensity and does not change the psychophysical function. However, other studies have shown that an increase in flow rate increases odor detectability[58,74,82] as well as odor intensity[57,79,80]. The different outcomes may be explained by a difference in feedback given to the observers regarding their inhalation behavior[90].

Recordings from the olfactory epithelium have shown that the magnitude of electrical activity increases with the velocity of the applied odor vapor[76]. The discharge rate of olfactory nerves also increases with flow rate of odorous air of constant concentration[5,93,94]. The neurophysiological studies were performed on animal preparations through which the odorous gas was usually sucked. Such preparations behave differently from an intact breathing animal. Comparisons between human and animal olfactory data should therefore be made with great care.

Apart from the olfactory neurons, the nasal mucosa contains free nerve endings of the trigeminal nerve. These nerve endings can be stimulated by a number of chemical and physical variables, and the activity of these neurones interacts with the olfactory nerve response[95]. Several odors are significant irritants, especially at high concentrations. In subjects with unilateral destruction of the trigeminal nerve, the trigeminal component could account for approximately 30% or more of the total perceived intensity of different substances[25]. Doty and associates[33] verified the role of trigeminal input for odor intensity perception by comparing anosmic to normal persons. It is impossible to control for the trigeminal effect on odor perception in humans. All information on odor perception must be viewed as a result of inputs from both the olfactory and the trigeminal nerve.

Sensation measurement methods

Odor evaluation may focus on different descriptors of the odor sensation: detectability of odors, discrimination between odors, perceived odor intensity, odor intensity pattern or profile, odor quality and preference, and finally, acceptability of the odor.

The detectability of odors is commonly determined by the use of classic threshold methods[41,61]. In environmental studies, the method most commonly used for expressing the level of odors is essentially based on the absolute odor threshold as expressed by the number of dilutions necessary to arrive at odorlessness (mixtures). The absolute detection threshold for single chemical substances varies widely. Recognition thresholds (including identification of quality) are generally higher than detection thresholds (detection of the mere presence of the stimulus). Threshold values are to a large extent defined by extra-stimulus factors such as the threshold measurement procedure, the quality of the olfactometer, the purity of the chemical substance, the sample of observers, etc.

Classic threshold theories assume the existence of a momentary absolute sensory threshold. On the other hand signal detection theory[14,41,50] claims that no absolute threshold exists. In signal detection theory sensory excitation from a repeated signal is assumed to have a defined distribution. Furthermore it is assumed that excitation from another origin than the stimulus, for example from spontaneous nerve activity, appears as an integrated part of the sensory response.

The greatest advantage of applying signal detection theory is that both positive and negative false responses can be estimated. Classic threshold methods can only correct for false positive responses. The main drawback of the signal detection approach is the small range of physical quantities that can be investigated within a reasonable number of observations.

In accordance with Weber's law, the ratio (Weber fraction), between the just noticeable difference and the intensity of the stimulus is assumed to be a constant and be characteristic for each sense modality. People can reliably resolve differences in odor concentrations in the range of about 10–50%. The differing results probably depend somewhat on the olfactometric techniques being used[26,85,102].

For odors, as for other sensory stimuli, perceived intensity increases as a power function of concentration[78]. For all odors studied the exponent of the power function is less than unity which means that the olfactory system attenuates the stimulus information more at high concentrations[9,24]. In the measurement of perceived odor intensity, direct scaling methods are the most common. Earlier, such evaluations consisted of simple judgments of the rank order of odor intensity (e.g., weak, moderate, or strong). On such a scale, the interval between categories is not defined. This category or rank order scale does not permit a precise quantification of the odor sensations.

By magnitude estimation or magnitude production methods, the test subjects can quantify their sensations along a broader and more detailed scale that can be related to reference odors. In advanced cases, a battery of odor references are used intermixed with the series of test gas presentations. Such references in combination with transformation procedures allows for comparison of odor sensations from different test objects or compounds[8,21]. Another method is equal-intensity matching with a reference matching variable. Different equipment has been developed for such purposes (e.g., 'finger-span matching', Ekman et al.[38]; 'hydrogen sulfide odor matching', Lindvall and Svensson[65]; 'n-butanol odor matching', Moskowitz et al.[72]). For further information on scaling methods, consult Marks[69] and Baird and Noma[4] and particularily for the scaling of odors, Cain and Moskowitz[30] and Lindvall[63].

Theories on olfactory coding (which are dealt with in another chapter of this book) are intimately linked to various ideas of odor classification. A classification of odorous compounds can be made by grouping the chemicals according to how congruently they function in mixtures or in cross-adaptation[7,54]. Experiments on discrimination of odor intensity and quality can also be used for obtaining information on odor quality[46,56].

While much of the earlier research on odor quality was aimed at classifying odor substances, more recent research has been oriented towards a mapping of odor qualities. One way of studying odor maps or spaces is to use multidimensional scaling techniques based on similarity/difference judgments. The data are analyzed according to different mathematical models[31,39,51]. Doty et al.[34] have proposed standardized quality identification tests for different odors. This approach aims at testing broad parts of the human odor sensitivity spectrum, mainly for use in medical examinations.

To some degree odor pleasantness/unpleasantness can be judged by the same techniques used for scaling odor intensity[44,65,73]. One problem with judgments of pleasantness/unpleasantness is that observers vary much more in their hedonic judgments than in their intensity judgments[9,73]. Unpleasant odors form a special problem in air pollution control. Because odor pollution is often difficult to analyze by chemical methods, owing to its complexity and low concentration levels, sensory analysis is frequently used in field experiments[59]. From a methodological point of view it should be emphasized that in psychophysical studies it is critical that the perceived intensity of odors be controlled if qualitative and hedonic aspects are to be separated.

The extent to which unpleasant odors are annoying to a community must ultimately be assessed by scaling annoyance in epidemiological studies. Only then can all the conditions that determine the acceptability of an odor be considered, e.g. living and exposure conditions and observer attitudes towards the source[64]. In annoyance surveys using self-rating questions, relevant psychometric methods should be used[15]. As with other sensation measurements, annoyance measurements should result in calibrated measures that permit comparisons between different objects (exposed areas), fulfilling the assumptions for commonly used statistical procedures, and thus enabling the determination of meaningful dose-response relationships.

Quality control and quality assurance

As with other measurements obtained in the natural sciences, sensory measures must be calibrated. The expression 'calibration' is used here in its broad sense. Sometimes, calibration is necessary to validate the odor measurements, at other times, to increase comparability between the results from different studies. In such analytical control, odor references or standards are necessary. More recent investigations have used reference substances such as acetone, hydrogen sulfide, dimethyl monosulfide and pyridine[6,9,13,20,65]. In order to calibrate sensory scales it is not enough to set the scale value for one stimulus to an equal level and then transform data by multiplication. A safer approach is to match for equal-intensity with a matching continuum or to use a Master Scale for scale calibration[8,19,21,65,72].

It is evident from the literature that different laboratories often obtain very different results for absolute odor threshold determinations of single compounds[61]. The reason for this may be small chemical differences in the odorants tested or differences in the psychometric approach and in the dose/exposure equipment. A simple standardization of the olfactometric procedure is not to be sought because the aims of the research with olfactometers differ considerably and flexibility has to be retained. But there is a definite need to introduce a set of calibration procedures to make it easier to compare results from different laboratories. Such quality assurance or quality control is especially important in applied research and when sensory procedures are used in environmental control.

Quality assurance refers to all steps which may be taken to ensure that data are reliable. As presently discussed in the World Health Organization, quality assurance covers the utilization of scientifically and technically sound practices for the collection, transport and storage of samples, the laboratory analysis, as well as the recording, reporting and interpretation of results. More specifically, quality control has two components: One is external quality control, which is a system for objective checking of laboratory performance by an external group, and the other is internal quality control which is a set of procedures used by the staff of a laboratory for continuously assessing results as they are produced in order to decide whether they are reliable enough to be released. It is not sufficient that laboratory analyses are subject to internal quality control procedures alone. To ensure accuracy of results from an individual laboratory and to guarantee comparability among different laboratories, external quality assurance must also be practised.

Much environmental research concerns sensory thresholds. Since the goal is to arrive at absolute threshold values for detection, the need for quality control is evident. A comparison of odor thresholds for one single compound can be made in the following way. First, one must introduce a reference odorant to be determined by the laboratory in the same context as the test odorant. This gives a practical check on such intervening factors as a possible biased selection of observers and differences in adaptive state. Second, when the investigator has decided upon a certain absolute odor threshold of the test odorant, it is recommended that this specific threshold concentration be studied by a signal detection approach. As mentioned before, methods based on signal detection theory permit a check not only of the existence of false positive responses on the part of the observer but also the existence of false negative responses. This means that an observer who does not perform satisfactorily, for example due to lack of motivation, will not distort the results. A high detectability index, as measured by the signal detection approach, of the threshold concentration of the test odorant would indicate that the threshold determination was not properly done. Of course there is a need to agree upon the detection level to be accepted.

In many applied contexts, signal detection methods are superior to classic threshold methods. The technique is less dependent on background factors of a social-psychological nature. The method is not independent of sensory and physiological factors such as adaptation, varying background noise levels, etc. Therefore, it needs to be standardized for practical use. From a psychological point of view, the method is limited in that only detectable differences are measured. However, unlike absolute threshold values, it has been possible to relate meaningfully indices of detectability to perceived odor strength[14,41]. Clearly, in quality assurance of odor measurement the introduction of well defined odor reference substances is a primary requirement. Such a reference odorant is a prerequisite in the laboratory calibration of both threshold studies and odor intensity studies. Securing results with a signal detection method furnishes supplementary internal checks on the reliability of the detection measures obtained by classic methods.

Moskowitz et al.[72] has proposed a standardized way to express the perceived intensity of odors. The technique is based on the use of a reference scale of n-butanol. Its psychophysical power function was estimated from the results of four different laboratory experiments to have an exponent of 0.66 and a multiplicative constant of 0.261. They suggest that n-butanol should serve as a standard odor reference for matching odorants in terms of perceived odor intensity. The results of the intensity matches (expressed in n-butanol concentration) may then be expressed not only in units of concentration but also in terms of subjective odor intensity (by transforming with the aid of the standardized power function for n-butanol).

An equal-sensation matching procedure for obtaining calibrated unpleasantness scales has been suggested by Lindvall and Svensson[65] and applied to the odor measurement of complex gas mixtures (combustible animal manures). They used hydrogen sulfide as the reference gas and a matching procedure of successive approximation developed for fast and simple measurement in applied or field contexts[89]. The calibrated equal-sensation matching method has been carefully checked in repeated investigations as to its validity as well as practical reliability[87,88].

One of the central problems in assessing perceptions of odors is that different persons make judgments widely separated in time, context, and compounds. This makes it difficult to compare judgments between experiments because it is clear that individual differences exist in people's perception of odors and in their response behavior, and thus also in their estimates of equal-sensation matches. Berglund and associates have solved this problem by constructing a Master Scale with a reference odor that can be used as a common reference for all judgments of odors independent of the judgment peculiarities of individual subjects serving in the specific experiment. Such a scale provides a defined unit of measurement of the attribute while the procedure for obtaining it will not destroy the information about the observer's individual differences in scaling performance. When applied to a psychophysical problem, the target odor can be expressed in terms of the perceptual or physical units of the master function[17,19,21].

The introduction of reference odors in the psychophysical experiment requires that the reference odor does not distort the detection and perception of the target odor. The psychophysical scaling of the master substance and the target odor jointly should not affect either of the two scales of perceived odor intensity, i.e., no specific interaction should take place. Furthermore, the reference master substance should be technically easy to produce and measure, and perceptually distinct and easy to discriminate in small steps over a wide range of perceived intensities.

It is important which version of a direct scaling method is used for obtaining the odor intensity estimates. For example, the use of a 'homo-quality' standard can diminish the response range for weak stimuli more than a 'hetero-quality' standard will do. Although not conclusive, the current data would support a matching procedure, either involving the matching of numbers (free-number estimation) or cross-modal matching of other modalities[17].

It has also been shown that range effects are important in odor measurement. When stimulus range is varied, a common finding is that the exponent of the psychophysical function is increased when concentration range is decreased. The range effect may be attributed to scaling biases but also to a true sensory process. The Master Scale has been shown to diminish this scaling bias[8].
In summary, the use of a master scale function would provide the following advantages: 1) serve as an indicator of observer scaling behavior, 2) be used for calibrating perceptual scales, 3) make standardization possible by the aid of the psychophysical function of the master substance, 4) control for the range effect of perceptual scales.
Part of the variation in sensory odor measurement is due to differences in sensitivity within panels and panel members. This variability is partly caused by differences in age, physiological state, anatomical characteristics, etc. But usually these differences are not predictable. Therefore, it is important that test subjects employed for odor measurements be selected so that the effect of these factors is controlled.
The ideal solution would be to use large samples from well defined population groups. Usually, practical considerations require the use of smaller groups, 'odor panels', selected with respect to odor sensitivity and consistency. After being trained in the experimental task, such panels have proved themselves to be faster, more sensitive and consistent at reporting than large probability samples. These considerations may outweigh the lack of representativeness of the small panel.
The age of the subjects is a main determinant of odor sensitivity. If the purpose of the odor measurement is to estimate the odor incidence in the surroundings of an industrial plant, the ages of the members of the panel should mirror the population age distribution. But, if the purpose of the measurement is to compare different odor sources, cleaning devices, or odor profiles of complex gas mixtures, the investigator will usually gain by employing fairly young test subjects. Such a panel will show more consistent sensitivity. In practice, there is no important difference in sensitivity between sexes or between smokers and nonsmokers. The selection of panel members, however, should consider a broader range of intervening variables than discussed here[61,62,96,97].

Clinical studies

In clinical neurology, odor measurements are being used as part of the test battery in the neurological examination. Abnormalities of the sense of smell are many and varied[32,35,81]. The symptoms may involve quantitative changes (anosmia, hyposmia, and hyperosmia) as well as qualitative changes (peripheral or central parosmia). In testing the sense of smell in clinical practice, the perceptual task may focus on a number of functional features: sensitivity, capacity and tolerance, supraliminal intensity, quality discrimination, veridicality, and sometimes also physiological correlates[45]. Usually, sensory evaluation in clinical practice uses threshold methods, primarily for testing sensitivity. In real life, however, quality discrimination and veridicality are important, i.e., perception of differences between odor molecules and ability to identify odorants by name. Odor discrimination testing usually involves the comparison of successively presented stimuli because attempts to present two odors simultaneously to the separate nostrils tend to make it difficult for the test subject to separate the component parts. Such short-term odor recognition memory tests have been tried, i.e., by Engen and associates[43,68]. Recently, Doty et al.[34] have developed the University of Pennsylvania Smell Identification Test. It is a 40-item multiple choice test, each item consisting of odorant crystals microencapsulated on strips to be scratched by the subject and then to be smelled and labeled according to specified response alternatives. For clinical screening, the UPSI test is at present the most attractive approach.
Abnormalities of the sense of smell are known to be inherited. In recent years, there has been growing concern about occupationally acquired odor deficits. For instance, Ahlström et al.[1] reported recruitment effects (a steepened psychophysical function) of perceived odor intensity for workers exposed to petroleum products.

Population studies

A recurrent problem in environmental research is to quantify annoyance due to disturbing factors in the community, such as malodors. The typical approach has been the sociological survey, but one difficulty in such surveys is the selection of an attribute that adequately reflects people's conception of environmental factors. A further difficulty is the scaling of the environmental variables quantitatively, as they are perceived. Scales measuring the annoyance caused by odor but obtained from different populations will give different units of measurement, and annoyance scales cannot be compared adequately unless they are calibrated. Berglund and associates[12] proposed a calibration procedure in the scaling of odor annoyance by introducing a defined psychological unit of measurement into the data. For calibration purposes portable standard odors were presented and their annoyance scale values were compared to the annoyance scale values of previously experienced traffic noise. The procedure was applied to four odor-polluted areas around a pulp mill. Thurstonian scaling[92] was applied to the response frequencies obtained from a 400 person (probability) sample of interview responses. The Thurstonian solution permitted the calculation of a single measure (for each area) of odor annoyance with the same assumptions as with traditional calculations of proportions of respondents. Further, since the measurements were made on an interval scale, they allowed a grading of odor stimuli with respect to mean degree of annoyance in each area.
From a psychometric point of view the following recommendations are suggested to improve the annoyance scaling based on self-rating questions in epidemiological studies (Berglund, Berglund and Lindvall[15]):
a) Whenever economically possible, the distribution and average degree of population annoyance should be determined. b) To permit such scaling the questionnaire must include a large number of response categories (at least 6), preferably using only adverbs of degree as modifiers of the annoyance adjective. c) The survey should include questions on the annoyance evoked by several environmental agents, not only by the target factor. d) To allow for satisfactory data treatment, subsamples of respon-

dents must be comparatively large; ideally at least 200 persons are needed in each subsample to get a reliable population measure of annoyance. e) If areas or populations are to be compared, the annoyance scales must be calibrated. Such a calibration is particularly necessary when annoyance responses to different environmental agents are to be determined. To achieve this, at least two reference anchors must be introduced into the survey.

There is a strong need for the development of suitable reference anchors for practical work. Further, it is desirable that the quality of the annoyance measurements be raised above the currently usual rank order information. Several psychophysical procedures can be applied in the survey questionnaire and in the personal interview in order to reach this goal.

Epilogue

Theories and methods of odor evaluation are used as substitutes for chemical measurement, for investigating the contamination of odors, or for monitoring air pollution. These applications require deep knowledge in odor science but particularly in odor psychophysics, since the sense of smell of humans is involved. It is a fact that odor molecules are odorless if nobody smells them.

As with the natural sciences, the evolution of the research from the stationary laboratory into the natural field environment brings with it great possibilities, but also difficulties to be overcome. The real life situation will always be superior with regard to the representativeness of the stimulus and the representativeness of the population. On the other hand, field research is less promising for developing research methods and theory since it involves a trade-off between precision and representativeness.

In recent years applied odor psychophysics has created a great research tool in the mobile olfactometer, which allows subjects to breathe naturally when sampling the odorous gas mixtures of the environment (presented in hoods or chambers). The development of methods for measuring odor detection and perception during the sixties has now been supplemented with procedures for calibrating sensory scales. The calibration of odor scales is an example of this modern trend. Systems for quality assurance of odor measurements are currently under discussion. When the full potential of sensory methods has been realized in applied odor research, whether it involves personal interviews, questionnaires or field experiments, the measurement of subjective and of objective phenomena are indistinguishable.

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Speculations on receptor cells as analyzers and filters

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Key words. Odor biology; receptor cells; receptor morphology; analyzers.

The contributions to this volume document the rapid increase in knowledge of olfactory neuroscience which has occurred during the past decade and the exciting prospects for future progress. Much has been learned about the cell biology of olfactory neurons and other cells constituting olfactory tissues. The physiological and behavioral roles of chemosensory organs in a variety of organisms have been explored and a rational teleology is emerging. Anatomical and developmental knowledge is in a stage of explosive growth and, as a result, many of the naive assumptions of a decade ago are being discarded. The synthetic capabilities of fragrance chemists have led to what will probably be precise establishment of the chemical basis for perceptual experience. In spite of all this, there are major shortcomings in what we know and understand.

For the chemical senses of all organisms, from bacteria to primates, there are two central questions. 1. How do these senses work? 2. What do they do? Much of this volume addresses the second question. We know less about the first.

Bacterial chemoreception is best understood[30]. The complex chemotactic behavior of *Escherichia coli* has been dissected using genetic mutants. There are separate receptor proteins for each of the many different stimulus substances which can influence movement. Receptor messages are integrated by transducer proteins. These in turn modify the proteins which control the motile flagella. In higher organisms, although comparable mechanisms are postulated, the nature of the receptors on the sensory neurons is not known. Nor is it possible to predict how different receptor cells will differ in their responses to a stimulus or how the resulting differences in cellular activity are processed by the nervous apparatus to direct an orderly change in behavior.

In this chapter a variety of experimental evidence is interpreted to imply that olfactory receptor neurons are more than simple stimulus detectors. The hypothesis is advanced that the unusual morphological features of these cells and tissues are accompanied by biochemical and physiological specializations. These specializations within the sensory neurons serve to maximize signal-to-noise ratios, integrate accumulated stimulus action, and suppress responses which do not carry meaningful olfactory information.

A. Receptor morphology

The somata of the receptor neurons in vertebrates are located in epithelia lining the nasal cavity. Each neuron has a single dendrite which projects to the epithelial surface. It terminates in an olfactory knob from which grow either cilia or microvilli. Proximal to the knob tight junctions connect dendrites to the apical regions of enveloping supporting cells[4]. These junctions form a diffusion barrier which prevents ionic and stimulus substance fluxes between the receptor surface and the rest of the extracellular space of the epithelium. Receptor neuron dendrites lie in separate invaginations in supporting cells[11, 23]. These isolate each neuronal dendrite from its neighbors and (probably) allow rigorous control by the supporting cell of the ionic composition of the fluid surrounding the dendrite. Dendrites are of various lengths and small diameters. The cell bodies from which they grow are large. They are not enveloped by supporting cells. Instead they are jam packed against each other. The dendrites in vertebrates are 1–2 μm in diameter and 20–100 μm long. These long, thin processes expand dramatically in cross-sectional area to form cell somata, typically