# THEORIES OF OLFACTION: A REVIEW

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## INTRODUCTION

Modern man tends to relegate the olfactory sense to a position of secondary importance with respect to the auditory and visual senses. However, the purely aesthetic value of olfaction in the enhancement of flavor and the enjoyment of food, as well as the more important adaptive aspect which enables man to interpret his environment in the absence of visual sense, are not to be discounted in the evaluation of this little understood sensory system. A contributory factor to this secondary relegation of olfaction may be its relative inaccessibility to experimentation. This was one of the conclusions arrived at by Kalmus and Hubbard (1960). These investigators view olfaction not only as subjective phenomenon, but also as straddling the perennial gulf between the objective and the subjective. In spite of these difficulties, many investigators feel that the intrinsic values to be garnered in the study of olfaction are as many and diverse and they are unexplored. Snider (1964) feels that the study of olfactory phenomena may lead to unexpected benefits for mankind, such as improvements in industrial hygiene, progress in nutrition through the analysis of complex flavors of foods and drinks, the elimination of obnoxious odors, the synthesis of any desired odor, the possible development of an artificial olfactory apparatus or nose as an aid to criminologists and in anosmic prosthesis, and as a useful tool in diagnostic medicine.

Thus it would seem that this long neglected sensory area is in need of systematic, thorough investigation, both from the point of view of pure science as well as the more applied areas of psychology.

## PARAMETERS OF OLFACTORY STIMULATION

It would seem logical that no discussion of any sensory modality would be sufficient without a discussion of the basic stimulus parameters. Jones and Jones (1953) review some of the requisite properties of odorous substances which have been traditionally considered to be necessary for olfactory perception. In general, these conditions are as follows: (a) It must be to some degree volatile at room temperature, (b) it must be at least a trace soluble in water, (c) it must be within certain limits as to molecular weight (not too high), (d) it must be to some degree soluble in lipoids. Jones and Jones (1953) discuss the validity of these conditions and state that there is no absolute agreement between scientists on these points. Stevens (1951) reports that it is very probable that no one physical property alone is involved in the physical nature of the adequate stimulus. Stevens feels that in order for a substance to be "smellable," that substance must be volatile at ordinary temperatures and must also be soluble in lipoids.

In general, it may be stated that organic compounds make up the greatest class of odorous substances. The adequate stimulus is dependent upon volatility, solubility in lipoids, total molecular structure, and spatial arrangements within the different forms of the same compounds (Haagen-Smit, 1952). It should be noted that when one breathes through the nose the air stream does not pass over the olfactory receptors, but reaches them indirectly by radiation and convection currents (Wyburn, *et al.*, 1964).

In spite of the relative inaccessibility of the olfactory receptors, odorous substances can be detected at extremely low concentrations (Stevens, 1951). In terms of concentrations of molecules, it has been estimated that olfaction is ten thousand times as sensitive as the sense of taste (Moncrieff, 1946). Threshold values as obtained by the dilution method yielded threshold concentrations for ethyl mercaptan of $4 \times 10^{-5}$ milligrams per liter of air (Moncrieff, 1946). In general, the absolute threshold for smell varies considerably between individuals as within individuals from time to time, but all results tend to agree on a high degree of sensitivity on the part of the olfactory mechanism.

## PHYSIOLOGICAL MECHANISMS INVOLVED IN OLFACTION

The organ of smell is located on the wall of each side of the nasal cavity and is known as the olfactory epithelium (Wyburn, *et al.*, 1964). The olfactory epithelium is composed of three types of cells: (1) the pigmented columnar cells whose function is mainly one of support; (2) the basal cells which constitute the material upon which the epithelium is based; and (3) the olfactory receptor cells (Morgan and Stellar, 1950). The densely packed olfactory receptors range in density from 62,000/mm$^2$ in the pig (a microsmatic animal) to 127,000/mm$^2$ in the rabbia (a macrosmatic animal) with a total of one hundred million in the latter (Gasser, 1956). Biedler (1961) points out differences in receptor morphology which may be related to a differential sensitivity to odors and thus, may be as possible basis for odor quality discrimination. Neural projections leave these receptor cells and collect into bundles forming the olfactory nerve fibers. These fibers pass through the bony roof of the nasal cavity to terminate in the olfactory bulb. The olfactory bulbs develop from the cerebral hemispheres and thus, the olfactory neural apparatus is unique in that its receptors are directly connected with the cerebrum. The olfactory area of the cortex has connections with many other parts of the brain, and in this way makes its contribution to the sensory component of conscious activity (Wyburn, *et al.*, 1964).

Wyburn, *et al.* (1964), point out that the olfactory sense has an adequate neural apparatus to make use of the variables of the impulse code and sort out the information which it delivers to the cerebral cortex in terms of both the strength and diversity of smell properties of the stimulating substances. It has already been noted that there are structural differences in the olfactory receptors. Electrical changes caused by the potentials generated in the receptors can be recorded from the surface of the olfactory epithelium when it is stimulated by odorous substances. The amplitude of the electrical responses varies in different regions of the olfactory epithelium according to the density of the receptors, and the records confirm that localized groups of receptors are particularly receptive to different odors. The shape, the duration, and the latency period of the reported response is related to the strength of the stimulus (Wyburn, *et al.*, 1964).

## CLASSIFICATORY SYSTEMS OF OLFACTORY QUALITY

The early attempts at the formulation of olfactory theories centered around systems of classifying odors. Among the first of these systems was that proposed by the great taxonomist Linnaeus, who felt that plant odors could be placed into seven classes: (1) aromatic, (2) fragrant, (3) ambrosiac, (4) alliaceous, (5) hircine, (6) foul, and (7) nauseous. Haller in 1753 offered a threefold classification: (1) sweet-smelling or ambrosiac odors, (2) intermediate odors, (3) stenches. In addition to these theories, there were also two 18th century classifications based on chemical characteristics of the odoriferous substances, one by Lorry in 1784 and one by Foureroy in 1798. Previous to Zwaardemaker, there were five little-known attempts in the 19th century. In 1895, Zwaardemaker accepted the classification schema of Linneaus and added one class from Lorry's list and one class from that of Haller to give a total of nine primary odors: (1) ethereal, (2) aromatic, (3) fragrant, (4) ambrosiac, (5) alliaceous, (6) empyreumatic, (7) hircine, (8) foul, and (9) nauseous. Henning, in 1915, after extensive research, developed a classificatory schema involving six principal groups of odors which could be arranged in a geometric form known as Henning's Smell Prism. According to Henning, the odors could be placed in the following classes: (1) ethereal, (2) fragrant, (3) spicy, (4) resinous, (5) burnt, and (6) putrid (Boring, 1942).

Rimmel also proposed a theory which contained a very large number of classes. It should be noted that Rimmel's system of classification was intended for the perfume manufacturer, rather than as a systematic classification of odors on a physiological or constitutional basis. Crocker and Henderson have also proposed a theory whereby four kinds of smell nerves were postulated, corresponding to the following odor classes: (1) fragrant, (2) acid, (3) burnt, and (4) caprylic or goatlike. Any given odor may contain all four of these fundamental odors, and their relative degrees of stimulation were considered to be the determining factors governing the individuality of the odor (Moncrieff, 1946). Crocker and Henderson (Boring, 1942) also utilized the first numerical coding system to aid in the application of their classificatory system.

Some of the more recent theories proposing classifications of odors include Duncan and Amoore. Duncan (Wendt, 1952), using a technique identical to independent threshold determinations, obtained results suggesting the presence of a large, though limited number of primary odors. Those odors supposedly are based on receptor action, but Wendt (1952) did not specify the nature of the receptor action nor did he list the specific classes proposed by Duncan. Amoore (Benjamin, *et al.*, 1965) includes a classification of odors as part of a more comprehensive theory of olfaction. These classes are as follows: (1) camphoraceous, (2) pungent, (3) ethereal, (4) floral, (5) pepperminty, (6) musky, and (7) putrid.

In spite of the vast amount of work that has been concerned with the classification of odors, Jones and Jones (1953), in an excellent review, point out a few of the reasons for the abandonment of this approach by current olfactory theorists. Among these are the following: (1) some substances change odor quality with changes in concentration, (2) very similar odors may be caused by different compounds which differ greatly in molecular structure, (3) stereoisomers may have different odors, (4) compounds which are very similar chemically may have quite different odors, and (5) it has not been possible to predict the odor of a compound, or even whether it will be odorous, from a chemical structure. It should be noted that the recent classification put forth by Amoore has been able to overcome several of these criticisms as indicated by the number of investigations conducted by Amoore and his cohorts.

## MAJOR THEORIES OF OLFACTORY PERCEPTION

Because of the multiplicity and inadequacy of the earlier theories of olfaction, no attempt will be made in this paper to discuss these theories. Interested readers are referred to Moncrieff (1946), Boring (1942), or Jones and Jones (1953).

For practical purposes an arbitrary modification of the tentative classification of the theories of olfaction proposed by Jones and Jones (1953) will be utilized throughout the remainder of the paper.

I. *Radiation Theories*

The use of the term "radiation" may mislead a partially informed student of olfactory theories. In the system proposed by Jones and Jones (1953), radiation theories refer to theories which postulate emanations from the source of the odor in the form of waves or radiations. The theory of Teudt may be considered representative of this type of theory. Teudt states that electron vibrations in the atom or molecule set up vibrations in the surrounding medium, these in turn are reinforced by resonance. The olfactory nerves are assumed to have similar electrical vibrations with a minor differences between nerves, and molecules of odorous substances will reinforce those whose period of vibration corresponds to their own. The different rates of vibration are perceived as different odor qualities. Needless to say, these thories have long since been refused (Jones and Jones, 1953).

II. *Vibrational Theories*

A. Ultraviolet Theory

Heyninx (Moncrieff, 1946) pointed out that odorous substances which gave ultraviolet absorption bands consisted of molecules vibrating with a period equal to that of the ultraviolet light they absorbed. Differences in the qualities attributed to different odors would then be due to different frequencies of vibrations which could be determined from the ultraviolet absorption bands. Moncrieff (1946) argues that hydrogen cyanide and water have identical absorption bands but different odors. Jones and Jones (1939) point out various other inconsistencies which have led to the negation of the ultraviolet theories.

B. Raman Shift Theory

The Raman Shift is an optical phenomenon in which a substance radiated by light of one wavelength may give off wavelengths both shorter and longer than the original light. The difference between the wavelength of the light with which the substance is irradiated and the wavelength that is reflected is called the Raman Shift.

The first theorist to attempt utilization of the Raman Shift in an explanation of olfactory phenomena was Dyson in 1928. Dyson (Jones and Jones, 1953) believed that certain internal vibrations of the molecules were responsible for odor and that these intramolecular vibrations may be measured by utilizing the Raman Spectrum. All substances with odors have a Raman Shift between 140 and 350 millimicrons and substances with similar Raman Shifts have similar odors (Morgan and Stellar, 1950).

R. H. Wright (1961) has found evidence to support the theory of involvement of the Raman effect in olfaction; however, exceptions to the theory have been found. Young, Pletcher, and N. Wright (1948) have identified compounds which are characterized by the same odor, but exhibit different Raman Shifts, and also substances with different odors and identical Raman Shifts. Another criticism against Dyson's theory is that glycerin, which is odorless, has absorption bands in the Raman Spectrum (Jones and Jones, 1953).

C. Infra-Red Theories.

Early in the history of olfactory investigations, Faraday pointed out a relationship between odors and the infrared spectrum (Moncrieff, 1946). Glasser (1950) mentions that Ogle was the first to formulate an infrared theory of olfaction. Okle reasoned that since the auditory and visual receptors respond to waves, it might be assumed that the pigmentation in the nose also might respond to radiation and suggested that the radiation was within the infra-red spectrum.

Probably the most famous proponents of an infra-red theory of olfaction are Beck and Miles (1947). Utilizing insects in their experimentation, these investigators report that the receptor elements radiate selectively, depending upon size and shape, and when any odorous substance comes within the radiation field of the receptors, it causes them to lose energy because of the infra-red absorption characteristics of the substance. This loss of energy initiates the neural impulse. Because the receptors radiate selectively and the substances presumably have different infra-red absorption spectra, certain receptors will be stimulated by some substances and certain others by other substances (Beck and Miles, 1947).

Morgan and Stellar (1950) state that there are certain substances which smell (paraffin and carbon disulfide) but have no absorption curves within the infra-red spectrum. There are also others such as carbon dioxide and water vapor which possess no odorous properties but do exhibit absorption of infra-red radiation. In addition, the previously cited criticisms of Young, *et al.* (1948), with respect to the Raman Shift theories are also applicable to infra-red theories.

In the face of these criticisms, Miles (1949) attempted to reformulate his infra-red theory of olfaction by postulating that the odorous substance is absorbed as a film only one molecule thick on the surface of the olfactory receptor cells, and that cells, which contain an optically active compound, react chemically. This chemical reactivity of the receptor cells serve to initiate the neural impulse. It might be stated that in attempting to modify his theory, Beck has rendered it too cumbersome for practical use (Jones and Jones, 1953).

III. *Mechanical Theories*

Jones and Jones (1953) list only one purely mechanical theory, that of Banerji. This theory states that air movement in the nose sets the olfactory hairs into vibration, and this vibration is then modulated by odorous particles according to their own molecular weight and momentum. This theory has one observation in its favor, the fact that odor sensation occurs only when a stream of air is in motion through the nasal cavity. The major criticism of this theory is the fact that odor quality has not been found to be correlated with molecular weight. It should be noted that Ueki and Domino (1961), utilizing neurological investigations with maccaques, have found evidence suggesting the existence of mechanical receptors within the olfactory epithelium.

IV. *Stimulus Pattern Theories*

Perhaps the most extensive work in the electrophysiological area of olfaction has been conducted by Adrian (Weddel, 1955). The depth and detail of the findings of Adrian will not be discussed in this paper; however, Adrian has proposed a unique type of theory to explain olfactory qualities. In brief, this theory proposes that different odors stimulate maximally different regions of the olfactory membrane, and that the basis of this differentiation lies in the physical properties of the odors and the eddy currents in the nasal passage (Geldard, 1950). Adrian has revised his theory and now believes that spatial patterning, coupled with some temporal differences in time of arousal and response decay, is sufficient to account for quality (Jones and Jones, 1953). The major criticisms of Adrian's theory are that other experimenters have not been able to replicate his findings and that he does not account for olfactory stimulation (Jones and Jones, 1953).

V. *Chemical Theories*

The chemical theories contain many and diverse formulations relating olfaction to the chemical properties of the receptors and/or stimuli. Again, an extensive review of the chemical theories of olfaction will not be attempted in this paper, and the interested reader is referred to Jones and Jones (1953) and Moncrieff (1946).

Mullins (1955) has measured the olfactory thresholds for homologous series of paraffins, alcohols, and chloroparaffins, all of these having different solubility parameters. He postulates that there exists in the olfactory epithelium at least two, and probably more, types of receptors, each of which possesses a different solubility parameter. In addition to the property of solubility, the molecular shape of the molecule is also important in determining olfactory thresholds. It is theorized that the receptor membrances contain a number of pores of different size, which are distributed in random fashion over the receptor surface. An odorous molecule of the same size as the pore will excite this portion of the receptor surface, but will render insensitive all larger pores. The concentration necessary to excite some receptor types is more than sufficient to narcotize others; consequently, total response decline occurs and adaptation takes place. Very large molecules do not find a sufficient number of suitable pores to completely excite the membrane, thus, they have no odors. The major criticisms of this theory is that the hypothetical pores have not been demonstrated.

Another theory, that of Heusgham and Gerebtzoff (Pfaffmann, 1956) emphasizes properties of the receptors as a basis for a theory of stimulation. They provide a biochemical analysis of the lipids of the olfactory mucosa, with particular concern for the yellow pigment. Unfortunately, the many theories of this type attempt to explain only one or a few of the many aspects involved in olfaction.

Haagan-Smit (1952), a biochemist, also favors a chemical theory of olfaction. Specifically, Haagen-Smit postulates that odoriferous substances act by interfering with enzyme catalyzed reactions in the olfactory receptors. In addition, since enzymes are affected in their reactions by exceedingly small amounts of a variety of substances, this theory, according to Haagan-Smit, explains the high sensitivity and great range of our sense of smell. The rapid reversibility of the inhibitory effects of enzymes would account for the rapid recovery of the receptor systems to normal, thus enabling the perception of new odoriferous stimuli.

Stoll (Wenzel, 1954) reports still another theory on variations in odor associated with an homologous series of bicyclic farnesyl synthetic compounds. Intensity of odor, he feels, decreases with molecular weight and character of odor changes as well. He believes that both the intensity and character of odor are determined by the form and size of the molecules, while the functional groups are only partially influential. Stoll suggests that there are fewer receptive centers for relatively larger molecules.

Briggs and Duncan (Benjamin, *et al.*, 1965) have confirmed the presence of carotenoids in the olfactory epithelium of cows and dags; and have thus revived the old theory that carotenoids play an important role in olfaction, which is analogous to their role in vision. Moulton (Benjamin, *et al.*, 1965) criticized this theory on the grounds that he has demonstrated species differences in the distribution of these pigments in the olfactory mucosa. In some species, such as rats and pigs, thre is no evidence of carotenoid material in the receptor cells. Briggs and Duncan support their theory with evidence indicating that the recovery of the ability to detect odors in anosmics occurs following the administration of vitamin A. Other investigators disagree and ascribe vitamin A effects to non-specific changes that affect the nasal mucosa.

### VI. *Steric Theories*

Troland has proposed one of the very few theories which attempt to account for all of the psychophysical problems, and one of his key concepts is a steric factor (Jones and Jones, 1953). Troland provides for the mechanism of stimulation by postulating that molecules are adsorbed on the surfaces of the olfactory hairs or cells, which depolarizes the receptor and thus sets off the neural impulees. Olfactory quality is determined primarily by the timing of the nerve impulses, although Troland did not elaborate on this point. Intensity of odor is accounted for by either the total number of similarly excited fibers or by the total number of impulses in the olfactory nerve. He also suggests that olfactory qualities may be spread out in a type of uni-dimensional olfactory spectrum, rather than being classifiable into a definite number of basic types. Jones and Jones (1953) feel that Troland's theory is among the most sophisticated in the field.

Pauling (Jones and Jones, 1953) has proposed a "lock and key" theory of olfaction which he has derived from his studies of the specificity of antibodies and enzymes. This theory is attractive because olfactory responses appear to be of the same approximate order of specificity as the enzymes and antibodies response. In general, it appears that Pauling favors a "molecular shape" theory.

Wendt (1952) feels that the "site filling" theory of Moncrieff which postulates that the molecules of the receptors have surface structures into which the structures of odorous molecules can fit, has merit. Beets (Wendt, 1952) has voiced strenuous objections to Moncrieff's theory of a relationship between unsaturation, resonance, and odor on the grounds that the alleged increase in molecular flexibility with resonance or unsaturation is not true.

Davies and Taylor studied the activity of odorants in accelerating the process of hemolysis of the red blood cells. Their data supports a theory of penetration of the sense cells by the olfactory stimuli (Pfauffmann, 1956). Needless to say, their theory has been hotly disputed, leading to a revision by Davies and Taylor (1959). Their new theory attempts to account for olfactory phenomena utilizing the molecular shape, size, and partition properties of the odorous molecules. The theory accounts for the olfactory threshold of a number of substances, but does not take into account odor quality or the relation between intensity of sensation and odor concentrations.

VII. *Phase Boundary Theories*

Phase boundary theories are primarily concerned with the mechanism by which the receptors are stimulated, although they may be secondarily concerned with the problem of quality. Kremer (Jones and Jones, 1953) developed an olfactory theory dependent on an assumed similarity between narcotics and odor stimuli. He believed that odorous substances were first dissolved in the mucus, then either absorbed into the olfactory cells or adsorbed onto the surface. In either event, the cellular metabolism would be upset and the neural impulse initiated. No explanation of olfactory quality is offered. A brief discussion of other theories which may be classified as phase boundary theories are listed by Jones and Jones (1953).

VIII. *Enzyme Theories*

Among the more modern approaches to the problem of olfactory stimulation are the enzyme theories, in which the primary effect of an odorous substance is thought to be on the enzymes of the olfactory cells. Kristiakowsky (Jones and Jones, 1953) believes that the basic principle underlying olfaction is a chemical reaction involving the enzymes, that the initiation of certain enzymes contained in the olfactory cells is responsible for odor.

Baradi and Bourne (Wendt, 1952) have also proposed a theory of olfaction which is based on enzyme activity. It is assumed that there are several active enzymes present in the olfactory epithelium. Odor compounds have the ability to inhibit these enzymes. This selective inhibition alters the relative concentration of various compounds at the receptor and thereby initiates the neural response.

Lauffer (Wendt, 1952) has developed a more sophisticated theory of the action of molecular configuration. Lauffer surveyed nonolfactory biological processes, particularly from the standpoint of biochemistry, and found mechanisms which might fit the requirements of the olfactory processes. He suggested that enzyme action is the most likely candidate. Enzymes, like all proteins, are macromolecules that form addition compounds by means of minor attractive forces, such as hydrogen bonds, which may also determine their shape and specific activity. The weakness of these forces makes it necessary that a molecule fit closely against the enzymes over an extensive area in order for the addition compounds to be formed.

The molecule-enzyme alliance Lauffer has suggested stretches or unfolds the molecule so that points normally unexposed might become capable of chemical reaction. Thus if the molecules of the odorant produce their effects by combining with protein molecules such as enzymes, the importance of molecular shape is clear. Lauffer felt that the action by which excitation is produced is interference with some vital process through the alteration of the enzyme or enzymes concerned.

In the preceding discussion of olfactory theories, the inadequacies of the formulations are evident. Pfaffman (1956) has stated that it is very unlikely that any satisfactory theory of olfaction can result from the consideration whereby one aspect of the olfactory process receives undue weighting, or from the erroneous assumption that olfactory perception is related to some physical parameter of the stimulus. In view of the preceding, most of the theories of olfaction remain inadequate.

The most promising theory at present is that proposed by Amoore (1963). Amoore's view is that odor quality depends largely on the shape and size of the stimulating molecule. Partly on the basis of subjective assessments of odor quality, he has deduced the existence of seven primary odors (camphoraceous, pungent, ethereal, floral, pepperminty, musky, and putrid). Amoore goes beyond early theorists by specifying the shape and size of five hypothetical receptor sites which correspond to five of the primary odors. The two remaining classes of odors, pungent and putrid, are thought to depend not on the molecular shape and size, but on the electrical status of the odorant molecule. Amoore has worked out the structural formulas for each of the five primary odors for which receptors are postulated and has built three-dimensional models of their atomic units (Snider, 1964). For example, Amoore found that the 100 compounds having a camphor-like odor all had about the same shape (spherical) and the same diameter (seven angstroms). He has further determined the characteristic shape and size of the remaining four primary odors. Johnston, Rubin, and Amoore (Snider, 1964) have put the theory to empirical test and have found that it is possible to synthesize a molecule to certain shapes and predict its odor accurately.

Thus far, no serious objections to the theory have been justly raised and Amoore has been able to predict as well as explain olfactory phenomena through an application of his theory. The only major drawback to the theory is that Amoore does not attempt to explain the actual stimulation processes whereby receptor functioning is initiated, but Benjamin, *et al.* (1965), suggest a possible incorporation of some of the more accurate formulations of other theorists which explain the initiation process (Davies and Dravnieks). Although this theory is still in need of further empirical investigations, it is felt by the majority of the scientific community and by the author of this paper that this theory is the most promising at the time.

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ABSTRACT

The purpose of this paper is to present a critical review of the major olfactory theories. Included are discussions of olfactory stimulus parameters, sensory physiology, and various systems of odor classification such as those of Henning, Zwaardemaker, or Crocker and Henderson. The major theories of olfaction described include the radiation theory of Teudt; the electromagnetic vibrational theories of Beck and Miles, Dyson, and Heyninx; the mechanical theory of Banerji; the stimulus pattern theory of Adrian; the chemical theories of Haagen-Smit or Mullins; the steric theory of Troland; the Phase Boundary theory of Kremer; the Enzyme theory of Lauffer; and the Stereochemical theory of Amoore. Current research in this area is also presented.

RESUMEN

Este trabajo tiene como propósito el presentar una revisión crítica de las teorías olfatorias más importantes. Se incluyen discusiones sobre parámetros de estímulos olfatorios, fisiología sensorial, y varios sistemas de clasificación de olores como los de Henning, Zwaardemaker, Crocker y Henderson. Entre las teorías descritas se incluye la teoría de radiación de Teudt; las teorías de vibración electromagnética de Beck y Miles, Dyson y Heyninx; la teoría mecánica de Banerji; la teoría de patrones de estímulos de Adrian, las teorías químicas Haagen-Smit o de Mullins; la teoría de Troland, la teoría de límites de fase de Kremer, la teoría enzimática de Lauffer, y la teoría estereoquímica de Amoore. También se presenta la investigación actual en esta area.

RESUMO

O propósito dêste trabalho é apresentar uma revisão crítica das principais teorias olfatórias. Incluem-se discussões de parâmetros de estímulo olfatório, fisiologia sensorial, e vários sistemas de classificação de odôres tais como os de Henning, Zwaardemaker, e Crocker e Henderson. As teorias principais de olfato descritas incluem a teoria de radiação de Teudt; as teorias electromagnéticas vibratórias de Beck e Miles, Dyson, e Heyninx; a teoria mecânica de Banerji; a teoria de padrão de estímulos de Adrian; as teorias químicas de Haagan-Smit ou Mullins; a teoria atômica-molecular de Troland; a teoria de limite de fase de Kremer; a teoria de enzima de Lauffer; e a teoria estereoquímica de Amoore. Pesquisas neste campo são também revistas.