

## **A Phenomenological Model of the Perceived Intensity of Single Odorants**

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*(Received 15 September 1981, and in final form 12 August 1982)*

The response of a model olfactory system to a single odorant is quantified by interconnecting three separate stimulus–response relationships. Together, these relationships encompass the deposition of odorant molecules onto an olfactory organ, their movement to the dendrite of the olfactory receptor neuron, their subsequent induction of action potentials, and the processing of induced and spontaneous action potentials by the central nervous system, resulting in perception and a behavioral response. Phenomena discussed within the context of the model include the behavioral threshold, central summation of responses from a number of olfactory neurons, and the effect of organ shape on olfactory detection.

The intent of the model is to provide a quantitative conceptual framework for designing and interpreting experiments relating sensory input to perception and behavior. Its utility is particularly evident for insect olfaction since it enables insect sex pheromone behavioral thresholds to be estimated from the literature when bioassays or electrophysiological studies are not possible. It also derives a physiologically meaningful method for comparing behavioral thresholds among different animals, and permits comparisons of different kinds of behavioral responses in the same species. Vertebrate olfaction is treated briefly in a discussion of the effect of sniffing on the threshold of detection.

### **1. Introduction**

When the olfactory organ of an animal is stimulated, a number of chemical and physiological events must occur before the central nervous system (CNS) perceives an odor. Ultimately, the perceived intensity of the sensation is influenced by many factors, including the rate of adsorption of odorant to the exposed surfaces of the olfactory organ, the rate of transport from these surfaces to the underlying olfactory receptor neurons, the number and sensitivity of the receptor neurons, and the procedure by which the CNS evaluates their output. The quantitation of such influences is a

central problem in olfactory psychophysics (Neuhaus, 1953; Stuver, 1958; Teichman, 1959; Kafka, 1970; Kaissling, 1971; Menco, 1977; Hornung & Mozell, 1977; Moulton, 1977).

An example from insects illustrates the kinds of questions that a quantitative treatment of olfaction must answer. Many insects emit volatile chemicals called sex pheromones that selectively attract and sexually excite individuals of the opposite sex. A major concern in the implementation of insect control procedures by use of such chemicals is the minimum detectable concentration, which is usually measured behaviorally (Mankin *et al.*, 1980). In some instances, it would be of practical benefit if the threshold could be estimated from easily obtained physiological and morphological parameters rather than by bioassay. However, the great diversity in the size and shape of insect antennae makes it difficult to determine which morphological parameters have the greatest importance. The silkworm moth, *Bombyx mori* L., has a large, feathery antenna, for example, while the cabbage looper, *Trichoplusia ni* (Hübner), has a thread-like antenna. Yet, both insects have comparable thresholds for their respective sex pheromones,  $10^3$ – $10^4$  molecules/cm<sup>3</sup> (Kaissling & Priesner, 1970; Sower, Gaston & Shorey, 1971). Thus, a question is raised immediately whether these morphological differences affect the threshold. This and similar questions led us to develop the model derived below.

The derivation is obtained by combining two stimulus-response relationships from the psychophysical, chemical engineering, and neurophysiological literature. One is a power function relating the activity of an olfactory receptor neuron to physical, physiological, and morphometrical parameters that determine the stimulus intensity. The other is an equation from signal detection theory that defines a criterion by which a stimulus of low intensity can be distinguished from a background of spontaneous neural activity. In examining the derivation, the reader should bear in mind that we do not intend to derive either the most simple or the most complete model possible, nor to describe the discrimination process. For example, the power function describing the response of an olfactory neuron can be simplified to a linear equation when the odorant concentration is near threshold. The response also can be described in terms of a hyperbolic function, a more general polynomial function, or a Weber–Fechner logarithmic function (Rushton, 1961). Portions of the model are applicable to contact chemoreception, particularly those parts dealing with the processing of information after it is transduced by the sensors (see e.g. Fredman, 1975). This aspect will not be discussed, however.

In later sections the model is expanded by incorporating a measure of how intensely an above-threshold olfactory stimulus is perceived. The

expanded version is applied to bioassays that measure the magnitude of different types of behavioral response to the same olfactory stimulus, showing the underlying commonalities in the different dose-response curves. For example, it is shown how bioassays measuring percentage response and those measuring response latency can be compared directly.

A concluding section discusses the types of olfactory systems for which the model is likely to have utility and considers how variations in the exposed surface area of an olfactory neuron, the number of olfactory neurons stimulated, and the spontaneous activity of olfactory neurons affect the behavioral threshold. The vertebrate olfactory threshold is considered briefly. A number of applications of the model to insect olfaction are discussed in Mankin & Mayer (1983).

## 2. Model

The first olfactory system to be modeled in this report is schematized in Fig. 1. It comprises a total of  $n$  independent sensors connected to a central

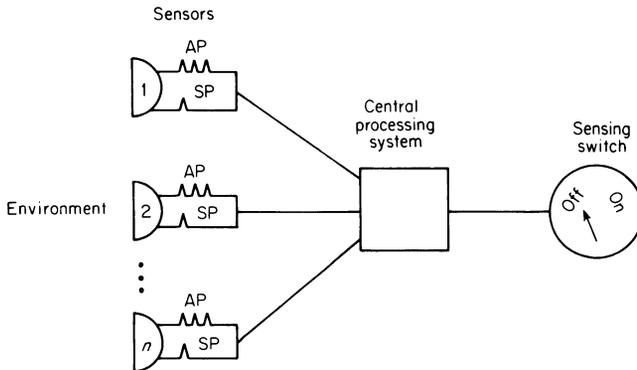


FIG. 1. Schematic of a model olfactory system comprising a total of  $n$  sensors, a central processing system, and a sensing switch. Symbols: AP (stimulus-activated pulses); SP (spontaneous pulses).

processor that can be in either a quiescent or an excitatory state, as signified by a sensing switch. An expanded version is considered later in section 6. For simplicity, we limit the initial system to three activities: (1) the sensors independently transmit odorant-activated pulses as well as spontaneous pulses to the central processor; (2) the central processor, analogous to a locus of converging neurons in the brain, counts the pulses from the sensors

and determines whether the total rate of incoming pulses exceeds some fixed response criterion level; and (3) when the rate exceeds the criterion level the processor switches from a quiescent to an excitatory state that decays back to quiescence after the stimulus ceases. The first two actions of the model system are represented by an equation that expresses the rate of emission of pulses in terms of the stimulus intensity. The third action is represented by another equation giving the response criterion in terms of the rate of arrival of pulses at the central processor. These are conceptually separate processes and are considered separately in the next two sections.

Before deriving the relationship between the stimulus and the pulse rate in the model system, it is necessary to consider briefly the physical units of stimulus intensity. To provide more physiological meaningfulness, we represent the stimulus intensity for this report by the rate of adsorption of odorant to a number of independent sensors rather than by the conventional units of odorant concentration. In a real olfactory system, the rate of adsorption to an individual sensor depends primarily on the odorant concentration, but it also depends somewhat on the turbulence in the stimulus airflow and the interactions between the odorant molecules and the sensor surface molecules (Judeikis & Stewart, 1976). Such interactions include van der Waal forces and hydrogen bonding (Regnier & Goodwin, 1977). Because of the complexity of these factors, the rate of adsorption cannot be calculated from adsorption theory, but experimentally measured rates of deposition to surfaces can usually be fitted to

$$m_a = CSK, \quad (1)$$

where  $m_a$  (units: moles/sec) is the mean rate of adsorption to a sensor surface of area  $S$  ( $\text{cm}^2$ ),  $C$  (moles/ $\text{cm}^3$ ) is the mean odorant concentration in the stimulus air, and  $K$  (cm/sec) is an empirically measured deposition velocity of odorant to the sensor. The deposition velocity is a commonly measured parameter in studies of gas and pollutant adsorption (Thom, 1968; McMahan & Denison, 1979).

The difficulties of measuring the deposition velocity of odorant to an olfactory organ are alleviated somewhat by the fact that adsorption is a nonspecific process. The deposition velocity of most chemicals varies within the limits, 0.1–10 cm/sec (McMahan & Denison, 1979), which is relatively narrow compared to the  $10^3$ – $10^4$ -fold variations of odorant concentration normally occurring in the atmosphere. We have measured the deposition velocity of two different sex pheromones to several different insect antennae and found values that lay within even narrower limits, 0.2 to 6 cm/sec (Mankin & Mayer, unpublished data). It is thus convenient and realistic

to assume that  $K = 1$  cm/sec in the model system. Our rationale for representing the stimulus intensity in terms of  $m_a$  rather than  $C$  will become more evident as the derivation proceeds. Except where explicitly stated, the remainder of this report deals with the model system rather than a real olfactory system.

### 3. Response of a Model Sensor

Because power function have been very successful as approximate representations of psychophysical relationships (Stevens, 1975), we adopt the following equation to describe the rate of pulse emission by a sensor in terms of the rate of adsorption of odorant:

$$M_p = b_1(M_a + b_2)^b, \quad (2)$$

where  $M_p$  (number/interval) is the mean number of pulses elicited from an independently acting sensor during the test interval in which the pulses are monitored,  $b_1$ ,  $b_2$ , and  $b$  are regression constants (number/interval), and  $M_a$  (number/interval) is the mean number of odorant molecules adsorbed by the sensor per interval. The mean rate of adsorption to the sensor is related to the odorant concentration in the stimulus air by the equation:

$$M_a = N_a t_i C S K, \quad (3)$$

where  $N_a$  is Avogadro's number ( $6.02 \times 10^{23}$ /mole) and  $t_i$  (sec) is the duration of the test interval. The quantities,  $N_a$  and  $t_i$ , are included in equation (3) solely to express  $M_a$  in normalized units of number per interval rather than the units of moles per second. This conversion simplifies the later parts of the derivation. The quantities,  $b_1$  and  $b_2$ , in equation (2) are constants in the model but it should be noted that they may vary with time in a real olfactory system (see e.g. Kaissling, 1976; Koshland, 1980).

Equation (2) is difficult to interpret as it stands, but it can be converted into a form where the parameters have a more intuitive meaning. Two such parameters are a noise factor, representing the spontaneous activity of the cell, and a response transduction (gain) factor, representing the rate of pulses produced by a single stimulus molecule. To perform the conversion we apply the binomial theorem or, less restrictively, a Taylor series expansion to obtain:

$$M_p = b_1 b_2^b + b b_1 b_2^{b-1} M_a + b(b-1) b_1 b_2^{b-2} M_a^2 / 2 + \dots \quad (4)$$

This can be simplified by noting that if  $M_a$  nears zero the  $M_a^2$  and higher-order terms become negligible. It is convenient to define

$$q = b_1 b_2^{b-1}, \quad (5)$$

where  $q$  is a kind of response compliance, the average number of pulses activated by an odorant molecule adsorbed to the sensor, and

$$M_s = b_1 b_2^b, \quad (6)$$

where  $M_s$  is the spontaneous activity of the sensor. Then,

$$M_p = M_s + qM_a. \quad (7)$$

Equation (7) can be interpreted as showing that at low stimulus intensities the rate of emission of pulses by a sensor is the sum of a rate of spontaneous emission,  $M_s$ , plus a rate of stimulus-activated emission,

$$M_o = qM_a, \quad (8)$$

where  $M_o$  (number/interval) is the mean number of odorant-activated pulses emitted per interval by a sensor. Necessarily, equation (8) is valid only when  $M_a$ , the rate of adsorption, nears zero.

Inspection of equation (2) in view of equations (5) and (6) provides insight into how the variation in the response of a sensor to different odorants affects the magnitude of the regression coefficients in the power function. The coefficient,  $b_1$ , is determined primarily by the units for stimulus and response (in this case number per interval). The ratio,  $q/M_s$ , is equal to  $b/b_2$ , so it is appropriate to interpret  $b$  as a correlate of the intrinsic response or gain of the sensor and  $b_2$  as a correlate of the intrinsic noise. It follows, then, that if a sensor is differentially sensitive to two odorants, the stimulus-response power functions for each odorant should have different values of the exponent,  $b$ . The higher value of  $b$  should occur for the odorant to which the sensor is more responsive. It also follows that a sensor with a higher rate of spontaneous activity should have a larger  $b_2$ .

#### 4. The Response Criterion for Detection of a Stimulus

In the next phase of the modeled detection process, a central processor analyzes the incoming pulses from the sensors. The central processor monitors the total rate of incoming pulses, and sets the sensing switch activating the excitatory state on the basis of a fixed response criterion. The concept of a response criterion has its origins in signal detection theory (Green & Swets, 1974). The theory examines a hypothetical detector system

with a large number of sensors that send both induced and spontaneous pulses to a central processor, the output from no single sensor being dominant. According to the central limit theorem, the distribution of the rate of spontaneous pulses inputted to the processor tends toward normality. Consequently there is a probability,  $p$ , that the rate of spontaneous input pulses exceeds  $\mu + Z\sigma$ , where  $\mu$  is the mean rate of spontaneous input pulses,  $\sigma$  is the standard deviation, and  $Z$  is the normal correlate of  $p$ , i.e. it is the horizontal axis on a plot of the normal distribution. For example, when  $Z = 1$ ,  $p = 0.1587$ , and when  $Z = 2$ ,  $p = 0.0228$ .

Now, suppose that the hypothetical detector receives spontaneous noise pulses at the mean rate of  $\mu_0 \pm \sigma_0$ . If the detector has a measured probability,  $p_0$ , of registering a signal during an interval when no stimulus is presented, then it can be inferred that there is a critical normal correlate of  $p_0$ , call it  $Z_0$ , such that

$$\mu_c = \mu_0 + Z_0\sigma_0. \quad (9)$$

The quantity,  $\mu_c$ , is the response criterion, the rate of input at which the detector first enters the excitatory state. Pirenne & Marriot (1959) proposed a similar criterion for vision. The response criterion cannot be measured directly, but it can be estimated by determining the mean and variance of the input noise along with the probability of a spontaneous response.

To apply equation (9) to the model olfactory system, we can estimate the mean and variance of the noise pulses carried to the central processor by noting that a series of pulses from either a single neuron or a group of nerve fibers can be modeled approximately by a Poisson distribution (Cox & Lewis, 1966; Kaissling, 1971). Because the sensors are analogous to peripheral olfactory receptor neurons, we assume here that the output from each sensor is described by the Poisson equation:

$$p_{M_s}(x) = M_s^x \exp(-M_s)/x! \quad (10)$$

where  $M_s$  is the spontaneous activity (see equation (6)), and  $p_{M_s}(x)$  is the probability that a particular integral number,  $x = 0, 1, 2, \dots$ , of spontaneous pulses occurs during a given interval when the mean number per interval is  $M_s$ . The Poisson distribution has two properties that simplify the model calculations: (1) the mean and variance of the distribution are equal (Cox & Lewis, 1966); and (2) the distribution of the sum of two Poisson distributions with means,  $M_1$  and  $M_2$ , is a Poisson distribution with the mean,  $M_1 + M_2$  (Box, Hunter & Hunter, 1978). Thus, if  $n_{t,x}$  is the number of intervals in which exactly  $x$  pulses arrive at the central processor,  $n$  is the number of sensors, and  $N$  is the total number of intervals, then the probability that  $x$  spontaneous pulses reaches the central processor during

a given interval is

$$n_{i,x}/N = p_{nM_s}(x). \quad (11)$$

The mean and variance of the rate of input pulses is  $nM_s$ .

An estimate of the response criterion for the central processor of the model system is obtained as follows. First, three quantities are measured: the number of sensors,  $n$ ; the mean rate of emission of spontaneous pulses from a sensor,  $M_s$ ; and the probability,  $p_0$ , that the sensing switch (see Fig. 1) activates the excitatory state spontaneously. From  $p_0$ ,  $Z_0$  is determined by reference to a table of the normal distribution. Then the criterion for activation of the excitatory state is calculated from the equation:

$$\mu_c = nM_s + Z_0(nM_s)^{1/2}, \quad (12)$$

which is a special case of equation (9). To keep the units consistent, it is necessary to assign the units of (number of pulses/interval)<sup>1/2</sup> to  $Z_0$ .

While this procedure specifies a practical method for estimating an animal's response criterion, nothing is specified about how the animal itself would determine the mean noise level if it did process threshold stimuli according to equation (12). It is not difficult to imagine several plausible averaging mechanisms, however. For example, in a model of bacterial chemotaxis MacNab & Koshland (1972) postulated that bacteria have a memory. An attractant-chemoreceptor complex activates two different enzymes that catalyze respectively the synthesis and degradation of a regulator chemical,  $x$ , at different rates. The concentration of  $x$  must rise above a critical level before the bacterium responds. Presumably, the central processor could operate similarly, with a change in the spontaneous signal level resulting in the change of a mean level of some critical chemical, e.g. a neurotransmitter. The response criterion would be analogous to the critical level of  $x$  in the MacNab-Koshland model.

## 5. Analysis of Factors Affecting the Excitatory State

The central processor can be switched into an excitatory state either by a level of spontaneous pulses that exceeds the criterion or by an odorant concentration of some minimum intensity,  $T$  (moles/cm<sup>3</sup>), hereafter called the switch threshold. Because of its analogy with the behavioral threshold, the switch threshold is one of the most important parameters in the model.

To obtain a relationship determining  $T$  from parameters of the model, it can be assumed that  $T$  is the minimum concentration of odorant at which the value of  $M_0$  in equation (8) for a single sensor is sufficiently large that the total input to the central processor from all the sensors rises above the

response criterion. In other words when  $C = T$ , then  $M_0 = M_t$ , where  $M_t$  is the minimum rate of induced pulses needed to obtain the excitatory state. According to equation (12), the minimum rate of induced pulses is

$$M_t = Z_0(nM_s)^{1/2}/n = Z_0(M_s/n)^{1/2}. \quad (13)$$

(Note that if the sensors are stimulated selectively, equation 13 must be modified as discussed in the Appendix.) To relate  $M_t$  to the threshold, we first combine equations (3) and (8), obtaining

$$N_a C = M_0 / q t_i S K. \quad (14)$$

Since, by definition,  $C = T$  when  $M_0 = M_t$ , equation (14) can be rewritten in terms of  $M_t$  and combined with equation (13), yielding

$$N_a T = Z_0(M_s/n)^{1/2} / q t_i S K, \quad (15)$$

which expresses the threshold for switching to the excitatory state in terms of phenomenological parameters.

## 6. Responses to Above-Threshold Stimuli

Heretofore the excitatory state of the model system has been analogized as a two-way switch, but a more realistic representation of olfactory perception would grade the intensity of the excitatory state in proportion to the stimulus magnitude. It is convenient to assume that the proportionality is described via a power function of the form frequently used to represent the psychophysical response by humans to stimuli of a number of different modalities (Stevens, 1975):

$$I = I_0(C - \tau)^\beta. \quad (16)$$

where  $I$  is the intensity of the excitatory state,  $C$  (moles/cm<sup>3</sup>) is the odorant concentration,  $\tau$  (moles/cm<sup>3</sup>) is the threshold, which either can be estimated from  $T$  in equation (15) or calculated as a regression constant, and  $I_0$  and  $\beta$  are regression constants.

It is of interest to generalize further by considering an example where the excitatory intensity cannot be monitored directly, but the system exhibits an observable response that is graded with respect to stimulus intensity. Although equation (16) cannot be determined in this case, two important parameters,  $\tau$  and  $\beta$ , can be estimated from the power function for the observable response. Ideally, if the observable response,  $R$ , is proportional to the excitatory intensity, then

$$R = R_0(C - \tau)^\beta \quad (17)$$

where  $R_0$  is a regression constant. The two exponents should be equivalent because both the excitatory state and the observable response are induced by the same sensors, and the exponent is primarily a measure of the sensor transduction characteristics (section 3). In a real olfactory system, however, a number of physiological factors could interfere with the expression of the observable response, or the response might be so complex that it would be only marginally indicative of excitatory intensity. These effects would tend to decrease the exponent in the observable-response power function relative to the exponent in equation (16). Sensory adaptation would increase both exponents without changing their relative order. Consequently, if the excitatory exponent were unknown, the observable-response exponent could be set as a lower limit for the perception exponent. Similarly, the observable-response threshold cannot be lower than the excitatory threshold, so in the absence of knowledge about the excitatory threshold, the observable-response threshold could be set as an upper limit.

## 7. Comparisons with Previous Analyses

There are two formal differences between the proposed model and most previous treatments of olfaction: the form of the mathematical representation for the basic stimulus-response relationship of olfactory acuity, and the assumptions about the process of adsorption to the olfactory organ. For perspective, we will consider the differences briefly in this section, but it should be noted that these issues have little bearing on the overall validity of the model.

In contrast to equation (2), most previous analyses of olfaction (e.g. Tucker, 1963; Kaissling, 1969) have represented the rate of emission of action potentials in terms of a hyperbolic equation. Kaissling (1971) has also considered a modification of the hyperbolic equation that takes into account the electrical properties of the olfactory neuron. The resultant equation is flatter than the hyperbolic curve and closely resembles the power function of equation (2). Another frequently hypothesized form of stimulus-response relationship is a Weber-Fechner logarithmic function (Rushton, 1961; O'Connell, 1975; Den Otter, 1977). In the paper that follows, all three curves are considered for the case of pheromonal olfaction in *B. mori*. Each of them provides a good fit to the data, so the curves cannot be distinguished statistically. Apparently, the differences in the choice of stimulus-response function have little effect on the predictions of the model.

By contrast, the differences in the assumptions about the deposition of odorant molecules to the olfactory organ result in considerable differences

in the predictions of deposition velocity. Adam & Delbrück (1968) and Murray (1977) assume that every odorant molecule which contacts the olfactory organ is adsorbed, while it is assumed in the model that the adsorption rate is determined by equation (1). The effect of choosing one assumption over the other can be calculated by referring to equation (47) in Adam & Delbrück (1968):

$$J \approx 0.5 CSD/r, \quad (18)$$

where  $J$  (moles/sec) is the rate of adsorption of odorant to a cylinder of area  $S$  ( $\text{cm}^2$ ),  $D$  ( $\text{cm}^2/\text{sec}$ ) is the diffusion coefficient of the odorant and  $r$  (cm) is the radius of the cylinder. To estimate what this means in terms of deposition velocity, we note that according to equation (3),

$$K = M_a/N_a t_i CS = J/CS. \quad (19)$$

Next, comparing equation (18) with equation (19), we see that

$$K \approx 0.5 D/r. \quad (20)$$

The magnitude predicted by Adam & Delbrück (1968) for the deposition velocity of odorant to an insect olfactory sensillum thus can be calculated from the radius of an insect olfactory sensillum of about  $10^{-4}$  cm (Kaissling, 1971), and the diffusion coefficient, which for most odorants falls within the range  $0.01$  to  $0.1 \text{ cm}^2/\text{sec}$  (Mankin *et al.*, 1980). The predicted deposition velocity is about  $10^2$ – $10^3$  cm/sec, two to three orders of magnitude above experimentally measured values in the literature (McMahon & Denison, 1979).

Because of this difference in the way the model and Adam & Delbrück (1968) treat the adsorption process, the two analyses make different predictions concerning the effects of shape on olfactory acuity. If the deposition velocity is high, an adsorbent surface collects all the odorant in its vicinity, which results in a concentration gradient that increases the deposition velocity. The gradient is inversely proportional to the radius of curvature of the surface, so a slender, thin object would be predicted to have a greater deposition velocity than a blunt, thick object. However, there is a negligible gradient around a surface adsorbing at a low deposition velocity of  $1 \text{ cm}/\text{sec}$ , so the difference in shape would be of little importance relative to the difference in surface area. Kaissling (1971) predicted from Adam & Delbrück's work that a feathery insect antenna should be a more efficient odorant filter than a thread-like antenna. However, if  $K$  is about  $1 \text{ cm}/\text{sec}$  for both types of antenna, then any differences in filtering ability would be based on differences in surface area (which indeed are usually consider-

able). This difference in predictions undoubtedly can be resolved experimentally.

### 8. Olfactory Systems To Which The Model Is Applicable

Theoretically, by analogizing an olfactory neuron as a sensor, an action potential as a pulse, a part of the *CNS* as the central processor, and the behavioral response as an indication of a central excitatory state, we can apply the model to any real olfactory system. However, the extreme complexity of real systems belies the simplicity of the original assumptions in the model, and some of the parameters may be difficult to determine. Two parameters in particular are extremely difficult to measure in most vertebrates: the number of olfactory neurons sensitive to the odorant being tested, and the effective surface area from which a cell collects the odorant. When these parameters cannot be determined for a vertebrate system, the model can still be applied to make some general predictions about the limits of detectability and the important physical parameters involved in detection.

An example where the model can be applied to vertebrate olfaction is a current controversy about the effects of nasal air flow on the odor intensity perceived by humans (Schneider *et al.*, 1963; Rehn, 1978; Teghtsoonian *et al.*, 1979). The model clarifies some of the issues involved. According to equation (1), the velocity of the carrier air is of only minor importance; the rate of adsorption of odorant, which is relatively insensitive to velocity, is the primary parameter. As the speed of the flow increases, however, the level of turbulence also increases (Judeikis & Stewart, 1976), enhancing the mixing of odorant-laden air with air just above the olfactory epithelium. This effect may account for the finding that response intensity increases up to a point with increases in the stimulus flow rate. It also may explain why many animals sniff when they are exposed to low concentrations of an odorant. Several quick sniffs generate much more turbulence than a single, low-speed inhalation, consequently increasing the supply of odorant to the olfactory epithelium.

One requirement restricting the applicability of the model is that stimulus-response relationships must be established for both the behavior of the whole animal and the electrophysiological response of single, peripheral olfactory neurons. The animal must be able to communicate its detection of an odor, or else respond behaviorally in some reflexive or near-reflexive manner. If an identical behavioral response is also elicited by other nonolfactory stimuli, it may be difficult to ascertain whether a spontaneous behavioral response in the absence of the odor is not an

artifact due to inadvertent stimulation by the nonolfactory cue. This problem may result in the overestimation of  $p_0$ . Also, the constants in the power function of equation (2) are not strictly constant in a real olfactory system. The magnitude of these constants in the power function of a single olfactory neuron can vary with time and the pattern of previous stimulation because of adaptation. Such differences are magnified in comparisons among different olfactory neurons. Even neurons that respond to the same odorant exhibit considerable variation in their response curves (O'Connell, 1975). Thus, equation (2) can be applied to real olfactory systems only if the responses of a number of neurons are averaged in tests conducted under a fixed experimental paradigm.

There are, however, many animals for which a number of the conditions of the model can be satisfied. The Lepidoptera are particularly suitable for analysis. The number of olfactory neurons on a moth antenna and the effective surface from which a neuron collects odorant can be estimated relatively easily because the morphology of a sensillum often indicates the functionality of its olfactory neurons. Inspection of morphologically distinct sensilla by microscopy thus allows an estimate of the number of olfactory receptor neurons of a given type.

Another advantage provided by insects is that, in many species, the neurons in a majority of the olfactory sensilla are sensitive to one or more of the sex pheromones for that species, and the behavioral response to the sex pheromone tends to be stereotypical. The pheromonal response has been studied in detail in several insects, as well as the morphology and electrophysiology of sensilla that bear pheromone-sensitive olfactory neurons, so many of the parameters in the model can be estimated from values already in the literature.

Bearing in mind the above caveats about applicability, we now conclude by mentioning some phenomenological relationships derived in the model that can (and should) be tested experimentally.

The predictions in equation (15) about the relationship between the behavioral threshold and the number and surface area of olfactory receptor neurons are in general agreement with the pattern implemented through natural selection in a number of animals with highly developed olfactory acuity. These macrosmatic animals have olfactory organs of large surface area with a large number of olfactory neurons, just as equation (15) predicts would be optimal. Data from insect studies pertinent to the predictions about behavioral thresholds are presented in Mankin & Mayer (1982).

The effect on the threshold when a change occurs in the spontaneous activity of the olfactory receptor neurons, and the effect of a change in the probability that the central excitatory state becomes activated

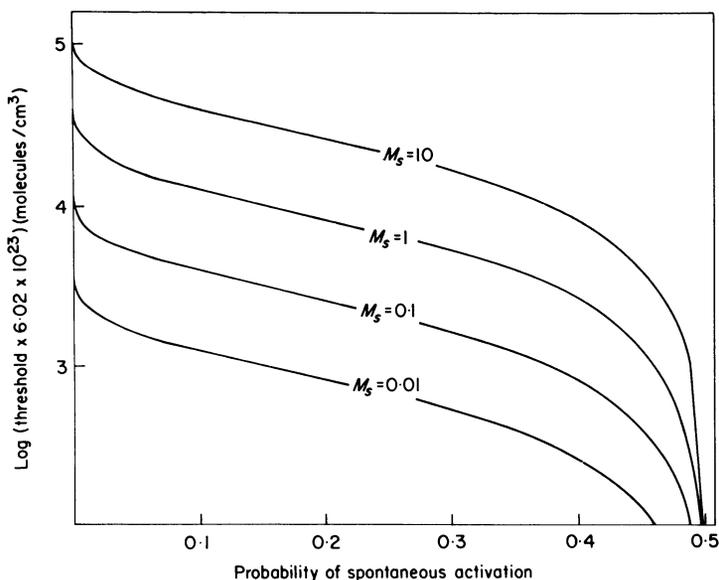


FIG. 2. Effect of changing the probability of a spontaneous activation of the excitatory state,  $p_0$ , and/or the spontaneous activity of a single sensor,  $M_s$  (pulses/interval), on the sensing threshold.

spontaneously are shown in Fig. 2, where the parameters  $q$ ,  $t_i$ , and  $K$ , are set to 1, and  $n$  and  $S$  are set arbitrarily to  $10^4$  and  $10^{-6}$   $\text{cm}^2$ , respectively. According to Fig. 2, an evolutionarily optimized olfactory neuron would have a low spontaneous activity, although this has not been experimentally demonstrated. One shortcoming of the model is that, in an optimized system, the probability of spontaneous activation of behavior would be large (Fig. 2). This does not take into account other factors that work toward minimizing spontaneous behavioral responses in the absence of stimuli, e.g. predation of unconcealed animals searching for odorant sources, and the energy requirements of searching forays. However, the model does indicate that a low rate of spontaneous activation, i.e. a minimized spontaneous behavioral response, theoretically can occur without significantly raising the threshold.

The expansion of the model to above-threshold responses shows how different bioassays might be compared even when they measure different kinds of response. In the case of insect pheromone bioassays for example, one behavioural response could be percentage wing flutter (orthokinesis) and the other, percentage upwind flight (anemotaxis). The criterion that anemotaxis must occur is more stringent than the criterion of orthokinesis,

so the anemotactic threshold should be higher than the orthokinetic threshold, both being higher than the perceptual threshold. Both responses are amenable to bioassays that could test these predictions. Similarly, the exponent for the anemotactic response should be smaller than the exponent for the orthokinetic response, both being slightly smaller than the exponent for perception. If two different bioassays of the same odor yielded different values for the threshold and the exponent in the response power function, then it could be expected that the response measure most indicative of perception was the one that yielded the power function with the highest exponent and the lowest threshold. The latter point is discussed in Mankin & Mayer (1983).

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## APPENDIX

### Summation of Responses from Single Olfactory Cells

There are two cases to consider in examining how a change in the number of sensors stimulated affects the switch threshold. If all the sensors are stimulated but the number of sensors changes, then the effect on the threshold is described by equation (15). However, if the number of sensors,  $n$ , remains constant while the number stimulated,  $n'$ , changes, then equation (13) must be modified to

$$M_t = Z_0(nM_s)^{1/2}/n'. \quad (\text{A1})$$

As a result, equation 15 converts to

$$N_aT = Z_0(nM_s)^{1/2}/qt_iSKn'. \quad (\text{A2})$$

The primary difference between equation (15) and equation (A2) is that, in the former, the threshold is inversely proportional to the square root of the number of sensors, and in the latter, the threshold is inversely proportional to the number of stimulated sensors. There is no practical difference between the two equations because they both are highly simplified, imprecise representations of central nervous processes.