

# The Adaptation of the Moth Pheromone Receptor Neuron to its Natural Stimulus

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**Abstract.** We analyze the first phase of information transduction in the model of the olfactory receptor neuron of the male moth *Antheraea polyphemus*. We predict such stimulus characteristics that enable the system to perform optimally, i.e., to transfer as much information as possible. Few *a priori* constraints on the nature of stimulus and stimulus-to-signal transduction are assumed. The results are given in terms of stimulus distributions and intermittency factors which makes direct comparison with experimental data possible. Optimal stimulus is approximately described by exponential or log-normal probability density function which is in agreement with experiment and the predicted intermittency factors fall within the lowest range of observed values. The results are discussed with respect to electroantennogram measurements and behavioral observations.

**Keywords:** Pheromone receptor, Information processing, *Antheraea polyphemus*

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## INTRODUCTION

The main task of neuronal sensory systems is to "encode" information about the animal's environment into its internal representation. Physiological reasons limit the range of neuronal responses and consequently not all stimulus states can be encoded with equal reliability. The stimulus-response relation describes the reliability of encoding and thus implicitly provides such stimulus characteristics that maximize the information capacity of the neuron. One of the first studies of stimulus-response function with respect to maximizing the information gain was done on large monopolar cells (LMC) in the compound eye of the fly [1]. The LMC is a graded potential cell which codes the contrast fluctuations. The contrast levels in natural fly's habitat were measured by objective methods (photodiode) and the resulting characteristics were compared with those predicted from the stimulus-response curve. It was shown that LMCs are adapted to the animal's ecology as the natural stimulus maximizes the cells' performance. The following studies, e.g., Atick [2], Bialek and Owen [3], Hateren [4], Hornstein et al. [5], Laughlin [6], confirmed that the natural signals are processed optimally by sensory systems. Nevertheless, the majority of available studies consider the visual system only. In this paper we parallel the pioneering work by Laughlin [1], adapting the method to suit the specificity of invertebrate olfactory system.

Orientation towards food and mate, especially in insects, is an olfactory-controlled behavior which relies on the detection of odorant molecules delivered from the source. The atmospheric turbulence causes strong mixing of the air and creates a wide spectrum of spatio-temporal variations in the signal. The largest eddies are hundreds of meters

in extent and may take minutes to pass a fixed point, while the smallest spatial variations are less than a millimeter in size and lasts for milliseconds only [7, 8]. The mean concentration of the odorant decreases monotonically with the distance from the source, however, the relation for concentration fluctuations and thus for instantaneous magnitude of the signal is more complicated. Due to the inhomogeneous mixing very high concentration values can be found in a wide range of distances from the source, though their frequency decreases with distance [7]. An important characteristic of the detected signal is its intermittency, i.e., the fraction of time during which non-zero concentrations are detected. It has been shown [9, 10] that the natural signal is highly intermittent in a wide range of experimental conditions. The signal is present less than 50% of the total time, usually even smaller intermittency is detected, e.g., Murlis et al. [10] report 20% in measurements of pheromone dispersion in natural conditions close to the source. Various types of ion detectors are usually employed for measurements, though Baker and Haynes [11], Murlis et al. [10] have also used electroantennogram responses. The description of the complicated and inhomogeneous structure of the detected odorant concentrations requires an approximative approach and statistical methods are usually employed. The probability density function over the whole stimulus range is the most convenient descriptor of the signal [7, 8, 10, 12, 9].

The variations in the concentration of the stimulus are essential for the insect to locate the source of the stimulus. The animal loses direction to the source and its upwind flight gets "arrested" if it gets into a cloud of homogeneously distributed pheromone [13, 14]. Experiments in tunnels have shown that characteristics like frequency and intensity of the intermittent stimulus play a key role in maintaining the proper direction of flight [15]. The insect's sensory system differs from the ion detector and thus the level of temporal and spatial detail the receptor neuron perceives is limited by both physical and biochemical reasons [11, 16, 17]. In other words, not all the information pheromone signal potentially carries can be processed. We analyze the first phase of information transduction in the olfactory receptor of the male moth *Antheraea polyphemus*. The external stimulus (the odorant) is given by the temporal concentration of the major component of the sex pheromone, the (E,Z)-6,11-hexadecadienyl acetate. The response of the system (the internal signal) is the graded concentration of activated receptor molecules. This process of transduction represents the first stage in the cascade of events finally leading to generation of action potential. The detailed analysis of the first phase provides insight into the information processing at the single-receptor level. We may paraphrase the fundamental data processing inequality [18]: if some information does not pass the first stage, it cannot reappear in any sequential stage of the processing. The first stage of transduction cascade therefore sets constraints on the final performance of the receptor.

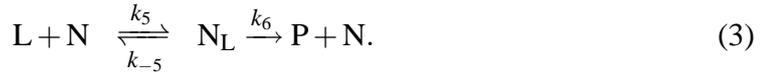
The goal of this paper is to characterize the performance of the stimulus-to-response transformation, namely to find and describe the optimal stimulus (or the class of optimal stimuli) that maximizes the performance. Mathematical basis for this task is provided by the statistical theory of information and the proposed method can be used in similar or more general situations. Similarly to LMCs studied in [1] the response of the first-stage information transduction in the olfactory neuron is a graded signal. Likewise, the experimental measurements of odorant plume concentration characteristics in the animal's habitat were performed by objective devices (ion detectors). The comparison

of predicted and natural stimulus reveals how well the receptor is adapted or "tuned" to the signals it encounters most often.

## METHODS

### The model of the odorant receptor

The first stage of information processing in the olfactory sensory neuron is described by the transformation of the external signal (the odorant concentration in the air) to the internal signal (the concentration of activated receptors). The model of odorant receptor we consider here was developed by Kaissling and Rospars [19] and represents a modified version of the original model developed by Kaissling [16]. The modification has no impact on the obtained results (verified numerically) though it simplifies the original model in terms of required parameters and variables. The chemical reactions form the following chain:



The network (1)–(3) includes the external ligand (the odorant)  $L_{\text{air}}$ , its uptake  $L$  and reversible binding to a receptor  $R$ , the reversible change of the complex  $R_L$  to an activated state  $R^*$  (the internal signal), a reversible binding of  $L$  to a deactivating enzyme  $N$  (see Kaissling and Rospars [19] for details) and an irreversible odorant deactivation by changing of the complex  $N_L$  to  $P+N$ . The concentrations of the eight species involved are denoted by square brackets and the values are functions of time. For simplicity we omit to denote the explicit dependence on the time variable  $t$  and adopt the following notation for the individual concentrations:  $L_{\text{air}} = [L_{\text{air}}](t)$ ,  $L = [L](t)$ ,  $R = [R](t)$ ,  $R_L = [R_L](t)$ ,  $R^* = [R^*](t)$ ,  $N = [N](t)$ ,  $P = [P](t)$  and  $N_L = [N_L](t)$ .

The total concentration of the receptor molecules,  $R_{\text{tot}} = R + R_L + R^*$ , does not change over time as well as the total concentration of the deactivating enzyme,  $N_{\text{tot}} = N + N_L$ , remains constant. The evolution of the reactions (1)–(3) in time given the external signal  $L_{\text{air}}$  is fully described by five first order ordinary differential equations (4)–(8) and two

algebraic equations (9) and (10):

$$\frac{dL}{dt} = k_i L_{\text{air}} - k_3 LR + k_{-3} R_L - k_5 LN + k_{-5} L_N \quad (4)$$

$$\frac{dR_L}{dt} = k_3 LR - k_{-3} L_R - k_4 L_R + k_{-4} R^* \quad (5)$$

$$\frac{dR^*}{dt} = k_4 R_L - k_{-4} R^* \quad (6)$$

$$\frac{dL_N}{dt} = k_5 LN - k_{-5} L_N - k_6 L_N \quad (7)$$

$$\frac{dP}{dt} = k_6 L_N \quad (8)$$

$$R = R_{\text{tot}} - R_L - R^* \quad (9)$$

$$N = N_{\text{tot}} - L_N. \quad (10)$$

The state of the system at any given time,  $S(t) = \{L(t), R_L(t), R^*(t), L_N(t), P(t)\}$ , is given by the actual values of the involved variables and we assume that at  $t = 0$  the concentrations  $L, R_L, R^*, L_N$  and  $P$  are zero. The values of parameters were determined by Kaissling [16] and Kaissling and Rospars [19], we summarize them in Tab. 1.

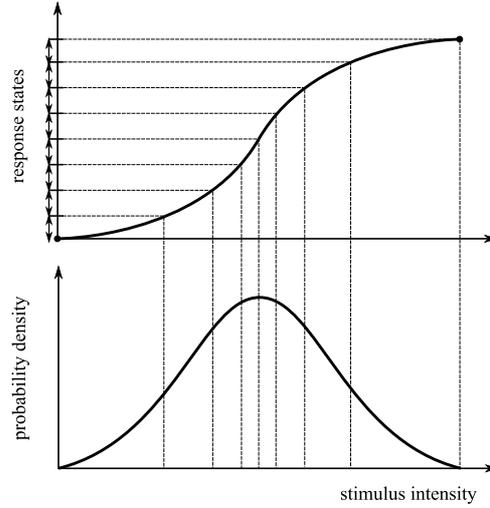
**TABLE 1.** Summary of the odorant receptor model parameters [16, 19].

$k_3$	$= 0.209 \text{ s}^{-1} \mu\text{M}^{-1}$	$k_{-3}$	$= 7.9 \text{ s}^{-1}$
$k_4$	$= 16.8 \text{ s}^{-1}$	$k_{-4}$	$= 98 \text{ s}^{-1}$
$k_5$	$= 4 \text{ s}^{-1} \mu\text{M}^{-1}$	$k_{-5}$	$= 98.9 \text{ s}^{-1}$
$k_6$	$= 29.7 \text{ s}^{-1}$	$k_i$	$= 29000 \text{ s}^{-1}$
$R_{\text{tot}}$	$= 1.64 \mu\text{M}$	$N_{\text{tot}}$	$= 1 \mu\text{M}$

The differential equations (4)–(8) follow the law of mass action for chemical reactions. In reality, the response of the system is not deterministic. The value fluctuates due to the stochastic effects like spatial inhomogeneities in the distribution of reactants. If the concentrations of reactants are high enough above single-molecular levels then the fluctuations are relatively small and can be neglected. However, for small doses the situation is more complicated and the stochastic effects have to be described properly [20]. In this paper we thus do not investigate the effect of extremely small odorant doses. The value of  $R^*$  corresponding to one activated receptor molecule per neuron is approximately  $10^{-6.2} \mu\text{M}$  [19] which is far below the values considered in this paper.

## Optimal stimulus reconstruction

The main task of the first-stage of signal processing in the olfactory receptor neuron is to transform the input signal (the odorant concentration) into its internal representation (the concentration of activated receptors). The neuron performs optimally if it preserves as much information about the input as possible. According to the information theory, information is transmitted only if the input varies randomly [18]. From this point of view a homogeneous cloud of odorant would carry zero information. The exact amount

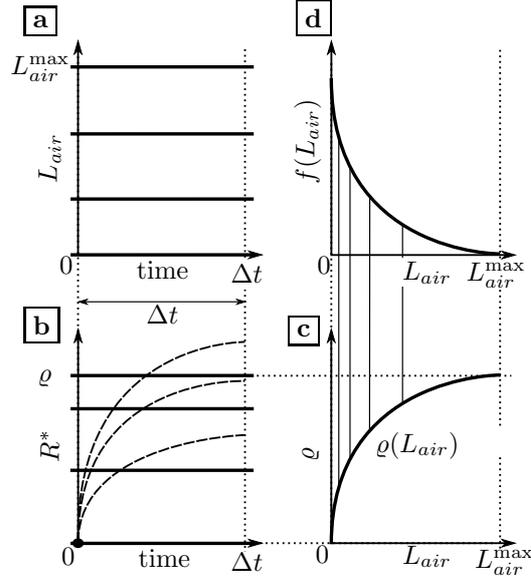


**FIGURE 1.** The amount of information the neuron can transfer is limited by the finite range of possible response states. Furthermore, the minimal stimulus increment that changes the response state is not constant over whole the stimulus range. The amount of transferred information therefore depends both on the range of stimulus and on the frequency with which particular concentration values occur. If the neuron performs optimally then all response states have to be used equally likely, which in turn uniquely determines the optimal stimulus probability density function (adapted from Laughlin [1]).

of transferred information is determined from the stimulus-response relationship. The problem therefore lies in relating two signals,  $L_{\text{air}}$  (the stimulus) and  $R^*$  (the response). The information, however, is not transmitted at a time instant, rather we assume that it is gained within a time interval. Therefore we divide the time axis into "windows" or "bins" of length  $\Delta t$ , i.e., we do not consider any temporal details below  $\Delta t$ . The stimulus is represented by a constant value of concentration  $L_{\text{air}}$  in the time window and the response,  $\rho$ , to such stimulation is the average value of activated receptors taken over the corresponding time window  $\rho = \langle R^* \rangle_{\Delta t}$ . This simple set-up allows us to test the performance of the receptor model at different levels of temporal resolution.

The most important factor limiting the information transfer is the bounded range of responses  $\rho$  due to finite number of receptor molecules per neuron. Once the maximum number of receptor molecules is activated no higher stimulus concentration can be encoded. Furthermore, the neuron can perceive a change in stimulus value differently depending on the basal stimulus concentration. The amount of transferred information therefore depends both on the range of stimulus  $L_{\text{air}}$  and on the frequency with which particular concentrations values occur, see Fig. 1. In other words, the description of  $L_{\text{air}}$  in each selected time window is given in terms of probability density function  $f(L_{\text{air}})$ .

The information theory [18, 21, 1] describes the optimal stimulus characteristics implicitly: the system performs optimally if all possible response values are used with equal frequency. In the following we describe the "step-wise" method to obtain such stimulus characteristics that equalize the output usage. First we compute the reaction of the system to all possible stimuli in the first time window,  $(0, \Delta t)$ , given the zero initial condition at  $t = 0$ , see Fig. 2a. For each stimulus the response  $\rho$  is the average number of activated receptors in  $(0, \Delta t)$ , Fig. 2b. The relation between  $L_{\text{air}}$  and  $\rho$  describes the



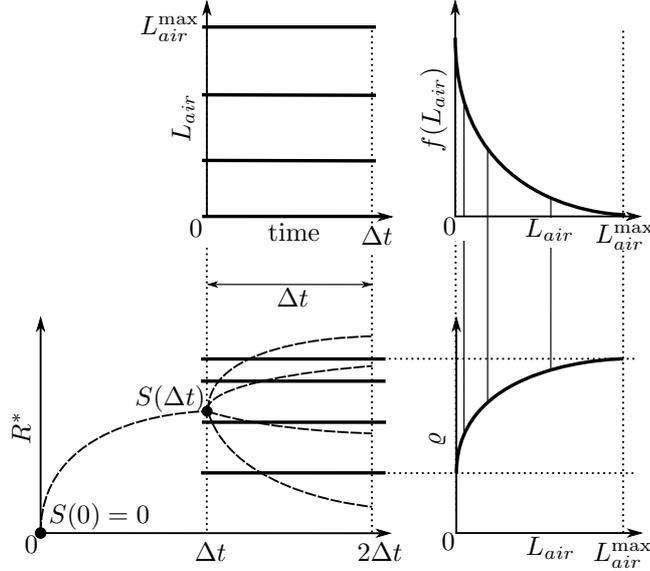
**FIGURE 2.** Stimulus optimization in the first time window  $(0, \Delta t)$ . (a) The stimulus  $L_{\text{air}}$  is a constant function bounded inside  $[0, L_{\text{air}}^{\text{max}}]$  (several examples shown). (b) Starting from zero at  $t = 0$  the time development of  $R^*$  (dashed line) is averaged ( $\rho$ ) over the first time window (solid line). (c)  $\rho$  "encodes" the stimulus value so the stimulus-response curve  $\rho(L_{\text{air}})$  can be constructed. (d) The stimulus-response curve uniquely determines such stimulus probability density function  $f(L_{\text{air}})$  that all responses  $\rho$  are used equally likely.

stimulus-response curve,  $\rho(L_{\text{air}})$ , Fig. 2c. Conditioned that all responses have to be used with equal frequency, the stimulus cumulative distribution function can be related to  $\rho(L_{\text{air}})$ . The optimal stimulus probability density function  $f(L_{\text{air}})$  can be then written as

$$f(L_{\text{air}}) = \frac{d}{dL_{\text{air}}} \left[ \frac{\rho(L_{\text{air}}) - \rho_{\text{min}}}{\rho_{\text{max}} - \rho_{\text{min}}} \right], \quad (11)$$

where  $\rho_{\text{min}}$  resp.  $\rho_{\text{max}}$  are the minimal resp. maximal response values encountered in the time window, Fig. 2d. Once the optimal stimulus probability density for the time  $(0, \Delta t)$  is known we use it to select one stimulus value. The reaction of the system to this particular stimulus is computed, the state of the system  $S$  at  $t = \Delta t$  is determined and we can proceed to the next time window  $(\Delta t, 2\Delta t)$ . Note that the information transfer in this system has a memory, i.e., the current state is affected not only by the current stimulus but also by the history of stimulation. Therefore the state of the system  $S(\Delta t)$  must be taken into account for evaluation of the response in the time window  $(\Delta t, 2\Delta t)$ . The optimization proceeds similarly in  $(\Delta t, 2\Delta t)$ : we again compute the time course of the activated receptor concentration ( $R^*$ ) and determine their averages ( $\rho$ ) under all possible stimulus conditions, Fig. 3. The optimal stimulus probability density function in  $(\Delta t, 2\Delta t)$  is determined again by employing formula (11). After selecting one random stimulus value the process continues into the following time window. The range of  $\rho$  and the shape of  $f(L_{\text{air}})$  may change from one window to another.

The actual amount of transferred information in each step can be estimated from the available response range. If we divide the range  $(\min \rho, \max \rho)$  into  $n$  bins (that cannot



**FIGURE 3.** Stimulus optimization in the second time window  $(\Delta t, 2\Delta t)$ . One particular stimulus value is drawn randomly from  $f(L_{air})$  reconstructed in the first time window  $(0, \Delta t)$ . The corresponding response and the state of the system  $S(\Delta t)$  are computed. In the second time window  $(\Delta t, 2\Delta t)$  the responses and their averages are determined again for all stimulus values (taking into account the state system at  $t = \Delta t$ ). The stimulus-response curve and the corresponding stimulus probability density function are determined and the process is carried into the next time window.

be divided any further) the amount of information which can be transferred is  $\log_2 n$  bits [18]. For each time window we thus compute the estimate of transferred information, here denoted as obtainable information,  $I_{obt}$ , in bits as

$$I_{obt} = \log_2 \left( \frac{\max \rho - \min \rho}{\Delta \rho} \right), \quad (12)$$

where the division factor  $\Delta \rho$  is set prior to the optimization process. We adopt the convention that  $I_{obt} = 0$  if the coding range is smaller than  $\Delta \rho$ . The factor  $\Delta \rho$  corresponds to the minimal number of activated or deactivated receptor molecules the system perceives as a change. We set the minimal value to 100 molecules which consequently gives  $\Delta \rho = 10^{-4.2} \mu\text{M}$ . Substituting for  $\Delta \rho$  into formula (12) and taking into account that the maximal concentration of activated receptors is  $R^* \approx 0.24 \mu\text{M}$  [19] yields the maximum information gain  $I_{obt} \approx 12$  bits. We furthermore assume that  $\Delta \rho$  does not depend on the length of the time window.

## RESULTS

### Single-pulse stimulation

First we examine the behavior of the model under the stimulation with a single pulse of unlimited duration. Setting the left-hand sides of equations (4)–(8) equal to zero gives

the asymptotic value of  $R^*$  as a function of the constant  $L_{\text{air}}$ ,

$$R^* = (1 - Q_4)R_{\text{tot}} \left[ \frac{K_{d3}Q_4}{K_{m5,6}} \left( \frac{k_6 N_{\text{tot}}}{k_i L_{\text{air}}} - 1 \right) + 1 \right]^{-1}, \quad (13)$$

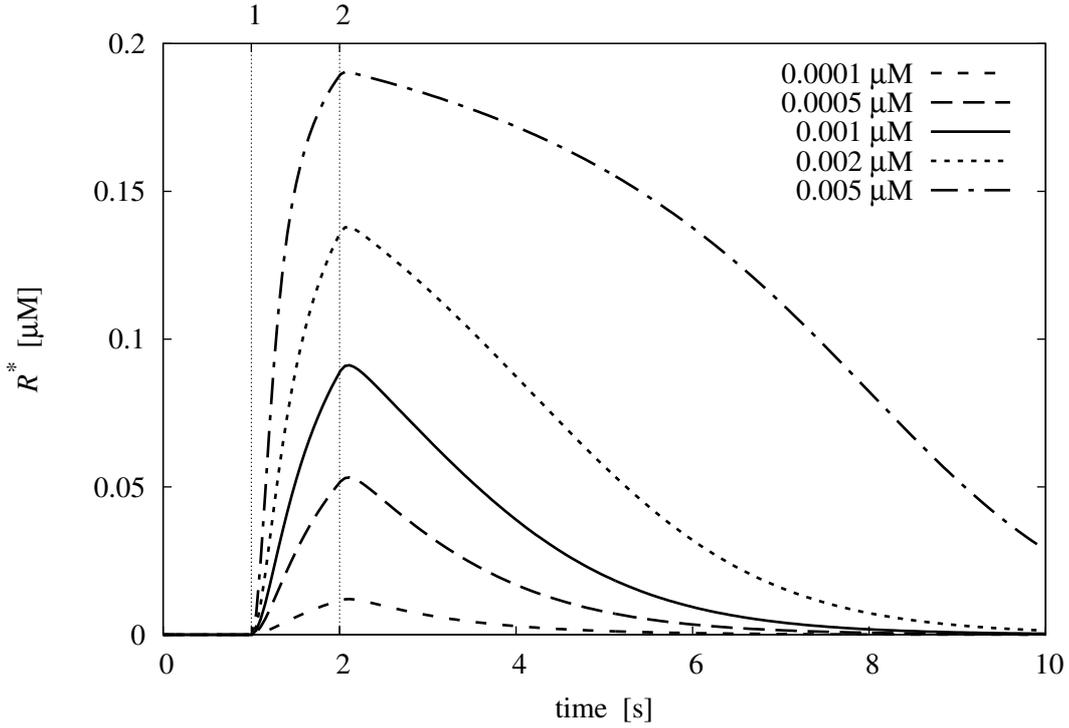
[19], where  $K_{d3} = k_{-3}/k_3$  corresponds to the dissociation constant of ligand and receptor,  $Q_4 = k_{-4}/(k_4 + k_{-4})$  and  $K_{m5,6} = (k_{-5} + k_6)/k_5$  are the Michaelis constants of the ligand and the deactivating enzyme. Using the values from Tab. 1 we find that the dose-response relationship (13) is almost perfectly linear with the maximum concentration of the activated receptors  $\max R^* = (1 - Q_4)R_{\text{tot}} \approx 0.24 \mu\text{M}$  [19]. The minimal concentration of infinite duration that activates the maximal number of receptors is  $L_{\text{air}} \approx 0.001 \mu\text{M}$ .

Next we examine the response of the system to a constant stimulation of limited duration. In Fig. 4 we see the time course of  $R^*$  given several different values of  $L_{\text{air}}$  from  $0.0001 \mu\text{M}$  to  $0.005 \mu\text{M}$ . The stimulation starts at  $t = 1$  s and lasts for 1 s. We see, that the system responds differently even for stimulus concentrations higher than the minimum concentration which evokes asymptotically maximum number of activated receptors (the asymptotic maximum  $L_{\text{air}} = 0.001 \mu\text{M}$ ). In other words, values  $L_{\text{air}} > 0.001 \mu\text{M}$  can be distinguished only if the duration of the stimulus pulse decreases. However, the duration of the falling phase gets progressively longer which has important consequences on distinguishing details in sequences of large stimulus values. During the simulations we avoid extremely small doses of odorant due to the validity of the mass action law. For the same reason we do not set the length of the time window  $\Delta t$  close to zero. The smallest value we allow is  $\Delta t = 0.2$  s which is near the upper value of the experimentally observed range [17]

## Multi-pulse stimulation

First we employ the optimization process directly, i.e., under the condition of stimulus being permanent but varying. In the first example we set the level of temporal detail to  $\Delta t = 0.2$  s. The upper bound on stimulus value is  $L_{\text{air}}^{\text{max}} = 0.1 \mu\text{M}$ , which is  $1000\times$  the concentration sufficient to reach the asymptotic maximum and therefore the stimulus range can be considered unrestricted.

The results are presented in Fig. 5. The plots show the state of the system in each time window (time is on the horizontal axis). The first row shows the optimized stimulus value which is randomly drawn from the optimal probability density function in each time window. The chosen stimulus value in turn determines the behavior of the system in the next time window due to the memory effect. The second row is the reaction of the system to the optimized stimulus and the third row shows the transferred (or obtainable) information. We see, that the performance of the system is not stable in time, i.e., the obtainable information  $I_{\text{obt}}$  monotonically decreases. The reason lies in the prolongation of the falling phase of  $R^*$ , see Fig. 4. The response range is initially bounded from below by  $\min \rho = 0 \mu\text{M}$  (we start from zero initial condition) but due to the memory effect the actual value of  $\min \rho$  increases in subsequent time windows. The upper limit of responses,  $\max \rho$ , does not change because it is given by the physical properties of



**FIGURE 4.** Response  $R^*$  of the system to pulsed stimulation (from  $t = 1$  s to  $t = 2$  s) of varying intensity. The limited duration of the pulse allows the system to detect  $L_{\text{air}}$  higher than  $0.001 \mu\text{M}$  (solid line), for which the system saturates asymptotically. Note the significant prolongation of the falling phase with increasing stimulus value.

the system. Consequently, the response range decreases and  $I_{\text{obt}}$  finally (and inevitably) reaches zero no matter how large is the stimulus value. The instability of the system is reflected also in the time development of optimal stimulus probability density function,  $f(L_{\text{air}})$ , see Fig. 6. Stimulus probability density function  $f(L_{\text{air}})$  in the first time window, which corresponds to maximal  $I_{\text{obt}}$ , can be approximated by the exponential probability density function

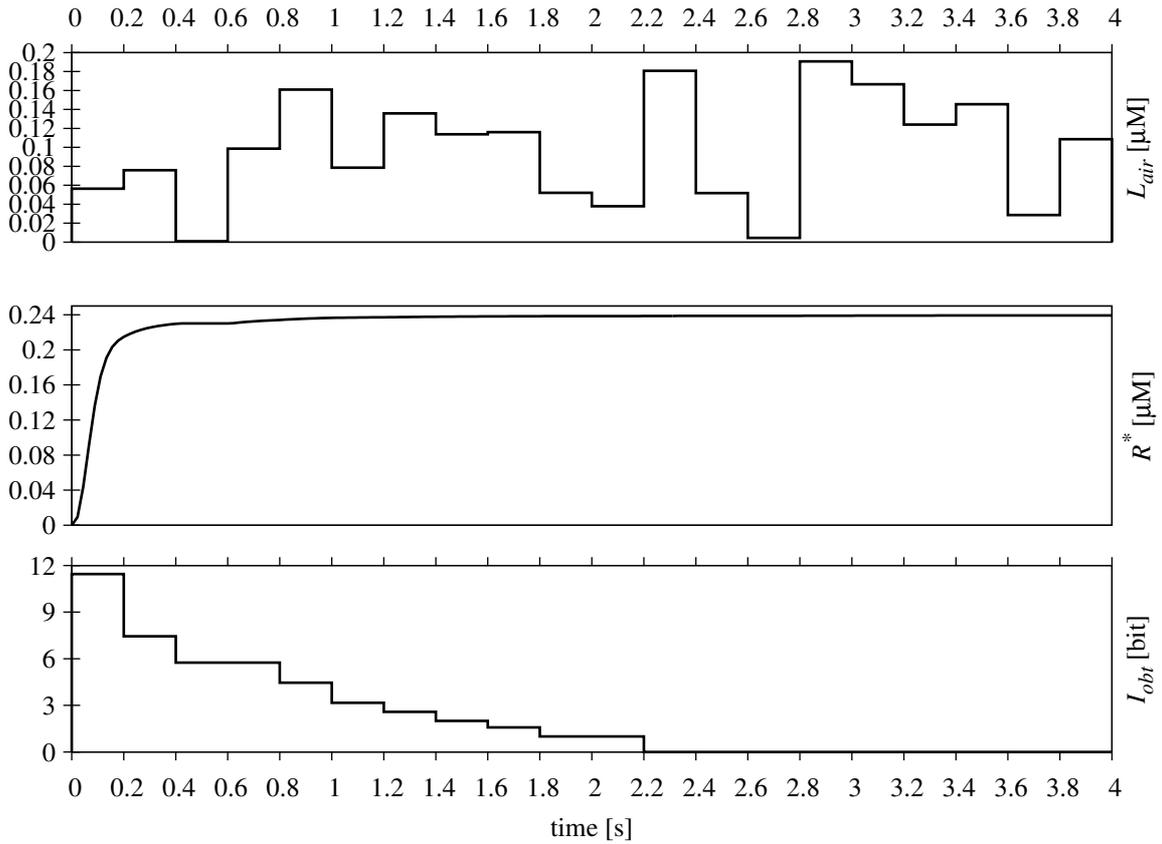
$$f(L_{\text{air}}) = \frac{1}{\lambda} \exp(-L_{\text{air}}/\lambda), \quad (14)$$

with mean value  $\lambda = 0.03 \mu\text{M}$ . A better fit, in this case, is provided by the log-normal distribution

$$f(L_{\text{air}}) = \frac{1}{x\sigma\sqrt{2\pi}} \exp\left[-\frac{(\ln x - \mu)^2}{2\sigma^2}\right], \quad (15)$$

with  $\sigma = 1.5 \mu = -3.6$  and mean value  $0.08 \mu\text{M}$ . In subsequent time windows  $f(L_{\text{air}})$  transforms into uniform distribution over the whole stimulus range meaning that there is no stimulus value preference once no information can be encoded.

The system can be stabilized by limiting the upper stimulus range to its asymptotic maximum  $L_{\text{air}}^{\text{max}} = 0.001$ , i.e., the response range is zero if stimulated constantly by  $L_{\text{air}}^{\text{max}}$ . The result is presented in Fig. 7. The temporal detail of the stimulus (the time window

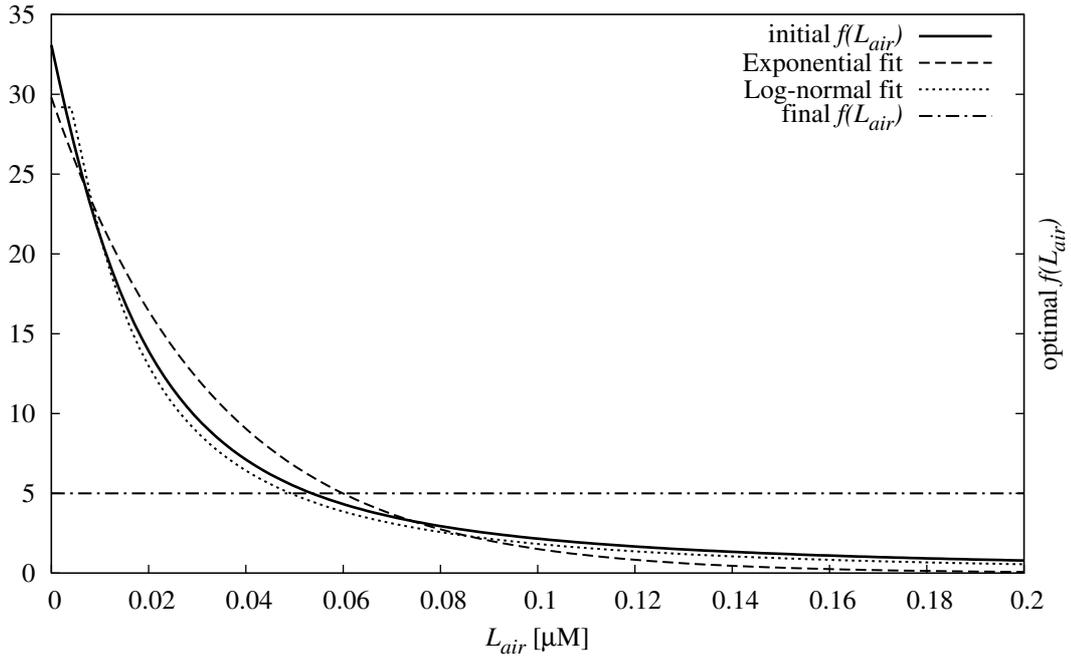


**FIGURE 5.** Optimal stimulus reconstruction:  $\Delta t = 0.2$  s and  $\max L_{air} = 0.1 \mu\text{M}$ . The three plots show (from top): the sample stimulus course, the response of the system  $R^*$ , and the corresponding obtainable information  $I_{obt}$ . The maximum stimulus value is chosen high enough to show the range accepted by the system at the selected temporal detail level. Initially, the optimal stimulus probability density function  $f(L_{air})$  coincides with the exponential probability density but changes towards uniform distribution. The obtainable information  $I_{obt}$  decreases quickly due to the effect of memory. After  $t = 2.2$  s no information is encoded. The effect of memory therefore disables high-precision coding for a prolonged period of time.

$\Delta t$ ) is set to 0.4 s. We see that though the performance is stable now the obtainable information is always below 12 bits and the full encoding capacity is never used. The optimal stimulus probability density is also stable in time. Its shape resembles the uniform probability density function, nevertheless it is slightly skewed towards higher values.

### Intermittent stimulation

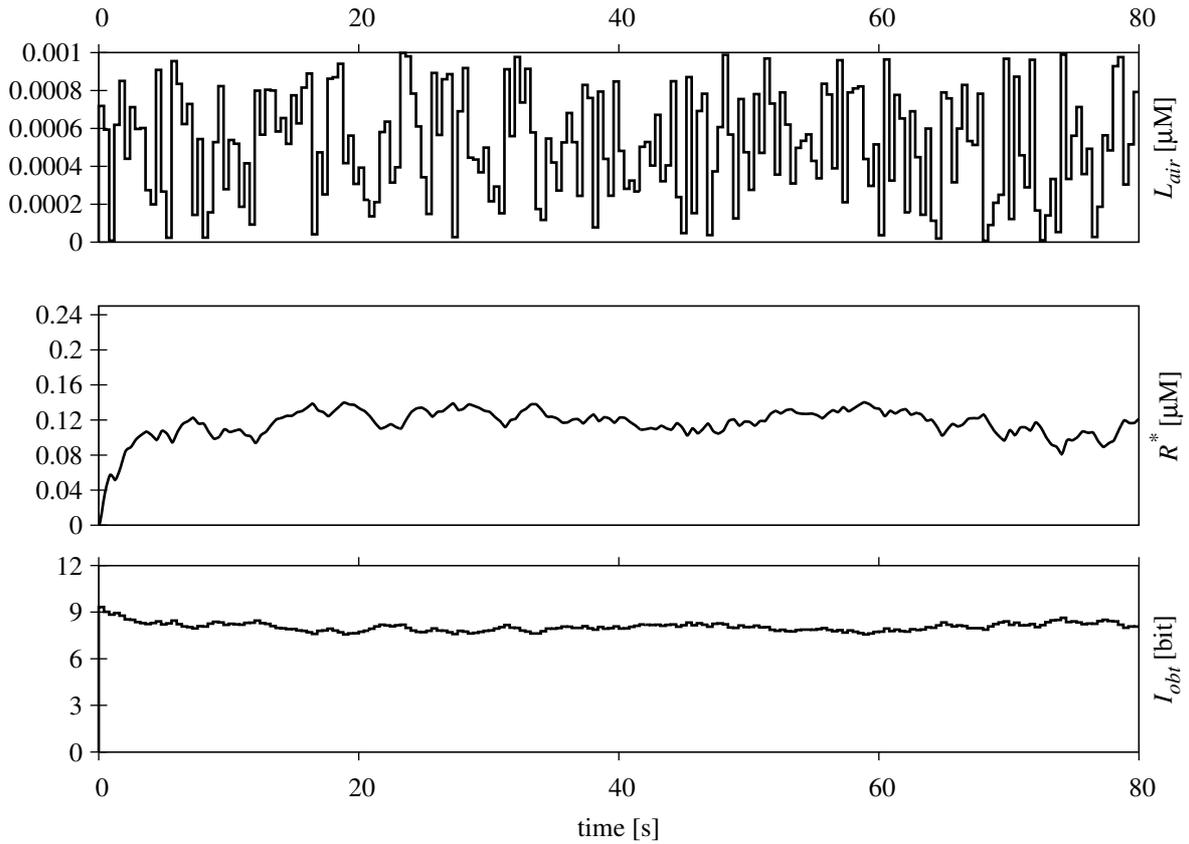
The sample optimization process illustrated in the previous examples was carried out under the condition of signal presented in every time window. Another possibility to obtain stable performance and to avoid saturation effects is to leave the stimulus range virtually unrestricted and let some time windows to contain no signal. The fraction of



**FIGURE 6.** Optimal stimulus probability density functions  $f(L_{\text{air}})$  for the case of persistent stimulation with unrestricted concentration values in Fig. 5. The initial  $f(L_{\text{air}})$  which corresponds to maximal information transfer can be roughly approximated by the exponential or better by the log-normal probability density function. The final  $f(L_{\text{air}})$  when no information is transferred is uniform over the whole stimulus range.

the total recording time where the signal is present is called intermittency and it is well known that for natural signals its value is very low, almost always less than 50 % [7, 8]. Murlis et al. [10] report intermittency of naturally dispersed odorant plume as low as 10 % or 20 % in the range of meters from the source.

The final example shows a possibility to predict the optimal intermittency value. We are interested in encoding the signal with maximum sensitivity whenever possible. This condition sets the limits on the recovery time needed after one particular stimulus is presented. Whenever the obtainable information decreases below 11 bits (the threshold for optimal performance) we let the following time windows contain no signal until  $I_{\text{obt}} > 11.5$  bits again. The intermittency allows the system to "reset" and perform in optimal state again. The result for  $\Delta t = 0.4$  s and  $L_{\text{air}}^{\text{max}} = 0.03 \mu\text{M}$  is shown in Fig. 8. The optimal stimulus probability density function is stable in time (whenever the stimulus is present) and can be described by the exponential probability density function (14), this time with  $\lambda \approx 0.005 \mu\text{M}$ . The intermittency predicted in this case is 7 %. However, the intermittency value is directly dependent on the threshold value of  $I_{\text{obt}}$  for optimal performance and the threshold value for zero signal.

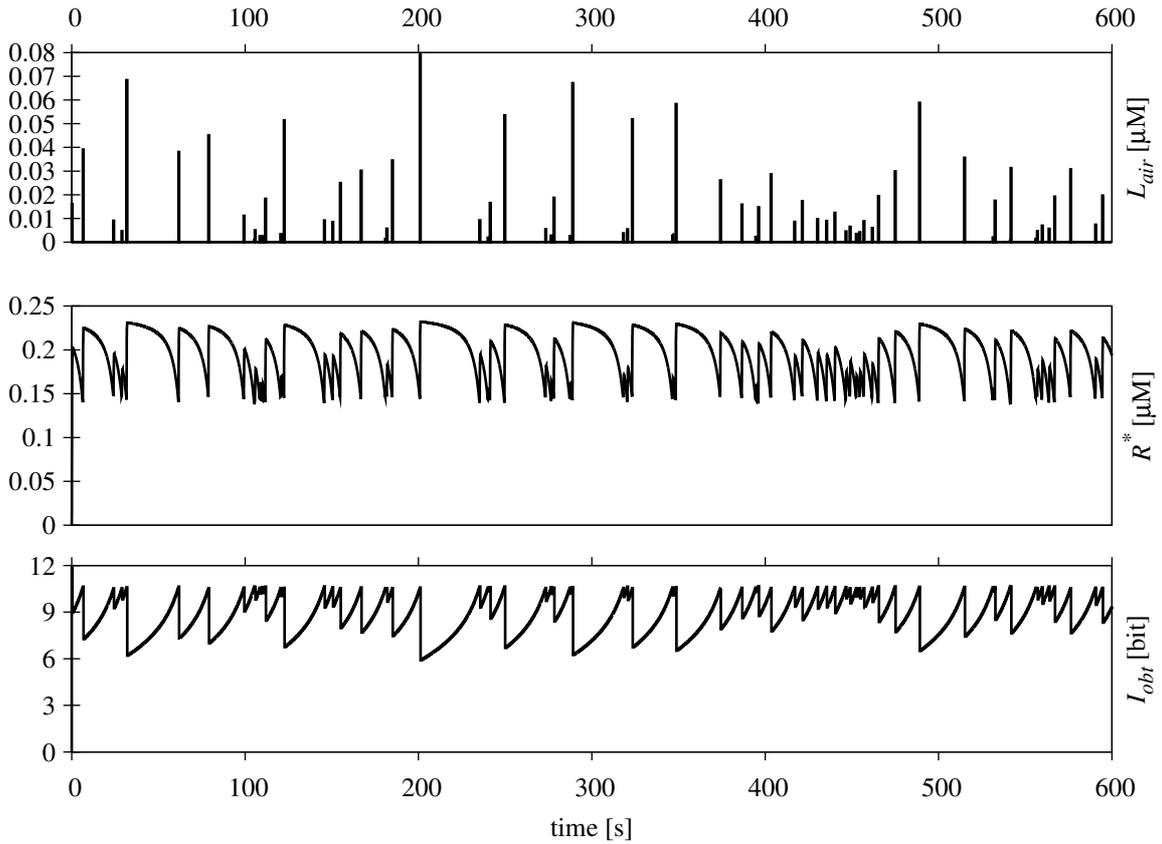


**FIGURE 7.** Reconstruction of optimal stimulus :  $\Delta t = 0.4$  s and  $L_{air}^{max} = 0.1 \mu\text{M}$ . The upper range of stimulus is limited by the asymptotic maximum in order to stabilize the performance of the system under persistent stimulation. However, the obtainable information is always below 12 bits and the full encoding capacity is never used.

## DISCUSSION

It is impossible to characterize the optimal stimulus distribution without restricting either the maximum pheromone concentration or by considering the intermittent nature of stimulation, since the performance of the system may be unstable in time, see Fig. 5. We discuss the two possible considerations separately:

1. The signal is present all the time but its upper bound is limited, which prevents the responses from saturation (Fig. 7). The optimal probability density function is skewed towards higher stimulus values depending on the level of temporal detail  $\Delta t$ . However, continuous stimulation with higher stimulus may lead to the saturation of activated states, decrease in transferred information and consequent loss of correct direction of flight for the insect. Such situations have been observed close to the source [22] leading to flight "arrestment" of the male moths. This behavioral change can be explained using the obtained results. Once the transferred information decreases to zero, there is no way for the animal to tell whether it



**FIGURE 8.** Reconstruction of optimal stimulus including intermittency:  $\Delta t = 0.4$  s and  $\max L_{\text{air}} = 0.3 \mu\text{M}$ . The periods of zero signal are predicted by the model under the condition of optimal signal coding, so the system performs optimally and  $f(L_{\text{air}})$  is stable in time (whenever the signal is present). The optimal stimulus probability density function is described by the exponential probability density. The resulting intermittency factor is 7 %.

is flying in the odorant plume or in a clean air. The observed zigzag pattern and counterturns then lead to decrease in the stimulus value and to the reset of the coding process. It has been observed [23] that after extremely strong pheromone stimulation the recovery time may take up to minutes.

2. The upper bound of the signal is unrestricted but the signal is highly intermittent (Fig. 8). We found that the shape of optimal stimulus probability density can be well approximated either by the exponential or log-normal models. This is in full agreement with experimental data [7, 12, 9]. The intermittency is characteristic for natural signals [10]. The values of intermittency predicted by our model are rather in the lower range usually observed in experimental data (10–20 % reported by Jones [7], 10–40 % by Murlis et al. [10] depending on the experimental conditions). The value obtained by our method ( $\approx 7\%$ ) is mainly due to the condition of optimal performance whenever non-zero stimulus is present. The threshold value for zero signal also affects the intermittency factor greatly (this affects the experimental data as well [7, 9]). Another (hypothetic) possibility lies in more rapid deactivation of

the receptors.

The coding range is widest if the initial concentration of activated receptors  $R^*$  is zero. In other words the first stimulus encounter is coded with finest precision and the situation progressively worsens (Fig. 5). This observation is also confirmed experimentally, though not directly, from the electroantennographic measurements of pheromone plume structure. Baker and Haynes [11] found, that after the burst of stimulus is encountered only several first peaks may be followed by the response.

## CONCLUSIONS

We find that the optimization of information transfer in the model of the odorant receptor is complicated by the "memory effect" and the response saturation. If we leave the range of possible stimulus intensities unrestricted then intermittency must be taken into account. The stimulus probability density function that maximizes the information transfer can be well approximated by the exponential model which is in agreement with experimental data. The predicted intermittency is in the lower range of experimentally observed values. The obtained results are put into correspondence with behavioral observations, namely the upwind flight arrestment reported in homogeneous plume clouds or very close to the source.

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