



## Time-Dependent Solutions for a Cable Model of an Olfactory Receptor Neuron

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A mathematical model for an olfactory receptor neuron is investigated. The physiological and anatomical background required for the construction of a mathematical model are explained. The model, which has been described previously, has three components, including the sensory dendrite on which are found the receptor proteins themselves, and others consisting of a passive cable leading to a trigger zone and axon. In the present paper, we pursue an analytical approach for determining the change in time of the receptor potential in the important case of a subthreshold square pulse of odorant stimulation delivered uniformly at the sensory dendrite. Then, the input current increases in time to its asymptotic value. This latter condition means that we can use a Green's function approach in order to obtain accurate representations for the solution for the entire length of the nerve cell. In the case of finite cables the solution is obtained as an infinite series which is shown to converge and can be easily used to find the depolarization at all space and time points of interest. A steady-state result is obtained directly by solving the relevant ordinary differential equation. For a semi-infinite cable an explicit expression is found for the voltage as a function of time and space variables involving a single integral. However, the exact expression follows from this for the steady-state result. The analytical results obtained are compared to numerical solutions and employed to investigate the effect of varying the position of the trigger zone and the electronic length of the neuron.

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### 1. Introduction

We are concerned in this paper with the quantitative aspects of the olfactory transduction process, in which an olfactory receptor neuron is stimulated by the arrival of odorant molecules. These molecules are recognized by receptor proteins on the sensory dendrite of the receptor cell. The structure of the system has made us turn to cable models for neurons, whose applicability to motoneuron soma-dendritic

components was first investigated in the pioneering works of Rall (1960, 1964, 1967; see Segev *et al.*, 1995). The present work continues that in our previous articles (Lánský *et al.*, 1994; Rospars *et al.*, 1996; Vermeulen *et al.*, 1996) in which we have formulated a mathematical model for the olfactory receptor neuron.

In that model the neuron is divided into three compartments. The first compartment represents the sensory dendrite which contains the olfactory receptor molecules. The voltage along this sensory component was assumed to satisfy, with biophysical justification, a cable equation with an input current incorporating an excitatory reversal potential triggered by odorant stimulation. The membrane

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parameters of the cable were assumed to be uniform along its length. This is an accurate representation of the properties of the actual dendrite of the receptor neurons of male moths that respond to the components of the sexual pheromone released by conspecific females (Kaissling, 1986, 1987). The sensory dendrite of this neuron is believed to bear only one type of receptor protein. Moreover, the variation in diameter of this unbranched dendrite, which can be as long as 300  $\mu\text{m}$  in some species, is small over most of its length (Keil, 1984), and can thus be approximated by a cylinder. This neuron is one of the most thoroughly studied olfactory receptor neurons; a survey of its anatomical, neurophysiological and biochemical features can be found in Kaissling (1986, 1987) and Stengl *et al.* (1992) (see also Breer, 1994; Shepherd, 1994).

Adjoining the sensory component is a dendritic and a somatic region in which there is no activation of conductance changes by odorant molecules. In this part of the cell, depolarization spreads passively. Thus, the second component of the model consists of a traditional linear passive cable. The third component of the model consists of a spike-generating region or trigger zone where action-potentials develop when threshold conditions are met or exceeded.

In our investigations of the mechanism of the transduction process we have obtained complete steady-state results for a model of the above kind in the case where the cable length was semi-infinite (Rospars *et al.*, 1996). This model was further studied by Vermeulen *et al.* (1996) for a model neuron of finite length. In these articles as in the present one, the voltage distribution along the neuron was obtained when the sensory dendrite was uniformly stimulated by various concentrations of odorant molecules of a single species activating a corresponding set of receptors sites. The use of a spatially extended input along the cable is new and distinguishes the present investigation from previous ones for model neurons with point stimulations (Rinzel & Rall, 1974; Jack *et al.*, 1981).

In order to develop a theory of the olfactory transduction process, we attempt in this paper to determine time-dependent solutions for the electrical potential along the neuron from the onset of stimulation when the odorant intensity rises from zero to a constant value. As our first attempt to solve this problem using an analytical approach, we will present exact time-dependent solutions under the assumption that the stimulation is subthreshold.

## 2. Analytical Time-dependent Solutions

Let  $x$  be the distance, measured in space constants, from the distal end of the sensory component, and suppose that this component, containing the olfactory receptor sites, extends from  $x = 0$  to  $x = x_1$ . We denote the reversal potential for the permeating ions at the sensory membrane by  $V_E$  and let  $V = V(x, t)$  represent the depolarization at  $x$  at time  $t$ , where time is measured in membrane time-constants. Suppose also that the length of the entire cylinder representing the neuron is  $L$  where  $L \leq \infty$ . Then  $V$  satisfies (see for example Rall, 1959; Tuckwell, 1988b, Ch. 7) the partial differential equation

$$V_t = V_{xx} - V + g(x, t)(V_E - V). \quad (1)$$

Here  $g(x, t)$  represents the induced conductance increase and subscripts represent differentiation with respect to the subscripted variables.

We will assume the following simple scheme for the activation of receptors by arriving odorant molecules. The receptor site is in two possible states, in one of which the ion channels are closed, and in the other the ion channels are open. This is tantamount to the classical theory of drug action (Del Castillo & Katz, 1957) and was employed in the present context by Lánský and Rospars (1993). The opening and closing of ion channels can be regarded as a birth and death process, as in Lam and Lampard (1981). However, because we are considering an essentially deterministic model, we will employ the mean number of open channels to represent the conductance increase due to the stimulation by odorant molecules. Thus, assuming that initially no receptors are activated, the conductance increase may be represented by a function of the form

$$g(x, t) = \bar{g}(1 - e^{-vt})[H(x) - H(x - x_1)] \quad (2)$$

where  $\bar{g}$  depends on several parameters including the receptor density (Rospars *et al.*, 1996),  $v$  depends on parameters related to transport of odorant molecules and transduction mechanisms including transition probabilities for opening and closing of ion channels, and  $H(\cdot)$  is the unit-step function, equal to zero for negative arguments and equal to unity otherwise. The difference of step-functions in (2) ensures that the conductance change  $g(x, t)$  only occurs from  $x = 0$  to  $x = x_1$  where receptor sites and their associated ion channels are located, and tends, for  $0 < x < x_1$ , to the asymptotic steady-state value  $\bar{g}$  with time constant  $1/v$ . Both constants  $\bar{g}$  and  $v$  are expected to depend on the intensity of stimulation i.e. on the concentration of the odorant molecules (for the dependence of  $\bar{g}$  on concentration, see Rospars *et al.*, 1996).

This approach can be generalized to the case of a sensory dendrite bearing several types of receptors and an odorant stimulus constituted of several types of molecules. Then, (1) becomes

$$V_i = V_{xx} - V + (V_E - V)[H(x) - H(x - x_1)] \times \sum_{i=1}^n \bar{g}_i (1 - e^{-v_i t}) \quad (3)$$

where  $i, i = 1, 2, \dots, n$ , indicates each species of odorant molecule-receptor combination. However, it will simplify the expressions which follow if we drop the summation over  $i$  in (3) and consider only one type of odorant-receptor combination, as in the case of the insect receptor neurons responding to components of sexual pheromones.

We assume that initially the entire receptor is at resting potential. Thus, the initial condition is

$$V(x, 0) = 0, \quad 0 \leq x \leq L. \quad (4)$$

Furthermore, throughout this article, a sealed-end condition will be employed at  $x = 0$ , so that there we have boundary condition

$$V_x(0, t) = 0, \quad t \geq 0. \quad (5)$$

The partial differential eqn (1) cannot be solved directly using a Green's function because of the term  $(V_E - V)$ . However, we are able to find analytical solutions for the equation

$$V_t = V_{xx} - V + \bar{g}V_E[H(x) - H(x - x_1)](1 - e^{-vt}), \quad (6)$$

which derives from (1) under the assumption that

$$V \ll V_E \quad (7)$$

that is, when the response to stimulation is uniformly well below the reversal potential. It is expected that assumption (7) will be valid under conditions of weak stimulation, which constitutes a physiologically important situation. The corresponding assumption for the input parameter  $\bar{g}$  is that it be small enough to ensure that relation (7) is satisfied. This approximation can also be interpreted as the injection of a current density  $I(x, t)$  given by the rightmost term of (6).

Equation (6), in conjunction with the boundary conditions, is in the form of a standard linear cable equation and can thus be solved using the appropriate Green's function. It will be a useful simplification to utilize the linearity or superposition principle (Tuckwell, 1988a, p. 191) to decompose the solution as

$$V(x, t) = U(x, t) - W(x, t), \quad (8)$$

where  $U$  satisfies

$$U_t = U_{xx} - U + \bar{g}V_E[H(x) - H(x - x_1)], \quad (9)$$

and  $W$  satisfies

$$W_t = W_{xx} - W + \bar{g}V_E e^{-vt}[H(x) - H(x - x_1)]. \quad (10)$$

The boundary and initial conditions for  $U$  and  $W$  are the same as those for  $V$ .

We will consider the cases of (a) a finite-cable, with  $L < \infty$ , and a sealed-end condition at  $x = L$ ,

$$V_x(L, t) = 0; \quad (11)$$

and (b) a semi-infinite cable, with  $L = \infty$ , with the usual boundary requirement of boundedness at infinity.

### 3. Solutions for a Finite Cable

In the case of a finite cylinder of length  $L$  and with both ends sealed, the Green's function is given by

$$G(x, y; t) = \frac{e^{-t}}{L} \left\{ 1 + 2 \sum_{n=1}^{\infty} \cos\left(\frac{n\pi x}{L}\right) \cos\left(\frac{n\pi y}{L}\right) \exp\left(-\frac{n^2\pi^2 t}{L^2}\right) \right\} \quad (12)$$

(Tuckwell, 1988a). Substitution of this in the following standard formula,

$$V(x, t) = \int_0^L \int_0^t G(x, y; t - s) I(y, s) ds dy \quad (13)$$

with current density  $I = \bar{g}V_E[H(x) - H(x - x_1)]$  [see (9)] gives

$$U(x, t) = \frac{\bar{g}V_E}{L} \left\{ x_1(1 - e^{-t}) + \frac{2L}{\pi} \sum_{n=1}^{\infty} T_n \right\}, \quad (14)$$

where

$$T_n(x_1; x, t) = \frac{1}{nk_n} \cos\left(\frac{n\pi x}{L}\right) \sin\left(\frac{n\pi x_1}{L}\right) (1 - e^{-k_n t}), \quad (15)$$

and  $k_n = 1 + n^2\pi^2/L^2$ . Similarly, substitution of (12) in (13) with current density  $I = \bar{g}V_E e^{-vt}[H(x) - H(x - x_1)]$  given by (10), gives  $W(x, t)$ , but certain values of  $v$  need special attention. When  $v$  is not equal to  $1 + n^2\pi^2/L^2$  ( $n = 0, 1, \dots$ ), we have

$$W(x, t) = \frac{\bar{g}V_E}{L} \left\{ \frac{x_1}{1 - v} (e^{-vt} - e^{-t}) + \frac{2L}{\pi} \sum_{n=1}^{\infty} T_n^* \right\}, \quad (16)$$

where

$$T_n^*(x_1; x, t) = \frac{1}{nk_n^*} \cos\left(\frac{n\pi x}{L}\right) \sin\left(\frac{n\pi x_1}{L}\right) \{e^{-vt} - e^{-k_n t}\}, \quad (17)$$

with  $k_n^* = k_n - v$ . In the special case  $v = 1$  we find that  $W$  simplifies to

$$W(x, t) = \frac{\bar{g}V_E}{L} e^{-t} \left( x_1 t + \frac{2L^3}{\pi^3} \sum_{n=1}^{\infty} T_n^{**} \right), \quad (18)$$

where

$$T_n^{**}(x_1; x, t) = \frac{1}{n^3} \cos\left(\frac{n\pi x}{L}\right) \sin\left(\frac{n\pi x_1}{L}\right) \left\{ 1 - \exp\left(-\frac{n^2 \pi^2 t}{L^2}\right) \right\}. \quad (19)$$

From these expressions the response can be calculated for all  $x$  and  $t$ . The exceptional cases  $v = 1 + n^2 \pi^2 / L^2$  ( $n = 1, 2, \dots$ ) would require further special treatment of a singular term in the series for  $W$ .

#### THE STEADY STATE

The steady-state distribution of potential (6) under assumption (7), which we denote by  $V^*(x)$ , must satisfy the ordinary differential equation

$$V^{*''} - V^* = -\bar{g}V_E[H(x) - H(x - x_1)], \quad (20)$$

(primes indicating differentiation) and, in the present case we require  $V^{*'}(0) = V^{*'}(L) = 0$ . It is found that this steady-state solution is given by, firstly,

$$V^*(x) = \bar{g}V_E \left( 1 + \frac{\sinh(x_1 - L)\cosh(x)}{\sinh(L)} \right), \quad (21a)$$

when  $0 < x < x_1$ , and by

$$V^*(x) = \bar{g}V_E \frac{\sinh(x_1)\cosh(x - L)}{\sinh(L)}, \quad (21b)$$

when  $x_1 \leq x \leq L$ . Here  $V^*(x)$  is continuous at  $x = x_1$  and furthermore it is clear that  $V^*(x)$  is bounded for all  $x$ . This latter fact enables us to see that the series involved in the determination of  $V$  converge, because we always have  $V(x, t) < V^*(x)$ , for all  $x$  and all  $t$ .

#### 4. Solutions for a Semi-infinite Cable

For the case  $L = \infty$  but with the same boundary condition as above at the origin, the Green's function is (Tuckwell, 1988a)

$$G(x, y; t) = \frac{e^{-t}}{\sqrt{4\pi t}} \left\{ \exp\left(-\frac{(x-y)^2}{4t}\right) + \exp\left(-\frac{(x+y)^2}{4t}\right) \right\}. \quad (22)$$

On using this function in conjunction with the given current density we now obtain, after some manipulations,

$$U(x, t) = \frac{\bar{g}V_E}{2\sqrt{\pi}} \int_0^{x_1} \int_0^t \frac{e^{-(t-s)}}{\sqrt{t-s}} \left\{ \exp\left(-\frac{(x-y)^2}{4(t-s)}\right) + \exp\left(-\frac{(x+y)^2}{4(t-s)}\right) \right\} ds dy.$$

If we now put  $T = t - s$ , then since when  $s = 0$ ,  $T = t$  and when  $s = t$ ,  $T = 0$  and since  $dT = -ds$ , we get

$$U(x, t) = \frac{\bar{g}V_E}{2\sqrt{\pi}} \int_0^{x_1} \int_0^t \frac{e^{-T}}{\sqrt{T}} \left\{ \exp\left(-\frac{(x-y)^2}{4T}\right) + \exp\left(-\frac{(x+y)^2}{4T}\right) \right\} dT dy.$$

To simplify this we put, for the contribution from  $\exp(-(x-y)^2/4T)$ ,  $z = x - y$  so that when  $y = 0$ ,  $z = x$  and when  $y = x_1$ ,  $z = x - x_1$ . Since  $dz = -dy$ , this contribution is

$$U_1(x, t) = -\frac{\bar{g}V_E}{2\sqrt{\pi}} \int_x^{x-x_1} \int_0^t \frac{e^{-T}}{\sqrt{T}} \exp\left(-\frac{z^2}{4T}\right) dT dz.$$

In the contribution from  $\exp(-(x+y)^2/4T)$ , we put  $z = x + y$  so that when  $y = 0$ ,  $z = x$  and when  $y = x_1$ ,  $z = x + x_1$ . Since here  $dz = dy$ , the second part of  $U$  is

$$U_2(x, t) = \frac{\bar{g}V_E}{2\sqrt{\pi}} \int_x^{x+x_1} \int_0^t \frac{e^{-T}}{\sqrt{T}} \exp\left(-\frac{z^2}{4T}\right) dT dz.$$

Combining  $U_1$  and  $U_2$  into a single expression gives

$$U(x, t) = \frac{\bar{g}V_E}{2\sqrt{\pi}} \int_{x-x_1}^{x+x_1} \int_0^t \frac{e^{-T}}{\sqrt{T}} \exp\left(-\frac{z^2}{4T}\right) dT dz.$$

We may now use the standard integral (Gradshteyn & Ryzhik, 1965)

$$\int_0^t \frac{e^{-T-(x^2/4T)}}{\sqrt{T}} dT = \frac{\sqrt{\pi}}{2} \left\{ e^{-|x|} \operatorname{erfc}\left(\frac{|x|-2t}{2\sqrt{t}}\right) - e^{|x|} \operatorname{erfc}\left(\frac{|x|+2t}{2\sqrt{t}}\right) \right\}$$

where  $\operatorname{erfc}(\cdot)$  is the complementary error function, to convert the expression for  $U$  to

$$U(x, t) = \frac{\bar{g}V_E}{4} \int_{x-x_1}^{x+x_1} \left\{ e^{-|z|} \operatorname{erfc}\left(\frac{|z|-2t}{2\sqrt{t}}\right) - e^{|z|} \operatorname{erfc}\left(\frac{|z|+2t}{2\sqrt{t}}\right) \right\} dz. \quad (23)$$

Here one can obtain  $U$  at any  $x$  and  $t$  by a simple integration. Similarly, a simple expression can be obtained for  $W(x, t)$  and hence  $V(x, t)$ . In addition, an explicit formula can be obtained for the steady-state distribution of potential along the entire neuronal cable, as we now demonstrate.

#### THE STEADY STATE

The steady-state potential in the case of a semi-infinite cable can be found from the expression for  $U(x, t)$  on taking the limit  $t \rightarrow \infty$ . Note that there is no contribution from  $W$ . Using the facts that  $\operatorname{erfc}(-\infty) = 2$  and  $\operatorname{erfc}(\infty) = 0$ , we have

$$V(x, \infty) = \frac{\bar{g}V_E}{2} \int_{x-x_1}^{x+x_1} e^{-|z|} dz.$$

One has to distinguish now the cases  $x \leq x_1$  and  $x > x_1$ . After some algebraic considerations we finally obtain,

$$V^*(x) = \bar{g}V_E(1 - e^{-x_1} \cosh(x)), \quad 0 \leq x \leq x_1 \quad (24a)$$

and

$$V^*(x) = \bar{g}V_E e^{-x} \sinh(x_1), \quad x \geq x_1. \quad (24b)$$

Note that (24b) applies at the neuron's trigger zone.

### 5. Numerical Results and Discussion

In the case of a finite neuron, we have obtained analytical series approximations for conditions of weak stimulation. These analytical solutions were obtained for (6) using the appropriate Green's function. Since one may solve this equation by numerical techniques, such as the Crank–Nicolson

method (see, for example, Mascagni, 1989) we decided to investigate the relative efficiencies of these two methods of solution.

We computed the receptor potential  $V(x, t)$  using the series solution truncated at a small number  $p$  of terms. We also solved (6) numerically using the Crank–Nicolson finite-difference scheme. Letting the numerical solution be  $\tilde{V}(x, t)$  we determined the relative error  $(\tilde{V} - V)/\tilde{V}$ . Results for this quantity are shown in Figs 1(a) and (b). In Fig. 1(a) we plot the relative error vs the number of terms in the series solution at  $x = 0.5$ ,  $t = 1.0$  with  $\bar{g} = 0.15$  and  $v = 1$ , for two values of cable length,  $L = 1.5$  and  $L = 10.0$ , representing the extremes of physiological lengths. The solution can be seen to be accurately (within 1%) represented by only a few terms when  $L = 1.5$ , whereas about 12 terms are required when  $L = 10$ . [It is known that the series solution obtained using the

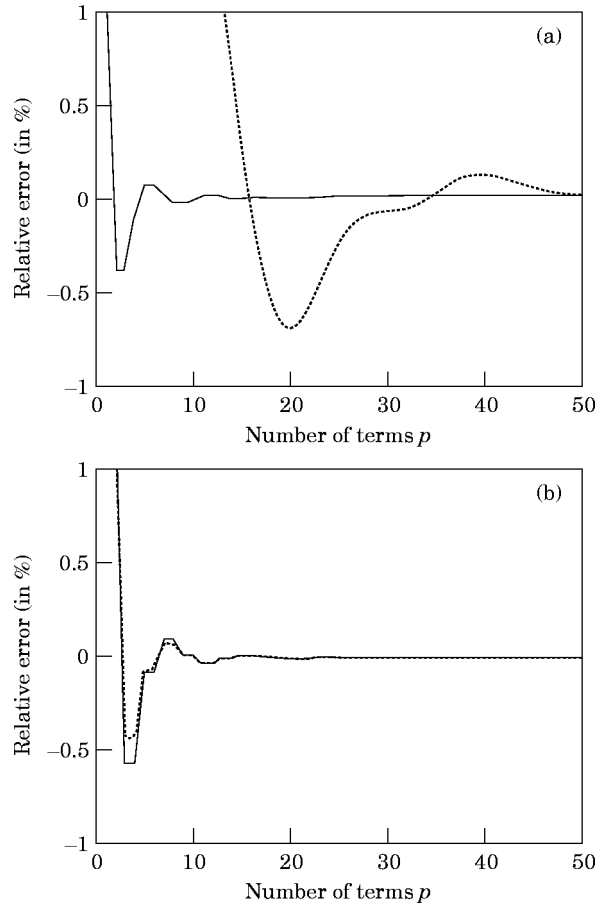


FIG. 1. Relative error  $(\tilde{V} - V)/\tilde{V}$  on receptor potential  $V = V(x, t)$  given by (8) with respect to solution  $\tilde{V}$  obtained by numerical integration of (6), as a function of the number  $p$  of terms kept in the infinite series of (14), (16) or (18). (a) For neuron lengths  $L = 1.5$  (solid line) and  $L = 10$  (dotted line) with  $1/v = 1$ . (b) For time constants  $1/v = 0.5$  (solid line) and  $1/v = 5$  (dotted line) with  $L = 2$ . Parameters:  $x_1 = 1$ ,  $x = 0.5$ ,  $t = 1$ ,  $\bar{g} = 0.15$ ,  $V_E = 100$ .

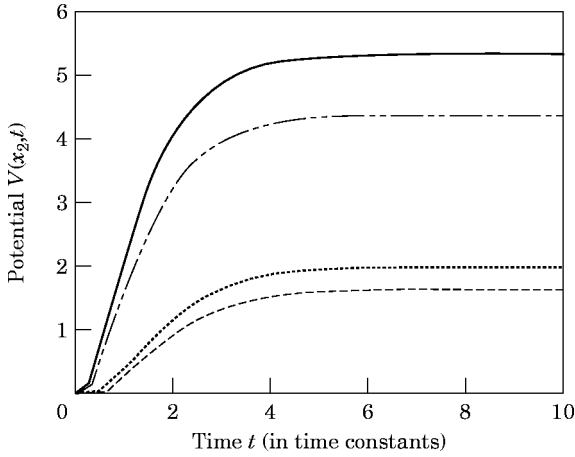


FIG. 2. Evolution in time of the receptor potential  $V(x_2, t)$  at the neuron's spike trigger zone  $x_2$ . Effect of altering the position  $x_2$  of the trigger zone such that  $x_2 = 1.2$  (solid line),  $x_2 = 1.4$  (dash-dotted line),  $x_2 = 2.2$  (dotted line) and  $x_2 = 2.4$  (dashed line), for a fixed region of stimulation (from 0 to  $x_1$ ) at a fixed intensity of stimulation. Parameters:  $x_1 = 1$ ,  $L = 5$ ,  $\bar{g} = 0.15$ ,  $v = 2$ ,  $V_E = 100$ .

eigenfunction expansion representation (12) for the Green's function converges rapidly at moderate and large values of  $t$ ; see Rinzel & Rall (1974).] In Fig. 1(b) we show the effect of varying  $v$ , the reciprocal of the time constant for transport and transduction of odorant molecules. These results indicate that the relative error is both small and insensitive to the magnitude of  $v$  as there is little change when  $v$  varies by an order of magnitude. When  $p = 20$  the relative error is less than 1% over the entire range of physiological values of  $L$  and for  $p = 50$  it is less than 0.1%.

There is therefore an obvious advantage of less computational time in using the analytical representations of the solutions, especially when simulating a large array of receptor neurons. When we use analytical methods, the potential at a given time  $t$  can be computed directly whereas if we use numerical methods to calculate the potential at time  $t$ , we need to iteratively evaluate the solution over the entire interval  $(0, t]$ .

We have used the results of Sections 3 and 4 to compute values of the depolarization at various positions on the receptor neuron for various values of the parameters. Our first calculations were for finite cables and were designed to investigate the effects of varying the position  $x_2$  of the neuron's trigger zone with all remaining parameters fixed. In Fig. 2 we show the results for  $V(x_2, t)$  as a function of time, the latter being in time constants. The value  $x_1 = 1$  (in space-constant units) is chosen because it is believed to represent accurately the actual neuroanatomical arrangement in the case of a moth sex-pheromone receptor neuron (Kaissling, 1987). The value  $L = 5$

was chosen also as a representative length, enabling the trigger zone to be placed both close to the region of stimulation (e.g.,  $x_2 = 1.2, 1.4$ ) and fairly remote from it (we chose the values 2.2. and 2.4). It can be seen from the figure that the latency to reach a given depolarization (e.g. 1) is much larger in the case of a long passive dendrite. However, the steady state is reached within the same time (about 5 time constants) whatever the length of the passive dendrite. It can be seen also that the change in voltage induced by the same change  $\Delta x_2 = 0.2$  is much greater when the trigger zone is close to the region of stimulation than it is when the trigger zone is further away. From these results we deduce that larger coding errors of stimulus intensity could be induced when the trigger zone is too close to the region in which the receptor molecules are found. This conclusion is based on the assumption that the receptor uses a firing frequency code for intensity. However, we are not concerned here with supra-threshold stimulation but seek only general principles which may be deduced using an analytical approach.

It is also of interest to see the effects of changing the overall electrotonic length of the neuron. The coding may be strongly position-dependent and in particular depend on the location of the receptor proteins in relation to other cell components, including the axon which terminates in the brain. In Fig. 3 we show the variations in  $V(x_2, t)$  for fixed  $x_1$ ,  $x_2$ ,  $\bar{g}$  and  $V_E$  for values of  $L = 2.0, 2.5$  and  $10.0$ . It can be seen that the magnitude of the response at the trigger zone is affected greatly by increasing the length from 2 to 2.5 but past such values of  $L$ , relatively little

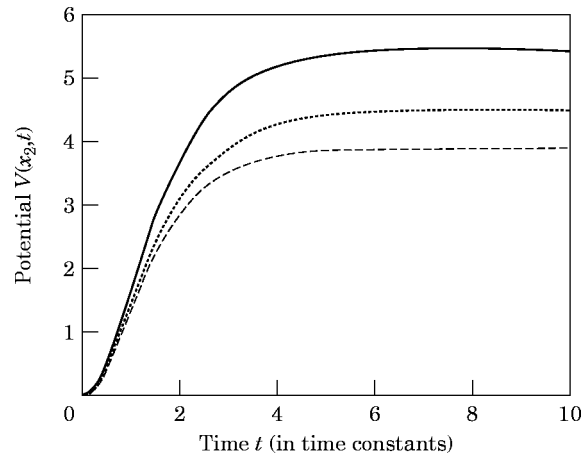


FIG. 3. Evolution in time of the receptor potential  $V(x_2, t)$  at the spike trigger zone  $x_2$ . Effect of altering the electronic length  $L$  of the cable representing the neuron at a fixed intensity of stimulation. Shown for  $L = 2$  (solid line),  $L = 2.5$  (dotted line) and  $L = 10$  (dashed line). Parameters:  $x_1 = 1$ ,  $x_2 = 1.5$ ,  $\bar{g} = 0.15$ ,  $v = 2$ ,  $V_E = 100$ .

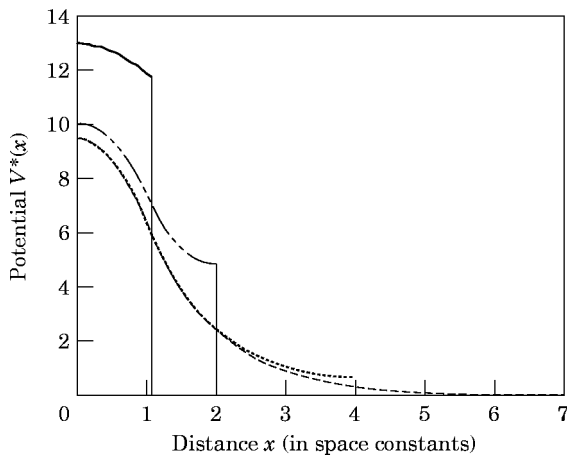


FIG. 4. Steady-state distributions of the receptor potential  $V^*(x)$  throughout the neuron for cable lengths  $L = 1.2$  (solid line),  $L = 2$  (dash-dotted line),  $L = 4$  (dotted line) and  $L = \infty$  (dashed line) and for fixed conditions of stimulation. The results for finite cables are obtained from (21a) and (21b), that for an infinite cable from (24a) and (24b). Parameters:  $x_1 = 1$ ,  $\bar{g} = 0.15$ ,  $V_E = 100$ .

change in response occurs as  $L$  increases. This implies that cells with smaller overall electrotonic lengths are more sensitive and this sensitivity is decreased as the length increases. There may here be an analogy with the well-known size principle, exposed for motoneurons (Henneman *et al.*, 1965; Burke, 1973; Traub, 1977).

The final set of numerical results is displayed in Fig. 4. Here are shown the steady-state distributions of potential for various cable lengths and for fixed values of  $x_1$ ,  $\bar{g}$  and  $V_E$ . For  $L = 1.2$  there is little variation in  $V^*$  over the entire neuron. In the probably more realistic cases, with  $L \geq 2$  (note that  $x_1 = 1$  by assumption) it can be seen that the rate of decline in potential is quite large, but when  $L$  becomes very large ( $L = \infty$ ) the potential distribution over the distal dendrite including the region of stimulation and possibly over the trigger zone is practically independent of  $L$ . The results of Figs 3 and 4 indicate that there may be an optimal value of  $L$  (perhaps between 1.5 and 3) beyond which value little change in response over the sensory part  $[0, x_1]$  or over the passive region  $[x_1, x_2]$  occurs and in fact where the response over these regions is quite pronounced, even for conditions of weak stimulation as have been assumed throughout this study.

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