An Efficient Algorithm for Cable Theory,
Applied to Blowfly Photoreceptor Cells and LMC's

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Abstract. A both simple and efficient algorithm is presented that yields the voltages and currents in an arbitrary cable structure. The algorithm consists of the following steps: 1. The cable structure is divided into homogeneous cable segments; 2. Each cable segment is considered as a two-port, and replaced by an equivalent circuit consisting of discrete elements; 3. The resulting equivalent scheme of the whole cable structure is solved with an algorithm for ladder networks (or, if the structure is not tree-like, with a network analysis program), which yields the input and output voltages and currents of each cable segment; and if required 4. The voltage and current distribution in each segment is determined from the input and output voltages and currents. The algorithm is applied to blowfly photoreceptor cells and LMC's, i.e., neurons that receive their main input from the photoreceptor cells. The photoreceptor cells are especially interesting as a model, because cells that receive light from the same direction are coupled by gap junctions between their axon terminals (Chi and Carlson 1976; Ribi 1978; Shaw and Stowe 1982). This coupling can be conveniently analyzed with the help of the algorithm presented. The LMC's are interesting as a model, because they are long (500 μm) and narrow (2 μm), and there has been some debate over the question whether they conduct their signals passively or by an active mechanism (Zettler and Järvi-Lehto 1973; Wilson 1978; Shaw 1984b). We will see, that the assumption of passive signal conduction is consistent with all existing data on the LMC's.

1 Introduction

This article serves two purposes. First, it presents a fast and efficient algorithm for solving by computer the cable equation in an arbitrary cable structure. Second, it presents several applications of the algorithm to cells in the blowfly eye that are subject to intense investigation.

The theory on which this algorithm is based is not new. For many special cases solutions in closed form of the cable equation have been obtained (Jack et al. 1975). For more complicated structures other approaches are necessary, e.g. the equivalent cylinder concept (Rall 1959), the use of a network analysis program on compartmental models (where short cable segments are approximated by RC-circuits, Rall 1964; Segev et al. 1985), or the design of a calculus for handling treelike cable structures (Butz and Cowan 1974; Koch and Poggio 1985). This article tries to integrate the last two approaches: cable segments are replaced by equivalent circuits consisting of discrete elements, and an algorithm for the resulting equivalent circuit of the whole cable structure is developed. The difference with previous compartmental models is that the equivalent circuit is an exact description of the cable segment and not an approximation. From it we can obtain the entire current and voltage distribution in the cell.

The theory is applied to blowfly photoreceptor cells and LMC's, i.e., neurons that receive their main input from the photoreceptor cells. The photoreceptor cells are especially interesting as a model, because cells that receive light from the same direction are coupled by gap junctions between their axon terminals (Chi and Carlson 1976; Ribi 1978; Shaw and Stowe 1982). This coupling can be conveniently analyzed with the help of the algorithm presented. The LMC's are interesting as a model, because they are long (500 μm) and narrow (2 μm), and there has been some debate over the question whether they conduct their signals passively or by an active mechanism (Zettler and Järvi-Lehto 1973; Wilson 1978; Shaw 1984b). We will see, that the assumption of passive signal conduction is consistent with all existing data on the LMC's.

2 Theory

2.1 The Cable Equation

The cable equation is most easily derived in the frequency domain (e.g. Scott 1970; Koch and Poggio 1985). A cable is then represented by distributed complex impedances $z_a$ and $z_m$, the impedances of the axoplasm and the membrane respectively (Fig. 1A). Ohm's law and current conservation lead to the
Fig. 1. A The cable shown has a distributed impedance of the axoplasm $Z_a$, and a distributed impedance of the membrane $z_m$. $i_a$ is the axial current in the cable, $i_m$ the membrane current, and $v$ the membrane voltage. B A cable segment considered as a two-port, with voltage $v_1$ and current $i_1$ at the one port, and $(v_2, i_2)$ at the other. C The shown T-network is an equivalent circuit for the two-port of B. The impedances $z_{11}$ and $z_{12}$ are given in the text following equations (Koch and Poggio 1985)

\[
v = i_m z^2_m , \tag{1}
\]

\[
\frac{dv}{dx} = -i_m z_a , \tag{2}
\]

\[
\frac{di_m}{dx} = -i_m , \tag{3}
\]

with

\[
z_a = r_a = \frac{R_a}{\pi a^2} , \tag{4}
\]

\[
z_m = r_m \left[ \frac{1}{\jmath \omega c_m} = \frac{r_m}{1 + \jmath \omega c_m r_m} \right] , \tag{5}
\]

\[
r_m = \frac{R_m}{2\pi a} , \tag{6}
\]

\[
c_m = 2\pi a C_m , \tag{7}
\]

where all currents and voltages are in the frequency domain, as they will be in the remainder of this article; $v$ is the membrane potential $[V]$, $i_m$ the membrane current per unit length cable $[A/m]$, $i_a$ the axoplasmic current $[A]$, $r_a$ the axoplasmic resistance per unit length cable $[\Omega/m]$, $r_m$ the membrane resistance per unit length cable $[\Omega/m]$, $r_m$ the membrane resistance $[\Omega m^2]$, $c_m$ the membrane capacitance per unit length cable $[F/m]$, and $C_m$ the membrane capacitance $[F/m^2]$. Differentiating (2) to $x$, substituting (3), and using (1) yields (Koch and Poggio 1985)

\[
\frac{d^2v}{dx^2} = g^2v , \tag{8}
\]

with

\[
g = \left( \frac{z_a}{z_m} \right)^{1/2} . \tag{9}
\]

Although $g$ depends on $\omega$, it does not depend on $x$, thus the cable equation (8) is a simple second order differential equation with general solution

\[
v = A \exp (-gx) + B \exp (gx) , \tag{10}
\]

where $A$ and $B$ are constants determined by the boundary conditions of the actual configuration.

2.2 A Cable Segment as a Two-Port

As Fig. 1B shows, a cable segment can be considered as a two-port, with a voltage $v_1$ and current $i_1$ at the one port, and a voltage $v_2$ and current $i_2$ at the other. This way of representing a cable segment is especially appealing when we are not interested in the whole current and voltage distribution in the segment, but only in the input/output behaviour. This is often the case when studying neurons, where synapses are the natural input and output sites. But it is in fact quite easy to find the whole current and voltage distribution if necessary, as will be shown in Sect. 2.5.

There are several schemes giving the relations between voltages and currents of a two-port (e.g. Kinariwala et al. 1973), of which we shall use here the $z$-parameter scheme

\[
v_1 = z_{11} i_1 + z_{12} i_2 , \tag{11}
\]

\[
v_2 = z_{21} i_1 + z_{22} i_2 = z_{12} i_1 + z_{11} i_2 , \tag{12}
\]

where $[z_{ij}]$ is a $2 \times 2$ matrix giving the voltages when the currents are known. But any combination of two of the four voltages and currents ($v_1, v_2, i_1, i_2$) will yield the other two with the help of (11) and (12), if $[z_{ij}]$ is known. The second equation in (12) follows from symmetry (see Fig. 1B).

The boundary conditions for the cable segment of Fig. 1B ($v(x=0)=v_1$, $v(x=l)=v_2$, $i_m(x=0)=i_1$, and
\[ i_4(x=l) = -i_2 \] lead to
\[ z_{11} = \frac{z_a \exp(gl) + \exp(-gl)}{g \exp(gl) - \exp(-gl)} = \frac{z_a \cosh(gl)}{g \sinh(gl)}, \quad (13) \]
\[ z_{12} = \frac{2}{g} \frac{\exp(gl) - \exp(-gl)}{\exp(gl) + \exp(-gl)} = \frac{1}{g \sinh(gl)}, \quad (14) \]

where \( l \) is the length of the segment, and (10) and (2) were used. The impedance \( z_{11} \) is the input impedance of the cable with open-ended output \((i_4 = 0)\), \( z_{12} \) is the transfer impedance \((v_3/i_2)\) with open-ended output. These equations are well-known in cable theory [cf. Butz and Cowan 1974, (42)].

### 2.3 A Cable Segment as a T-Network

A convenient way to represent (11) and (12) is depicted in Fig. 1C. The behaviour of this network is identical to that of (11) and (12), as can be easily checked. The T-network as an equivalent scheme for a cable segment has several attractive features. First, it is easy to handle, e.g. for drawing the equivalent scheme of an arbitrary cable structure. Second, closed loops can be dealt with as well as tree-like structures. Third, the continuous cable has been reduced to a lumped circuit (Fig. 1C), by which the distributed impedances (13) and (14) can be obtained. This allows the use of a network analysis program for solving complicated cable structures without much extra computational effort compared to compartmental models, as used by e.g. Rall (1964) and Segev et al. (1985). Finally, the equivalent scheme leads to ladder networks, which are easily solved with the algorithm demonstrated below.

### 2.4 Solving Ladder Networks

The solution of a ladder network by computer is efficiently done with the algorithm of Kinariwala et al. (1973). This is illustrated by the example of Fig. 2. Suppose we apply a voltage \( v_1 \) at the beginning of the circuit, and we want to know the voltage \( v_3 \) and the current \( i_1 \). We then first assume that the voltage \( v_4 \) at the far end of the circuit is 1; this means that we normalize all voltages and currents to \( v_4 \). Then we work our way backwards through the circuit (for a particular frequency \( \omega \))

\[ v_4 = 1, \]
\[ i_3 = v_4/z_6, \]
\[ v_3 = v_4 + i_3 z_3, \]
\[ i_2 = i_3 + v_3/z_4, \]
\[ v_2 = v_3 + i_2 z_2, \]
\[ i_1 = i_2 + v_2/z_2, \]
\[ v_1 = v_2 + i_1 z_1, \]
\[ A_{13} = v_3/v_1, \]
\[ A_{11} = i_1/v_1. \]

Although \( v_4 = 1 \) will generally not be the case, the ratio of any two voltages or currents will be correct, because the circuit is linear. Thus \( A_{13} \) is the ratio of \( v_3 \) and \( v_1 \) (at frequency \( \omega \)), and \( A_{11} \) the input admittance of the circuit. If we multiply the applied voltage \( v_1 \) (i.e. the component of \( v_1 \) with frequency \( \omega \)) with \( A_{13} \), we get the resulting voltage \( v_3 \), multiplication with \( A_{11} \) yields \( i_1 \). Going through (15) for all relevant frequencies yields all voltages and currents in the circuit. In the computer (15) is conveniently implemented as a function or subroutine.

For tree-like cable structures, e.g. dendritic trees (Koch et al. 1982), the ladder algorithm can also be used. Each branch is then considered as a separate ladder, for which the input impedance follows from the algorithm. This input impedance is then used for the circuit of the parent branch.

### 2.5 The Voltage and Current Distribution in a Cable Segment

Once we have determined the input and output voltages and currents of a cable segment, we can find the voltage and current distribution for that segment as follows

\[ v(x) = \frac{z_a}{g} \frac{i_1 \cosh(gl-x) + i_2 \cosh(gx)}{\sinh(g)} \], \quad (16) \]
\[ i_a(x) = \frac{i_1 \sinh(gl-x) - i_2 \sinh(gx)}{\sinh(g)} \], \quad (17) \]
\[ i_m(x) = g \frac{i_1 \cosh(gl-x) + i_2 \cosh(gx)}{\sinh(g)} \], \quad (18) \]

where \( l \) is the length of the segment, \( x \) the distance from the \((v_1, i_1)\)-port (see Fig. 1B), and (16) follows from (2), (10), and the boundary conditions. Equations (17) and (18) follow from (16), (2), and (1). To find the voltage and current distribution in the whole cable structure, the cable is divided into cable segments and converted to T-networks, and the ladder algorithm applied (or a network analysis program). If currents are injected at
several places, the resulting voltages and currents in the cable structure can be found from superposition: the responses to each current injected add. From this the input and output voltages and currents of the cable segments follow, which finally yields the voltage and current distribution in each segment through (16)-(18).

3 Example: An Isolated Photoreceptor Cell

The cell body of a fly photoreceptor cell is an elongated structure, about 250 μm long and 5 μm wide. Along the cell body lies the rhabdomere, a light-guiding structure containing the photopigment. Absorption of light leads to a depolarizing receptor potential. At the bottom of the cell a short axon, about 35 μm long and 2 μm wide, conducts the receptor potential to the synaptic zone in the lamina. In the lamina, second and higher order neurons process the signal further. An isolated photoreceptor cell is shown schematically in Fig. 3A, its equivalent circuit in Fig. 3B. As an approximation we assume that photocurrent (or current applied through a microelectrode) enters the cell only halfway along its cell body. Applying the algorithm of Sect. 2.4 to this circuit yields

\[
\begin{align*}
\frac{v_4}{i_4} &= 1, \\
\frac{v_3}{i_3} &= v_4/z_1, \\
\frac{v_2}{i_2} &= \frac{v_3}{i_3} + \frac{v_2}{z_1}, \\
\frac{v_1}{i_1} &= \frac{v_2}{i_2}, \\
\frac{R_{ii}}{A_{14}} &= \frac{v_4}{i_4}, \\
\frac{R_{lg}}{A_{14}} &= \frac{v_4}{i_1},
\end{align*}
\]

(19)

where the leftmost cable segment is assumed to be open ended at the left side, and thus reduces to a single load \(z_{11}\). \(R_{11} = v_4/i_1\) in (19) is the input impedance of the cell, \(A_{14} = v_4/v_1\) the transfer efficiency of voltage from the cell body to the terminal, and \(R_{14} = v_4/i_1\) the transfer impedance from the cell body to terminal. Going through (19) for various frequencies yields Fig. 4. We used for the membrane resistance of the cell a value \(R_m = 8 \text{ kΩ cm}^2\), and for the terminal resistance 100 MΩ (Van Hateren 1986). For further details see the legend of Fig. 4. We see in Fig. 4 that the input impedance \(R_{11}\) of the cell drops appreciably for frequencies higher than about 100 Hz. The phase of \(R_{11}\) behaves for low frequencies like that of an RC-circuit (which has a phase asymptote of \(-\pi/2\)) for high frequencies like that of an infinite cable (which has a phase asymptote of \(-\pi/4\)). This can be understood by realizing that only low frequencies can see the whole cell because of the finite propagation velocity in the cable. Thus for high frequencies the cell acts like an infinite cable.

The group delay \(t_g\) follows from the definition of group velocity (see e.g. Scott 1970)

\[
t_g = -\frac{d\phi(\omega)}{d\omega},
\]

(20)

where \(\phi(\omega)\) is the phase as a function of the angular frequency \(\omega\). The group delay of \(R_{14}\) (Fig. 4) is a measure of the delay between the current injection (e.g. caused by the phototransduction process) and the resulting voltage response in the cell body. It is for this example approximately 2 ms; this is only a small part of the total delay between illumination of a photoreceptor and the voltage response in the cell – about 20 ms for dark-adapted fly photoreceptor cells. Further, the group delay of \(A_{14}\) shows that the delay between voltage applied in the cell body and a voltage response in the terminal is mainly determined by the time constant of the cell, and not by the transport through the axon.

The response in the time domain (Fig. 4, lower left) is the voltage response (in mV) to a short (0.125 ms) current pulse of unit area (i.e. containing a charge of 1 pC). It was obtained by transformation of the current pulse to the frequency domain with a FFT (2048 points, time window 64 ms), multiplication by the appropriate transfer function, and transformation back to the time domain. The fast initial transient of the response is due to the redistribution in the cell of
Fig. 4. An example of calculations for an isolated photoreceptor cell according to the circuit of Fig. 3B. \( R_{11} = \frac{v_1}{i_1} \) is the input impedance of the cell, \( A_{14} = \frac{v_4}{v_1} \) the voltage transfer from cell body to terminal, and \( R_{14} = \frac{v_1}{i_1} \) the transfer impedance from the cell body to the terminal. The upper two rows show the transfer functions of \( R_{11}, A_{14}, \) and \( R_{14} \). The frequency \( f \) is in Hz, with \( f = \frac{\omega}{2\pi} \), where \( \omega \) is the angular frequency. In the upper row \( R_{11} \) and \( R_{14} \) are in M\( \Omega \), \( A_{14} \) is dimensionless. The second row from above shows the phase in radians, the third row the group delay in ms. The lowest row shows voltage responses (in mV) to either a 0.125 ms, 8 nA current pulse (\( R_{11} \) and \( R_{14} \)), or a 0.125 ms, 8 mV voltage pulse (\( A_{14} \)). Parameters: membrane resistance of cell body and axon: 8 k\( \Omega \) cm\(^2\); intracellular resistivity: 100 \( \Omega \) cm; membrane capacitance of cell body and axon: 1 \( \mu \)F/cm\(^2\); length of cell body: 250 \( \mu \)m; diameter: 5 \( \mu \)m; length of axon: 35 \( \mu \)m; diameter: 2 \( \mu \)m; terminal resistance: 100 M\( \Omega \), capacitance: 2.2 F. Because the microvilli of the rhabdomere contain most of the membrane area in the cell body, this must be taken into account (Hardie et al. 1981). We assume that the rhabdomere contains a membrane area of 40 \( \mu \)m\(^2\) per \( \mu \)m of its length (see Van Hateren, 1986).

The voltage transfer \( A_{14} \) in Fig. 4 shows that voltage fluctuations up to about 1 kHz are transmitted efficiently from cell body to terminal. Higher frequencies, however, are attenuated strongly. The group delay of \( A_{14} \) is in the order of 100 \( \mu \)s, much smaller than the delay of 2 ms measured by Scholes (1969). If the delay is actually 2 ms, it is certainly not a delay due to propagation through the cable. Figure 4 (middle below) shows also the voltage response (in mV) in the terminal to a 0.125 ms voltage pulse of 8 mV in the cell body.

Finally, the transfer resistance \( R_{14} = R_{11} A_{14} \), relating the current injected in the cell body to the resulting voltage response in the terminal, is shown in the right column of Fig. 4. For low frequencies the amplitude and phase characteristics are mainly determined by \( R_{11} \), for high frequencies mainly by \( A_{14} \). The figure at the lower right shows the response to a current of unit area in the cell body.
4 Example: 6 Coupled Photoreceptor Cells

In the example presented above, the photoreceptor cell was treated as an isolated unit. In reality, however, this is not the case. In the neural superposition eye of the blowfly 6 photoreceptor cells that look into the same direction – but through different facet lenses – converge to one and the same column in the lamina (Braitenberg 1967). These 6 cells are coupled by gap junctions between the axon terminals in the lamina (Shaw and Stowe 1982), chiefly between next-neighbours in the ring of terminals (Shaw 1984a). A model for this system is shown in Fig. 5A. Although this structure has a loop, our ladder algorithm still applies when we use the symmetry. Suppose we inject a current $i_1$ in one cell, and we want to know the voltage $v_4$ in its terminal (see Fig. 5A, and 3B for details of the cell into which current is injected). Then the procedure goes as follows:

\[
\begin{align*}
v_7 &= 1, \\
i_7 &= 0.5v_7/z_1, \\
v_6 &= v_7 + i_7 R_g, \\
i_6 &= i_5 + v_6/z_1 + v_6/z_1, \\
v_5 &= v_6 + i_5 R_g, \\
i_5 &= i_4 + v_5/z_1 + v_5/z_1, \\
v_4 &= v_5 + i_4 R_g, \\
i_4 &= 2i_5 + v_4/z_1, \\
v_3 &= v_4 + i_4(z_11 - z_12'), \\
i_3 &= i_4 + v_3/z_12', \\
v_2 &= v_3 + i_3(z_11 - z_12 + z_11' - z_12'), \\
i_2 &= i_3 + v_2/z_12, \\
v_1 &= v_2 + i_2(z_11 - z_12), \\
i_1 &= i_2 + v_1/z_11, \\
R_{14} &= v_4/i_1,
\end{align*}
\]

where $R_{14}$ is the transfer impedance from cell body to terminal for the cell into which current is injected; $z_1$ is the input impedance of a cell as seen from the terminal (see Fig. 3B), again determined by going through the appropriate ladder network (Fig. 3B)

\[
\begin{align*}
v_1 &= 1, \\
i_2 &= -v_1/z_11, \\
v_2 &= v_1 - i_2(z_11 - z_12), \\
i_3 &= i_2 - v_2/z_12, \\
v_3 &= v_2 - i_3(z_11 - z_12 + z_11' - z_12'), \\
i_4 &= i_3 - v_3/z_12', \\
v_4 &= v_3 - i_4(z_11' - z_12'), \\
z_1 &= -v_4/i_4.
\end{align*}
\]

The situation is even more complicated than this, however, because the extracellular space in the lamina is separated from the extracellular space in the retina by a resistance barrier (Shaw 1975). This gives rise to large extracellular potentials in response to light, which presumably have a role in the gain control of the synapse (Shaw 1981; Van Hateren 1986). A model of this extended system is shown in Fig. 5B. The loop at the terminals is now more complicated than without resistance barrier, and can not be solved with the algorithm. It leads to 4 equations with 4 unknowns, which are readily solved (see Appendix). The remaining parts of the system can again be considered as a ladder network.

For current entering only 1 cell (e.g. by illuminating only 1 cell, for experimental examples see Van Hateren 1986) we get Fig. 6, for currents entering all 6 cells (e.g. by illuminating 6 cells) we obtain Fig. 7. We may compare the results in Fig. 6 to those in Fig. 4, the case of an isolated photoreceptor cell. The main difference is that the photoreceptor cell of Fig. 6 is somewhat faster than an isolated photoreceptor: the amplitudes of $R_{14}$ and $R_{14}$ in Fig. 6 cut off at higher frequencies than in Fig. 4, the group delays of $R_{14}$ and $R_{14}$ are shorter, and the slow transients of the responses to current pulses are faster. The voltage transfer $A_{14}$ is comparable, except that it is about two times smaller in Fig. 6 than in Fig. 4 (see the amplitude characteristics for low frequencies, and the response to a voltage pulse of unit area). $R_{14}$ is reduced as well. All differences mentioned above arise from the fact that in Fig. 6 the photoreceptor is loaded by the resistance of the gap junctions and the other cells in series with them (see Fig. 5B), whereas the isolated photoreceptor cell of Fig. 4 is not. This extra load reduces the input resistance and time constant of the cell – this is similar to what happens when the resistance $R$ of an RC-circuit is reduced. Furthermore, it reduces the voltage transfer...
Fig. 6. An example of calculations for 6 coupled photoreceptor cells (see Fig. 5B), with current injected in 1 cell (e.g. by illuminating only 1 cell). $R_{11}$, $A_{14}$, and $R_{14}$ are defined for this cell similarly to the definitions in Fig. 4, the parameters and dimensions are also the same. Further parameters: $R_0 = 25 \, \text{MO}, R_b = 2 \, \text{MO}$

$A_{14}$, $A_{14}$ would be zero in the extreme case of an infinite load (i.e. a zero load resistance).

Figure 7 (currents entering all 6 cells) is very similar to Fig. 4 (an isolated photoreceptor cell). The reason is that if the voltages in all terminals are equal, no current flows through the gap junctions, which means that it looks as if there are no gap junctions. The only difference with the case of an isolated photoreceptor cell is the presence of a barrier resistance $R_b$ (see Fig. 5B), which causes extracellular field potentials in the lamina. These potentials slightly reduce the load via the terminal impedances $z_t$ on the photoreceptor cells.

5 Example: A Large Monopolar Cell

The 6 photoreceptors of the previous section, which look into the same direction, project to the Large Monopolar Cells (Kirschfeld and Franceschini 1968; Braitenberg 1967), which in turn conduct the signal electrotonically to the next neuropile, the medulla (rev. Shaw 1984b). The LMC's are interesting from our present point of view, because they are long (approximately 500 µm) and slender (2 µm), and are thus expected to display strong cable properties.

Figure 8 shows a model of an LMC. The impedance $z_5$ is the impedance of the postsynaptic membrane of the LMC in the lamina, i.e. its input load. The axon is considered as a cable segment, with impedances $z_{11}$ and $z_{12}$. The output load $z_t$ is the impedance of the terminal of the LMC in the medulla. An example of calculations on this model is shown in Fig. 9. $R_{11} (=v_1/i_1)$ is the input impedance of the LMC, $A_{12} (=v_2/v_1)$ the voltage transfer from postsynaptic membrane to terminal, and $R_{12} (= R_{11}A_{12} = v_2/i_1)$ the transfer impedance from postsynaptic
Fig. 7. The same as Fig. 6, but now for currents injected in all 6 photoreceptor cells (e.g. by illuminating them all)

membrane to terminal. For the axon we assume a length of 500 μm, and a diameter of 2 μm. The membrane resistance of the axon is not known; it is taken here as $R_m = 10 \text{kΩ} \text{cm}^2$ (see Zettler and Järvilehto 1973). This value is large enough to be consistent with the small attenuation along the axon observed in these neurons (Zettler and Järvilehto 1973). We assume that it is mainly $z_s$ that determines

the input impedance of an LMC (about 10 MΩ, Zettler and Järvilehto 1973), and take $z_t = 10 \text{MΩ}$. The output load $z_t$ is not known either; we assume for the moment $z_t = 1000 \text{MΩ}$.

We see in Fig. 9 that the delay between current injection in the lamina and a voltage response in the terminal is now mainly determined by the cable delay (see $A_{12}$). The first reason for this is the length of the axon, the second the very short time constant of the postsynaptic membrane (see $R_{11}$). Furthermore, the attenuation along the cable is limited ($A_{12} = 0.7$ for $f < 100$ Hz), whereas the input resistance of the cell is low (because of the low resistance of the postsynaptic membrane). Thus, as already argued by Wilson (1978), this may explain the measurements of Zettler and Järvilehto (1973), who measured a low input resistance which they thought to indicate an active mechanism for the conduction because of the small attenuation found along the axon.
Fig. 9. An example of calculations for an LMC (see Fig. 8). $R_{11} (= v_i/i_i)$ is the input resistance of the LMC, $A_{12} (= v_2/v_1)$ the voltage transfer through the axon, and $R_{12} (= R_{11} A_{12} = v_2/i_i)$ the transfer impedance from the postsynaptic membrane to the terminal. Parameters: membrane resistance of the axon: 10 kΩ cm²; intracellular resistivity: 100 Ω cm; membrane capacitance: 1 µF/cm²; length of the axon: 500 µm, diameter: 2 µm; resistance at the postsynaptic membrane: 10 MΩ, capacitance: 2.2 pF; resistance at the terminal: 1000 MΩ.

A low impedance current source (e.g. the postsynaptic membrane) driving an axon with a high membrane resistance combines advantages of both: the attenuation along the axon is small because of its high membrane resistance, and the system can transmit high frequencies because of the low impedance of the current source. This may be compared to the way coaxial cables are used in electronics: these cables have a very high resistance from core to shield (cf. a high membrane resistance). If they were charged, discharging would take a long time, thus their frequency response would be very poor. But usually these cables are driven by low impedance sources, that actively charge and discharge the cable, which results in a far better frequency response.

An interesting feature of electrotonic conduction is that the input and output are not strictly separated: any change in the output load not only changes the output, but also affects voltages arising at the input. This is especially important because the LMC's are connected to other neurons in the lamina by synapses in both directions (Strausfeld and Nüssel 1980). Therefore, a change in the medulla might in principle change the behaviour of the lamina network. Whether this property is desirable or not, and whether it is used or not by the fly, is not known at present. Nevertheless, it is possible to predict how this antidromic information transfer could be minimized or maximized. Note that changing the properties of the cable itself (e.g. its membrane resistance) will not change the transport efficiency exclusively in one direction, unless the membrane resistance is not uniform. An efficient way, however, to cause unidirectional signal transmission is illustrated in Fig. 10, which shows $A_{12}$ as a function of
the output load for a few relevant frequencies. If the input load were e.g. 10 MΩ, the antidromic voltage transfer $A_{21}$ would be about 0.06 (this can also be found from Fig. 10 because the input load does not influence the voltage transfer $A_{12}$, and we may reverse input and output). Thus a large terminal resistance then results in highly unidirectional (orthodromic) transmission, whereas equal loads at both sides of the cable would yield complete bidirectionality.

Conclusion

The examples have shown that the representation of cable segments by T-networks is well suited for handling cable structures, especially when the ladder algorithm is applied. More complicated structures than dealt with here, e.g. dendritic trees with many branches, are equally easy to handle. A major advantage of the ladder algorithm is its simplicity: each step is a clear, short statement, which substantially reduces the risk of errors.

The algorithm is also very fast: using a Fortran77 program for a cable structure consisting of 100 cable segments takes only 26 ms CPU-time per frequency on a Cyber 170/760 mainframe. On a Data General Eclipse S/140 minicomputer it takes 360 ms, and even on a relatively small microcomputer (Data General Desktop 20, without hardware floating point) a workable 4.7 s. Another nice property of the algorithm is that the CPU-time is linearly related to the number of cable segments in an arbitrary tree-like cable structure.

The ladder algorithm only works for cable structures without loops [except in special cases as in (21)]. The T-network, however, is also useful when there are loops, because it reduces the continuous cable structure to a circuit with discrete elements. A network analysis program can then be used for analyzing the circuit (Segev et al. 1985). This is also a way to treat nonlinear membranes (Bunow et al. 1985), insofar they can not be linearized (Koch 1984).

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Appendix

With $v_7 = 1$ in Fig. 5B, Kirchhoff's laws lead to 4 equations with 4 unknowns ($v_4$, $v_5$, $v_6$, and $v_3$). Solving these equations yields

$v_4 = (hk - gl)/(ak + gd)$,
$v_5 = (d/k)v_4 + l/k$,
$v_6 = (-c/(2a))v_1 + b/(2a)$,
$v_7 = (-bc/(2a^2) - c/a)v_1 + b^2/(2a^2) - 1$,

where

$a = z_1 z_t$,
$b = R_g z_t + z_1 R_g + 2z_1 z_t$,
$c = z_1 R_a$,
$d = R_g z_t$,
$f = z_t^2 + 6R_g z_t$,
$g = b^2 c/(2a^2) + bc/a + c/2$,
$h = b^3/(2a^2) - 3b/2$,
$k = f + bcd/a^2 + 3cd/a$,
$l = b^2 d/a^2 + bd/a - d$.

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