A cable model for coupled neurons with somatic gap junctions

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Abstract. A cable model is presented for a pair of electrotonically coupled neurons to investigate the spatial effects of soma-somatic gap junctions. The model extends that of Poznanski et al. (1995) in which each neuron is represented by a tapered equivalent cable attached to an isopotential soma with the two somas being electrically coupled. The model is posed generally, so that both active and passive properties can be considered. In the active case a system of nonlinear integral equations is derived for the voltage, whilst in the passive case these have an exact solution that also holds for inputs modelled as synaptic reversal potentials. Analytical and numerical methods are used to examine the sensitivity of the soma potentials (in particular) to the coupling resistance.

1 Introduction

Evidence for neuronal coupling within the hippocampal subfields CA3, CA1 and dentate gyrus has been given by Schuster (1992), MacVicar and Dudek (1980a,b, 1981), and MacVicar et al. (1982). Schmalbruch and Jahnsen (1981) have observed gap junctions between CA3 pyramidal neurons, and it is these that are thought to mediate the electrical coupling. However, such coupling has not been taken into account when attempts have been made to estimate the passive electrical parameters of such neurons and may cause significant distortions in the results (Getting 1974; Rall 1981; Skrzypek 1984; Publicover 1989).

As a first step in the cable analysis of investigating the effects of coupling on synaptic potentials and the passive spread of electrical signals, Poznanski et al. (1995) considered two exponentially tapered equivalent cylinders that were coupled through their isopotential somas. The analysis of the model investigated the effect of the coupling resistance and somatic shunt parameter on the potential response at the two somas for synaptic input at selected points along one of the coupled neurons. However, the mathematical analysis was restricted to determining the potential at the two somas, and moreover only partial analytic expressions were obtained with completion of the solution being given by numerical techniques. Here we provide a complete analytical solution for the model. Moreover, we extend the solution to include synaptic reversal potentials as well as to allow for more general taper types (as given Evans 2000), of which the exponential is one particular type. These extensions give the model greater flexibility in its realistic representation of dendritic trees by equivalent cylinders. The representation of synaptic input as a conductance change rather than a current source on the dendrites is generally more appropriate, since the latter is only really satisfactory at the soma or on proximal dendrites with a dual patch clamp.

The motivation for obtaining an analytical solution for the passive case is twofold. First, when the solution is expressed as a weighted series of time-dependent exponentials, it gives the explicit dependence of the voltage amplitude terms and time constants on the model parameters and hence information on their relative effect and importance as well as aiding the practical determination and extraction of such parameters. Secondly, it provides a reference solution against which numerical and analytical solutions of extended models can be compared. Moreover, the model is presented generally so that extension to include active membrane properties can be made, with the solution presented here being of relevance in the reduction of such equations to a system of nonlinear integral equations.

The structure of the paper is as follows. In Sect. 2 the boundary-value problem for the model is described. Since the principal part of the governing equations are linear, in Sect. 3 an explicit expression for the Green’s function is derived which is used in Sect. 4 to reduce the problem for the potential to a system of integral equations. The system of integral equations is solved explicitly in the linear case and is applicable to passive membranes or linearized active membranes. Sections 5 and 6 explore the coupling parameter dependence of the solution. In Sect. 5, the simplification of the Green’s function in the limits of weak and strong coupling is discussed, whilst in
Sect. 6 we illustrate through a numerical example the coupling parameter dependence of the solution at the somas. The responses to specific excitatory and inhibitory synaptic reversal potentials are explicitly considered.

2 The mathematical problem

We consider two neurons, each represented by a single tapering equivalent cylinder and coupled at their isopotential somas through a gap junction. The model for the tapering equivalent cylinder is described in Evans (2000), where for the case of interest here the number of equivalent cylinders \(N\) representing each neuron is taken to be one \((N = 1)\) and the taper types are restricted to the same class of six taper functions, namely, the hyperbolic cosine-squared (HCS), hyperbolic sine-squared (HSS), trigonometric cosine-squared (TCS), exponential (EXP), square (SQU), and uniform (UNI). A schematic illustration of the model is shown in Fig. 1.

The mathematical statement of the equations for this model is as follows:

\[
\begin{align*}
\frac{1}{R_{junc}} \left( v_2 + \tau_2 \frac{\partial v_2}{\partial t} \right) &= \frac{1}{\lambda_{a_2}^* r_{a_2}^*} \frac{\partial v_2}{\partial Z_2} \\
&= I_{junc}(t) - \left( \frac{v_2 - v_1}{R_{junc}} \right) \; ; \\
\text{at } t = 0, \quad v_1 = h_1(Z_1), \quad v_2 = h_2(Z_2),
\end{align*}
\]

where for tapering equivalent cylinder \(i\) \((i = 1 \text{ or } 2)\) we have that:

\[
v_i(Z_i, t)
\]

is the potential [volts] at tapering electrotonic distance \(Z_i\) and time \(t\) (s) in cylinder \(i\),

\[
L_i
\]

is the total tapering electrotonic length of cylinder \(i\),

\[
F_i(Z_i)
\]

is the geometric ratio function \((F_i(0) = 1)\),

\[
D_0^i = D_s^*(0)
\]

is the diameter at \(Z_i = 0\),

\[
\lambda_{a}^* = \left( \frac{\mu a^*}{4 \pi \rho_i^a}\right)^{1/2}
\]

is the characteristic length parameter of a cylinder of diameter \(D_0^i\) (cm),

\[
D_i = D_s^*(Z_i)^{2/3}
\]

is the diameter at tapering electrotonic distance \(Z_i\) (cm),

\[
\lambda_{a}^* = \lambda_{a}^* \left( Z_i \right)^{1/3}
\]

is the characteristic length parameter (cm),

\[
\tau_{m_1} = \frac{1}{\rho_i^a \pi D_i^2}
\]

is the axial resistance per unit length \((\Omega \text{cm})\),

\[
\tau_{m} = \frac{1}{\rho_i^a \pi D_i^2}
\]

is the axial resistance per unit length of a uniform equivalent cylinder of diameter \(D_0^i\) (\(\Omega \text{cm}\)),

\[
\tau_{s_i} = R_{s_i} C_{s_i}
\]

is the somatic time constant \((s)\) of soma \(i\),

\[
R_{s_i}
\]

is the lumped resistance \((\Omega)\) for soma \(i\), which can include a shunt resistance,

\[
C_{s_i}
\]

is the lumped capacitance \([F]\) for soma \(i\),

\[
I_i
\]

is an applied current to the soma of neuron \(i\),

\[
I_i(Z_i, t; v_i)
\]

is an applied current to equivalent cylinder \(i\),

\[
h_i(Z_i)
\]

is the initial voltage in cylinder \(i\),

\[
R_{junc}
\]

denotes the junctional resistance \((\Omega)\) between the somas of the two neurons.

In this model, the axial current through the gap junction resistance is \((v_2(t, t) - v_1(0, t))/R_{junc}\), and we have allowed for differing somatic time constants and soma resistances for both neurons. We have assumed no axial current flow at the ends of the neurons i.e. sealed-end terminations, although extension to mixed end boundary conditions is straightforward. The geometric ratio functions \(F_i(Z_i)\) \((i = 1, 2)\) belong to the six types discussed in Evans (2000). The boundary conditions (5) and (6) belong to the six types discussed in Evans (2000).