Assignment 2

Branched Cylinders: Dendritic Tree Approximations

Submission: Moodle (single compressed file including results/explanations and Matlab files)

The aim of this computer laboratory is to explore some of the time independent electrical properties of single branched cables. Branched cables are an important means of modelling the passive electrical properties of axonal and dendritic trees. Consideration will be restricted to trees exhibiting only one order of branching (see Figure 1) however the principles elaborated upon here are easily extended to higher order trees.

Consider the following first order branched cable:

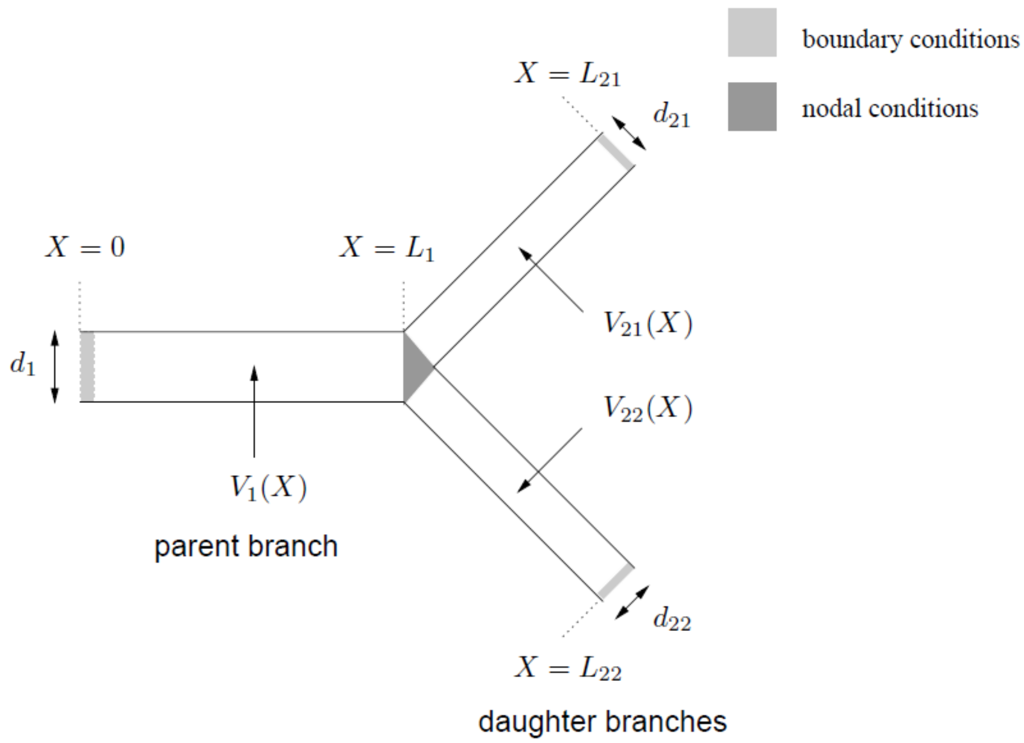

Figure 1: First order binary cable consisting of a parent branch and two daughter branches.

where V_1, V_{21} and V_{22} are the membrane potentials of the respective branches. d_1, d_{21} and d_{22} are the diameters of the parent and daughter branches respectively and X is axial distance in terms of the dimensionless **electrotonic distance** $X = x/\lambda_c$. It should be noted that λ_c need not be the same for all branches.

At **steady state** the membrane potential of each branch will satisfy

$$\frac{d^2V}{dX^2} = V \qquad (1)$$

and thus a **general solution** for the membrane potential as a function of electrotonic distance will be

$$\begin{aligned} V_1(X) &= A_1 e^{-X} + B_1 e^{X} & 0 \leq X \leq L_1 \\ V_{21}(X) &= A_{21} e^{-X} + B_{21} e^{X} & L_1 \leq X \leq L_{21} \\ V_{22}(X) &= A_{22} e^{-X} + B_{22} e^{X} & L_1 \leq X \leq L_{22} \end{aligned} \quad (2)$$

For a specific solution **6 constraints** are required in order to determine the **6 constants** $A_1, B_1, A_{21}, B_{21}, A_{22}$ and B_{22}. The constraints are determined from

- boundary conditions - conditions at the cylinder terminals
- nodal conditions - conditions at the branch points

1. Boundary conditions

Specifying the boundary conditions provides **3 constraints**. For example

- an applied current I_{app} is injected at the inner conductor at $X = 0$ then

$$\left.\frac{dV_1}{dX}\right|_{X=0} = -(r_i\lambda_c)_1 I_{app} \quad (3)$$

$(r_i\lambda_c)_1$ is just notational shorthand for the value of $r_i\lambda_c$ for the parent cylinder. The same notation applies to the daughter cylinders.

- the terminal ends of the daughter branches are held at rest (killed ends) i.e.

$$V_{21}(L_{21}) = V_{22}(L_{22}) = 0 \quad (4)$$

2. Nodal conditions

Specifying nodal conditions provide the **remaining 3 constraints**. Thus assuming no applied currents other than at the terminals (see boundary conditions)

- the membrane potential *must* be continuous at the nodes thus

$$V_1(L_1) = V_{21}(L_1) = V_{22}(L_1) \quad (5)$$

- current is conserved at the nodes (branch points) i.e.

$$\frac{-1}{(r_i\lambda_c)_1}\left.\frac{dV_1}{dX}\right|_{X=L_1} = \frac{-1}{(r_i\lambda_c)_{21}}\left.\frac{dV_{21}}{dX}\right|_{X=L_1} + \frac{-1}{(r_i\lambda_c)_{22}}\left.\frac{dV_{22}}{dX}\right|_{X=L_1} \quad (6)$$

The left hand side is the current flowing out of the end of the parent cylinder whereas the right hand side is the current flowing into the daughter cylinders.

3. Solving for the constants

By writing out the equations following from the constraints in full, and performing substitutions and differentiations as required the following is obtained

$$\begin{aligned}
A_1 - B_1 &= (r_i\lambda_c)_1 I_{app} && \text{applied current at beginning of parent cylinder} \\
\left.\begin{aligned} A_{21}e^{-L_{21}} + B_{21}e^{L_{21}} &= 0 \\ A_{22}e^{-L_{22}} + B_{22}e^{L_{22}} &= 0 \end{aligned}\right\} & && \text{daughter terminals held at rest} \\
\left.\begin{aligned} A_1e^{-L_1} + B_1e^{L_1} - A_{21}e^{-L_1} - B_{21}e^{L_1} &= 0 \\ A_{21}e^{-L_1} + B_{21}e^{L_1} - A_{22}e^{-L_1} - B_{22}e^{L_1} &= 0 \end{aligned}\right\} & && \text{continuity of } V \text{ at branch node} \\
-A_1e^{-L_1}/(r_i\lambda_c)_1 + B_1e^{L_1}/(r_i\lambda_c)_1 + A_{21}e^{-L_1}/(r_i\lambda_c)_{21} - & \\
B_{21}e^{L_1}/(r_i\lambda_c)_{21} + A_{22}e^{-L_1}/(r_i\lambda_c)_{22} - B_{22}e^{L_1}/(r_i\lambda_c)_{22} &= 0 && \text{conservation of current}
\end{aligned} \tag{7}$$

> **Question 1**
> By referring to the general solution (2) and the equations of constraints (3)-(6) convince yourself of the truth of equations (7).

By defining

$$\mathsf{x} = \begin{pmatrix} A_1 \\ B_1 \\ A_{21} \\ B_{21} \\ A_{22} \\ B_{22} \end{pmatrix} \tag{8}$$

equations (7) can be rewritten as the following **matrix equation**

$$\mathsf{Ax} = \mathsf{b} \tag{9}$$

where

$$\mathsf{b} = \begin{pmatrix} (r_i\lambda_c)_1 I_{app} \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix} \tag{10}$$

and

$$\mathsf{A} = \begin{pmatrix}
1 & -1 & 0 & 0 & 0 & 0 \\
0 & 0 & e^{-L_{21}} & e^{L_{21}} & 0 & 0 \\
0 & 0 & 0 & 0 & e^{-L_{22}} & e^{L_{22}} \\
e^{-L_1} & e^{L_1} & -e^{-L_1} & -e^{L_1} & 0 & 0 \\
0 & 0 & e^{-L_1} & e^{L_1} & -e^{-L_1} & -e^{L_1} \\
-e^{-L_1}/(r_i\lambda_c)_1 & e^{L_1}/(r_i\lambda_c)_1 & e^{-L_1}/(r_i\lambda_c)_{21} & -e^{L_1}/(r_i\lambda_c)_{21} & e^{-L_1}/(r_i\lambda_c)_{22} & -e^{L_1}/(r_i\lambda_c)_{22}
\end{pmatrix}$$

Question 2
By performing the matrix multiplication of equation (9) show that you obtain equations (7).

MATLAB can find the solution of $Ax = b$ by `x = A\b`.

Load the definition of matrix A by loading the cable.m file to MATLAB, and the cable parameters of Table 1.

parameter	MATLAB variable	value	units
d_1	d1	75	10^{-4} cm
d_{21}	d21	30	10^{-4} cm
d_{22}	d22	15	10^{-4} cm
R_m	Rm	6	$10^3\,\Omega\,\mathrm{cm}^2$
R_c	Rc	90	$\Omega\,\mathrm{cm}$
L_1	l1	1.5	–
L_{21}, L_{22}	l21, l22	3.0	–
I_{app}	iapp	1	10^{-9} A
$(r_i\lambda_c)_1$, $(r_i\lambda_c)_{21}$, $(r_i\lambda_c)_{22}$	rl1, rl21, rl22	–	Ω
π	pi	3.14159...	–
R_s	Rs	1	$10^6\,\Omega$

Table 1: Parameters, and the corresponding MATLAB variables to be used, for a single branched cable having the electrical properties of the crab giant axon.

Question 3
By defining b determine the values of the coefficients of equation (2) assuming the boundary and nodal conditions of sections 1 and 2. Make sure you define b as a **column vector**

Question 4
By using the coefficients found above and assuming that the coefficient array is stored in the variable x ordered according to equation (8) plot the steady-state voltage profile in each branch by executing the following sequence of commands

```
>> y1 = linspace(0,l1,20)
>> y21 = linspace(l1,l21,20)
>> y22 = linspace(l1,l22,20)
>> v1 = x(1)*exp(-y1) + x(2)*exp(y1)
>> v21 = x(3)*exp(-y21) + x(4)*exp(y21)
>> v22 = x(5)*exp(-y22) + x(6)*exp(y22)
>> plot(y1,v1,'y-',y21,v21,'r-',y22,v22,'b-')
>> xlabel('X (dimensionless)')
>> ylabel('V (volts)')
>> title('Steady-state voltage - E5')
```

What do you note about the steady state voltage profile in the two daughter branches?

4. Solutions for different boundary conditions

By modifying individual entries of the coefficient matrices A and b solutions to equations (2) can be found for different boundary conditions.

Based on your experience of performing questions (1)-(4), plot the steady-state voltage profiles for each of the boundary conditions in Figure 2.

Note:

- only individual rows of A and b need to be modified.
- for example the boundary conditions of 2(a) require
  ```
  >> A(2,:) = [0 0 -exp(-l21) exp(l21) 0 0]
  ```
- the boundary conditions of 2(b) require in addition to the above change that
  ```
  >> A(3,:) = [0 0 0 0 -exp(-l22) exp(l22)]
  ```
- the boundary conditions of 2(c) require in addition to the modification for 2(a)
  ```
  >> b(1) = 0; b(2) = rl21*iapp
  ```
- the boundary conditions of 2(d) require in addition to the modifications for 2(c)
  ```
  >> b(3) = rl22*iapp
  ```

Question 5
What is the meaning of the positive right hand sides of $dV_{21}/dX|_{X=L_{21}}$ and $dV_{22}/dX|_{X=L_{22}}$ in 2(c) and 2(d)?

Question 6
Recalculate the coefficients of equation (2) and replot the steady-state voltage profile for the boundary conditions of Figure 2(b) and 2(d) for d_{21} = d_{22} = 47.2470 $\times$ 10^{-4} cm. What do you notice?

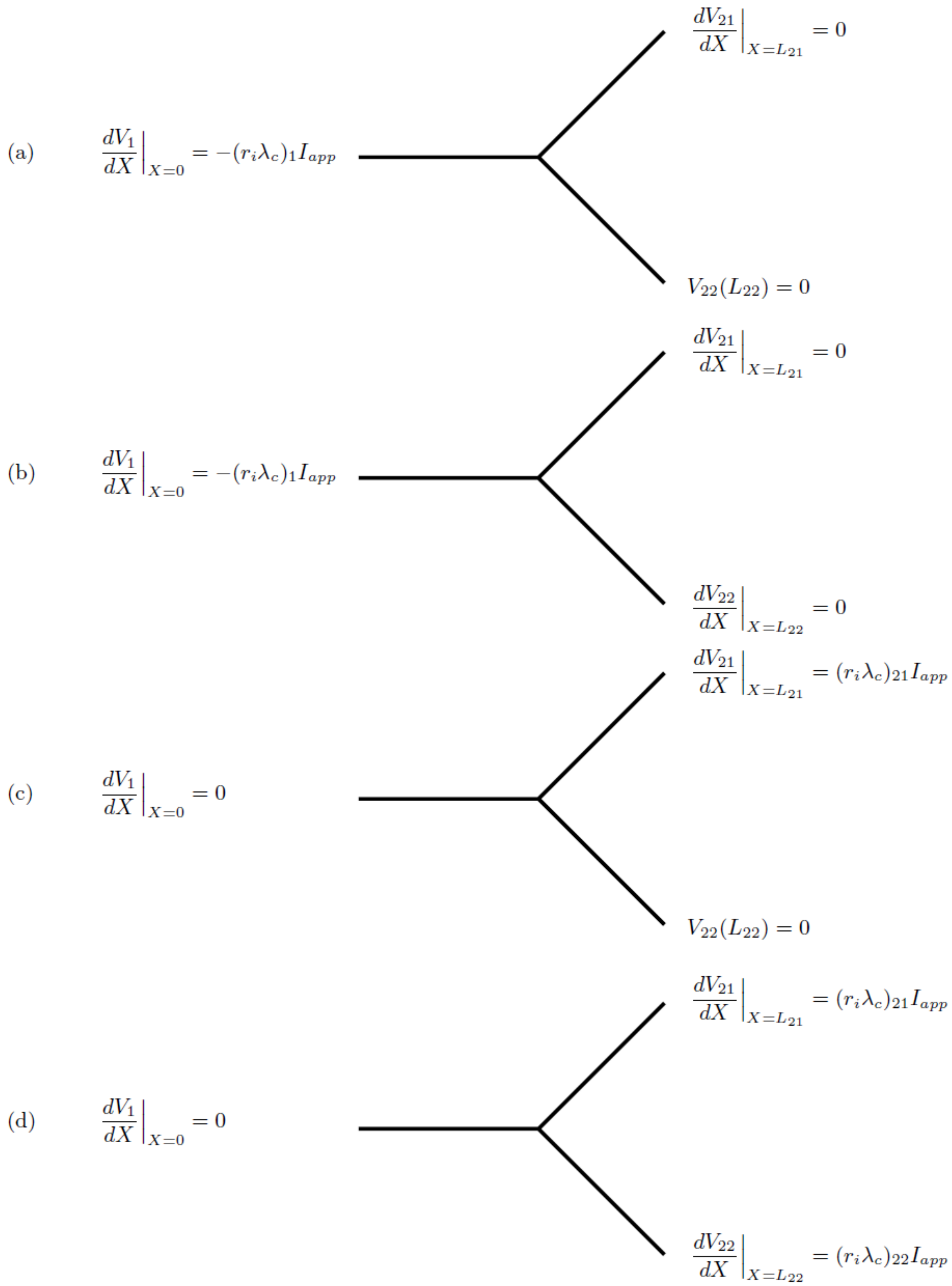

Figure 2: Single branched cable for different boundary conditions.