The sinoatrial (SA) node is a group of self-oscillatory cells in the heart which beat rhythmically and initiate electric potentials, producing a wave of contraction that travels through the heart resulting in the circulation of blood. The SA node is an inhomogeneous collection of cells which have varying intrinsic frequencies. Experimental measurements of these frequencies have shown that the peripheral cells of the SA node have a higher natural frequency than do the interior cells. This is surprising to us since in 1:1 phase-locked motion of two oscillators of different frequency, the oscillator with the higher frequency leads the other oscillator by a phase angle. If the wave originates in the center of the SA node as one expects, then the interior cells would be leading in a 1:1 phase-locked motion and should therefore have a higher frequency than the peripheral cells. Our objective in this work is to explain this discrepancy between intuition and the measured results, and to determine possible advantages of having cells of lower frequency in the interior. Using a model of the SA node consisting of three coupled phase-only oscillators, we show that increased robustness of synchronized behavior (represented by a larger region of parameter space) comes as a result of the experimentally observed distribution of frequencies in the SA node. Associated with the loss of synchronized behavior is a complicated series of bifurcations called the “devil’s staircase”. We use our system to derive a 1D discontinuous map which exhibits the devil’s staircase, and we analyze its dynamics.

1. Introduction

The sinoatrial (SA) node is a collection of self-oscillatory cells in the heart which control the rhythmic beating of the heart. Electric potentials are initiated in the SA node and propagate to atrial muscle, causing a wave of contraction resulting in the circulation of blood. The SA node is not a homogeneous collection of cells in terms of functionality, anatomy or electrophysiology [10]. Kodama and Boyett [4] investigated how electrical activity varies within different regions of the SA node. They experimentally found the spontaneous cycle length of cells in the central part of a rabbit SA node to be longer than that of cells in the peripheral region. This difference in cycle length corresponds to the interior cells having a lower frequency than the peripheral cells. Since the electric potential is expected to be initiated in the center of the SA node one would expect the center cells to have a higher frequency than the peripheral cells which is contrary to the results of Kodama. An objective of our work is to offer an explanation of this discrepancy.

We choose to model the SA node as three coupled phase-only oscillators [3]. Previous works in modeling the SA node include Cai et al. [1], where a biologically motivated coupled two cell model, governed by membrane currents, was considered. Numerically studying this model Cai et al. [1] describe the possible regions of motion to be: individual oscillation, entrained motion and complex oscillation. These observations may be interpreted as unsynchronized motion, synchronized

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motion and transitional bifurcations, respectively. The simple three phase-only oscillator model we will discuss captures each of these different types of motions. We will give a numerical approximation of the boundaries of the regions in parameter space corresponding to each type of motion. The parameter space is a plane with coordinates consisting of the two coupling coefficients. Michaels et al. [5] also describe these three types of motion when considering an $N \times N$ array of biologically modeled oscillators and note the active role the Farey sequence and devil’s staircase play in giving some order to the region of complicated dynamics. The devil’s staircase involves an infinite sequence of complicated bifurcations within a finite region. In our system this series of bifurcations occurs as we move through the region of 1:1:0 locking to the region of 1:1:1 locking. To transition between these two phase-locked motions the system must undergo $n:n:m$ phase-locked motion, for all values of $n$ and $m$ such that $m/n < 1$ [6]. Viewing the steady state behavior for all $n:n:m$ phase-locked motions, we note a common feature of the plots. Using this common feature we derive a 1D discontinuous map which also exhibits the devil’s staircase. A similar map has been studied by Veerman [9]. It has also been suggested as a step towards understanding ventricular parasystole by Courtemanche et al. [2].

2. Two coupled oscillators

In this section we show that in 1:1 phase-locked motion of two oscillators of different frequency, the oscillator with the higher frequency leads the other oscillator by a phase angle.

Modeling each as a phase-only oscillator, we have the equations

\[
\dot{\theta}_1 = \omega_1 + \beta_{12} \sin(\theta_2 - \theta_1) \\
\dot{\theta}_2 = \omega_2 + \beta_{21} \sin(\theta_1 - \theta_2)
\]

where $\theta_i$ is the phase of the $i$th oscillator, $\omega_i$ is the stand-alone frequency of the $i$th oscillator, and the coupling coefficient $\beta_{ij} \geq 0$ represents the effect of oscillator $j$ on oscillator $i$, as shown in Fig. 2. Defining the phase difference $\phi = \theta_1 - \theta_2$, we have

\[
\dot{\phi} = \omega_1 - \omega_2 - (\beta_{21} + \beta_{12}) \sin \phi
\]

For phase-locked motion we require that

\[
\dot{\phi} = 0 \Rightarrow \sin \phi = \frac{\omega_1 - \omega_2}{\beta_{21} + \beta_{12}}
\]

Now, if $\omega_1 > \omega_2$, then $\sin \phi > 0$, i.e., $0 < \phi < \pi$, i.e., oscillator 1 leads oscillator 2 by a phase angle $\phi$. Thus if oscillator 1 represents the interior cells in the SA node, while oscillator 2 represents the cells in the periphery, and if $\omega_2 > \omega_1$ as in Fig. 1b, then the signal originates in the periphery of the SA node and propagates inward, into the interior of the SA node, and

Fig. 1. (a) Schematic representation of the heart: SA = SA node, RA = right atrium, LA = left atrium, RV = right ventricle, LV = left ventricle, and (b) schematic representation of the SA node, showing the experimental result that the frequencies $\omega_2$ of cells in the periphery are greater than the frequencies $\omega_1$ in the interior.

Fig. 2. Schematic representation of two phase-only oscillators.
the periphery of the SA node. For these two oscillators, $\omega_2 > \omega_1$?

In order to explore this question we study a more complete model of the SA node.

3. Three oscillator model

In this work we model the SA node region of the heart by three coupled phase-only oscillators:

\begin{align*}
\dot{\theta}_1 &= \omega_1 + \beta_{12} \sin(\theta_2 - \theta_1) \\
\dot{\theta}_2 &= \omega_2 + \beta_{21} \sin(\theta_1 - \theta_2) + \beta_{23} \sin(\theta_3 - \theta_2) \\
\dot{\theta}_3 &= \omega_3 + x \sin \theta_3 + \beta_{32} \sin(\theta_2 - \theta_3)
\end{align*}

(5) \quad (6) \quad (7)

where $\theta_i$ is the phase of the $i^{th}$ oscillator, and the coupling coefficient $\beta_{ij} \geq 0$ represents the effect of oscillator $j$ on oscillator $i$, as shown in Fig. 3.

The first equation represents cells lying in the center of the SA node, while the second equation represents cells lying in the periphery of the SA node. For these two oscillators, $\omega_i$ represents their uncoupled frequency. The third equation represents non-oscillatory cells lying outside of the SA node. For the third oscillator, the parameters $\omega_3$ and $x$ determine its uncoupled behavior. We therefore restrict $x$ and $\omega_3$ such that when oscillator 3 is uncoupled from oscillators 1 and 2, it will have an equilibrium point. This restriction gives the condition

\[
\frac{|\omega_3|}{x} \leq 1
\]

(8)

To model regular heart beating we choose parameters $\omega_1$ and $\omega_2$ such that phase-locked motion of first two oscillators takes place when they are uncoupled from the third. Phase-locked motion of (5) and (6) with $\beta_{23} = 0$ occurs when

\[
\left| \frac{\omega_2 - \omega_1}{\beta_{12} + \beta_{21}} \right| \leq 1
\]

(9)

4. Equilibria

Equilibrium points, corresponding to no oscillations, are solutions of

\begin{align*}
0 &= \omega_1 + \beta_{12} \sin(\theta_2 - \theta_1) \\
0 &= \omega_2 + \beta_{21} \sin(\theta_1 - \theta_2) + \beta_{23} \sin(\theta_3 - \theta_2) \\
0 &= \omega_3 + x \sin \theta_3 + \beta_{32} \sin(\theta_2 - \theta_3)
\end{align*}

(10) \quad (11) \quad (12)

Rearranging (10) we obtain the following condition for equilibrium:

\[
\sin(\theta_1 - \theta_2) = \frac{\omega_1}{\beta_{12}} \Rightarrow \left| \frac{\omega_1}{\beta_{12}} \right| \leq 1
\]

(13)

Summing (10) times $\beta_{21}$ and (11) times $\beta_{12}$ we obtain another condition for equilibrium

\[
\sin(\theta_2 - \theta_3) = \frac{\beta_{21} \omega_2 + \beta_{21} \omega_1}{\beta_{12} \beta_{23}} \Rightarrow \left| \frac{\beta_{12} \omega_2 + \beta_{21} \omega_1}{\beta_{12} \beta_{23}} \right| \leq 1
\]

(14)

Substituting the first of (14) into (12), we obtain a third condition for equilibrium

\[
\sin \theta_3 = -\frac{\beta_{12} \beta_{23} \omega_3 + \beta_{12} \beta_{22} \omega_2 + \beta_{21} \beta_{32} \omega_1}{x \beta_{12} \beta_{23}} \Rightarrow \left| \frac{\beta_{12} \beta_{23} \omega_3 + \beta_{12} \beta_{22} \omega_2 + \beta_{21} \beta_{32} \omega_1}{x \beta_{12} \beta_{23}} \right| \leq 1
\]

(15)

To simplify the analysis we reduce the number of parameters by choosing values for $\omega_3$, $\beta_{12}$, $\beta_{21}$, and $x$ such that the inequalities given in (8) and (9) are satisfied. We set

\[
\beta_{12} = 1, \quad \beta_{21} = 1, \quad \omega_3 = 1, \quad x = 2
\]

(16)

![Fig. 3. Schematic representation of the three phase-only oscillator model where $\beta_i$ represents the effect of oscillator $j$ on oscillator $i$.](image)

- $\omega_1$ is the frequency of oscillator 1.
- $\omega_2$ is the frequency of oscillator 2.
- $\omega_3$ is the frequency of oscillator 3.
- $\beta_{12}$ is the coupling coefficient between oscillator 1 and oscillator 2.
- $\beta_{21}$ is the coupling coefficient between oscillator 2 and oscillator 1.
- $\beta_{23}$ is the coupling coefficient between oscillator 2 and oscillator 3.
- $\beta_{32}$ is the coupling coefficient between oscillator 3 and oscillator 2.

The coupling coefficients determine the phase relationship between the oscillators.
To further simplify the analysis we apply the constraint
\[ x_2 = \frac{3}{C_0} x_1 (17) \]

Our system of Eqs. (5)–(7) now becomes
\[ \dot{\theta}_1 = \omega_1 + \sin(\theta_2 - \theta_1) \]  
\[ \dot{\theta}_2 = 3 - \omega_1 + \sin(\theta_1 - \theta_2) + \beta_{23} \sin(\theta_1 - \theta_2) \]  
\[ \dot{\theta}_3 = 1 + 2 \sin \theta_3 + \beta_{32} \sin(\theta_2 - \theta_3) \]  

where we assume that \( \omega_1, \omega_2, \beta_{23}, \beta_{32} \) are positive. The conditions for equilibrium (13)–(15) then become
\[ \sin(\theta_1 - \theta_2) = \omega_1 \quad \Rightarrow \quad \omega_1 \leq 1 \]  
\[ \sin(\theta_2 - \theta_3) = \frac{3}{\beta_{23}} \quad \Rightarrow \quad 3 \leq \beta_{23} \]  
\[ \sin \theta_3 = -\frac{1}{2} \frac{3\beta_{32}}{2\beta_{23}} \quad \Rightarrow \quad \beta_{32} \leq \beta_{23}/3 \]  

If (21) is satisfied then (22) and (23) define a region in the \( \beta_{23}, \beta_{32} \) plane where all three oscillators are at rest. In this region the effect of non-oscillatory cells which lie outside the SA node on the oscillatory cells lying inside the SA node has become large and the phase-locked motion no longer persists. If the inequalities (22) and (23) are replaced by equalities, we obtain conditions for saddle node bifurcations:
\[ \beta_{23} = 3, \quad \text{if} \quad \beta_{32} \leq \beta_{23}/3 \]  
\[ \beta_{32} = \frac{\beta_{23}}{3}, \quad \text{if} \quad \beta_{23} \geq 3 \]  

Fig. 4 shows these two lines corresponding to saddle node bifurcations of equilibria, as well as the region where (22) and (23) are satisfied and the system is at equilibrium.

5. Phase-locked motions

If any of the inequalities (21)–(23) are violated, the system will not exhibit equilibria. Instead we find that it exhibits phase-locked periodic motions. One of these periodic motions is 1:1:1 phase-locking of all three oscillators. This behavior represents normal functioning of the heart. See Figs. 5 and 6.

Another periodic motion is found to be 1:1:0 phase-locking. In this case oscillators 1 and 2 are 1:1 phase-locked and when they oscillate through 2\( \pi \) radians oscillator 3 has a net zero phase change. See Figs. 7 and 8.
A final possible periodic motion is 1:0:0 phase-locking. In this case only oscillator 1 is oscillating through 2\(\pi\) radians during which time oscillators 2 and 3 each have a net zero phase change. See Figs. 9 and 10.

Numerical integration of Eqs. (18)–(20) gives approximate boundaries in the \(b_{23}, b_{32}\) plane for the regions containing the periodic motions or equilibrium points. Figs. 11–15 are the results of repeated numerical integration for discrete values in the \(b_{23}, b_{32}\) plane. After integrating it is determined which of the periodic motions the system is exhibiting or if it is at equilibrium. This can be accomplished by inspection of \(\theta_i\) vs. \(\theta_j\) plots as shown for example in Figs. 6, 8 and 10. However, this process can be automated either by numerically generating a Poincare map or through use of a fast Fourier transform (FFT) [8].

In Figs. 11–15 the *, +, × and o, respectively represent 1:1:1 phase-locked motion, 1:1:0 phase-locked motion, 1:0:0 phase-locked motion and the equilibrium state of the system. Black squares represent \(n:m:m\) phase-locked motions which
are encountered in the transition between 1:0:0 phase-locked motions and 1:1:1 phase-locked motions. As shown in Fig. 11 n:n:m phase-locked motions occur in the transition between 1:1:0 phase-locked motions and 1:1:1 phase-locked motions.

Moving through Figs. 11–15 $\omega_1$ is being decreased by 0.2 and $\omega_2$ increased by 0.2 so that the sum of $\omega_1$ and $\omega_2$ is held constant at 3, Eq. (17). Recalling the conditions for equilibrium (21)–(23), we see that equilibrium points only emerged in the last of our series of figures, Fig. 15. At the beginning of the sequence of figures $\omega_1$ is almost twice as large as $\omega_2$. Moving through the figures we see the region of 1:0:0 locking, the x region, shrinking as the regions of 1:1:1 and 1:1:0 locking grow. Finally when $\omega_1 = 1$ is reached the 1:0:0 region disappears and is replaced with equilibrium points. The boundary of this equilibrium region is fixed and the boundary curves are known. The boundary of this region is made up of the two lines of saddle node bifurcation, Eqs. (24) and (25). Therefore, the 1:1:1 locked region can no longer expand into this region and the rate of its growth is almost zero as $\omega_1$ is further decreased. This growth of the 1:1:1 region as $\omega_1$ is decreased

Fig. 7. Steady state time history of 1:1:0 phase locking for $\omega_1 = 1.5$, $\omega_2 = 1.5$, $\beta_{23} = 0.5$, $\beta_{32} = 0.5$.

Fig. 8. 1:1:0 Phase locking for $\omega_1 = 1.5$, $\omega_2 = 1.5$, $\beta_{23} = 0.5$, $\beta_{32} = 0.5$. 
suggests a benefit of having a lower intrinsic frequency in the center of the SA node than that of the peripheral cells. A growth of the area of parameter space in which a particular motion is seen to occur can be interpreted as increased robustness of that motion. Through the series of figures we have shown that modeling the center cells of the SA node with a lower frequency than the peripheral cells results in increased robustness of the 1:1:1 phase-locked motion. This is a desirable result since 1:1:1 phase-locked motion corresponds to rhythmic beating of the heart.

6. The devil’s staircase

We focus now on the n:m:m and n:n:m phase-locked motions which occur in the transitions between the 1:1:1, 1:1:0 and 1:0:0 phase-locked motions, cf. Fig. 11. Although these motions occur in a small region of parameter space, they may
be an important source of cardiac arrhythmias [2]. We begin by inspecting the shape of a typical 2:2:1 phase-locked motion, see Fig. 16, which was generated using numerical integration. Here we have set
\[
\theta_1 = x + \pi/2, \quad \theta_2 = y + 2\pi, \quad \theta_3 = z + 3\pi/2
\]
for convenience. We seek to abstract from such data a simple “toy” system which exhibits qualitatively similar dynamics.
Fig. 16 reveals that \( x \) and \( y \) are 1:1 phase-locked. We have found that this is a common feature of the motion of the system for varying values of the coupling coefficients. Thus we hypothesize that to investigate phase-locked behavior in the region of the devil’s staircase we need only focus on the \( y \) vs. \( z \) projection of the 3D motion, as the pertinent characteristics of the 3D motion will be captured in this 2D projection. Figs. 17 and 18 show the \( y \) vs. \( z \) projection of Fig. 16 as well as the associated time history of \( y \) and \( z \). Note that \( y \) completes 2 cycles in the time that \( z \) completes one cycle.

Fig. 13. Regions of phase-locked motions for \( \omega_1 = 1.4, \omega_2 = 1.6 \). The \( * \), \( + \) and \( \times \), respectively represent 1:1:1 phase-locked motion, 1:1:0 phase-locked motion, and 1:0:0 phase-locked motion. Black squares represent \( n:m:m \) phase-locked motions.

Fig. 14. Regions of phase-locked motions for \( \omega_1 = 1.2, \omega_2 = 1.8 \). The \( * \), \( + \) and \( \times \), respectively represent 1:1:1 phase-locked motion, 1:1:0 phase-locked motion, and 1:0:0 phase-locked motion.
In contrast to Fig. 17, which shows steady state behavior, Fig. 19 shows a field of transient trajectories. Note the accumulation of trajectories in the neighborhood of \( y = z = 0 \).

Concentrating on the region about the origin, we consider a flow box with vertices at \((-1, -1), (-1, 1), (1, 1)\) and \((1, 1)\) as shown in Fig. 20. We assume that trajectories flow into the box on the left or bottom sides, then flow out on the top or right sides. We parameterize the left and bottom sides with a parameter \( s \) which goes from \(-1\) to \(1\), and the top and right sides with a parameter \( q \), which also goes from \(-1\) to \(1\) as shown in Fig. 20. Each point on the left and bottom sides of the flow box corresponds to a unique value of \( s \), and each point on the right and top sides corresponds to a unique value of \( q \). Initial values of \( s \) are integrated until they reach a \( q \) value. Plotting \( q \) vs. \( s \) we obtain a curvy line, Fig. 21. In order to obtain a simplified

**Fig. 15.** Regions of phase-locked motions and equilibrium points for \( \omega_1 = 1, \omega_2 = 2 \). The \( \ast, +, \times \) and \( \circ \) respectively represent 1:1:1 phase-locked motion, 1:1:0 phase-locked motion, 1:0:0 phase-locked motion and the equilibrium state of the system.

**Fig. 16.** A 2:2:1 phase-locked motion. This is the steady state behavior for \( \omega_1 = 1, \omega_2 = 2, \beta_{13} = 2.9 \) and \( \beta_{23} = 1.022877 \), obtained by numerical integration. The upper left plot is the motion plotted in three-dimensions. The remaining three plots show the projections of this three-dimensional motion.
model of this system we make a bold approximation by replacing this curvy line with a straight line of slope $M$ and therefore have the mapping

$$q = sM + M - 1$$  \hspace{1cm} (27)

Eq. (27) gives a mapping from $s$ to $q$. We also need a mapping from $q$ to $s$, which we get by assuming trajectories leaving the top of the box re-enter the flow box through the bottom at the same value of $z$, that is, such that the exit and re-entry points are vertically aligned. Similarly we assume that a trajectory which leaves the flow box on the right hand side will re-enter it at the same value of $y$, that is, such that the exit and re-entry points are horizontally aligned.

---

**Fig. 17.** A 2:2:1 phase-locked motion. This is the steady state behavior for $\omega_1 = 1, \omega_2 = 2, \beta_{32} = 2.9$ and $\beta_{32} = 1.022877$, obtained by numerical integration. This is a blow-up of the lower right plot of Fig. 16. Cf. Fig. 18.

**Fig. 18.** Plots of $z$ and $y$ vs. time for the motion shown in Fig. 17. Note that between the two points marked D, $z$ has gone around $2\pi$ whereas $y$ has gone around $4\pi$. 

---
These assumptions give the discontinuous mapping from \( q \) to \( s \)

\[
  s = \begin{cases} 
    q + 1 & \text{if } q < 0 \\ 
    0 & \text{if } q = 0 \\ 
    q - 1 & \text{if } q > 0 
  \end{cases}
\]  

(28)

Combining the two mappings, (27) and (28), we find the one dimensional map

---

**Fig. 19.** Trajectories obtained by numerical integration for the same parameters as the steady state in Fig. 17. Initial conditions are spread along the left side \((s = -\pi)\) and bottom \((y = -\pi)\) of the plot.

**Fig. 20.** Flow box has been superimposed in Fig. 19. The arrows indicate that trajectories enter along the \(s\)-axis and leave along the \(q\)-axis.
This derived 1D map is comparable to a circle map [6] which is known to exhibit the devil’s staircase, and has been studied by Veerman [9]. For a slope $M > 1$ the map is chaotic. When $0 < M < 0.5$ the map has a single fixed point. Since we are interested in representing the n:n:m phase-locked motion with the mapping, we discard values of $M$ in both of these ranges. The mapping is then shown for a slope in the range of $0.5 < M < 1$ in Fig. 22. Features of the map that change as a function of the slope, $M$, are noted on the figure. Graphically, if we wish to iterate a point on the map forwards, we draw a 45° line, move horizontally to this 45° line and then vertically to intersect with the mapping to obtain the next point in the series. In

\[
f(s) = \begin{cases} 
    sM + M & \text{if} \quad -1 < s < 1/M - 1 \\
    0 & \text{if} \quad s = 1/M - 1 \\
    M(s + 1) - 2 & \text{if} \quad 1/M - 1 < s < 1 
\end{cases} \tag{29}
\]

Fig. 21. Mapping of $s$ to $q$. Pairs of $s, q$ values correspond to a trajectory entering the flow box at $s$ and leaving the flow box at $q$. A straight line is used to approximate the curvy line traced out by discrete $s, q$ pairs.

Fig. 22. Graphical representation of the mapping given by (29) for a slope in the range $0.5 < M < 1$. 
following this procedure we are in effect projecting the $f(s)$ value to the horizontal axis, making it the new $s$ value. Next we then find its corresponding $f(s)$ value. This process is known as a cobweb construction [7]. An example of this one dimensional map with a cobweb construction is shown in Fig. 23. In this figure the slope is $M = 0.7$ and a period 3 orbit emerges. This period 3 orbit is shown in the figure as a solid line while the approach to this periodic orbit is a dashed line. The approach to the periodic orbit has been removed in Fig. 24 and arrows have been added to fully understand the cobweb construction. A positive or negative value of $s$ means that the trajectory has entered through the bottom or left of the flow box, respectively. Entering through the bottom of the box means that oscillator 2 has completed one revolution, likewise entering through the left of the box means oscillator 3 has completed one revolution. We therefore define the winding number as the number of fixed points of the map with negative $s$ values divided by the number of fixed points with positive $s$ values. Since

\[
\text{Fig. 23. Map given by (29) with slope } M = 0.7 \text{ and cobweb construction. The iteration begins at } s = 0.5 \text{ and is labeled with a1. From this point the cobwebs may be followed to see the approach to the period 3 orbit, the first 5 steps have been numbered.}
\]

\[
\text{Fig. 24. Example of the one dimensional map given by (29) with } M = 0.7. \text{ For this slope the winding number is seen to be } 1/2.
\]
oscillators 1 and 2 are phase-locked in the region of the "devil’s staircase", as was shown in Fig. 16, a map with a winding number of $m/n$ serves to represent $n:n:m$ phase-locked motion. Courtemanche et al. considered a circle map as a theoretical means with which to study parasystole [2]. In their study a specific arrhythmia was modeled not only by the winding number but also by the sequence of the fixed points in the periodic orbit.

Discretizing the interval of $0.5 < M < 1$ we can compute the winding number for each value in this interval using Matlab. Plotting the winding number vs. $M$ yields the familiar picture of the "devil’s staircase", and is presented in Fig. 25.

7. Conclusions

The goal of this work has been to investigate a system of three coupled phase-only oscillators as a model for the SA node. This simple model was shown to exhibit both unsynchronized and synchronized motion as well as a complicated sequence of bifurcations separating these two behaviors. These features were observed by Cai et al. [1] and Michaels et al. [5] whose models of the SA node were much more biologically realistic. Therefore while our model is simplistic and not biologically detailed it is seen to have biological implications and was used to investigate the frequency discrepancy between the center and peripheral cells of the SA node. Through numerical integrations it was shown that an advantage of the center of the SA node having a lower frequency than the periphery is that 1:1:1 phase-locked motion, which corresponds to rhythmic beating of the heart, occurs for a wider range of system parameters.

A region of complicated dynamics was found and determined to be a devil’s staircase. This region is entered by transitioning from 1:1:0 to 1:1:1 phase locking. Inside the devil’s staircase there exists phase-locked motion of the form $n:n:m$ for all values of $m$ and $n$ such that $m/n < 1$. A 1D discontinuous map was derived which exhibits the characteristics of the devil’s staircase.

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