Firefly Synchronization

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Imagine an entire tree or hillside of thousands of fireflies flashing on and off all at once. Very few people have been fortunate enough to see this synchronization phenomenon, but it has been documented. As a result, many scholars have tried to model firefly synchronization, and even more generally, the synchronization of mutually coupled oscillators with random frequencies. Not all fireflies are able to completely synchronize their flashes, but most species can modify their natural frequency in an attempt to match stimuli of a different frequency. By treating the flash of each firefly as a stimulus, every firefly is attempting to dynamically synchronize its frequency with that of every other firefly. Modeling thousands of fireflies trying to flash in unison would result in thousands of complex coupled equations. Therefore, since the purpose of this project is to explore and simulate the effect of stimuli on firefly behavior, we will use the following simplified model found the chapter on Firefly Synchronization in Strogatz.

In this chapter, he examines a simple model of how firefly's flashing rhythm responds to flashing stimuli. This simple model was first developed by Ermentrout and Rinzel in 1984. Let the phase of the firefly's flashing be given by $\theta(t)$ where $\theta = 0$ corresponds to the instant when a flash is emitted. Assume this phase is 2π-periodic so that $\theta = 2\pi n$ (where n is any integer), also corresponds to a flash. Then $\dot{\theta}_0 = \omega$ represents its natural frequency - the frequency at which it flashes in the absence of stimuli. Now let there be a stimulus with 2π-periodic phase Θ; again $\Theta = 0$ corresponds to the instant the stimulus flashes. Its frequency is given by $\dot{\Theta} = \Omega$. We can think of any stimulus with this frequency as one type of stimulus.

We know know that if the stimulus flashes before the firefly, then it will speed up in an attempt to synchronize. Similarly, if the stimulus flashes after the firefly, then it will slow down. A simple model of this is

$$\dot{\Theta} = \omega + A\sin(\Theta - \theta) \tag{1}$$

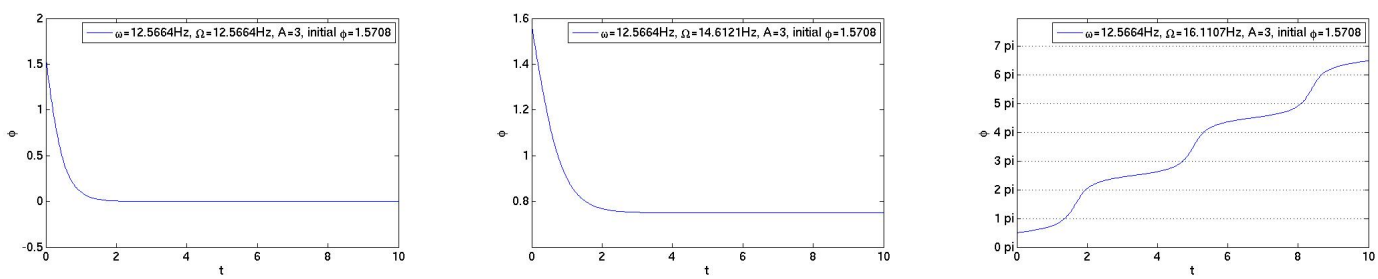
where A is the resetting strength of the firefly. This is a measure of the firefly's ability to change its instantaneous frequency in response to a stimulus. This definition implies that $A > 0$. From this equation, we see that if $0 < \Theta - \theta < \pi$, or in other words the stimulus is ahead of the firefly, then $\dot{\Theta} > \omega$ and thus the firefly speeds up. Similarly, if $-\pi < \Theta - \theta < 0$ and so the stimulus is behind the firefly, then $\dot{\Theta} < \omega$ and the firefly slows down. Let $\phi = \Theta - \theta$ denote the phase difference between the stimulus and firefly. This definition will become important in the analysis of the model to follow later. Since θ and Θ are 2π-periodic, so is their difference, ϕ.

Now that we have a model, we want to analyze the firefly's response to the stimulus. Scientists use the term entrainment to describe the situation in which the firefly is able to match its instantaneous frequency to that of the stimulus. This means that if entrainment occurs, the phase difference between the firefly and the stimulus, ϕ, approaches a fixed constant. If this constant is 0, then we say the firefly has synchronized with the stimulus and they flash simultaneously. If the constant is not equal to 0, then we say the firefly is phase-locked to the stimulus. Thus they have the same instantaneous frequency, but the firefly always flashes ahead or behind by a fixed amount. If entrainment does not occur, then the firefly will struggle to match the instantaneous frequency of the stimulus forever. Therefore ϕ will increase indefinitely but not uniformly. This is because ϕ increases slowly as the firefly tries to synchronize, then it increases rapidly through 2π, and the process repeats on the next beat cycle. This beat phenomenon is called phase drift.

We can plot ϕ versus time in order to classify the behavior of that system as phase synchronization, phase-locking, or phase drift. We can then plot $\dot{\phi}$ versus ϕ in order to analyze the stability of each behavior. To do so, first we need to find an equation for $\dot{\phi}$ in terms of ϕ. Using equation 1, we have

$$\begin{aligned} \dot{\phi} &= \dot{\Theta} - \dot{\theta} && (2) \\ &= \Omega - (\omega + A\sin(\Theta - \theta)) && (3) \\ &= \Omega - \omega - A\sin(\phi). && (4) \end{aligned}$$

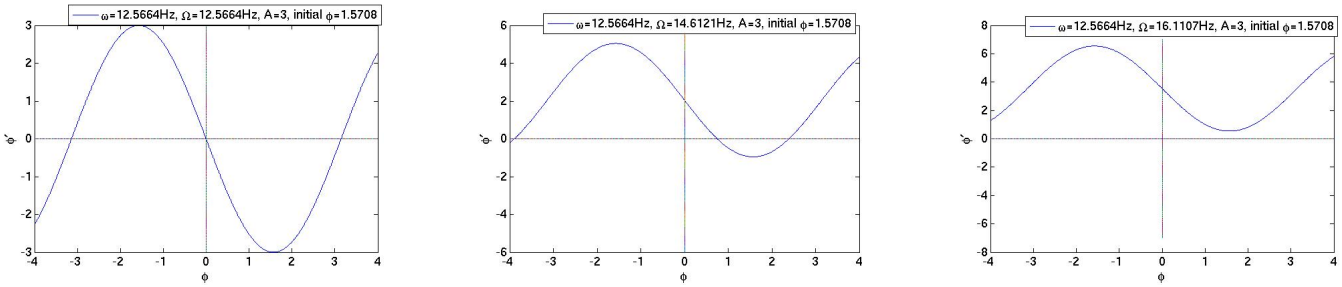
Now we can implement this equation as well as all necessary initial conditions and parameter values into the ODE45 solver in Matlab. ODE45 uses a fourth order explicit Runge-Kutta method. We then solve for ϕ at every time in the vector t, from 0 to tfinal in increments of 0.25 units, and plot the trajectory of ϕ. Note that for the ODE45 solver, we must give some initial condition on ϕ. Thus using different initial conditions and/or different system parameters (such as Ω, ω, and A), we can produce each of the three types of behavior. These are shown in Figure 1.



Phase Synchronization | Phase-Locked | Phase Drift

Figure 1: Phase Difference Trajectories

We can analyze the stability of these behaviors by examining the stability of the fixed points. To do so, we can plot $\dot{\phi}$ versus ϕ using equation 4 and the vector from -4 to 4 in increments of 0.01 units, respectively. As expected, three types of plots emerged: a stable fixed point at $\phi = 0$, stable fixed point at $\phi = c$ where c is some real constant, or no stable fixed points. Figure 2 shows these three behaviors.



Phase Synchronization Phase-Locked Phase Drift

Figure 2: Fixed Point Stability Analysis

For entrainment to occur, $\phi \to c$ as $t \to \infty$ (note that c can be equal to 0). Therefore for entrainment to occur in a situation, the stability analysis must show fixed points. In order to have fixed points, $\dot{\phi} = 0$, and thus,

$$0 = \Omega - \omega - A\sin(\phi) \tag{5}$$

$$\sin(\phi) = \frac{\Omega - \omega}{A}. \tag{6}$$

Since $-1 \leq \sin(\phi) \leq 1$, it must follow that

$$-1 \leq \frac{\Omega - \omega}{A} \leq 1 \tag{7}$$

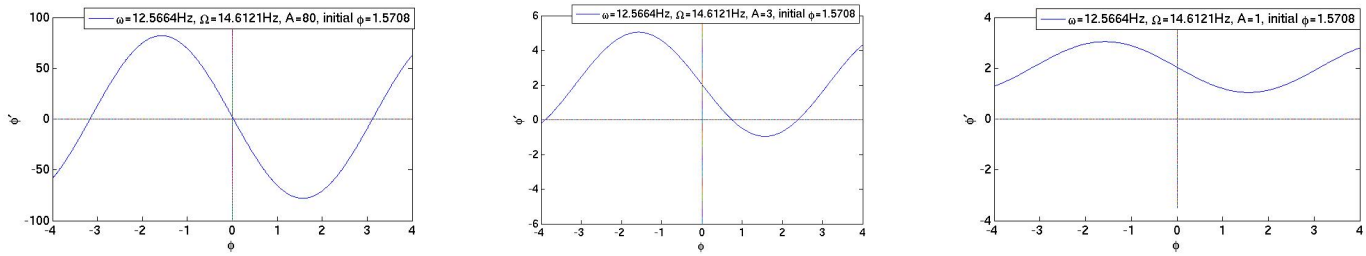
$$-A \leq \Omega - \omega \leq A \tag{8}$$

$$\omega - A \leq \Omega \leq \omega + A \tag{9}$$

in order for entrainment to occur. This is called the range of entrainment. This range implies that A must be larger than the difference in frequencies in order for entrainment to occur. In fact, in order for phase synchronization to occur, A must be much larger than $\Omega - \omega$. By measuring this range experimentally, one can find values for A for different species. There are a few species that can modify their natural frequency by almost 25% in order to entrain with the stimulus. Their A values must be huge! However, few species have large enough A values to perfectly synchronize with a stimulus. This could explain why firefly synchronization is so uncommon.

For a depiction of how the parameter A affects the behavior of the system, see Figure 3. Note that larger values of A allow phase synchronization while smaller values cause phase-locking and phase drift. This makes sense since A is proportional to how well the firefly can change its frequency to match that of a stimulus. Note also that the range of entrainment depends on the frequencies, not phases, of the firefly and stimuli. Therefore the initial phase difference does not affect the behavior of the system. This means that the cases in Figure 4 are equivalent to those in the phase-locking case of Figures 1 and 2. Changes in the initial ϕ might shift ϕ over time by $2\pi n$, but since ϕ is 2π periodic, the two behaviors are qualitatively equivalent.

The trajectory and phase plots offer insight into the model, but are sometimes difficult to understand. As a result, we also study a simulation of the fireflies' flashing rhythm in



Phase Synchronization Phase-Locked Phase Drift

Figure 3: Changes in values of A. Note the conditions of each plot are the same except for A. The plots indicate that changing the value of A affects the behavior of the system.

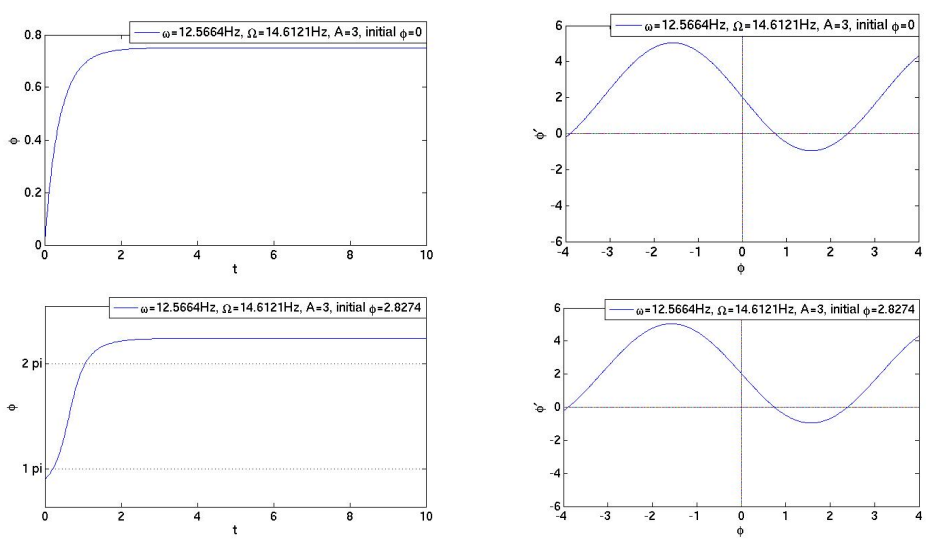


Figure 4: Changes in the initial ϕ. Note that the conditions of each plot are the same except for the initial ϕ. The plots show that changins this value does not affect the behavior of the system.

response to that of a stimulus. To make the simulation, we first make a 50 by 50 grid of fireflies and the stimulus. To randomly place fireflies within the grid irst make a 50 by 50 matrix of random real numbers between 0 and 1 using the command y=rand(50) in Matlab. Then let $y > 0.95$ in order to select only those matrix entries which are greater than 0.95. This assigns random positions for the group of fireflies of the same phase. Now to create the position of the stimulus, remove the center point by letting y(25,25)=0. Then create another 50 by 50 matrix of zeros, z=zeros(50), and place the stimulus at the center point with z(25,25)=1. We now have a grid to represent the position of the fireflies and a plane to represent the position of the stimulus.

In order to decide when the fireflies and stimulus should flash, recall that both the phases of the firefly and the stimulus are 2π-periodic. Therefore we want each flash only once every 2π units of time. To do this, we can flash the object at the instant in which sin(phase = 1 since sin = 1 only once every 2π. However, this would be very difficult to see since its such a brief moment. Therefore we use a Matlab's colormap in order to show the firefly and stimulus slowly turning on and off. Colormap is an 3-by-3 matrix of real numbers between 0.0 and 1.0. Each row is an RGB vector that defines one color. The kth row of the colormap defines the kth color, where map(k,:) = [r(k) g(k) b(k)]) specifies the intensity of red, green, and blue.[1]. In our simulation, let the stimulus be red and the firefly be green. Therefore, to show the stimulus flashing, we flash the stimulus at the moments in time in which $\sin(\Theta)) > 0.5$, and colormap assigns increasing intensities to the values 0.5-1. Thus the Matlab code for the stimulus reads $C(:,:,1) = z * (b(i)) * (b(i) > .5)$ where i is the instant in time and $b = \sin(\Theta) = \sin(\Omega i)$. We do the same for the firefly except we add some initial color to the fireflies in order to indicate their position. The fireflies flash according to $C(:,:,3) = y * ((a(i)) * (a(i) > .5) + .5 * (a(i) < .5)$ where $a = \sin(\theta) = \sin(\Theta - \phi)$. We assign $C(:,:,2) = zeros(50)$ since we do not want any green elements. To actually make the movie, we place these color map commands within a for loop that cycles from $i = 1$ to $i =$ length(t) where t=[0:0.25:tfinal]. At each cycle of the for loop, the mailer gets the image with the command, image(C), and then turns that image into a frame of the movie with F(i)=getframe. The result is a movie of randomly dispersed similar fireflies attempting to synchronize to a single stimulus. Each flash of the fireflies and the stimulus is divided into a discrete spectrum (updated every 0.25 units of time) of either blue or red, respectively.

We now have a model describing how a firefly reacts to a stimulus given some initial phase difference. We can extend this model to a group of fireflies of the same natural frequency reacting to any number of stimuli of the same frequency (given that the initial phase difference between any firefly and any stimulus is the same). Since frequency is a derivative of phase, we can think of this as a group of fireflies of the same phase and a group of stimuli of the same phase. Call this the *single stimulus case* for the single type of stimulus. But what happens when there are two types of stimuli? How will the fireflies react to two different frequencies? I have proposed two simplified models to explore this case; they are both derivatives of the previous single stimulus model. For both models, we will use the same parameters as we did previously, but now call the phase of the type 1 stimulus, Θ_1, and the phase of the type 2 stimulus, Θ_2. Similarly, their frequencies are given by $\dot{\Theta}_1 = \Omega_1$ and $\dot{\Theta}_2 = \Omega_2$. Let $\phi_1 = \Theta_1 - \theta$ be the phase difference between stimulus 1 and the firefly,

[1]This description of colormap is taken directly from Matlab's help files

and $\phi_2 = \Theta_2 - \theta$ be the phase difference between stimulus 2 and the firefly.

The first model predicts that the phase of the firefly changes according to

$$\dot{\theta} = \omega + A\sin(\phi_1) + A\sin(\phi_2) \tag{10}$$

while the second predicts

$$\dot{\theta} = \omega + A\sin\left(\frac{\phi_1 + \phi_2}{2}\right). \tag{11}$$

Call the first model the *multiple stimuli model* and the second the *average multiple stimuli model*. As in the derivation of the single stimulus model, we know $\dot{\phi}_1 = \dot{\Theta}_1 - \dot{\theta}$ and $\dot{\phi}_2 = \dot{\Theta}_2 - \dot{\theta}$. Substituting this into the two models, the first model yields

$$\dot{\phi}_1 = \Omega_1 - \omega - A\sin(\phi_1) - A\sin(\phi_2) \tag{12}$$

$$\dot{\phi}_2 = \Omega_2 - \omega - A\sin(\phi_1) - A\sin(\phi_2) \tag{13}$$

and the second yields

$$\dot{\phi}_1 = \Omega_1 - \omega - A\sin\left(\frac{\phi_1 + \phi_2}{2}\right) \tag{14}$$

$$\dot{\phi}_2 = \Omega_2 - \omega - A\sin\left(\frac{\phi_1 + \phi_2}{2}\right). \tag{15}$$

If the two stimuli have the same frequency, then $\Omega_1 = \Omega_2$. The phases of these stimuli are then given by $\Theta_1 = \Omega_1 t + \text{initial } \phi_1$ and $\Theta_2 = \Omega_2 t + \text{initial } \phi_2$ at time t. If initial $\phi_1 =$ initial ϕ_2, then $\Theta_1 = \Theta_2$ for all t. As a result, $\phi_1 = \phi_2$. In this case, we no longer have two types of stimuli, but instead one type of stimulus as in the single stimulus model. Therefore both models reduce to a single unique equation (in the sense that now $\dot{\phi}_1 = \dot{\phi}_2$). The multiple stimuli model becomes

$$\dot{\phi}_1 = \Omega_1 - \omega - 2A\sin(\phi_1) \tag{16}$$

and the average multiple stimuli model becomes

$$\dot{\phi}_1 = \Omega_1 - \omega - A\sin(\phi_1). \tag{17}$$

These models should be qualitatively the same as the single stimulus model, and thus equations 16 and 17 should be qualitatively the same as equation 4. Since only equation 17 agrees with equation 4, we must conclude that the average multiple stimuli model is more consistent.

Suppose now that $\Omega_1 = \omega$ but $\Omega_2 \neq \omega$ and initial $\phi_1 =$ initial $\phi_2 = 0$. Recall that $\dot{\theta}$ is driven by the sin term whose argument is the average of ϕ_1 and ϕ_2. Therefore even though $\phi_1 = 0$, $\phi_2 \neq 0$, and thus the sin term will either increase or decrease the frequency of the firefly. Once the firefly begins to change its frequency to match that of stimulus 2, ϕ_2 will increase or decrease, but then ϕ_1 will decrease or increase respectively. Once ϕ approaches 2π, it effectively resets to 0, and thus the same process occurs (ϕ_2 increases or decreases and ϕ_1 decreases or increases, respectively). Therefore the trajectories of ϕ_1 and ϕ_2 will be uniformly increasing and decreasing, or uniformly decreasing and increasing, respectively.

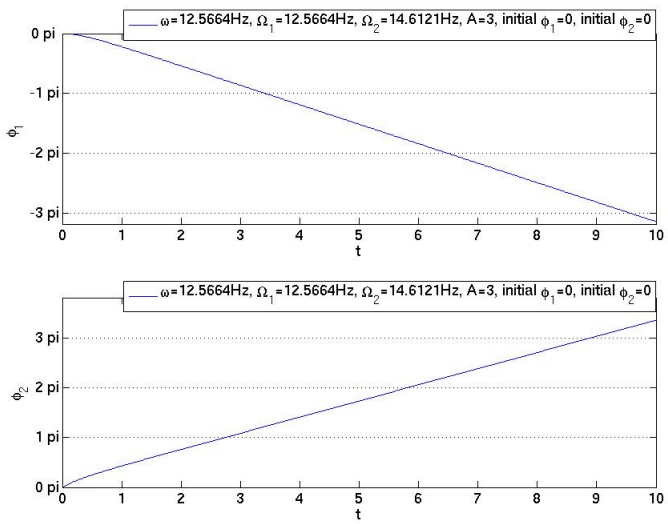


Figure 5: $\Omega_1 = \omega \neq \Omega_2$ and initial $\phi_1 =$ initial $\phi_2 = 0$

Thus the firefly will never entrain with either stimulus, but instead exhibit phase drift with both. See Figure 5 for a depiction of this behavior.

Looking at the same scenario, except now let initial $\phi_1 =$ initial $\phi_2 \neq 0$ as in figure 6. Here the initial phase difference affects the behavior of the system, unlike in the single stimulus model.

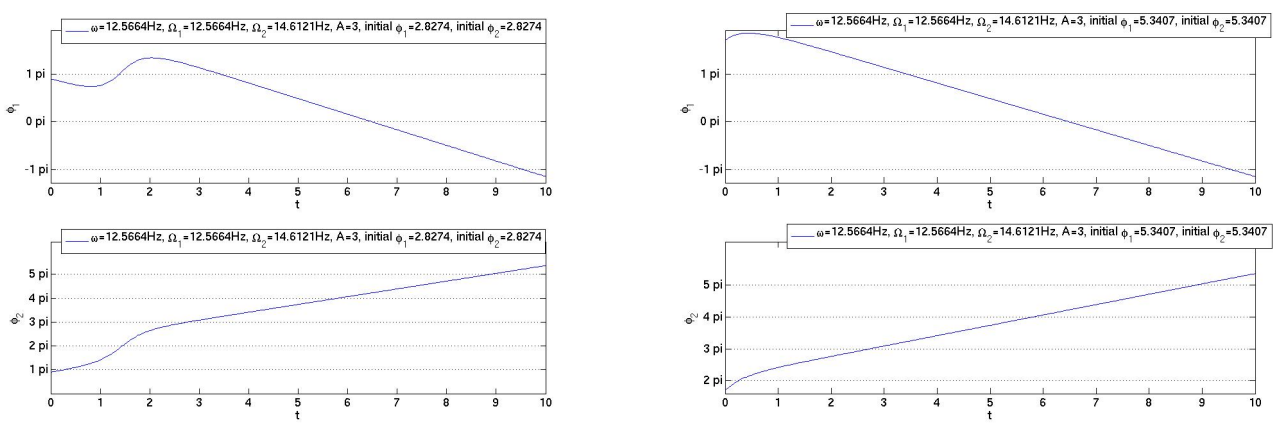


Figure 6: $\Omega_1 = \omega \neq \Omega_2$ and initial $\phi_1 =$ initial $\phi_2 \neq 0$

Interestingly enough, allowing $\Omega_1 \neq \Omega_2 \neq \omega$ produces the same behavior as displayed on the right hand side of figure 6. Therefore no matter the initial conditions nor the parameters, the firefly will always display phase drift from both stimuli in the average multiple stimuli model (unless the conditions and parameters are such that it reduces to the single stimuli model). Therefore the unique average multiple stimuli model, that is the one that differs from the single stimulus model, has no fixed points or stable behavior. In the previous single

stimulus model, we plotted $\dot{\phi}$ versus ϕ to find the fixed points. In the average multiple stimuli case, both $\dot{\phi}_1$ and $\dot{\phi}_2$ are dependent upon ϕ_1 and ϕ_2, and therefore we cannot use the same approach to find and classify fixed points. Fortunately the trajectories alone are enough to indicate that the unique model always shows phase drift and thus there are no fixed points. We can also see this by making another movie using colormap. We use the same commands as in the previous case, but now we represent the second stimulus with the green colormap. Therefore we replace $C(:,:,2) = zeros(50)$ with $C(:,:,2) = x * (c(i)) * (c(i) > .5$, where x=zeros(50) and x(25,35)=1 create the grid for stimulus 2, and $c = \sin(\Theta_2) = \sin(\Omega_2 i)$.

What do the results of these two models mean? Suppose there is a group of fireflies flashing with the same phase, and one firefly of a different phase lands in the group. Imagine also that the new firefly's phase is unaffected by that of the group. According to the single stimulus model, this new firefly is effectively a stimulus. The model suggests that the group can synchronize with the new firefly given a high enough value of A. However, if even one firefly in the group does not modify its frequency to match the newly introduced firefly, then this stubborn firefly becomes a stimulus. There are now two stimuli affecting the phase of the group. According to the average multiple stimuli model, no matter the phase of the stubborn firefly, the group will never be able to synchronize or even entrain to the stimuli. Therefore if any member of the group decides not to conform, the group will not be able to achieve a stable behavior. This could explain why firefly synchronization or even entrainment is such a rare phenomenon.

Strogatz, S. H. *Nonlinear Dynamics and Chaos, with Applications to Physics, Biology, Chemistry, and Engineering.* Reading, MA: Addison-Wesley, 1994.