

# Integrate and Firefly: Applying Neuroscience Models to Nature

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## Abstract

This paper reviews a set of papers seen in the Reference section, with Sarfati et al. (2023) serving as the main focus. Sarfati et al. (2023) explored how that in isolation from their peers, *Photinus carolinus* fireflies flash with no intrinsic period between successive bursts. Yet, when congregating into large mating swarms, these fireflies transition into predictability, synchronizing with their neighbors with a rhythmic periodicity. A mechanism for this emergence of synchrony and periodicity was proposed, and the principle was formulated in a mathematical framework. Remarkably, with no fitting parameters, analytic predictions from this simple principle and framework agreed strikingly well with data. Next, further sophistication was added to the framework using a computational approach featuring groups of random oscillators via integrate-and-fire interactions controlled by a tunable parameter. This agent-based framework of *P.carolinus* fireflies interacting in swarms of increasing density also showed quantitatively similar phenomenology and reduced to the analytic framework in the appropriate limit of the tunable coupling strength.

## Development of Theoretical Methods

A theoretical framework for modeling fireflies flashing dates back to a paper published in 1984, in which a simple one-variable model was posed that described synchronizing and desynchronizing of periodically stimulated fireflies. This model made a couple of assumptions: the first being that fireflies are inherently periodic, that is, if you are to take a firefly and look at it on its own, it will flash and recharge in a way that is periodic in nature. This paper describes the bursts that occurs with fireflies (multiple flashes at the same time) As these fireflies, who are already periodic independently, synching up as coupled oscillators. Ermentrout (1984). The assumptions made in this paper agrees with the overwhelming majority of fireflash synchronicity research in the sense that they all assume these fireflies to have periodicity in their flashing.

Recently, the paper that our research revolves around, Sarfati et al. (2023), took a drastically different approach to modeling this behavior of fireflies flashing and their synchronizing. Sarfati et al. (2023) A new controlled experiment was run in which collecting data showing the flash duration of a firefly became feasible and measurable, fireflies flashing no longer was modeled as inherently being periodic. From this data, it became evident that commonly the firefly that started a burst flashed for the longest, then followers flash in an already synchronized fashion. The findings from this research made it evident that fireflies should not simply be modeled in terms of periodic fireflies that happen to synchronize. From here, modeling the flashing of fireflies and describing this group periodicity became a more complex issue and thus required a more involved model to describe and simulate their behavior.

## Integrate and Fire model

As the research in the field has continually built on itself, as referenced in the abstract, the model has evolved and added complexity. In this modeling of fireflies lies a fascinating link to the neuroscience concept of the integrate and fire model. The integrate and fire model is used in the context of neuroscience in order to model certain neural systems and concepts. The integrate and fire model in neuroscience terms is expressed below:

$$C \frac{dV}{dt} = f(v) + I, T_m < t < T_{m+1}, m \in \mathbb{Z} \quad (0.1)$$

In this equation  $C$  represents the cell membrane capacity, and  $I$  represents the external input current into the cell, and  $f(v)$  represents the neurons activity properties. This model effectively models neural activity by integrating the membrane potential until it surpasses a threshold, denoted  $v_{th}$ , the neuron 'spikes'. When this occurs, an electrical pulse is released (the neuron spikes), following which there is a refractory period, where the neuron returns to its reset value, or  $v_r$ . Much of this can be taken and extrapolated to modeling fireflies.

## Principle of Emergent Periodicity

The fundamental paradigm behind the theoretical formulation is that: (1) each firefly waits a random time( $t$  drawn from  $b(t)$ ) before flashing again; (2) Upon flashing, a firefly instantly triggers all other fireflies to also flash. (3) After flashing, each firefly resets its internal waiting time to another random  $t$ . Under the assumption that the fireflies are identical, the probability distribution  $P_N(T_b)$  of the interburst interval  $T_b$  of a group of  $N$  fireflies is modeled as:

$$P_N(T_b) = N \left[ \int_{T_b}^{\infty} b(t) dt \right]^{N-1} b(T_b) \quad (0.2)$$

This distribution, as  $N \rightarrow \infty$ , converges to the Dirac-Delta function around the minimum interburst interval  $T_0$  of the individual fireflies:

$$\lim_{N \rightarrow \infty} P_N(T_b) = \delta(T_b - T_0) \quad (0.3)$$

## Computational Approach: Agent Based Simulation

The aforementioned Sarfati et al. (2023) paper presented a stochastic variant of the integrate-and-fire model, one which accounts for the variability in between firefly flashes while still holding the general structure of the integrate-and-fire model. Sarfati et al. (2023)

In this model, the internal state of firefly  $i$  is characterized by variables  $V$  and  $\epsilon$  whose evolution follows:

$$\frac{dV_i(t)}{dt} = \frac{1}{T_{si}} \epsilon_i(t) - \frac{1}{T_{di}} [1 - \epsilon_i(t)] + \epsilon_i(t) \sum_{i,j}^N \beta_{ij} \delta_{ij} [1 - \epsilon_j(t)] \quad (0.4)$$

where  $\epsilon_i$  is a binary variable that is 1 when an individual is charging (quiet) and 0 when an individual is discharging (flashing). The state of  $\epsilon_i$  changes to 0 when reaching the threshold voltage  $V = 1$ , and switches back to 1 when the firefly has finished discharging at the threshold ( $V = 0$ ). The time  $T_{di}$  represents the flash length and is drawn directly from observed data, and the time  $T_{si}$  represents the end-to-start interflash interval. This value comes directly from the data in the following way:  $T_{si} = T_{bi} - T_{di}$ , where  $T_{bi}$  represents the start-to-start inter-flash interval for firefly  $i$ , sampled from the input distribution envelope seen in [Figure 1](#) (a), and  $T_{di}$

represents the discharge time for firefly  $i$  sampled from the distribution of the discharge-time seen in [Figure 1](#) (b).

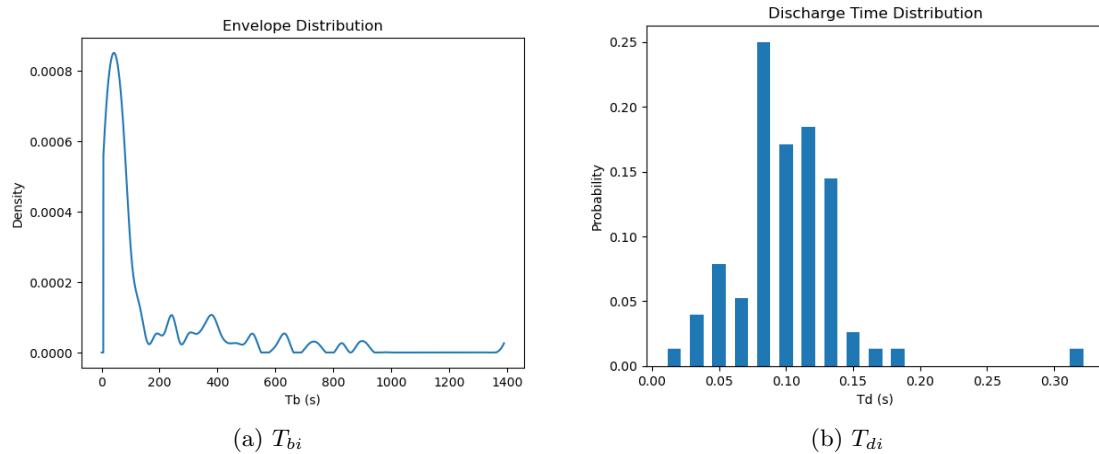


Figure 1: Shows the distributions that were sampled from for the simulation.

The firefly may be "pulled" towards flashing sooner if detecting the flashes of neighboring fireflies, which is represented in the framework by the third term. Here  $\delta_{ij} \in \{0, 1\}$  represents connectivity between agents and  $\beta_{ij}$  is the coupling strength. For simplicity, all-to-all connectivity ( $\delta_{ij} = 1, \forall(i, j)$ ) is used and the common interaction  $\beta_{ij} = \beta$  is varied.

The above is the standard equation for the integrate-and-fire (IF) scheme, with the crucial difference due to the introduction of stochasticity:  $T_{bi}$  is a random variable whose value is drawn from our experimental distributions seen in [Figure 1](#) (a) of interburst intervals, and  $T_{di}$  is a random variable whose value is drawn from our previously published data illustrating the distribution of firefly flash lengths. Each of these variables are sampled, for each agent, every time they switch state with  $\epsilon_i$  shifting from 0 to 1 or 1 to 0. In this stochastic IF framework the variability between flashes is accounted for, while maintaining the overall structure of the IF model. It is assumed that each firefly is identical, therefore, the same intrinsic probability distributions are used to sample from for each firefly.

This model is simulated for different values of  $N$  and  $\beta$ , and compared with the experimental data.

## Experiments

### Simulation Replication

This simulation exhibits a transition to group periodicity as interactions between agents are increased. We define the group interburst interval  $T_B$  as the time between one flash and the next flash produced by any other firefly in the swarm. For example, consider the case of  $N = 20$  in [Figure 2](#) (d). When  $\beta = 0$  each firefly behaves purely individually and interburst intervals tend to aggregate towards small values due to the random unsynchronized flashing of the  $N$  fireflies each with a flashing behavior typical of isolated individuals. This remains the case until the coupling strength,  $\beta$ , becomes large enough that there is enough of collective entrainment to align the flashes of the group. In these regimes, when one firefly flashes it quickly triggers all others. All agents then reset their charging time at roughly the same moment, and the smallest  $b$  selected by any individual firefly defines the duration between this flash and the group's next flash.

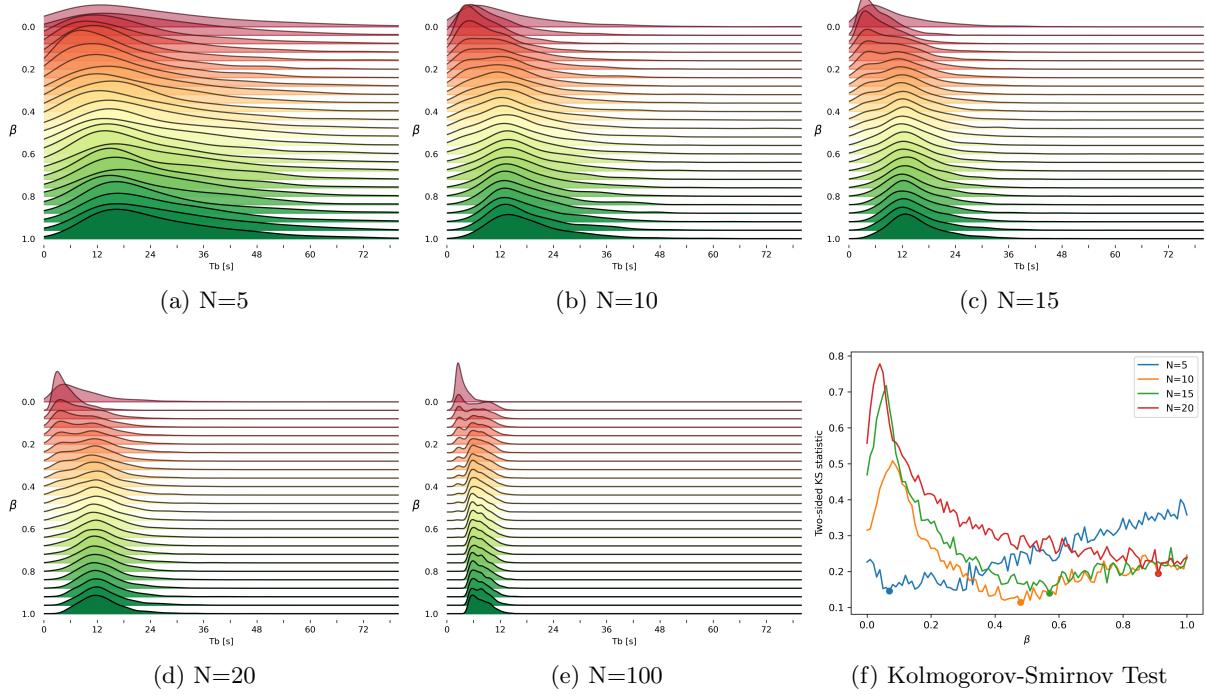


Figure 2: Shows the plots from our recreated simulations based on Sarfati et al. (2023). (a) For  $N = 5$ , the KS-statistic is minimum when  $\beta = 0.07$ . The peak of the histogram is at 10.2184 (b) For  $N = 10$ , the KS-statistic is minimum when  $\beta = 0.48$ . The peak of the histogram is at 10.2184 (c) For  $N = 15$ , the KS-statistic is minimum when  $\beta = 0.57$ . The peak of the histogram is at 10.2184 (d) For  $N = 20$ , the KS-statistic is minimum when  $\beta = 0.91$ . The peak of the histogram is at 10.2184 (e) For  $N = 100$ , the asymptotic behavior can be observed (f) KS-statistic for different values of  $N$  sweeping over  $\beta$

As a consequence, interburst intervals of the group,  $T_B$ , shift to a larger value corresponding to the smallest time between flashes for an individual firefly ( $T_{b0}$ ). This behavior can be seen easily in Figure 2, where wide distributions give way to progressively tighter shapes as  $\beta$  and  $N$  increase. We can quantify this transition by examining the characteristic peaks in the  $T_b$  distribution. Peaks with a value below the minimum of the input distribution occur when beta is small, and pulsatile coupling is thus weakly pulling the flashes towards each other. At each value of  $N$ , however, Figure 2 shows a sharp transition wherein the beta value becomes high enough to cause enough coupling gain to produce synchronous flashes and the alignment of the start of the next burst. This drives the pace of the flashing to be set by the first flasher, which as  $N$  increases becomes more likely to be on the lower end of the input distribution. The high-coupling peak is also naturally sharper at increasing  $N$ : at larger  $N$ , the probability that some  $T_{bi}$  approaches the minimum possible  $T_b$  is higher, resulting in more regularity the collective flashing pattern as seen in Figure 2 (e). As our simulation has a single fitting parameter, namely the coupling strength  $\beta$ , we conduct a detailed comparison of the simulation and experimental data to infer the most likely value of  $\beta$  for the *P.carolinus* system. A systematic parameter sweep over the values of  $\beta$  and  $N$  provides a set of  $T_B$  interval distributions Figure 2. We statistically compare the distributions generated by simulation with those obtained experimentally at each swarm density and find that the optimal values of  $\beta$  to match the empirical distributions cluster around when  $N \leq 15$  (and holds a higher value when  $N = 20$ ).

## Explorations

### Stochasticity of $T_{bi}$

From the model expressed in 0.4 we see that the intrinsic distributions of  $T_b$  and  $T_d$ , the coupling strength  $\beta_{ij}$  and the connectivity  $\delta_{ij}$  are all parameters that can be altered, which in turn would alter the resulting distribution of the group interburst interval  $T_B$ . The theoretical model 0.4 predicts that for any input distribution of  $T_{bi}$ , as the number of fireflies and the coupling between the fireflies increases, the  $T_B$  of the group approaches the minimum value in that the individual  $T_{bi}$  can take,  $T_0$ . In order to test this,  $T_{bi}$  is sampled from different probability distributions, and the behavior of  $T_B$  distribution of the group at high values of beta is compared. Initially,  $T_{bi}$  is set as a constant, set as 5, 40 and 300, and as the theoretical model predicts,  $T_B$  for the group peaks at values close to 5, 40 and 300 seen in Figure 3.

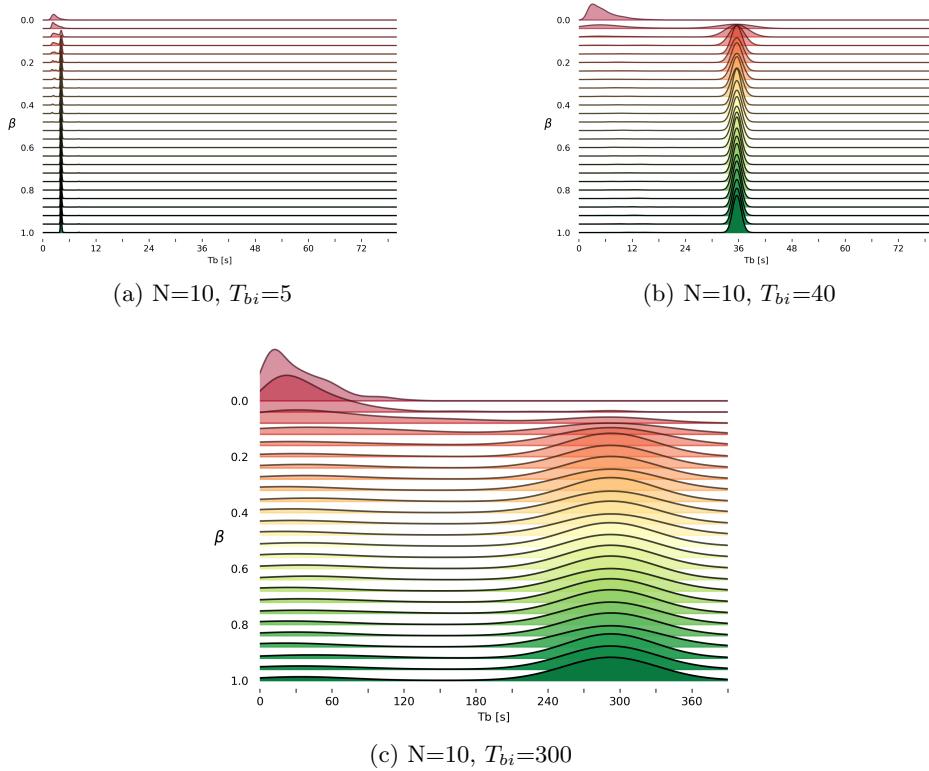


Figure 3: Starting with a simplified version of the model, where  $T_{bi}$  of the individual fireflies is fixed to constant values 5, 40 and 300

Stochasticity to  $T_{bi}$  is introduced to the model in the following manner : the envelope developed from a single firefly is multiplied by different constants, which has the effect of stretching the envelope by those constants. The minimum value of  $T_{bi}$  that can be sampled from the distributions, which happens to be 5.672 seconds, is also, thereby, multiplied by that constant. The theoretical model predicts that the peak of the distribution of  $T_B$  of the group should also be multiplied by that same factor, which is being observed in the simulations represented in Figure 4.

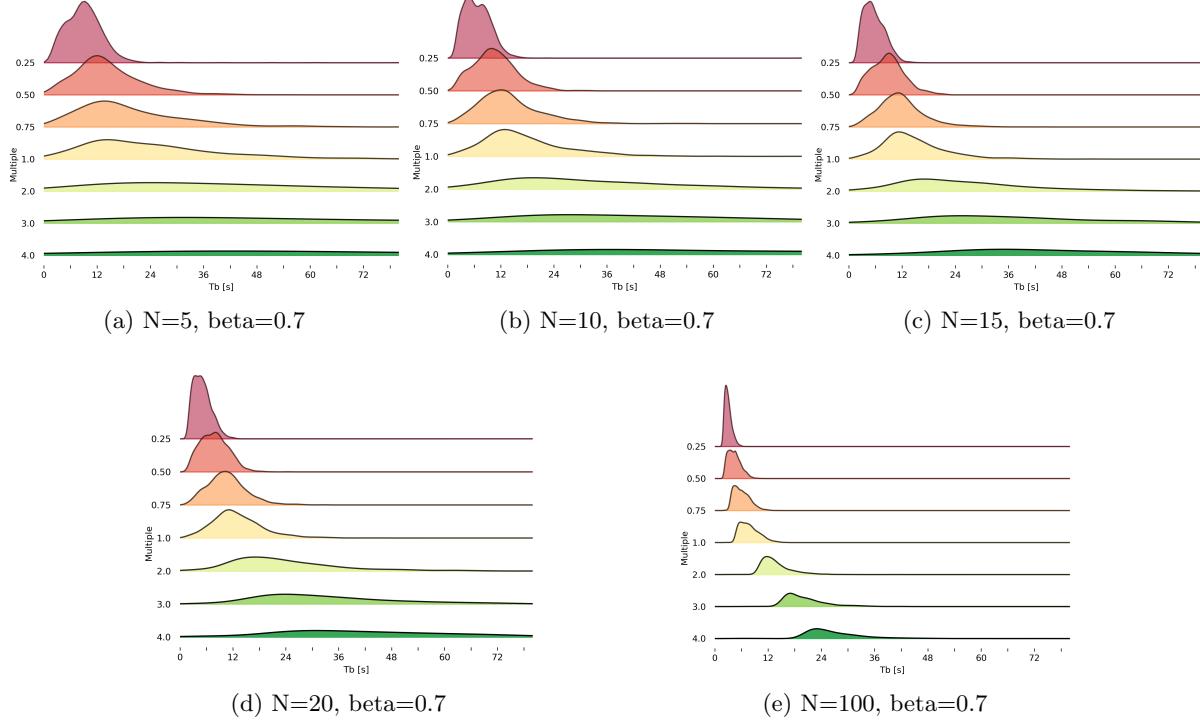


Figure 4: PDF of  $T_{bi}$  is scaled by a constant multiplying factor. For each value of  $N$ , the multiplying factor is swept across different values

### Adjacency Matrix

Going back to the stochastic integrate and fire model, the variable  $\delta_{ij}$  is something that can be altered and the effect on the group  $T_B$  distribution can be studied.  $\delta_{ij}$  is a binary variable that is either 1 if fireflies  $i$  and  $j$  are ‘neighbors’, i.e., the spatial distance between them falls below a threshold, and 0 if the distance between them is greater than this distance.  $[\delta_{ij}]$  is, therefore, a  $N \times N$  square matrix populated by 0’s and 1’s. In the original work by Sarfati et al. (2023), this matrix was uniformly set to be 1 for every entry of the matrix, that is, every firefly is assumed to be equally coupled with every other firefly in the swarm, whereas we are not making that assumption, and instead populating the matrix as follows: At time  $t = 0$ , spatial cartesian coordinates  $(x, y, z)$  of every firefly is sampled from a uniform distribution between 0 and 10 for  $x$ ,  $y$  and  $z$  representing the positions of the fireflies in a  $10 \times 10 \times 10$  cubical room. The euclidean distance between every pair of fireflies  $i$  and  $j$  is calculated, and if it is less than a threshold value, the  $\delta_{ij} = 1$  and 0 otherwise. It is assumed that the fireflies are stationary in time, so the adjacency matrix generated at  $t = 0$  is constant through the simulation.

First, keeping an arbitrary value of  $\beta = 0.7$  fixed, for  $N = 5, 10, 15, 20$ , different threshold values are considered, starting from 0 (no coupling), 2, 4, 6, 8, 10, 12 and no threshold (uniform coupling). For any fixed value of  $N$  and  $\beta$ , as the threshold distance is increased, the number of couplings for each firefly would increase, thereby pushing the peak of the group  $T_B$  distribution further to the right. This expected behavior is what is observed from the simulations as seen in Figure 5.

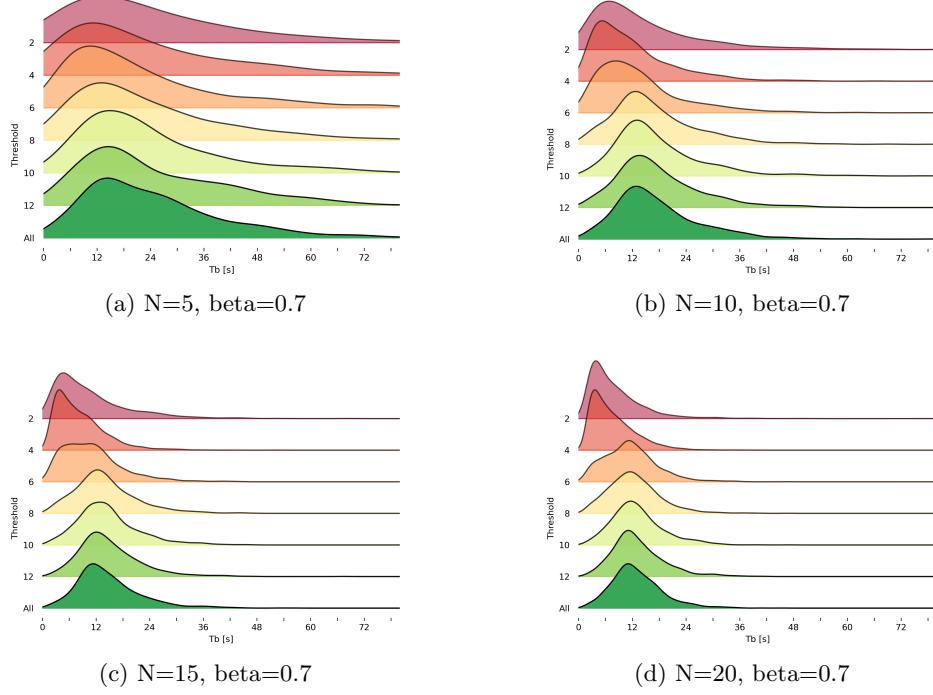


Figure 5: Adjacency Matrix Plots.  $\beta = 0.7$  is fixed, and for each value of  $N$ , different threshold distances are simulated.

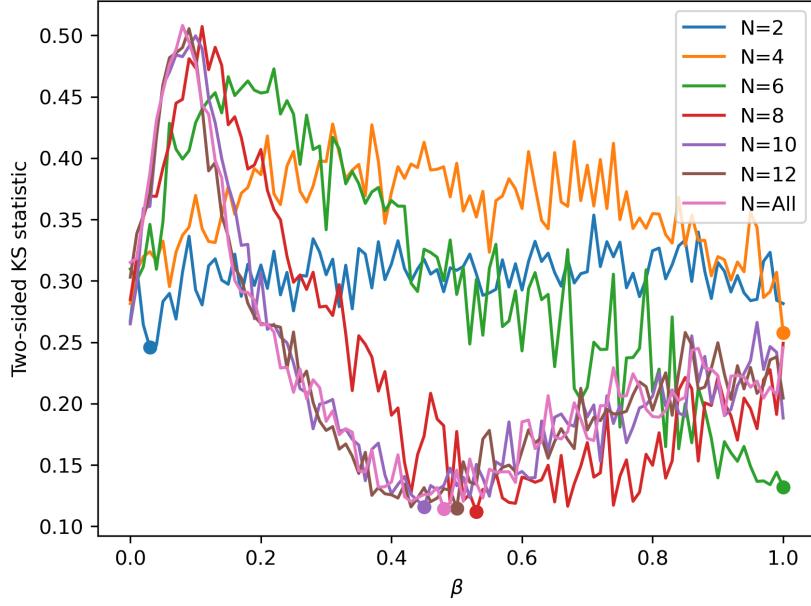


Figure 6: KS-Statistic for  $N = 10$ , for different threshold distances. KS-Statistic is minimum for threshold = 2 at  $\beta = 0.03$ , KS-Statistic is minimum for threshold = 4 at  $\beta = 1.0$ , KS-Statistic is minimum for threshold = 6 at  $\beta = 1.0$ , KS-Statistic is minimum for threshold = 8 at  $\beta = 0.53$ , KS-Statistic is minimum for threshold = 10 at  $\beta = 0.45$ , KS-Statistic is minimum for threshold = 12 at  $\beta = 0.5$ . KS-Statistic for threshold = 6 at  $\beta = 1.0$  for  $N = 5$  is 0.1514. Minimum KS-statistic for  $N = 5$  is 0.1455. KS-Statistic for threshold = 6 at  $\beta = 1.0$  for  $N = 15$  is 0.2212. Minimum KS-statistic for  $N = 5$  is 0.1400.

Then,  $N = 10$  is kept fixed, for the threshold values of 0, 2, 4, 6, 8, 10, 12,  $\beta$  is increased gradually from 0 to 1. For the resulting  $T_B$  group distribution, the Kolmogorov-Smirnov test is performed to compare it with the  $T_B$  group distribution obtained experimentally, at each value of  $\beta$ . The purpose of doing this test is to see if for any threshold value, the minimum KS test statistic is comparable to the minimum KS test statistic obtained from comparing the original model (with adjacency matrix 1) with the experimental data as seen in [Figure 6](#).

It was observed that when the threshold is 6, a minimum KS test statistic of 0.1320 occurs at  $\beta = 1$ . The original model from Sarfati23, for  $N = 10$  achieves a KS test statistic of 0.1143 at  $\beta = 0.48$ , which is comparable to the above KS test statistic. This suggests that, both the original model and the model with a threshold distance of 6 units, produce similar distributions of  $T_B$  of group.

To investigate this pattern further, the threshold distance is held fixed at 6 units and the  $\beta$  value is held fixed at 1, and the KS-test is performed for other values of  $N$  by comparing the distribution of group  $T_B$  with the experimental data. For every value of  $N$ , the minimum KS test statistic obtained for this combination of fixed  $\beta$  and threshold distance was observed to be comparable to the minimum KS test statistic obtained from comparing the original model and the experimental data. Furthermore, the original model achieves the minimum KS test statistic at different values of  $\beta$  for each value of  $N$ . This has given rise to a novel hypothesis that the integrate and fire model can be modified such that, when only the fireflies that are within a distance of 6 units are assumed to affect the behavior of firefly  $i$ , the evolution of  $V_i$  can be modeled as:

$$\frac{dV_i(t)}{dt} = \frac{1}{T_{si}}\epsilon_i(t) - \frac{1}{T_{di}}[1 - \epsilon_i(t)] + \epsilon_i(t) \sum_{i,j}^N \delta_{ij}[1 - \epsilon_j(t)]$$

where  $\beta_{ij}$  is observed to be 1, irrespective of the number of fireflies in the swarm. With the data available and the analysis performed, we make the claim that this suggested simplified model performs comparable to the original model statistically. The interpretation behind why this might be the case could be that, when the adjacency matrix is assumed to be uniform, the optimal value of  $\beta$  changes for each value of  $N$ ; this change is now captured by the adjacency matrix defined with a threshold value of 6 (for a 10x10x10 room) while keeping  $\beta$  fixed at 1. In the end, they both affect the third term in the model, so, stochastically they affect the evolution of  $V_i$  in time in a similar manner. Further rigorous analysis is required to study the behavior of the model and the KS test statistic for other values of threshold, and dedicated experimental setups focused on studying the effect of changing the threshold value to validate the above claim.

## Discussions

On recreating the plots that are reported in Sarfati et al. (2023), we found that the general behavior of the distribution of the group interburst interval  $T_B$  matches that we simulated match the respective distributions from the Sarfati et al. (2023). The peaks of the distribution, on increasing  $\beta$  shifts to the right, as expected, but the final values of  $\beta$  that minimized the KS-statistic, on comparing with the experimental data did not match exactly. The  $\beta$  values that were reported in Sarfati et al. (2023) for  $N = 5, 10, 15, 20$  respectively were 0.18, 0.13, 0.12, 0.64. But the  $\beta$  values that we got, that minimized the KS statistic were respectively 0.07, 0.48, 0.57 and 0.91. The inherent stochasticity of the model, and the marginal change in the distribution of  $T_B$  as  $\beta$  is increased beyond a point are possible reasons why this is taking place. When the stochasticity of  $T_{bi}$  is muted and set to fixed quantities as in [Figure 3](#), we see that the peak shifts to the constant value that  $T_{bi}$  is set. For higher values of the constants, it means the charging time for each firefly is higher. Thus, for the group as a whole, the variance

in the distribution is much higher than when the constants are smaller, like when they are fixed at 5, where the peak is sharp at that point.

From the experiments where the distribution of  $T_{bi}$  is changed, the group  $T_B$  distribution, at high values of  $\beta$  almost perfectly mirrors the changes to the  $T_{bi}$  distribution. This verifies the claim from the theoretical model that the peak of the final distribution occurs at the minimum value of  $T_{bi}$ . This behavior is replicated when the input distribution is scaled by different constants, and the peak of the final  $T_B$  of the group also gets scaled by the same constant. This reiterates that the computational model is well in line with the theoretical model. The introduction of the adjacency matrix is essentially an additional tuning parameter that can be used to fit the model with the experimental data. Mathematically, a matrix brings with it  $N^2$  parameters that can be tuned - whereas the original model that we have been working with only has the one parameter  $\beta$  to be tuned. But, a hypothesis such as the one elaborated in the previous section, where  $\beta$  is set to a constant, and the adjacency matrix is computed based on the distance between pairs of fireflies being lesser than or greater than a threshold value, reduces the possibility of over-fitting, while at the same time proposing a biologically plausible interpretation.

Integrate- and-fire models are extremely popular in the field of neuroscience- thus studying the behavior of a modified integrate and fire model, which has a stochastic element, could prove to be very useful in modelling groups of neurons. Since, in this model, the individual agents(fireflies) are assumed to be intrinsically aperiodic, but the final behavior of the group, still displays periodic behavior, this phenomenon can be used to model synchronisation between neurons, despite individual neurons not being periodic. Spiking neural networks are used extensively to model different neuroscientific phenomena, such as working memory, oscillations in motor neurons etc. By using these modified stochastic integrate and fire models, it might be possible to describe such phenomena even better. A recent paper published fills in the gap of nonlinear reset of membrane voltage that is missing from neural field theories from Ocker (2023). This could further produce a link between the model used here and neuroscience, as stochasticity was used in the aforementioned paper to describe the non-linear spike discharge.

## Conclusions

In conclusion, we simulated the computational model described in Sarfati et al. (2023) and statistically compared the distribution of  $T_B$  of the group with the experimental data. Using this we obtained the optimal values of  $\beta$  for every value of  $N$ . Then, we modified the model to study the behavior of the distribution of the group  $T_B$  when that of the individual fireflies  $T_{bi}$  are altered. The resulting behavior of the distribution match with the theoretical predictions, and verified the dependence of the group  $T_B$  distribution on the individual distributions. Finally, we reduced the assumption from the original model, that every firefly is uniformly coupled with every other firefly, and instead simulated the model for different values of threshold distances that generated different adjacency matrices. We claim that there could be a fixed threshold distance, in the real world, that would affect the coupling strength  $\beta$  between fireflies to be uniform, irrespective of the number of fireflies in the swarm, and from our analysis, we found that this distance was 6 units.

## Contributions

Eric: Worked on the theory of the model looking into the evolution of research in fireflies as well as potential further research into stochastic integrate-and-fire models. Also worked on changing

the coupling between fireflies and coded the adjacency matrix used for part of the research.

Peter: Focused on debugging and configuring the code provided from the GitHub repository that was used to recreate the simulations. Also adjusted the code to allow us to run the simulations where we adjusted the model. Lastly, was in charge of running the simulations (30+ hours of compute time) and generating the plots from the simulated data.

Krithikesh: Worked on creating a simplified code to alter the parameters and study their effects on the final distribution. Helped design the different tests that could be run to demonstrate the properties of the model, interpret the results and hypothesise on further improvements to the model.

## Materials Availability Statement

The data and code that support the findings of this study are openly available in the GitHub repository found at <https://github.com/PeterKinder/APPM5370>.

## References

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