

Slime Mold Team 1 Project Report

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1 Introduction

The *Physarum Polycephalum*, or true slime mold, is a large multi-nuclear cell which uses a network of tube-like structures called *pseudopodia* to connect food sources and ensure its survival. Much study has been done on the behavior and formation of the *pseudopodia*, with a special focus on the tendency to choose an efficient path between the food sources [1, 2, 4, 6, 9, 10, 12, 13]. When food is placed upon the slime mold, the organism will begin to send waves caused by biochemical oscillators throughout its plasmodium [4, 9, 10]. Through this process, *pseudopodia* perpendicular to the waves decay; those parallel are reinforced. It is believed that these biochemical waves play an integral part in the creation of an efficient path [9]. The exact connection, however, between the behavior and the biology of the *Physarum Polycephalum* is still unclear

There are two stages of development in the slime mold colony. The first stage is known as the searching or discovery. In this first and crucial growth stage, the primary goal of the *Physarum Polycephalum* is to find any and all food sources present in the region. Once food sources are discovered the second stage of growth begins. In this second stage of growth, the slime mold determines what tubes it will use to transport the nutrients throughout the organism. The purpose of our research is to construct a mathematical model that describes the formation of the tube networks within the plasmodium during the second stage of growth and development. We also aim to connect our model with the biology of the organism, resulting in a model which will further scientific and mathematical understanding of the *Physarum Polycephalum*.

While all of the mechanisms that drive the pattern of their formation are not entirely understood, much is known about the *pseudopodia* themselves: that the flux of protoplasmic sol through the *pseudopodia* plays an important role in their formation and reinforcement; that chemical oscillations drive the flux of the sol by changing hydrostatic pressure; that these chemical oscillations are stimulated by external factors, including food; that the source of the oscillations rotates between food sources [2, 4, 10, 11]. When considering the pattern of tubule formation, the bulk of research has focused upon the minimization of FT/TL : the ratio of the fault tolerance, the ability to withstand accidental disconnections of the tubes in the formation, to the total length of the tubes in the formation [12, 14]. Some researchers found that common *pseudopodia* patterns formed when this ratio was minimized include the

Steiner Minimum Tree, a Cycle formation that connects the outer edges of the food source formation, and a combination of the two [14].

A large problem with this global approach to modeling, however, is that it ignores the biology of the *Physarum Polycephalum*. While a minimized ratio of FT/TL may accurately describe the patterns that form, the slime mold does not grow with this final pattern in mind. Rather, it sends out chemical waves detecting potential food sources and then attempts to connect them to the rest of the organism in the most energy-efficient manner possible. Therefore, consideration of the local behavior of the *Physarum Polycephalum* is key to accurately predicting its behavior.

Intracellular communication plays a key role in network formation on the local level in the *Physarum Polycephalum*. Past research has focused upon three possible mechanisms of intracellular communication: electrical, chemical, and mechanical [5]. Long-range interaction via electrical potential has been shown to be unlikely in the plasmodium because the membrane potential decays within a short distance [5, 8]. The diffusion of chemical signals is also improbable because of the relatively large size of the organism [6]. It has been found, however, that active streaming of the protoplasm plays an important role in signal transduction, so mechanical communication is the most likely method of communication within the *Physarum Polycephalum* [3, 6]. While chemical communication does occur within the slime mold, mechanical communication is likely the primary method of communication within the cell.

The *Physarum Polycephalum*'s plasmodium consists of two layers, the outer gel (ectoplasm) and the inner sol (endoplasm), and a large volume of protoplasm which flows within the inner sol. Contractile actomyosin filaments line the interface between the two layers and produce mechanical oscillations, alternating waves of contraction and relaxation on the surface of the plasmodium [3, 6, 7]. This rhythmic contraction exerts pressure on the protoplasmic sol, causing it to flow through the tubes and out to other parts of the plasmodium [6]. The protoplasm streams rhythmically back and forth through the network of *pseudopodia*, driven by changes in hydrostatic pressure and distributing nutrients throughout the organism [2, 3]. The contractile activity is regulated by chemical oscillations based on a complex biochemical network [6]. The flux of this protoplasmic sol through the *pseudopodia* plays an important role in tubule formation [2, 4].

The movement of the entire *Physarum Polycephalum* is driven by a different mechanism than the protoplasm. The pressure that moves the protoplasm via chemical oscillations cannot move the external membrane itself [3]. The primary biochemical oscillators distributed in the plasmodium have the ability to oscillate independently of mechanical processes, so the plasmodium is treated as a system of coupled nonlinear oscillators, with each small piece tending to oscillate at a frequency determined by the local energy input and feedback conditions, as opposed to a fixed resonance [3, 6]. In the absence of external stimuli, the movement of the external membrane of the *Physarum Polycephalum* begins in a random direction. The slime mold extends like a sheet at the "frontal part" and intricate networks of veins develop toward the rear [5]. If at any point the *Physarum Polycephalum* senses food, the frequency

of the chemical oscillations increases [3]. Since the chemical oscillations are coupled with the mechanical oscillations, those increase as well, causing an increase in the thickness of the plasmodium [3, 6]. This also results in an increase in pressure on the protoplasmic sol, increasing the flux [3]. The plasmodium flows faster through a thicker *pseudopodia*, so we assert that when choosing among multiple paths the plasmodium migrates toward the site of increased flux.

The problem of efficient slime mold food distribution networks should be important not only to the organism and its researchers, but also to anyone who desires to create an efficient distribution network. Whether it is telephones, roads, or even bloodflow in the human body, the most efficient use of resources is critical in today's world.

Our research will further the understanding of the behavior of the slime mold *Physarum Polycephalum*. We will be studying the effect of food allocation on the choice of a network, as well as the manner in which the network is chosen.

2 Modeling the behavior of the *Physarum Polycephalum*

Our model of the behavior of the *Physarum Polycephalum* has undergone many changes throughout our research as we continually increased our understanding of the biology of the slime mold.

One thing that has not changed throughout our research is our underlying assumptions. We hold light, temperature, moisture, and other environmental variables constant. We also hold the amount of food placed at each node constant, assuming that a uniform mixture of oat flakes was used. The outcome of our lab experiments with uniform oat flake mixtures was similar to the outcome using solid oat flakes, so we feel that this is a valid assumption to make that will simplify our model. Our lab experiments also indicated that the placement of the slime mold culture does not play a crucial part in the path formation, so we do not take this variable into account in any of our models.

Our first model showed us the impracticality of a global approach. It consisted of the dimensionless ratio $SMT * FT/TL$, where SMT is the length of the Steiner Minimum Tree for that food formation, FT the probability that the network will not fragment if accidental disconnects occur at random places along the tubes, and TL the total length of the tubes in the formation [12, 14].

The tubule formation that maximized this relationship had the highest probability of forming. We added SMT to the ratio FT/TL in order to make TL dimensionless; FT was already dimensionless since it is a probability. Our hypothesis was that a network that has a high fault tolerance and low total length will be the most likely to form, so we wanted to maximize that ratio. We planned to include a probability factor that took into account the distance between two specific nodes in relation to the distance between all of the nodes.

We would have used this probability in combination with the ratio $SMT * FT/TL$ and other additions to our model to accurately predict the network formation of the *Physarum Polycephalum*. However, we found that this global model only described the outcome of the slime mold’s behavior and not the impetus behind its behavior. Therefore we abandoned it for a local model that focuses upon the reasons behind the tubule formations rather than focus solely upon the tubule formations themselves.

Our second mathematical model taught us that we should question our references, even if they are published in prestigious journals. This was a hard lesson to learn, and we wasted a lot of time attempting to use an equation presented by Kobayashi et al in [6] to measure pressure. The model itself was based on the flux equation using Poiseuille’s flow [2]. The equation is as follows:

$$Q_{ij} = \frac{D_{ij}}{L_{ij}}(p_i - p_j) \quad (1)$$

Q_{ij} is the flux through the *pseudopodia* M_{ij} connecting the nodes N_i to N_j assuming Poiseuille flow. p_i is the pressure at node N_i . L_i is the length of M_{ij} and D_{ij} is the conductivity. In order to make this equation dimensionless, we have made the units of the conductivity D_{ij} be $\frac{m}{kPa}$. The length, which is inversely proportional to the flux, is a distance, typically meters. The pressure, directly proportional to the flux, is measured in kilo-Pascals. This makes the units of our model as follows:

$$Q_{ij} = \frac{\frac{m}{kPa}}{m} * kPa = Q_{ij} = 1 \quad (2)$$

Therefore our model for flux is dimensionless and we were going to use it to determine the route that the *Physarum Polycephalum* will choose based on the hydrostatic pressure at each food node. We argued that the tube for which flux is the greatest is the tube that will remain in the steady-state structure of the tube network.

The calculation of pressure at small timesteps is impossible using the limited technology available to us, so we looked to outside sources for another way to calculate the pressure. That is when we attempted to use a set of equations by Kobayashi et al from [6]. It contains many unmeasurable variables, so we used the values for them that Kobayashi et al did. This resulted in an equation that depended solely on the placement of the food sources and the difference in pressure used in the flux would be dependent upon the relative position of the nodes from the center of the petri dish.

When we tested our experimental model on our lab experiments, we found many problems with this model. The most critical problem was that it could not be used to decide which of several paths connecting two nodes would be used in the steady-state of the *Physarum Polycephalum*. This came about because the model depended solely upon the position of the nodes, and the values for many of the variables used by Kobayashi et al in [6] were chosen to fit the data rather than the biology. The result was a pressure difference of 0, which we knew was incorrect. Therefore, we abandoned this set of equations and moved onto a new

calculation of pressure.

3 An Electrostatic Approach

After the failure of our first two models, we turned to a new approach, keeping in mind the problem of calculating a pressure field. Because we are investigating the relative positions of network tubes in *Physarum Polycephalum*, we opted to deal with the gradient of the pressure field, ∇P (a vector quantity) as opposed to the field itself (a scalar quantity). We propose a model that directly relates the gradient of the pressure with the gradient of electric potential in electrostatics as a means of approximating an initial network structure.

From the outset we considered the difficulty in experimental measurement of a pressure field. We opted instead to make certain assumptions about the nature of the pressure field and then test the results of those assumptions qualitatively against our findings in the lab.

In open conditions, fluid pressure can be approximated as the pressure in static conditions, so at a given point, we're dealing with hydraulic head at that point. The gradient then, is the vector gradient between hydraulic head measurements.

We consider each food source as a source of hydrostatic pressure. Further, add an equation for the conservation of mass each food source, and state that the pressure drops off as $\frac{1}{r}$, where r is the distance from the source. The gradient of the pressure is a vector field that points in the direction of the greatest rate of increase of the scalar pressure field, and whose magnitude is the greatest rate of change. Since pressure is falling off as a function of distance, we must use the negative gradient.

In electrostatics, the electric potential is a scalar field which also falls off as $\frac{1}{r}$. Its negative gradient is the electric field.

$$\mathbf{E} = -\nabla V \tag{3}$$

If we regard each food source as a point charge, we can look at the electric field for a given point charge distribution and draw conclusions about the analogous negative gradient of the pressure field for the same configuration of food sources.

The underlying argument here is that tube formation in *Physarum Polycephalum* will occur along the paths of the greatest difference in pressure, i.e. tubes will form along the lines of the vector field T where

$$\mathbf{T} = -\nabla P \tag{4}$$

where P is the pressure field.

The constant of proportionality in front of the $\frac{1}{r}$ dependence of both V and P is relative

to the values assigned to the nodes. For this reason we ignore the fact that the constants in each case won't be the same when we look at the field lines produced by a given point charge distribution. The constant of proportionality for electric potential is huge, but that is because point charges are on the order of 10^{-19} Coulombs.

The complication arises that with a distribution of point charges, we know (ideally) the charge of each point and therefore know which are sources and which are sinks. This is not the case given the same configuration of food sources. To remedy this, we must also assume that the pressure at each node depends on that node's nutritional value. We know that the nutritional value of each food source will decrease with increasing time. As a food source becomes less valuable, its resultant chemical oscillations in the plasmodium will decrease in amplitude [3]. Therefore, we also wish to implement a time-dependence. We make the assumption that this relationship is linear, though it may be worthwhile to investigate other non-linear relationships between node value and time. To keep things non-dimensionalized, we assign to each node a value of 1. If we assume that a food source is depleted after two days, we have:

$$P(t) = \begin{cases} 1 - \frac{t}{48} & t \in [0, 48] \\ 0 & \text{otherwise} \end{cases} \quad (5)$$

Where t is time in hours. As a method of assigning "charges" to each node, we first average the values of all nodes recognized by the slime mold. We then subtract this mean from each initial value. The resultant values are used as the "charge" of each node, which puts us in a position to calculate the vector gradient field between the nodes.

Biologically, the protoplasm extends like a sheet at the frontal part and intricate networks of veins develop toward the rear [5]. For simplicity in our model, we therefore assume that the plasmodium proceeds in a direction originating from the latest node it has encountered.

The locomotion of the plasmodia is by migration of up to 1 centimeter per hour, even under conditions of starvation for many days [15]. This motion is random without external stimuli [3]. For simplicity, we take migration speed as constant at $1 \frac{cm}{hr}$ as well as simply picking an initial direction.

4 Competition 4

4.1 Results for Team A

Figure 1 shows the formation chosen by Team A for the latest competition. Figure 2 shows the distance measurement between each node. We derived our pixel to centimeter conversion by the fact that the petri dish is 10 cm in diameter. Note that the slime mold was started at the bottom most point of the formation. We took this as its initial position.

The first movement was chosen to be from the initial point to the closest node when traveling

up and to the right. Figure 3 shows the values of the two nodes as well as the gradient field lines that result. The blue node is the starting point and the red node is the new food source. Note the positive value of the new node after the subtraction of the mean and the negative value of the starting node. The new food has become the “source” feeding into the “sink” that is the old node. We highlighted the expected path in Figure 4. It is simply the shortest of the field lines connecting the nodes.

Figure 5 shows the next movement as well as the values of each node and the resultant field. Movement is again up and to the right. Figure 6 shows the expected path between the newest node and the two previous nodes. Note that once again, subtraction of the mean has resulted in a positive value for the newest node and negative values for the first two nodes. Also note more negative value of the initial node leading to more field lines coming in from the new node. It’s value is more negative because consumption has taken place over a longer period of time.

Figure 7 shows the third movement as well as the values of each node and the resultant field. Movement is now to the left. Figure 8 shows the expected paths between the new node and the three previous. Notice that in this case, not enough time has elapsed to make the value of the last node negative. For this reason, the newest node does not form a path to last node, the former instead feeds into the first two nodes. Notice that the field line from the new node to the starting point passes through the location of the final node, and will thus be interrupted before reaching the original node.

Figure 9 shows the movement to the final node. Figure 10 shows the expected paths along the shortest field lines. The last node has again not yet become negative, but the top right node now has. From this, we see that the top left node feeds into the top right, while the newest node creates paths to the first two.

Figure 11 shows all of the path contributions from the individual steps as well as arrows indicating the direction of movement in each step, beginning with the bottom-most point. Figure 12 shows the network structure observed in the late stages of development of Team A’s competition colony. Paths resembling the results obtained from our model are highlighted. Notice that the junction of tubes between the four uppermost food sources is shifted up and to the left in the real colony, whereas our results indicate a junction closer to food source number 2. It seems that in the actual colony, much of the slime mold has migrated to this junction.

4.2 Results for Team Alpha

Figure 13 shows the formation chosen by Team Alpha for the latest competition. Figure 14 shows the distance measurement between each node. We derived our pixel to centimeter conversion by the fact that each box on the graph paper is one quarter of an inch and that there are 2.54 cm per inch.

We took the center node as the starting point for the slime. We picked the initial movement to be down and to the left.

Figure 15 shows the values of the two nodes as well as the gradient field lines that result. The blue node is the starting point (i.e. the center node in the overall formation) and the red node is the new food source (the bottom left node).

Once again note the positive value of the new node after the subtraction of the mean and the negative value of the starting node. The new food has become the “source” feeding into the “sink” that is the old node. We highlighted the expected path in Figure 16. It is simply the shortest of the field lines connecting the nodes.

We took the next movement to be directly to the right. Figure 17 shows the values of the three nodes as well as the gradient field lines that result. The new food represented by the bottom right node has now become the lone “source” feeding into the two old nodes.

In Figure 18 we’ve highlighted the expected path.

Figure 19 shows the result of movement to the final node. Here we see that that time interval elapsed is not sufficient to give the previous node a negative value. When we look at Figure 20 we see that, indeed, a path will tend not to form between the top and the bottom right nodes.

Figure 21 shows the combination of all the paths obtained in the individual steps. Figure 22 is a mirror image of the paths obtained. This network would result if the direction of motion was the mirror image of the one we chose.

Finally, Figure 23 shows the network structure observed in the late stages of development of Team Alpha’s competition colony. Paths resembling the results obtained from our model are highlighted. This bears striking resemblance to the network structure predicted when the path taken is the mirror image of the path outlined in the steps above (Figure 22).

5 Summary and Conclusions

We are attempting to model the tubular network formation of the *Physarum Polycephalum*. The literature and lab experiments have given us a fair grasp on what processes are taking place on the biological level when the plasmodium discovers a food source. Our primary concern is to mathematically determine how the slime mold decides which tubes to keep and which tubes to destroy in the determination of the steady-state network structure.

The model that we have at this point has evolved from a global approach to a local approach, and was driven by the outcomes of multiple lab experiments. The biggest difficulty that we encountered in the creation of our model was the determination of the difference in

pressure between each of the food sources. Our current model predicts the final formation of the tube network using an electrostatic analogy. With this electrostatic field implemented into the flux equation we have been able to very accurately determine what tubes the slime mold will choose to most efficiently transport nutrients.

Our mode is a promising approach to approximating network formations in slime mold. It is a new approach that our research indicates has never been done before. Finally, it relies on the biology of the slime mold but is not handicapped by the lack of clear understanding of all of the biological mechanisms on the microscopic level.

Our model does present some weaknesses as well. One is that the calculations are not automated, but rather must be done tediously by hand. This increases the possibility of human error and decreases the number of trials we are able to run. Another problem is that the model unrealistically stops after all food sources have been found. Since the slime mold does not know how many food sources we placed on the agar, it will continue searching after it finds the last one. A third problem is that we choose the initial direction of motion to be towards a food source, which is also not realistic. The initial direction of motion is random, but we were unable to find a suitable way to integrate that fact into our model. These last two weaknesses may explain why smaller tubes in the actual culture are seen to connect the main tubes that our model predicts.

6 Future Work

Since our model is new and groundbreaking, there are many possible directions in which that future researchers can go.

Further study can be with regard to non-linear time dependence on the decay of the value of hydrostatic pressure at a given food source as well as investigation into the possible paths that the slime could take in order to reach all food sources.

7 Appendix A: Procedure for application of electrostatic model

1. We measure the distance between all nodes. The distance is measured in pixels and then converted to cm .
2. We pick a starting point and an initial direction.
3. We then calculate the time it takes to reach the next node based on the distance between the nodes and a migration velocity of $1\frac{cm}{hr}$.

4. This time interval, t_1 , is then used to calculate the decreased value of the first node (whose initial value was 1, as stated in the section above)
5. The values of the first two nodes are averaged. The mean is subtracted from each initial value. These new values are used as the “charge” values to calculate the gradient field.
6. We then pick a new direction and again calculate the time it takes for the slime to travel from the last node to the new node, calling this time t_2 . We use both time intervals in the calculation of $P(t)$. The first node will have a value given by $P(t_1 + t_2)$, the second will have a value $P(t_2)$, and the new node will simply be 1.
7. These three values are again averaged, the mean subtracted from the values, and the result used as the “charge” of each node. We then calculate the gradient field again.
8. This process is repeated until all nodes have been reached.

8 Appendix B: Figures

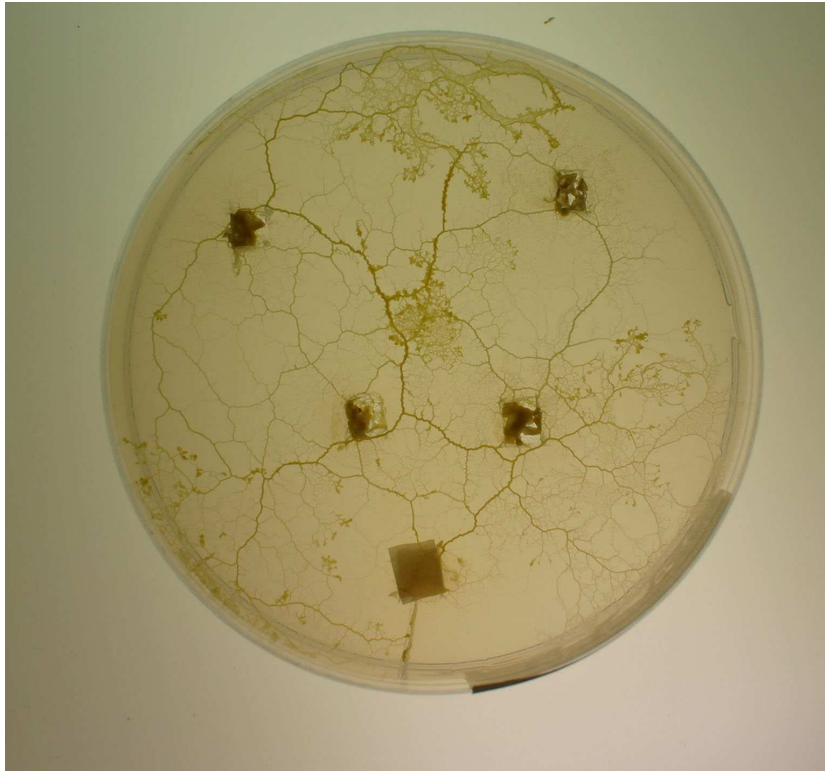


Figure 1: Team A's competition formation

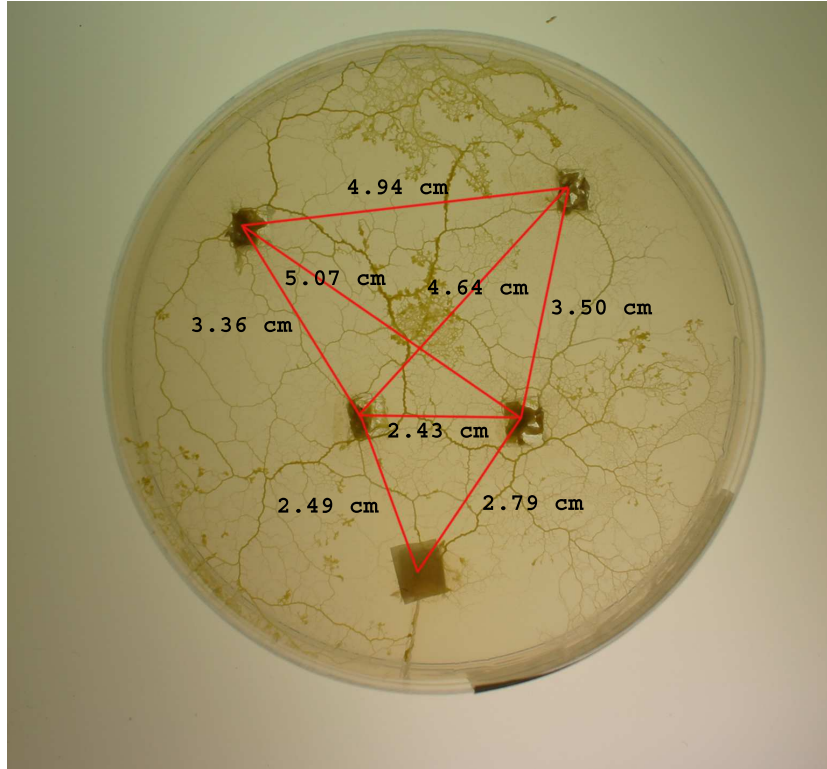


Figure 2: Length scale between each node.

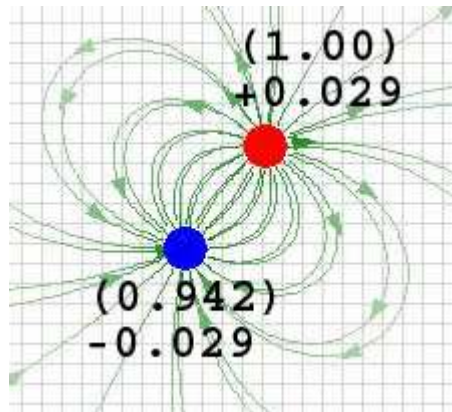


Figure 3: The first movement we chose for Team A's formation as well as the values of each node and the calculated gradient field. The values before the subtraction of the mean are given in parentheses.

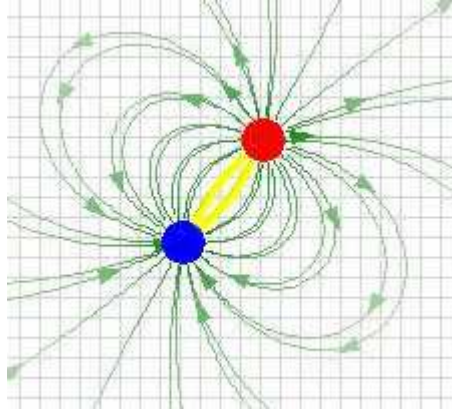


Figure 4: The first movement we chose for Team A's formation as well as the expected path between the nodes. This path is simply the shortest of the field lines connecting the two nodes.

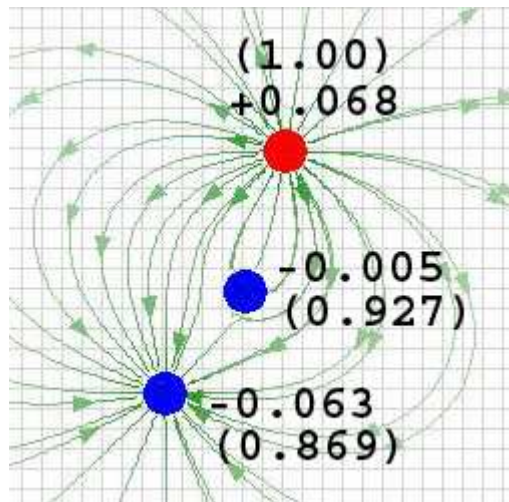


Figure 5: The second movement we chose for Team A's formation as well as the values of each node and the calculated gradient field. The values before the subtraction of the mean are given in parentheses.

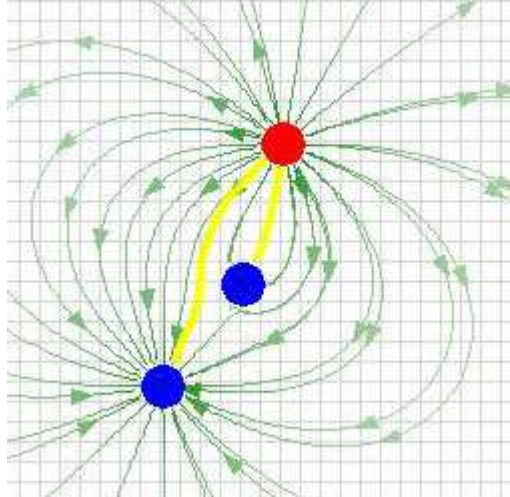


Figure 6: The second movement we chose for Team A's formation as well as the expected path between the nodes. This path is simply the shortest of the field lines connecting the two nodes.

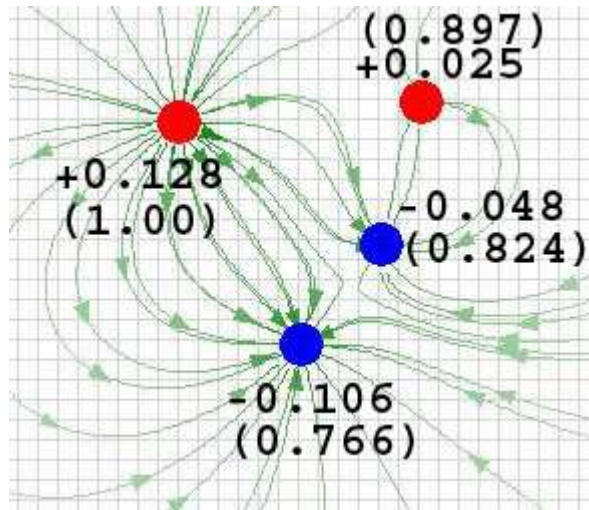


Figure 7: The third movement we chose for Team A's formation as well as the values of each node and the calculated gradient field. The values before the subtraction of the mean are given in parentheses.

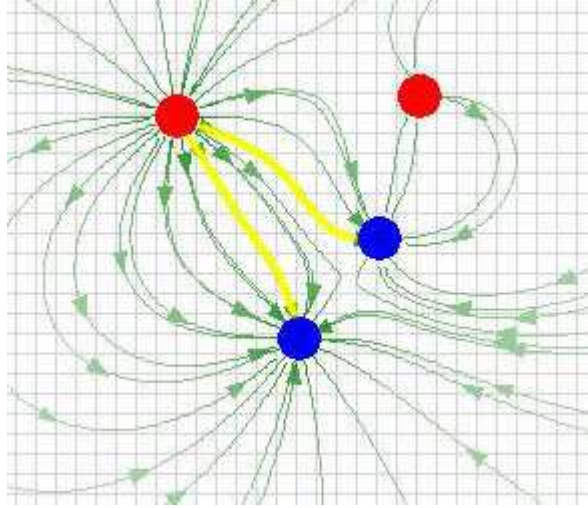


Figure 8: The third movement we chose for Team A's formation as well as the expected path between the nodes. This path is simply the shortest of the field lines connecting the two nodes.

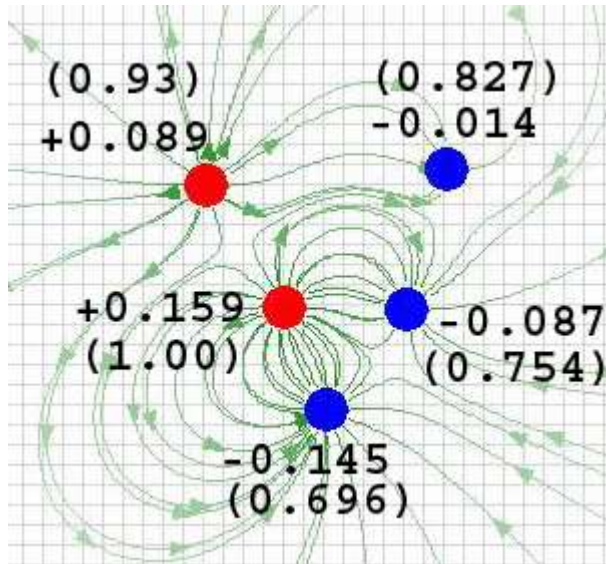


Figure 9: The final movement for Team A's formation as well as the values of each node and the calculated gradient field. The values before the subtraction of the mean are given in parentheses.

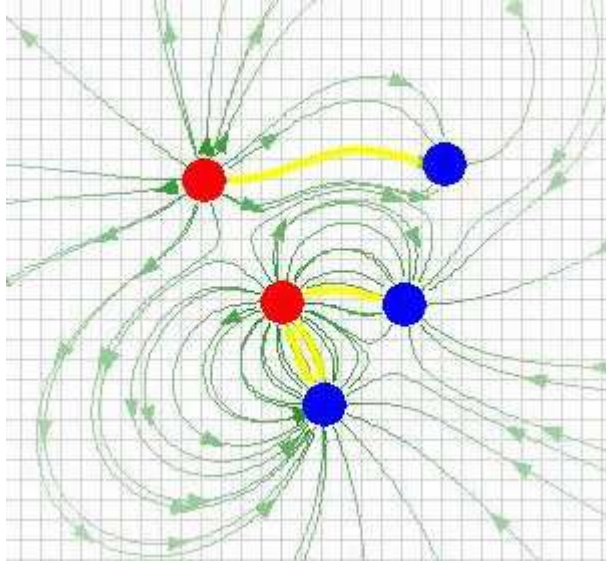


Figure 10: The final movement for Team A's formation as well as the expected path between the nodes. This path is simply the shortest of the field lines connecting the two nodes.

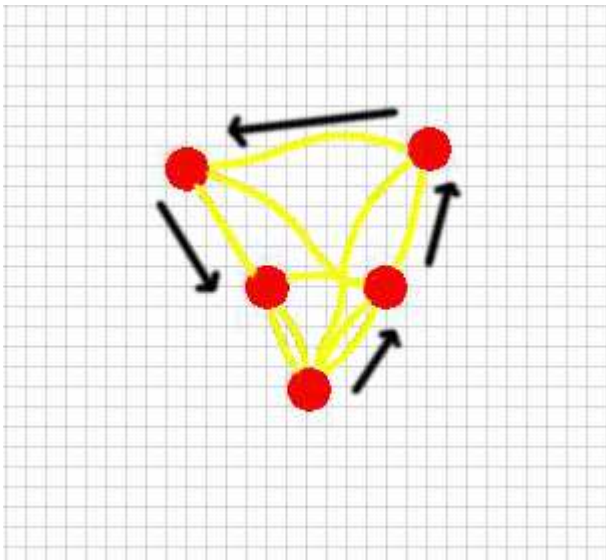


Figure 11: All of the path contributions from the individual steps. The black arrows indicate the directions of motion in order beginning with the bottom-most point.

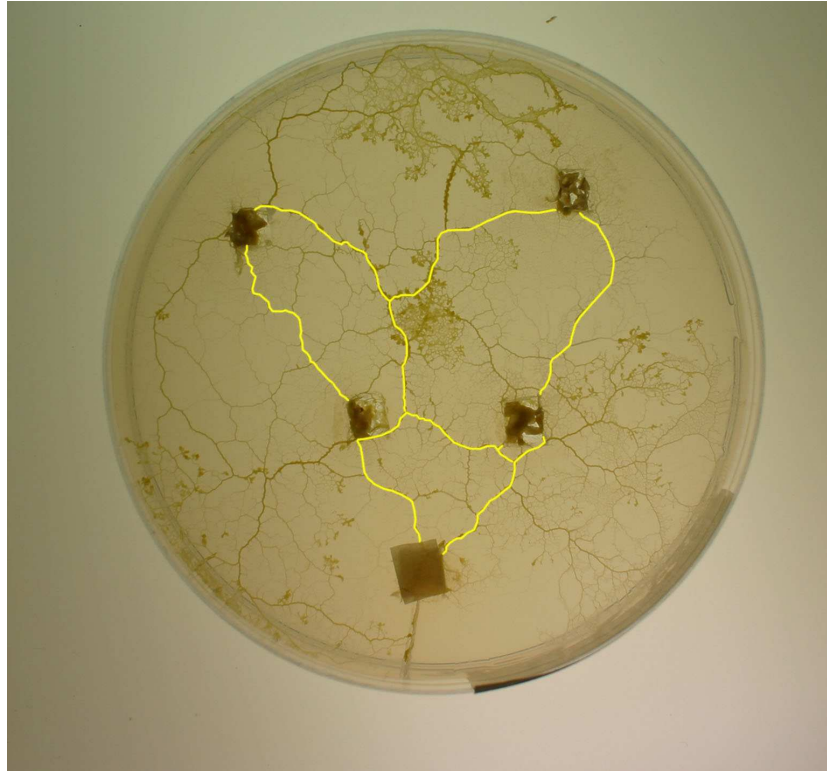


Figure 12: A comparison with the network structure observed in the late stages of development of Team A's competition colony.

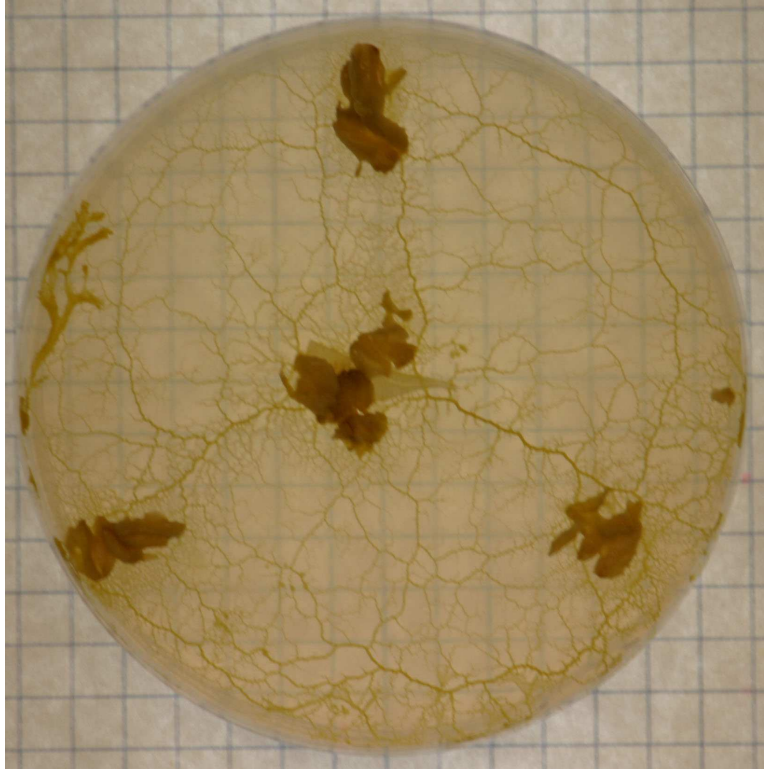


Figure 13: Team Alpha's competition formation.

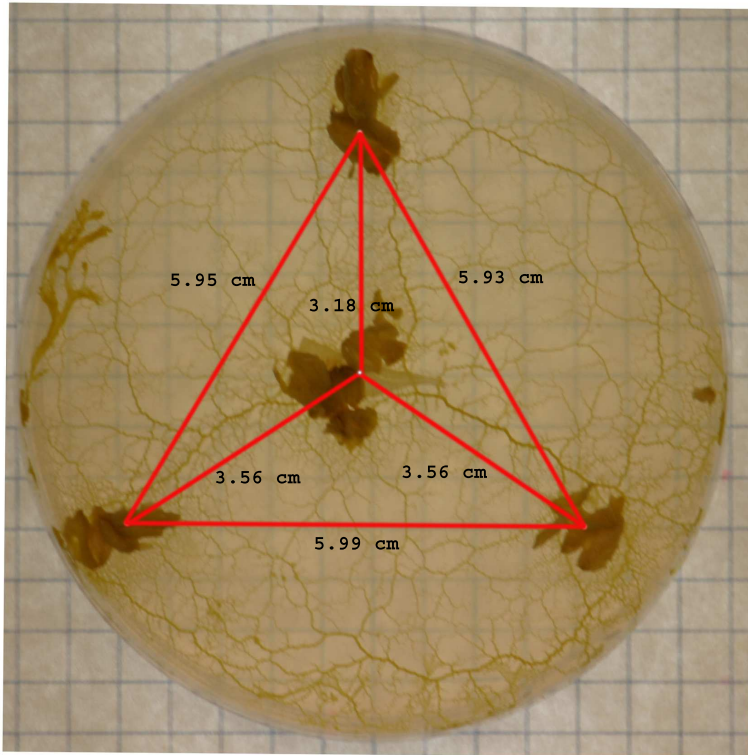


Figure 14: Length scale between each node.

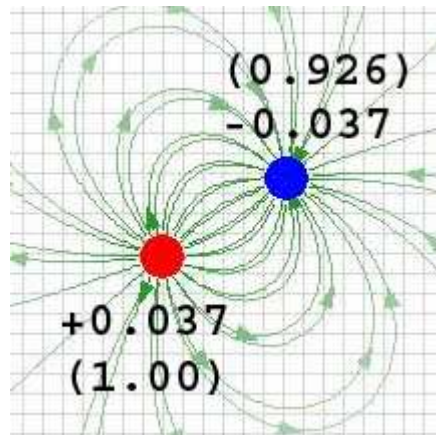


Figure 15: The first movement we chose for Team Alpha's formation as well as the values of each node and the calculated gradient field. The values before the subtraction of the mean are given in parentheses.

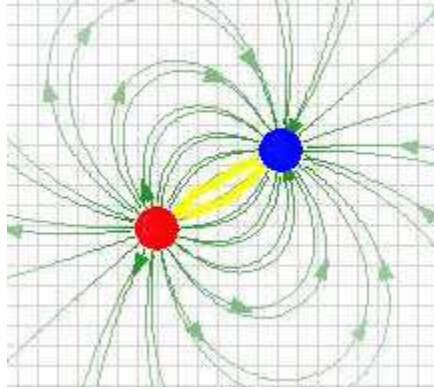


Figure 16: The first movement we chose for Team Alpha's formation as well as the expected path between the nodes. This path is simply the shortest of the field lines connecting the two nodes.

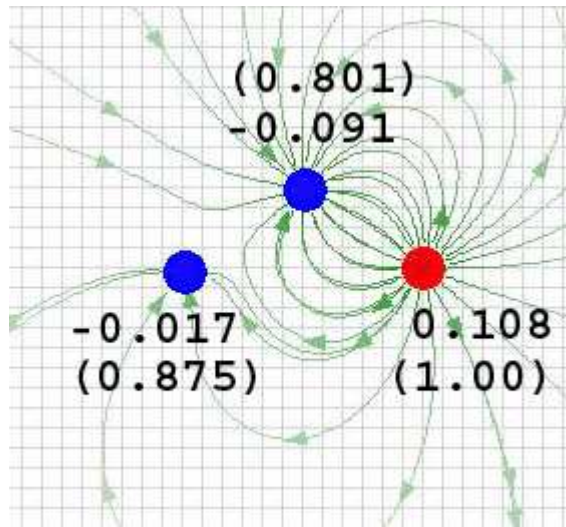


Figure 17: The second movement we chose for Team Alpha's formation as well as the values of each node and the calculated gradient field. The values before the subtraction of the mean are given in parentheses.

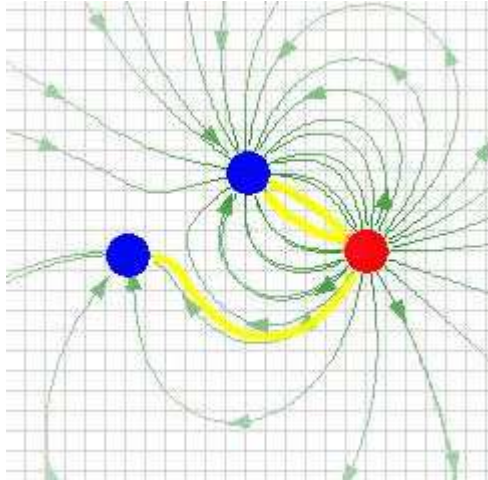


Figure 18: The second movement we chose for Team Alpha’s formation as well as the expected path between the nodes. This path is simply the shortest of the field lines connecting the two nodes.

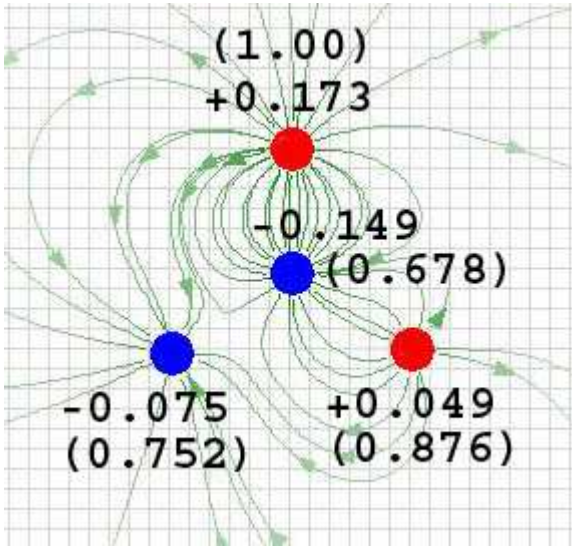


Figure 19: The final movement we chose for Team Alpha’s formation as well as the values of each node and the calculated gradient field. The values before the subtraction of the mean are given in parentheses.

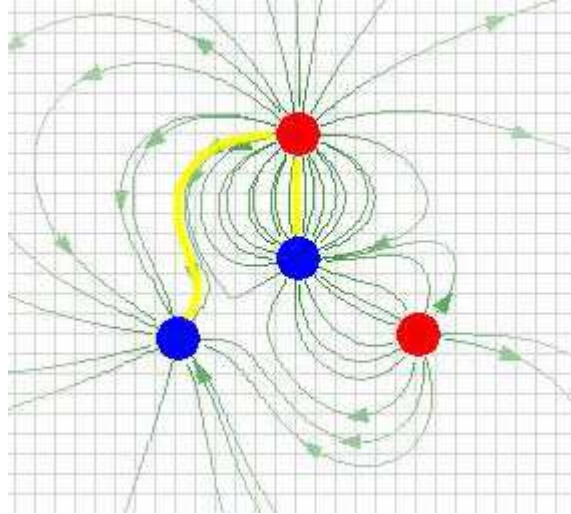


Figure 20: The final movement we chose for Team Alpha's formation as well as the expected path between the nodes. This path is simply the shortest of the field lines connecting the two nodes.

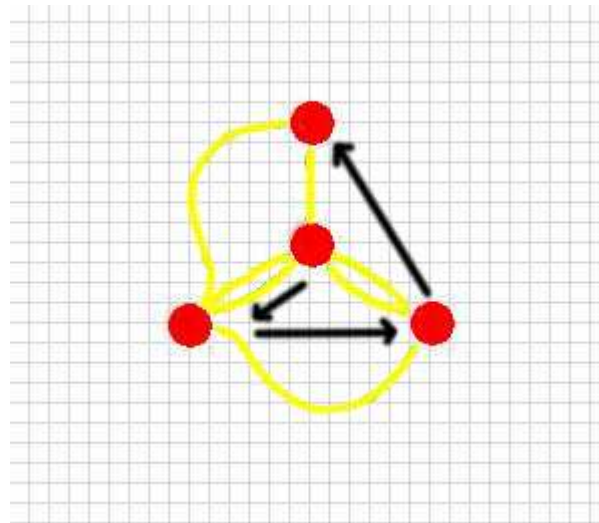


Figure 21: All of the path contributions from the individual steps. The black arrows indicate the directions of motion in order beginning with the center point.

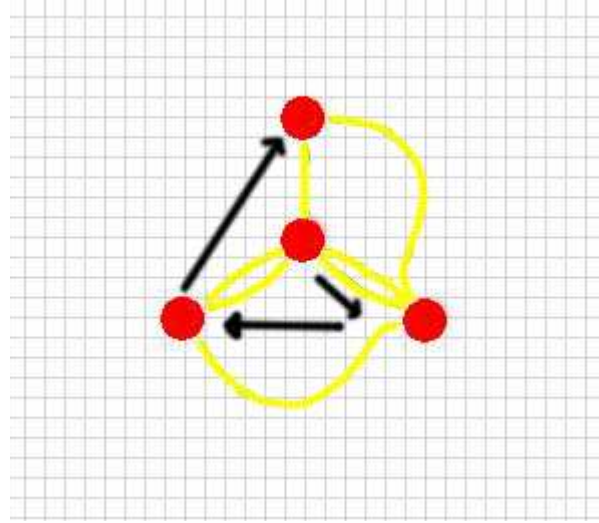


Figure 22: All of the path contributions from the individual steps of a scenario with the opposite initial direction. The black arrows indicate the directions of motion in order beginning with the center point.

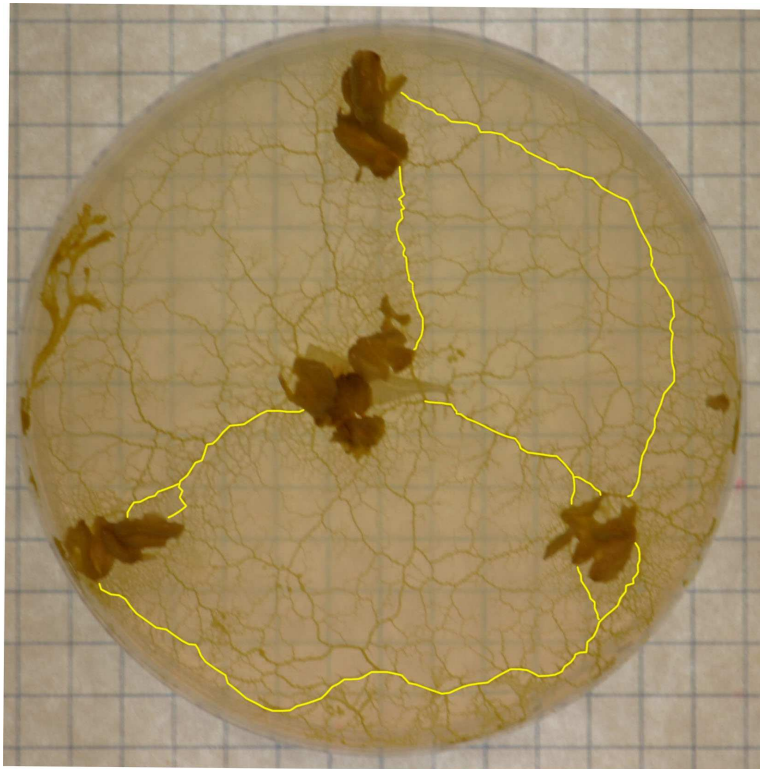


Figure 23: A comparison with the network structure observed in the late stages of development of Team Alpha's competition colony.

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