

Extraction and Investigation of Power Neurons in the *Caenorhabditis elegans* Connectome

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Abstract

Connectome analysis is the study of the brain's neurons and their connections (or synapses) to understand how brain regions communicate with each other and how the brain's structure affects its function. In recent years, researchers have reconstructed the complete connectomes of some organisms and have begun to analyze them in depth. One of the most studied connectomes is that of the nematode *Caenorhabditis elegans*, whose analysis has led to numerous discoveries. In this paper, we would like to make a contribution in this direction. In particular, by applying concepts and techniques of Complex Network Analysis, we want to test whether there are power neurons in this organism's connectome, i.e., neurons that are particularly important compared to the others. If so, we want to determine their characteristics and whether they form a backbone or not.

Keywords

Caenorhabditis elegans, Connectome, Power Neurons, Complex Network Analysis, Neuron Backbone, Brain Analysis

1. Introduction

The connectome maps all the neural connections (or synapses) in the nervous system. Its analysis reveals how the structure of the brain relates to its function, providing insight into processes like memory, learning, and attention, as well as brain behavior and its pathology. Research has linked connectome alterations to neurological disorders like autism [1], epilepsy [2, 3], Alzheimer's disease [4, 5, 6, 7], and Parkinson's disease [8, 9, 10], potentially leading to new therapies. Connectome studies are also affecting the development of advanced artificial neural networks, improving their learning and computational capabilities [11]. This vital area of research is growing rapidly so that the author of [12] clarifies that the study of connectomes allows us to reverse the usual sequence of explanation (i.e., from function to structure) to one that allows the prediction of function from structure. Connectome studies are actually divided into structural (physical connections) and functional (dynamic interactions) aspects; these

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represent to the connectome what hardware and software represent to computers. Functional connectomes are easily obtained using Magnetic Resonance Imaging; instead, reconstructing the structural connectome of the whole brain is challenging, although new methods based on advanced microscopy, positron emission tomography, and AI are emerging to accomplish this task.

Recent papers (e.g., [13, 14, 15, 16]) have shown that the distribution of neurons and their connections are neither completely random nor completely regular, suggesting that connectomes may be composed of a limited set of recurrent patterns. Examples of studies in this direction are the pioneering systematic investigations of neuronal connectivity in the nematode *Caenorhabditis elegans* (*C. elegans* for short) [17], as well as the detection of large-scale interregional pathways in the cerebral cortex of mammals, such as the rat [18], cat [19, 20, 21] and macaque monkey [22, 21].

Given the importance of connectome studies, two main lines of research are receiving much attention, namely: (i) the complete mapping of the connectome of increasingly complex organisms, and (ii) the definition of increasingly refined analyses on already known connectomes. The connectome of *C. elegans* was reconstructed as early as 1986 [13]; more recently, the complete connectome of *Ciona intestinalis* [23], *Platynereis dumerilii* [24] and *Drosophila melanogaster* at different developmental stages [25, 26, 27, 28, 29] have been made available. As for the *C. elegans* nervous system, as recently pointed out in [30], despite decades of research, the neural circuits that control its behavior are still not fully understood, and the roles of many neurons remain a mystery. The same paper reveals new circuits and functions of previously unstudied neurons.

In the meantime, the authors of [27] discovered the existence of a new type of neurons in the adult *Drosophila* connectome, which they called “rich club” neurons; they are a subset of neurons that tend to be more connected to each other than would be expected by chance alone.

The aim of this paper is to take a step forward in the analysis of the complex properties of connectome using advanced methods of Complex Network Analysis. In particular, we focus on the connectome of *C. elegans* and extend the concept of “rich club” neurons identified for *Drosophila* by considering not only degree centrality, as done in [27], but also the other three classical forms of centrality in Complex Network Analysis (i.e., closeness, betweenness, and eigenvector centralities), since each of them has very different properties and allows us to see the “strength” of a neuron from a different point of view. We call these neurons “power neurons”.

In particular, we first define the concept of power neuron and describe how to detect power neurons from the *C. elegans* connectome. We then perform several analyses, outlining the main properties of power neurons and showing that they indeed exert a strong influence on the other neurons of the connectome, forming a sort of backbone in it. In our opinion, this work serves as a first case study for defining a framework that can be applied to analyze the connectomes of increasingly complex organisms with the support of Complex Network Analysis concepts and techniques.

The outline of this paper is as follows: in Section 2, we present the dataset we used and define a complex network-based model to represent a connectome. In Section 3, we define the concept of power neuron and formulate an approach to detect power neurons from the *C. elegans* connectome. In Section 4, we characterize power neurons by discovering and describing

their main properties. Finally, in Section 5 we draw our conclusions and outline some possible future developments.

2. Dataset and connectome modeling

The data used in our research consists of the complete connectome (i.e., the set of all neurons and their connections) of *C. elegans*. This is one of the four organisms whose complete connectome is currently known (the other three are *Ciona intestinalis*, *Platynereis dumerilii*, and *Drosophila melanogaster*) and is one of the most studied in the literature. To retrieve the data for this connectome, we followed the instructions given in <https://www.wormatlas.org/neuronalwiring.html> and in [31]. Specifically, the authors provide the connectome in the form of an adjacency list. From this format we derived an adjacency matrix. With the latter structure, we were able to define the following network-based representation of the *C. elegans* connectome:

$$\mathcal{C} = \langle N, A \rangle \quad (2.1)$$

Here, N is the set of nodes of \mathcal{C} . There is a node $n_i \in N$ for each neuron in the connectome. Since there is a biunivocal correspondence between nodes and neurons, we use these two terms interchangeably in the following. A is the set of arcs of \mathcal{C} . There is an arc $(n_i, n_j) \in A$ if there is a connection from n_i to n_j . Since there is a biunivocal correspondence between arcs and connections, we use these two terms interchangeably in the following.

The brain of any organism is divided into (functional) areas, each of which groups together neurons that perform a specific function. Authors of different connectomes use different names for these functional areas; in the case of *C. elegans* they are called “ganglion groups”. In the following, however, we will use the term (functional) area because it is more abstract and more general, since it can be used for all organisms. Table 1 shows the functional areas of *C. elegans* with the corresponding description, while Table 2 shows the number of neurons for each area.

In Table 3, we report some basic measures related to the connectome network \mathcal{C} . Examining this table, we can see that the total number of neurons in *C. elegans* is small (279); the number of connections is not large (4,577), but the density is rather high compared to what occurs in other connectomes (to give an idea, the density in the connectome of *Drosophila melanogaster* is 0.0001). The average node indegree and outdegree are rather low (again, to give an idea, it is 40.25 in the connectome of *Drosophila melanogaster*). The average clustering coefficient is high, indicating a tendency for neurons to form clusters. The average path length and diameter have low values, indicating that signals originating from one neuron can quickly radiate to other neurons. Degree assortativity is essentially null, meaning that each neuron connects to other neurons regardless of whether or not they have a degree similar to its own.

3. Defining and detecting power neurons

For the definition of power neurons, we started with the results of [27], where the authors show the existence of a “rich club” of neurons in the adult *Drosophila* connectome. By the term “rich club” they mean a subset of neurons that tend to be more connected to each other than would be expected by chance alone. Using the network representation of the connectome shown in

<i>Area</i>	<i>Description</i>
anterior ganglion	It is a major integrative center that receives sensory inputs from amphid and cephalic neurons, coordinating movement and decision-making.
dorsal ganglion	It processes mechanosensory and chemosensory inputs, connecting to motor neurons to regulate head movements and responses to stimuli.
dorsorectal ganglion	It processes rectal sensory inputs and regulates waste expulsion while maintaining posterior body posture through motor neuron control.
lateral ganglion	It integrates sensory information from touch, temperature, and olfaction, relaying signals to the nerve ring for behavioral modulation.
lumbar ganglion	It is involved in reproductive behaviors, particularly in males, and integrates mechanosensory inputs from the tail to regulate movement.
posterolateral ganglion	It processes sensory signals for tail movements, withdrawal reflexes, and modulates responses related to body posture and external stimuli.
pre-anal ganglion	It coordinates rhythmic contractions involved in defecation, integrating sensory and motor signals related to posterior body functions.
retrovesicular ganglion	It relays signals between the nerve ring and ventral nerve cord, playing a crucial role in locomotion and body bending coordination.
ventral cord neuron group	It is a longitudinal network of motor neurons responsible for driving muscle contractions, enabling crawling and environmental navigation.
ventral ganglion	It contains motor neurons and interneurons that control movement, foraging, and coordinated body motions through the ventral nerve cord.

Table 1
Functional areas of *C. elegans* and their description

<i>Area</i>	<i>Number of neurons</i>
anterior ganglion	38
dorsal ganglion	6
dorsorectal ganglion	3
lateral ganglion	64
lumbar ganglion	24
posterolateral ganglion	14
pre-anal ganglion	12
retrovesicular ganglion	29
ventral cord neuron group	57
ventral ganglion	32

Table 2
Functional areas of *C. elegans* and number of their neurons

<i>Measure</i>	<i>Value</i>
Number of nodes (neurons)	279
Number of arcs (synapses)	4,577
Average node indegree	16.405
Average node outdegree	16.405
Density	0.059
Average Clustering Coefficient	0.337
Average Path Length	2.436
Diameter	5
Degree Assortativity	-0.092

Table 3
Main features of the *C. elegans* connectome

Equation 2.1, the “rich club” neurons could be defined as a set of neurons whose nodes are characterized by a high degree centrality and are connected more than would be expected by chance alone.

At this point, we thought of extending the concept of “rich club” neurons by considering not only degree centrality, but also other three classical forms of centrality in Complex Network

Analysis, since each of them has very different properties and allows us to see the “strength” of a neuron from a different point of view. Therefore, we define power neurons as those neurons whose corresponding nodes simultaneously belong to the top $X\%$ of nodes with the highest values of degree, closeness, betweenness and eigenvector centralities in the connectome network \mathcal{C} . Clearly, $X\%$ is a parameter whose value should be low and must be experimentally tuned. This definition is very strict in that it is by no means certain that a node belonging to the top $X\%$ of nodes with the highest values of one centrality will also belong to the top $X\%$ of nodes with the highest values of another centrality. For example, it is well known that in many network-modeled contexts, nodes with high values of degree centrality do not have high values of closeness centrality [32], and similar statements could be made for other centralities. Here, we even set the condition that a node must belong to the top $X\%$ of nodes with the highest values for *all* centralities. Based on the above reasoning, it can be expected that: (i) nodes with these characteristics (if they exist) will be few; (ii) nodes with these characteristics (if they exist) will be very strong.

Therefore, to see whether power neurons exist in *C. elegans*, it is necessary to study the distribution of the nodes of \mathcal{C} with respect to the four forms of centrality mentioned above. In Figure 1 we show such distributions.

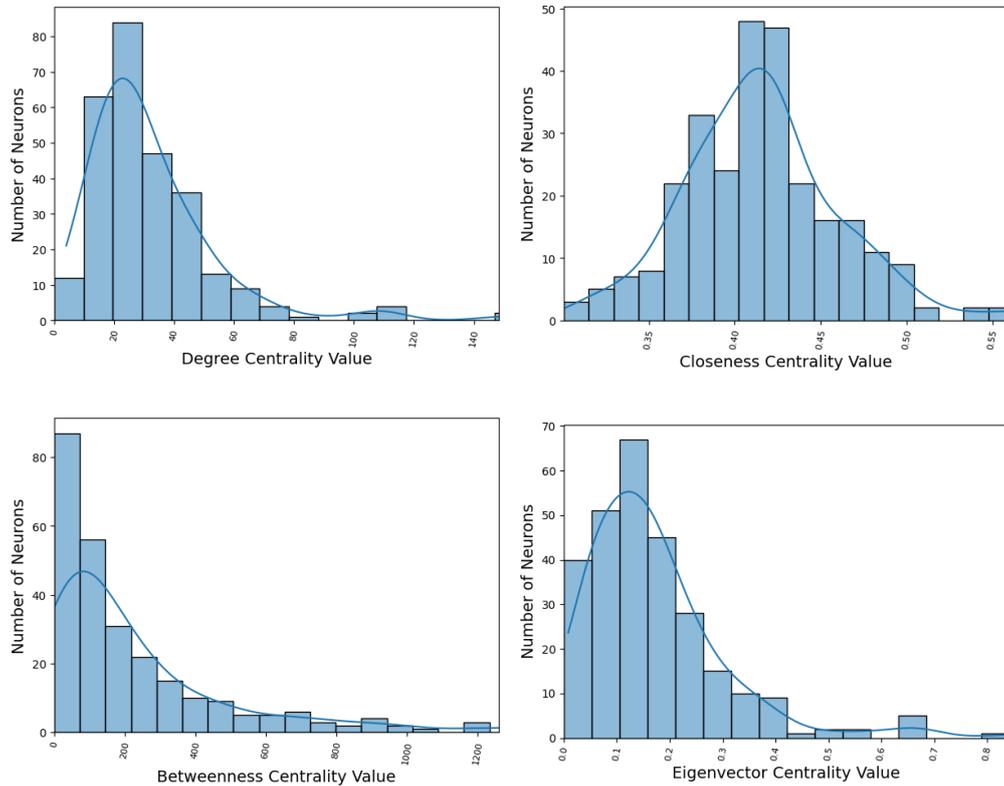


Figure 1: Distribution of the nodes of \mathcal{C} with respect to degree centrality (top-left), closeness centrality (top-right), betweenness centrality (bottom-left) and eigenvector centrality (bottom-right)

The distributions of nodes with respect to degree centrality is striking. In fact, such a distribution generally follows a power law [32] in complex networks. In this case, instead, we see an almost bell-shaped distribution, although the right side of the bell (i.e., the side with the highest degree centrality values) decays much more smoothly than the left side. The presence of the long right tail implies that there is a certain number of nodes with rather high degree centrality values. The distribution of nodes with respect to closeness centrality fully respects what is generally the case in complex networks; it is in fact a classical bell-shaped distribution [32]. The distribution of nodes with respect to betweenness centrality follows a power law, as might be expected from complex network theory [32]; that is, there are many nodes with low betweenness centrality and few nodes with high betweenness centrality. Finally, similar to degree centrality, the distribution of nodes with respect to eigenvector centrality does not reflect what would be expected from complex network theory (i.e., a power law distribution [32]). Instead, it is similar to that seen for degree centrality, with an almost bell shape and still a fairly long tail on the right side, and thus for high values of eigenvector centrality.

At this point, the question arises whether the nodes with the highest centrality values are always the same for all types of centrality, or whether they are different for each type. Complex network theory tends to rule out that they are always the same. However, we have at least two of the four distributions that differ from the standard, suggesting the need for further analysis to answer the previous question.

The first analysis to be done is to see if there are correlations between the different forms of centrality. For this purpose, the Spearman's correlation coefficient [33] can be calculated for each pair of centralities. This coefficient can take values in the real range $[-1, 1]$, where -1 (resp., 1) denotes a perfectly negative (resp., positive) correlation and 0 denotes no correlation. The results obtained are shown in Figure 2. Examining this figure, it can be seen that the Spearman's correlation coefficient is high or very high for each pair of centralities. This strengthens the hypothesis of the possible existence of nodes characterized simultaneously by high values of all four centralities.

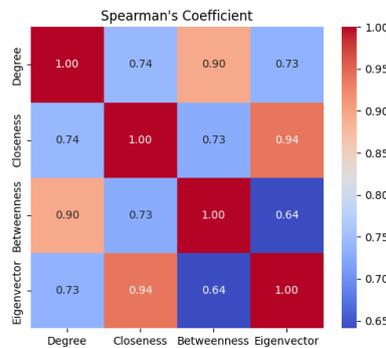


Figure 2: Values of the Spearman's correlation coefficient for each pair of centralities

At this point, as a further check, for each type of centrality, we constructed the set of the top 20% of neurons with the highest values. Then, for each pair of centralities, we calculated the intersection between the corresponding sets constructed in this way and computed the

percentage of neurons in the sets¹ that also belonged to their intersection. The results obtained are shown in Table 4. From the analysis of this table we can see that this percentage is not only significant for all pairs (which is not obvious because of what we said above about complex network theory), but is even higher than all our expectations. This allows us to say that there are certainly power neurons in the *C. elegans* connectome. The next step is to find them.

Centralities	
Degree & Closeness	78.18%
Degree & Betweenness	81.82%
Degree & Eigenvector	72.73%
Closeness & Eigenvector	85.45%
Betweenness & Closeness	72.73%
Betweenness & Eigenvector	65.45%

Table 4

Percentage of the nodes belonging to the intersection between the top 20% nodes for each pair of centralities

An essential step in finding power neurons is the tuning of X (see above). Obviously, X must be low; otherwise, the very concept of a power neuron as a neuron much more important than the others, which together with the other power neurons is able to condition the functioning of the whole connectome, would be meaningless. If the distribution of the nodes of \mathcal{C} with respect to degree, betweenness and eigenvector centralities followed a power law, the most obvious value we could think of to associate with X would be $X = 20\%$. In our case, we have seen that the distribution of nodes with respect to degree and eigenvector centralities does not follow a power law, but rather a bell shape with a long tail on the right. Intuitively, we can assume that X must be greater than 20%, although not by much. To determine what is a reasonable value of X , we calculated the percentage of common nodes for the four sets of top $X\%$ of neurons with the highest values of the four centralities as X varies. The result is shown in Figure 3.

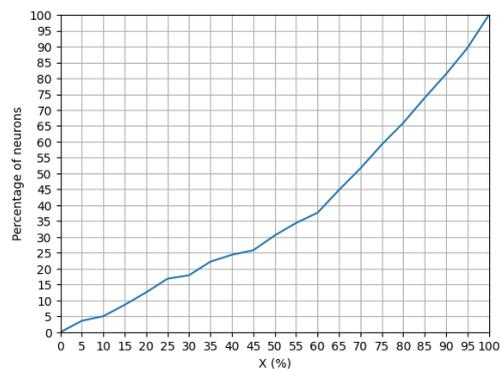


Figure 3: Percentage of the common nodes for the four sets of top $X\%$ neurons with the highest values of degree, closeness, betweenness and eigenvector centralities against X

The analysis of this figure shows that: (i) for values of X between 0% and 5%, the growth of the percentage of common nodes is high; (ii) for values of X between 5% and 10% this growth

¹Clearly, the two sets have the same number of neurons.

	<i>Number of neurons</i>	<i>Percentage neurons</i>	<i>Number of power neurons</i>	<i>Percentage of power neurons</i>
anterior ganglion	38	13.62%	0	0
dorsal ganglion	6	2.15%	0	0
dorsorectal ganglion	3	1.08%	2	4.26%
lateral ganglion	64	22.94%	25	53.19%
lumbar ganglion	24	8.60%	5	10.64%
posterolateral ganglion	14	5.02%	1	2.13%
pre-anal ganglion	12	4.30%	3	6.38%
retrovesicular ganglion	29	10.39%	8	17.02%
ventral cord neuron group	57	20.43%	0	0
ventral ganglion	32	11.47%	3	6.38%

Table 5
Number and percentage of neurons and power neurons in the connectome areas of *C. elegans*

is almost zero; (iii) for values of X between 10% and 25%, it is again high; (iv) for values of X between 25% and 30% it is almost zero; (v) beyond these values, it is again sometimes high and sometimes very low. For the reason seen above, it does not make sense to choose values of X greater than 30%; at the same time, it makes sense to choose values of X being not in the midst of a high growth, because in those cases a very small change in X would correspond to a very large change in the percentage of common nodes. Based on these considerations, the two possible values of X would be $X = 5%$, but this would result in a statistically insignificant number of power neurons (i.e., 10), or $X = 25%$. Our choice fell on the latter value.

At the end of this section, we can therefore conclude that there are power neurons in the *C. elegans* connectome, and that these correspond to the top 25% of neurons with the highest degree, closeness, betweenness and eigenvector centralities. The exact number of these neurons is 47 (i.e., 16.85% of the total number of neurons). In the next section, we will analyze some important properties that characterize them.

4. Finding the main properties of power neurons

Having found the power neurons in the *C. elegans* connectome, in this section we want to determine their most important properties. We start with some properties obtained directly by applying the semantics of centralities to the connectome. In particular, having a high degree centrality, power neurons have many connections and can thus act as hubs for other neurons. Having a high closeness centrality, they are connected to other neurons by short to medium paths; therefore, the information they transmit can reach the other connectome neurons very quickly. Having a high betweenness centrality, they are strategic nodes that can carry information between different areas of the connectome. Having a high eigenvector centrality, they are connected to other neurons with high eigenvector centrality. This allows us to hypothesize the presence of a backbone between them; later in this section we will see if this hypothesis is confirmed.

Already these properties tell us that power neurons are a small percentage of neurons that are very special, exceptionally well-connected, and influential.

In addition to these basic properties, we want to determine other properties of power neurons that will allow us to better characterize them. As a first step, we calculate the distribution of power neurons with respect to areas in *C. elegans*. Specifically, Table 5 shows the number and

percentage of neurons and power neurons for each area.

Looking at this table, we can see that the distribution of power neurons is not at all uniform across areas and does not even reflect the distribution of neurons across areas. In fact, we can see that more than half of the power neurons are located in the “lateral ganglion” area. This can be explained by the fact that this area is very important because it handles the transmission of sensory information related to touch, temperature, and olfaction to the nerve ring. The other two areas with a significant percentage of power neurons are “retrovesicular ganglion” and “lumbar ganglion”. Then, there are some areas with small percentages of power neurons, and finally three areas, namely “anterior ganglion”, “dorsal ganglion”, and “ventral cord neural group” that have no power neurons. If we look at the differences between the percentages of neurons and the percentages of power neurons in the areas, we can observe that the “lateral ganglion” area shows a very significant increase in the percentage of power neurons compared to the percentage of neurons. Other less significant increases are found for the “dorsorectal ganglion”, “lumbar ganglion”, “pre-anal ganglion”, and “retrovesicular ganglion” areas. Instead, decreases are observed for the “dorsal ganglion”, “posterolateral ganglion”, and “ventral ganglion” areas. Finally, two very significant decreases are observed for the “anterior ganglion” area and especially for the “ventral cord neuron group” area.

The next analysis is to compare the degree of all neurons and power neurons. The results are reported in Table 6. This table shows that the mean degree of power neurons is much higher than that of all neurons. This is not surprising given the definition of a power neuron. Rather, it is interesting to note that the median degree of power neurons is also significantly higher than that of all neurons. This implies that the overall degree distribution is shifted upward for power neurons. It is worth pointing out that if we multiply the mean degree of power neurons (72.72) by the number of power neurons (47), we get a total number of connections, and thus neurons directly connected to power neurons through an incoming or outgoing arc, of 3,471.84. Considering that the total number of neurons is 279, we can infer that there is a large overlap between the sets of neurons directly connected to a power neuron. Specifically, on average, each neuron is connected (via an incoming or outgoing arc) to about 12 different power neurons.

	<i>Degree</i>		<i>In-Degree</i>		<i>Out-Degree</i>	
	<i>Mean</i>	<i>Median</i>	<i>Mean</i>	<i>Median</i>	<i>Mean</i>	<i>Median</i>
All neurons	32.81	26.00	16.41	13.00	16.41	13.00
Power neurons	72.72	58.00	36.36	29.00	36.36	29.00

Table 6

Mean and median degrees of all neurons and power neurons in the connectome of *C. elegans*

We now want to see whether power neurons form a backbone, that is, whether they tend to connect more with each other than with other neurons. The possible existence of a backbone would be a very significant result, because it would lead us to say that there is a real structured organization among these nodes that allows them to strongly influence the whole *C. elegans* connectome, despite the fact that they are extremely few in number. To carry out this verification, we considered, in addition to the network \mathcal{C} associated with the connectome, the network \mathcal{P} induced by the power neurons, that is, the subnetwork of \mathcal{C} consisting only of the power neurons and the connections between them. For both networks we measured several parameters, namely

the number of nodes, the number of arcs, the average degree, the normalized average degree, the density, the average clustering coefficient, the diameter, the average shortest path, the size of the maximum connected component, and the degree assortativity. All these parameters are classical for Complex Network Analysis [32], except for the normalized average degree, which we introduce in this paper. It is defined as the ratio of the average degree to the number of nodes in the network. It is used to take into account the size of the network when evaluating the value of the average degree in different networks since the same average degree has very different implications for a very large or a very small network. Table 7 shows the parameter values obtained for networks \mathcal{C} and \mathcal{P} .

	\mathcal{C}	\mathcal{P}
Number of nodes	297	47
Number of arcs	4,577	686
Average degree	32.810	29.191
Normalized average degree	0.118	0.621
Density	0.059	0.317
Average clustering coefficient	0.337	0.444
Diameter	5	3
Average path length	2.436	1.710
Maximum connected component's size	279	47
Degree Assortativity	-0.092	-0.035

Table 7

Values of some basic parameters for networks \mathcal{C} (i.e., the complete network mapping the connectome) and \mathcal{P} (i.e., the subnetwork induced by power neurons)

This table provides us with several interesting insights. In particular, we have that:

- The density, the average clustering coefficient, and the normalized average degree in \mathcal{P} are greater than in \mathcal{C} ; all these values indicate that the power neurons have a greater propensity to connect with each other than other neurons.
- The diameter and average path length in \mathcal{P} are smaller than in \mathcal{C} , indicating that power neurons can communicate with each other faster than other neurons.
- The maximum connected component in \mathcal{C} includes 93.93% of the nodes, while that in \mathcal{P} includes 100% of the nodes. This means that every power neuron is connected to every other power neuron, while this is not the case for other neurons.

These findings all lead to the same conclusion, which is that there is indeed a backbone among the power neurons of *C. elegans*.

A final comment can be made about Table 7, although it has nothing to do with the existence of a backbone among power neurons. In fact, looking at this table, we can see that the degree assortativity is essentially null in both cases, meaning that both neurons and power neurons tend to connect with other neurons and power neurons regardless of the similarity or dissimilarity of the corresponding degrees.

All the results so far support the idea that power neurons are strategically placed in the connectome in such a way that they can pick up signals from certain areas (especially those in which they are most present) and route them to other (possibly distant) areas, thus allowing efficient propagation of signals among neurons.

As a further verification of this insight, we generated two network-based representations involving power neurons. In both networks, there is one node for each area; the size of the

node is proportional to the number of power neurons in that area. In the first network there is an arc between two nodes (areas) if there is at least one connection in \mathcal{C} between two neurons belonging to those areas such that at least one of them is a power neuron. The thickness of the arc is proportional to the number of connections that satisfy this property. The second network is analogous to the first, but it considers only those connections where both neurons involved are power neurons. Again, the thickness of the arc is proportional to the number of connections that satisfy this property. The purpose of both representations is to emphasize the role of power neurons in strategically connecting different areas to efficiently distribute information throughout the brain. Figure 4 shows the two networks thus obtained.

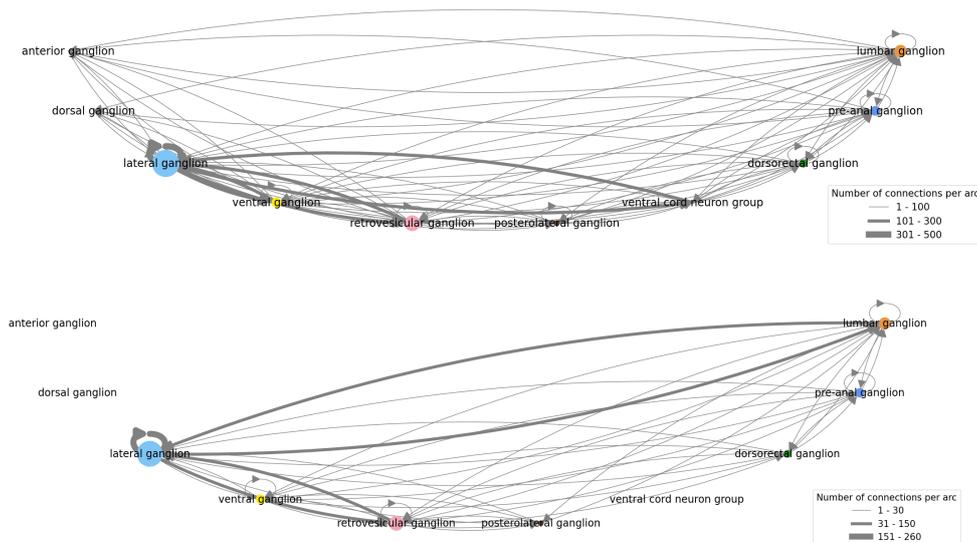


Figure 4: Connections between areas when at least one node of the arc is a power neuron (top) and when both nodes in the arc are power neurons (bottom)

Several considerations can be drawn from the analysis of this figure. First, consider the top side network, where at least one of the nodes in each arc is a power neuron. We can see that there are strong connections between “lateral ganglion” and “ventral ganglion”, “lateral ganglion” and “retrovesicular ganglion”, and “lateral ganglion” and “ventral cord neural group”. Note that there is also an extremely high number of “self-connections” in which both nodes belong to the “lateral ganglion” area; this peculiarity is not observed in any other area. There are indeed some other areas having self-connections, but these are generally limited in number. Let us now look at the bottom side network, where both nodes in each arc are power neurons. In this case, there are several changes compared to the previous case; in fact, the strongest connections are the self-connections involving the “lateral ganglion” area, and this is a confirmation compared to the previous case. Then, there are strong connections between “lateral ganglion” and “lumbar ganglion”, which in the previous case had connections, but not strong. The presence of a strong connection between “lateral ganglion” and “retrovesicular ganglion”, already seen in the top

side of the network, is also confirmed. In contrast, all the other pairs of areas show much weaker connections than in the top side network and also compared to the pairs of areas in the bottom side network already mentioned.

This last analysis concludes our discussion of power neurons in the *C. elegans* connectome. In the end, we can say that not only do they exist, but they are structurally organized to form a backbone capable of conditioning all the other neurons of the connectome and the functioning of the corresponding areas. They are able to collect signals from different areas of the connectome and then efficiently propagate them to all the other neurons. They are also responsible for the communication (and ultimately the functioning) of the connectome areas by promptly providing them with the information they need to function. Between certain areas of the connectome, there are privileged circuits involving power neurons that are essential for those areas to perform their assigned functions.

5. Conclusion

In this paper, we have defined an approach to search for power neurons in the *C. elegans* connectome, and once applied this approach and verified that power neurons really exist, we have presented an experimental campaign to characterize them. Our definition of power neuron is based on the definition of “rich club” neuron already found in the literature [27]. This definition is based on Complex Network Analysis and, in particular, on degree centrality. We believed that the idea of using Complex Network Analysis in this context was winning, and went further by considering closeness, betweenness and eigenvector centralities, in addition to degree centrality, in the definition of power neurons. The power neurons thus found first have several properties inherited from the application of the properties of the four centralities to the connectome. Moreover, through an extensive experimental campaign, we have identified additional important properties that characterize these neurons. Furthermore, we have seen that, although they are few, they form a backbone capable of influencing the functioning of all areas of the connectome.

As for further developments, we would first like to continue our studies in *C. elegans*. For example, we would like to verify the possible existence of frequent motifs in the connectome of this organism. In addition, we would like to extend our study of power neurons to one or more of the other three organisms (i.e., *Ciona intestinalis*, *Platynereis dumerilii*, and *Drosophila melanogaster*) whose complete connectomes are already known. Of course, as other complete connectomes become available, we would like to extend the study of power neurons and, more generally, the application of Complex Network Analysis concepts and techniques to these new connectomes as well.

Declaration on Generative AI

The authors have not employed any Generative AI tools.

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