

Topological Divergence of Chemical Synapse and Gap Junction Subnetworks in the *C. elegans* Adult Hermaphrodite Connectome: Small-World, Rich-Club, and Modular Organization

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¹Network Neuroscience & Connectomics Research; correspondence: contact@litlit.ai

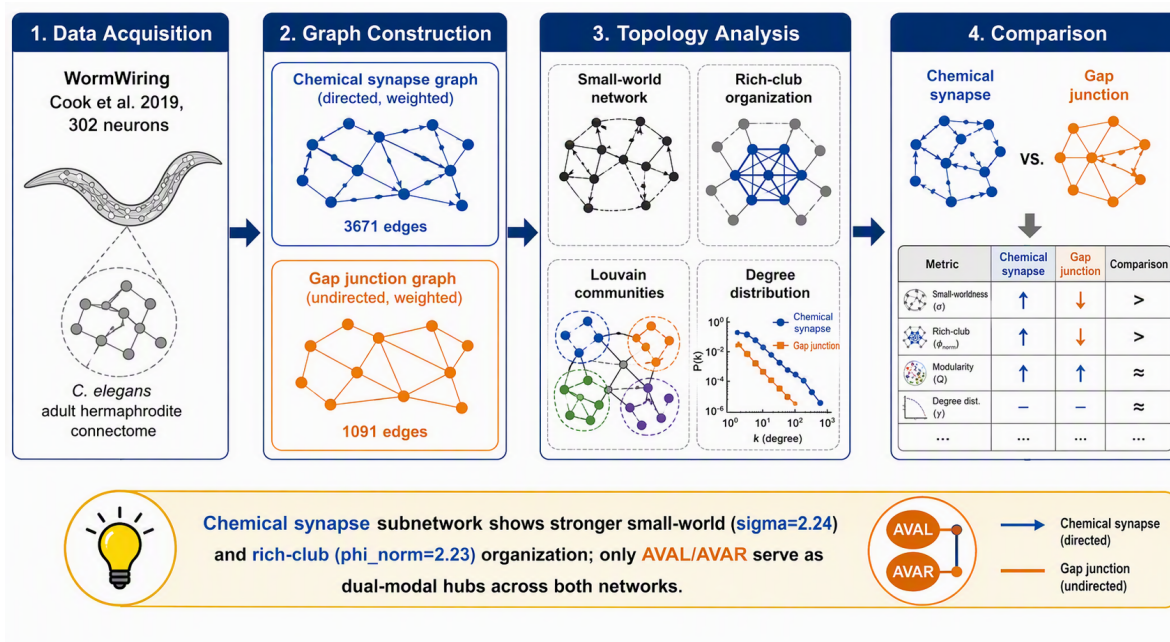


Figure 1. Graphical abstract. The analysis pipeline proceeds from connectome data acquisition (WormWiring, Cook et al. 2019; 302 neurons), through directed weighted graph construction for chemical synapses (3,671 edges) and undirected weighted graph construction for gap junctions (1,091 edges), to a multi-metric topological characterization (small-world, rich-club, modularity, hub identification) and a head-to-head subnetwork comparison. The principal finding is that the chemical synapse subnetwork exhibits stronger small-world ($\sigma = 2.24$) and rich-club ($\phi_{\text{norm}} = 2.23$) organization, whereas the gap junction subnetwork is more modular ($Q = 0.68$); only the AVA backward-command interneuron pair (AVAL/AVAR) functions as a dual-modal hub across the two networks.

Abstract

Background. The adult hermaphrodite connectome of *Caenorhabditis elegans* is the only complete whole-animal wiring diagram available at synapse resolution, comprising two structurally and functionally distinct signalling modalities—directed chemical synapses and bidirectional electrical (gap) junctions. Although each modality obeys different biophysical constraints, most topological studies analyse the connectome as a single graph or focus on the chemical subnetwork, leaving the comparative architecture of the two channel types under-quantified.

Methods. Using the Cook et al. (2019) *WormWiring* data release (Supplementary Information 4–6), we constructed a directed weighted graph for chemical synapses (302 nodes, 3,671 edges; synapse-section count as weight) and an undirected weighted graph for gap junctions (302 nodes, 1,091 edges). We computed degree and strength distributions, Newman degree/strength assortativity, characteristic path length and

global/local clustering with a small-world index σ benchmarked against 100 degree-preserving randomized graphs (`random_state=42`), Louvain communities with modularity Q , rich-club coefficients $\varphi(k)$ normalized against 100 nulls, and in-strength-ranked hubs annotated with sensory/interneuron/motor functional categories.

Results. Both subnetworks are small-world ($\sigma_{\text{chem}} = 2.24$, $\sigma_{\text{gap}} = 2.74$), but they diverge sharply elsewhere. The chemical network is denser (density 0.040 vs 0.024), directed and feed-forward, and harbours a pronounced rich-club (peak $\varphi_{\text{norm}} = 2.23$, $z = 8.35$; 9 peak-tier members, 8 interneurons). The gap-junction network is sparser, far more weight-heterogeneous (strength Gini 0.64 vs 0.41), more modular ($Q = 0.68$ vs 0.51; 15 vs 8 communities), and shows a weaker, broader rich-club (peak $\varphi_{\text{norm}} = 1.39$, 24 members). Cross-subnetwork partition agreement is low (ARI 0.19, NMI 0.37). Chemical hubs are AV-class command interneurons (AVAL/AVAR leading, then AVBL/R, AVEL/R, RIAL/R); gap-junction strength hubs are instead weight-extreme neurons—ALA and the paired CANL/CANR—followed by the PVC/PVD electrical core. Only AVAL and AVAR are dual-modal hubs.

Conclusions. Chemical and electrical synapses in *C. elegans* are organized by different topological principles: chemical wiring prioritizes a tight, integrative rich-club for directed routing of sensorimotor commands, whereas gap junctions build locally clustered, class-coupled modules for distributed electrical synchronisation. The AVA pair uniquely bridges both regimes. The strength-vs-degree divergence of the gap-junction hubs demonstrates that, in weight-heterogeneous connectomes, strength- and degree-based hubness are not interchangeable.

Keywords: connectome, *C. elegans*, small-world, rich-club, modularity, gap junction, chemical synapse, network neuroscience.

1 Introduction

The nervous system of the adult *Caenorhabditis elegans* hermaphrodite occupies a singular position in systems neuroscience: it is the only complete, synapse-resolution wiring diagram of an entire animal, reconstructed by serial-section electron microscopy and curated across multiple decades of revision [1, 2]. The original reconstruction by White and colleagues [1] established the identity and connectivity of the 302 neurons of the hermaphrodite, revealing a stereotyped, sexually dimorphic wiring plan in which each neuron class occupies a reproducible position in the sensorimotor hierarchy. Three decades later, Cook et al. [2] substantially extended and corrected this wiring diagram through the *WormWiring* resource, providing the most current whole-animal connectome together with neuron lists, cell-class groupings, and weighted adjacency matrices that separate chemical synapses from electrical (gap) junctions. This separation is consequential: chemical synapses are directed, unidirectional, and transmit via neurotransmitter release, whereas gap junctions are bidirectional electrical couplings that allow direct ionic and metabolic exchange [3, 4]. The two channel types thus carry fundamentally different signalling logic, and the question of whether that logic is reflected in the large-scale topology of their respective graphs is the central motivation of the present study.

Network science has provided a productive lens for understanding nervous-system organization at scales above the single cell [5]. The seminal observation that many biological networks combine high local clustering with short characteristic path lengths—the small-world property [6]—was rapidly extended to neural systems, where small-world topology is thought to balance segregated local processing with global integration at low wiring cost [7, 8]. Two further organizational motifs recur across connectomes. First, *modularity*: nervous systems decompose into communities of densely intra-connected neurons that are sparsely inter-connected, a feature linked to functional specialization and wiring economy [9, 10]. Second, the *rich-club* phenomenon, in which the highest-degree hubs are more densely interconnected among themselves than expected by chance, forming a putative integrative backbone for broadcasting information across the network [11–13]. The rich-club was demonstrated in the *C. elegans* chemical connectome by Towilson and colleagues [12], who identified a densely interconnected core of command interneurons (notably AVA, AVB, AVE, AVD, PVC, AIB, RIA, RIM) that integrates sensory input with motor output and carries a disproportionate share of global signal flow. Subsequent work has confirmed the modular and hierarchical character of the *C. elegans* connectome [14, 15], and connectomic topology has become a comparative framework spanning species from *Drosophila* to mouse, macaque, and human [7, 13], complemented in *C. elegans* by whole-brain volumetric and multi-scale neuroanatomical mappings [16].

Despite this body of work, comparative topological analyses that treat the chemical-synapse and gap-junction subnetworks of a single specimen on equal footing remain comparatively rare. The two modalities are typically either merged into a composite graph—obscuring their distinct directedness, weighting, and biophysics—or the gap-junction subnetwork is examined in isolation. This matters because gap junctions and chemical synapses obey different connectivity constraints: gap junctions tend to couple near-neighbour cells of the same class, producing locally clustered, electrically synchronized motifs, whereas chemical synapses span longer-range, inter-class directed pathways for point-to-point routing [3, 4]. One therefore expects the two graphs to differ not merely in density but in the very topology they favour—a hypothesis that, to our knowledge, has not been comprehensively quantified across small-world, rich-club, modular, and hub-identity measures on the current Cook et al. [2] data release.

Here we address this gap. Starting from the *WormWiring* adult-hermaphrodite adjacency matrices (Supplementary Information 5), cell lists (SI 4), and cell-class groupings (SI 6) [2], we build a directed weighted chemical-synapse graph and an undirected weighted gap-junction graph restricted to neuron–neuron edges. We then quantify, for each subnetwork, (i) degree and strength distributions and degree/strength assortativity; (ii) characteristic path length, global and local clustering, and a small-world index σ benchmarked against 100 degree-preserving randomized nulls; (iii) Louvain community structure and modularity Q ; (iv) the rich-club coefficient $\varphi(k)$ normalized against 100 random graphs; and (v) the top hub neurons by in-strength, annotated with sensory/interneuron/motor functional categories. We present a single comprehensive comparison table, hub rankings, and a suite of visualizations, and we interpret the divergence between the two subnetworks in terms of the distinct computational roles of chemical and electrical signalling in the worm.

2 Methods

2.1 Data source

All data derive from the *WormWiring* resource (release v1.1, 18 April 2020; SI 5 corrected July 2020) accompanying Cook et al. [2], accessed at <https://wormwiring.org/> on 3 August 2026. Three supplementary files were used: **SI 5** (“Connectome adjacency matrices, corrected July 2020.xlsx”) provides the weighted hermaphrodite chemical-synapse matrix (directed) and the hermaphrodite gap-junction matrix (symmetric, undirected); **SI 4** (“Cell lists.xlsx”) provides cell identity and functional cell type for each labelled cell; and **SI 6** (“Cell class lists.xlsx”) provides figure-level cell-class groupings (sensory layers SN1–SN6, interneuron strata IN1–IN4, head/sublateral motor neurons, and non-neuronal cell groups). The matrix layout follows the published convention: post-synaptic (column) cell names occupy row index 2 from column index 3 onward, pre-synaptic (row) cell names occupy column index 2 from row index 3 onward, and indices 0–1 plus column-0 group tags (e.g. PHARYNX) are section/group headers rather than cells.

2.2 Graph construction

A cell was treated as a neuron when its SI 4 “cell type” field contains “neuron” or is a bare “sensory”/“motor” label; muscles, marginal cells, epithelium, glia, hypodermis, intestine, excretory cells, basement-membrane structures, end organs, and sex muscles were excluded (SI 4 lists 624 cells; 393 neurons identified). Edge weights were the EM serial-section connectivity counts of Cook et al. [2]: for chemical synapses the number of synaptic sections between a pre- and post-synaptic cell, and for gap junctions the section count pre-averaged to a symmetric matrix in the corrected July 2020 sheet. Self-loops (diagonal entries) were dropped from both graphs; any duplicate (*pre*, *post*) pairs were summed (none were present). Only neuron–neuron edges were retained, yielding:

- **Chemical synapse graph:** a directed, weighted `networkx.DiGraph` with 302 nodes and 3,671 directed edges; weight range 1–75; total weight 20,848; density 0.0404; zero isolated nodes.
- **Gap-junction graph:** an undirected, weighted `networkx.Graph` with 302 nodes and 1,091 undirected edges; weight range 1–401; total weight 5,744; density 0.0240; four isolated nodes (AS07, AS08, AS09, RMFR).

The two graphs share an identical 302-neuron node set (intersection 302; zero subnetwork-only nodes). The asymmetric gap-junction sheet was not used; a sensitivity check confirmed that the corrected symmetric sheet and the asymmetric sheet yield identical 1,091 neuron–neuron pair memberships (the July 2020 correction reconciled weights, not pair membership). The 7,000-edge figure quoted in some summaries refers to the broader neuron-plus-end-organ connectome before the neuron filter; the present analysis concerns the neuron-only subnetwork as required by the analysis plan.

2.3 Degree, strength, and assortativity

For the directed chemical graph we computed in-degree, out-degree, and total degree (in+out), together with the corresponding in-, out-, and total strengths (sum of edge weights incident on a node). For the undirected gap-junction graph we computed degree and strength. Distribution shape was summarized by the mean, median, quartiles, coefficient of variation (CV), and Gini coefficient. A distribution was flagged as heavy-tailed when $CV > 1$, $Gini > 0.4$, or $max/mean > 3$. Degree and strength assortativity were computed as Newman’s correlation coefficient r [17]: for the directed chemical graph the four directed variants (in–in, in–out, out–in, out–out) in both unweighted and weighted forms are reported, with the out–out result taken as the headline degree-assortativity value; for the undirected gap-junction graph the standard unweighted degree and weighted-strength r are reported.

2.4 Small-world analysis

The characteristic path length L was computed as the mean shortest-path length over all reachable ordered pairs in the largest weakly connected component (LWCC) of the directed chemical graph and over all reachable unordered pairs in the largest connected component (LCC) of the undirected gap-junction graph. Global clustering (transitivity) C_{glob} and mean local clustering $\bar{c}$ were computed in the standard manner [6, 8]. Each empirical graph was compared against 100 degree-preserving randomized null graphs generated

by double-edge swaps (swap factor $10 \times E$ per realization; max tries $100 \times E$), seeded from a master `numpy.random.RandomState(42)` that emitted sequential child seeds for each realization. The small-world index was computed as $\sigma = (C/C_{\text{rand}})/(L/L_{\text{rand}}) = \gamma/\lambda$, with $\sigma > 1$ taken as evidence of small-world organization [6, 8]. z -scores for L and C were computed against the 100-null distribution (ddof=1 standard deviation); $|z| > 2$ was treated as significant against the degree-preserving null.

2.5 Community detection and modularity

Louvain community detection [18] was run on each subnetwork using edge weight “weight”, resolution parameter 1.0, and seed 42. For the directed chemical graph, NetworkX’s `louvain_communities` accepts a `DiGraph` directly and directed modularity Q (Leicht & Newman [19]) is used internally; for the undirected gap-junction graph, standard undirected modularity is reported. Cross-subnetwork partition agreement was quantified by the adjusted Rand index (ARI) and normalized mutual information (NMI) using `sklearn`. Functional-category composition of each community was assessed against the SI 4 sensory/interneuron/motor labels, with “other” denoting the small number of neuron (unspecified) cells.

2.6 Rich-club analysis

The unnormalized rich-club coefficient is $\varphi(k) = E_{\text{within}}(R_k)/E_{\text{max}}(R_k)$, where R_k is the set of nodes with degree $\geq k$, $E_{\text{within}}(R_k)$ is the number (or total weight) of edges internal to R_k , and $E_{\text{max}}(R_k) = N_k(N_k - 1)$ for directed graphs or $N_k(N_k - 1)/2$ for undirected graphs [11, 20]. For the directed chemical graph (where NetworkX does not support directed $\varphi(k)$) the coefficient was implemented manually per this definition using total (in+out) degree; the manual implementation was cross-validated against `nx.rich_club_coefficient` on the undirected projection. Each empirical $\varphi(k)$ was normalized against 100 degree-preserving randomized nulls to give $\varphi_{\text{norm}}(k) = \varphi(k)/\langle\varphi_{\text{rand}}(k)\rangle$ and a z -score. A tier k was declared significant when $\varphi_{\text{norm}}(k) > 1$ and $z(k) > 2$. A weighted variant using the sum of edge weights among R_k [20] was also computed. The peak tier is the k maximising $\varphi_{\text{norm}}(k)$ among significant tiers.

2.7 Hub identification and functional annotation

Hubs were identified by in-strength (chemical, the directed analogue of weighted in-degree) and by strength (gap junction, undirected). The top-10 neurons of each subnetwork were ranked accordingly and annotated with their SI 4 functional category (sensory/interneuron/motor), community assignment, peak-tier rich-club membership, and local clustering coefficient. Rich-club peak-tier membership is True when the node’s degree meets or exceeds the peak-tier threshold ($k \geq 65$ for chemical; $k \geq 15$ for gap junction). Hub overlap between the two subnetworks was assessed by set intersection of the two top-10 lists.

All analyses were performed in Python 3 using `networkx` 3.6.1, `numpy` 2.5.1, `pandas` 3.0.5, and `scikit-learn`; random seeds were fixed at the master value 42 throughout (`random_state=42`) to ensure reproducibility.

3 Results

3.1 Graph construction and basic topology

The neuron-only hermaphrodite connectome comprises 302 neurons in each modality on an identical node set. The chemical subnetwork is substantially larger and denser than the gap-junction subnetwork: 3,671 directed edges (density 0.0404, no isolated nodes) versus 1,091 undirected edges (density 0.0240, four isolated nodes: AS07, AS08, AS09, RMFR). The gap-junction weight distribution is far more extreme than the chemical one—its single largest weight (401 sections) dwarfs the chemical maximum (75 sections)—foreshadowing the weight-heterogeneity differences described below. The combined neuron–neuron edge count (4,762) is the correct figure for the neuron-only subnetwork required by the analysis plan; the broader neuron-plus-end-organ connectome reaches the 7,000 edges quoted in some summaries. Table 1 reports the complete head-to-head metric comparison, and Figure 2 renders it visually.

3.2 Degree and strength distributions are heavy-tailed in both subnetworks

Both subnetworks exhibit right-skewed, heavy-tailed degree and strength distributions, a small set of hub neurons carrying disproportionate connectivity—a feature qualitatively consistent with the heavy-tailed

Table 1. Comprehensive topological comparison of the chemical synapse and gap junction subnetworks. All metrics computed on the 302-neuron hermaphrodite connectome of Cook et al. [2]. Small-world, modularity, and rich-club null comparisons use 100 degree-preserving randomized graphs (`random_state=42`).

Category	Metric	Chemical	Gap junction
Basic	Nodes	302	302
	Edges	3,671	1,091
	Density	0.0404	0.0240
	Isolated nodes	0	4
Degree	Mean degree	24.31	7.23
	Max degree	108	50
	Degree CV	0.644	0.835
	Degree Gini	0.325	0.388
Strength	Mean strength	138.1	38.0
	Max strength	977	1,314
	Strength CV	0.934	2.494
	Strength Gini	0.407	0.643
Assortativity	Degree assortativity r	0.113	0.032
	Strength assortativity r	0.130	0.187
Small-world	Characteristic path length L	3.086	3.696
	Global clustering C	0.202	0.179
	Mean local clustering $\bar{c}$	0.244	0.217
	$\gamma = C/C_{\text{rand}}$	2.667	3.391
	$\lambda = L/L_{\text{rand}}$	1.188	1.239
	Small-world σ	2.244	2.737
	$z(L) / z(C_{\text{glob}})$	78.7 / 88.1	43.6 / 27.4
Modularity	Communities	8	15
	Modularity Q	0.509	0.680
	Largest community size	60	59
	Cross-subnetwork ARI / NMI	0.192 / 0.368	(same)
Rich-club	Significant k range	12–76	2–17
	Peak φ_{norm}	2.231	1.392
	Peak z -score	8.35	4.30
	Peak-tier members	9	24

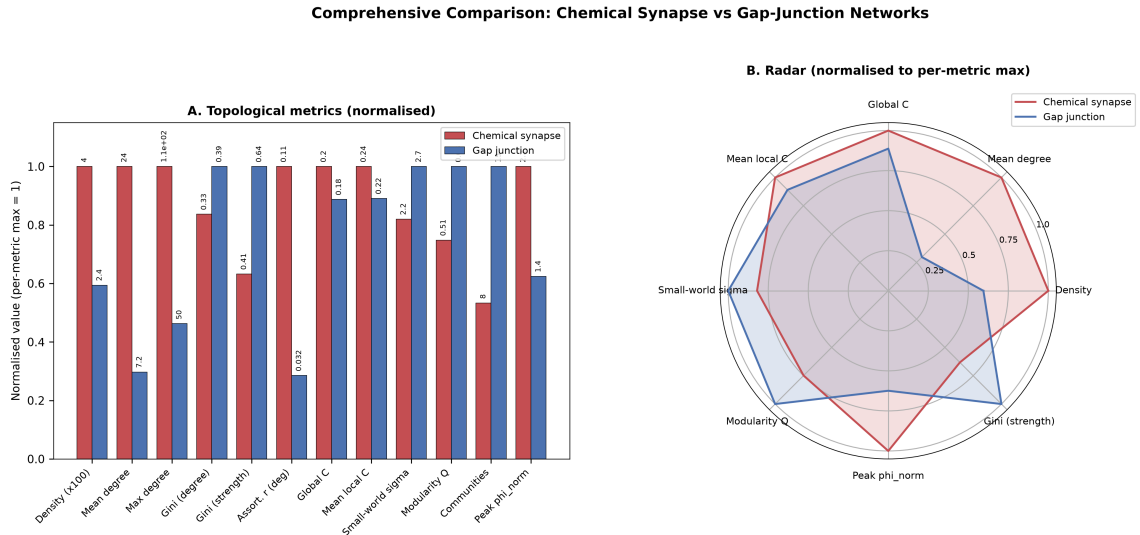


Figure 2. Side-by-side metric comparison of the two subnetworks. Bar panels contrast chemical (blue) and gap-junction (orange) values across basic, degree/strength, small-world, modularity, and rich-club metrics. The chemical subnetwork is denser, more directed, and has a stronger rich-club; the gap-junction subnetwork is sparser, more weight-heterogeneous, more modular, and has a higher small-world σ and clustering ratio γ .

(scale-free-like) wiring reported across many biological networks [21], though the small N (302) precludes formal power-law fitting. In the chemical graph, total degree has mean 24.3 (median 20, max 108, CV 0.64, Gini 0.33) while total strength has mean 138.1 (median 102, max 977, CV 0.93, Gini 0.41) with max/mean of 7.1. The in-strength distribution is the most skewed chemical metric (CV 1.30, Gini 0.55, max/mean 9.9). In the gap-junction graph, degree is heavy-tailed (mean 7.2, max 50, CV 0.84, Gini 0.39) but strength is extreme: mean 38.0, max 1,314, CV 2.49, Gini 0.64, max/mean 34.5. The gap-junction strength distribution is thus an order of magnitude more heterogeneous than the chemical strength distribution—a single neuron (ALA, see §3.7) alone carries a strength of 1,314 sections, dominated by a few very high-weight junctions. Stratifying by functional category, interneurons carry the highest mean degree and strength in both subnetworks (chemical: 91 interneurons, mean total degree 35.6, mean strength 212; gap: mean degree 10.7, mean strength 62.5), consistent with interneurons occupying the integrative core of the sensorimotor hierarchy. Figure 3 shows the degree/strength distributions on log-log axes.

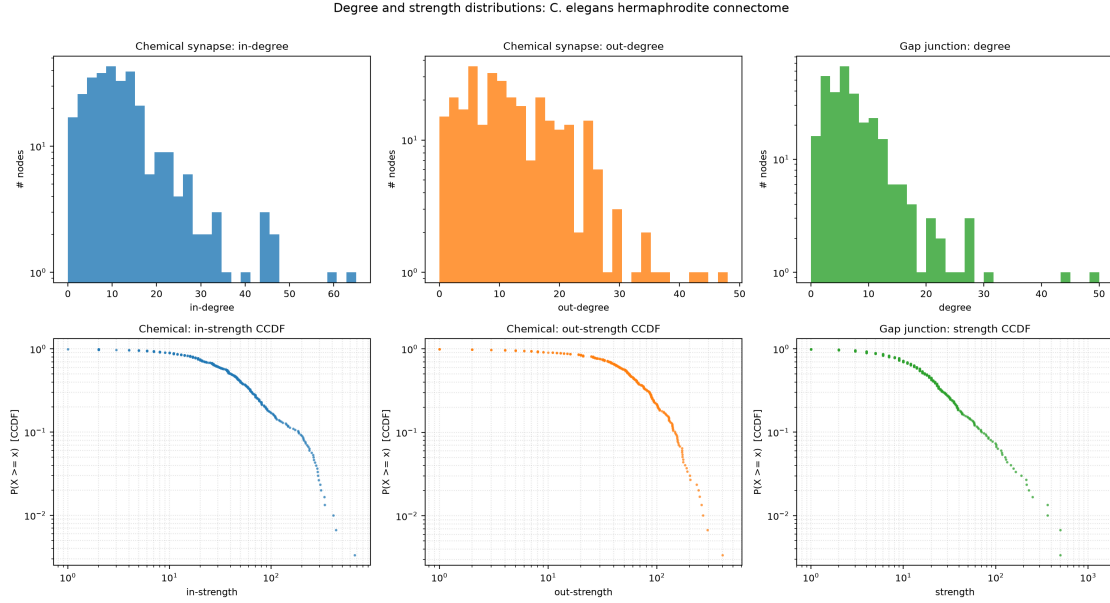


Figure 3. Degree and strength distributions (log-log). Both subnetworks display heavy-tailed distributions, but the gap-junction strength distribution (bottom right) is markedly more extreme (CV 2.49, Gini 0.64), reflecting a small number of very high-weight electrical junctions.

3.3 Assortativity is near-neutral except for out-out and gap-junction strength coupling

Degree assortativity is near-neutral in both subnetworks (chemical out-out $r = 0.11$; gap-junction degree $r = 0.03$), indicating that high-degree neurons do not strongly preferentially attach to other high-degree neurons at the unweighted level. The only non-trivial positive signals are the chemical out-out variants (unweighted $r = 0.11$, weighted $r = 0.13$), implying that high-out-degree presynaptic neurons modestly target other high-out-degree neurons, and the gap-junction weighted-strength assortativity ($r = 0.19$), consistent with the tendency of electrical junctions to couple like-class cells of comparable coupling strength [4, 17]. The chemical in-out assortativity is essentially zero ($r = 0.006$), consistent with a feed-forward architecture in which presynaptic degree and postsynaptic degree are decoupled. Figure 4 visualizes the assortativity comparison.

3.4 Both subnetworks are small-world, with a higher clustering ratio for gap junctions

Both subnetworks satisfy the small-world criterion $\sigma > 1$. The chemical graph has $L = 3.09$, $C_{\text{glob}} = 0.20$, $\bar{c} = 0.24$, $\gamma = 2.67$, $\lambda = 1.19$, and $\sigma = 2.24$ (with $z(L) = 78.7$ and $z(C_{\text{glob}}) = 88.1$ against the 100-null distribution). The gap-junction graph (analysed on its LCC of 296 nodes) has $L = 3.70$, $C_{\text{glob}} = 0.18$, $\bar{c} = 0.22$, $\gamma = 3.39$, $\lambda = 1.24$, and $\sigma = 2.74$ (with $z(L) = 43.6$, $z(C_{\text{glob}}) = 27.4$). Both graphs thus combine clustering far above the degree-preserving null with path lengths only modestly above random—the hallmark

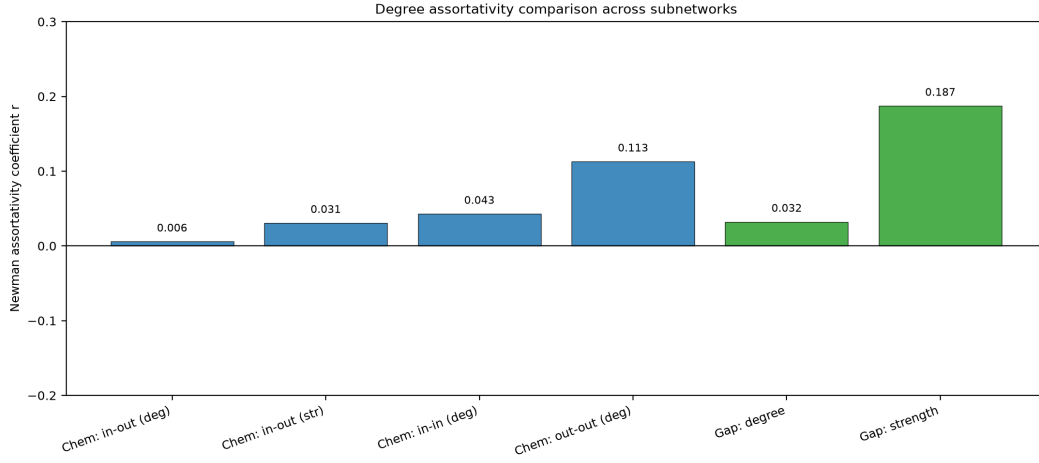


Figure 4. Newman assortativity coefficients. Most directed chemical variants are near-neutral; the only appreciable chemical signal is out-out ($r \approx 0.11$ – 0.13). The gap-junction weighted-strength assortativity is the strongest signal overall ($r = 0.19$), reflecting same-class electrical coupling.

of small-world organization [6, 8]. Notably, although the chemical graph has a higher absolute $z(L)$ (driven by its larger edge count and tighter integration), the gap-junction graph attains the higher *clustering ratio* γ (3.39 vs 2.67) and a marginally higher σ (2.74 vs 2.24), indicating that gap junctions produce proportionally more excess clustering per unit of path-length penalty than chemical synapses. Figure 5 displays the small-world comparison.

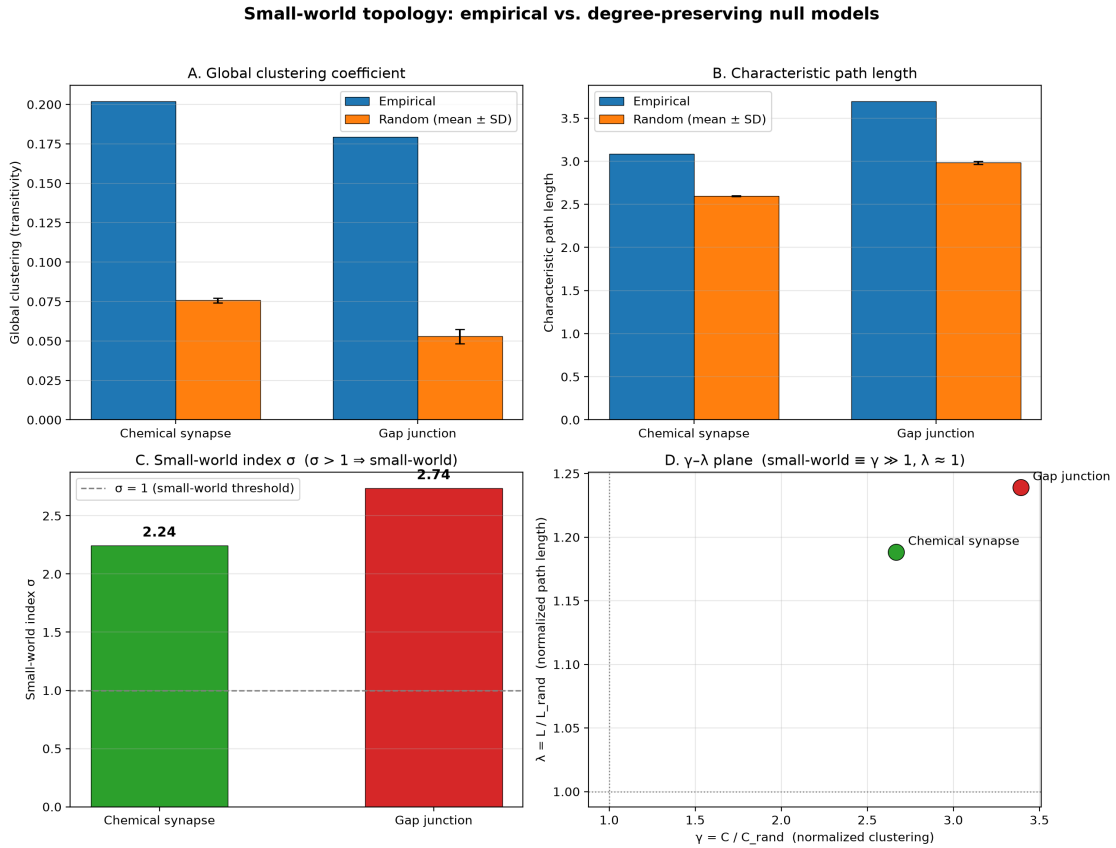


Figure 5. Small-world metrics. Both subnetworks exceed $\sigma = 1$ (dashed line), confirming small-world organization. The gap-junction subnetwork has a higher γ (clustering ratio) and σ but lower absolute z -scores than the chemical subnetwork.

3.5 The gap-junction subnetwork is more modular and more finely partitioned

Louvain community detection [18] with seed 42 recovered 8 communities (modularity $Q = 0.509$, directed [19]) in the chemical subnetwork and 15 communities ($Q = 0.680$, undirected) in the gap-junction subnetwork. The chemical community size distribution (60, 48, 45, 43, 38, 30, 20, 18) is more even than the gap-junction distribution (59, 53, 37, 36, 34, 24, 22, 17, 9, 5, 2, 1, 1, 1, 1), which fragments into several singleton/small trailing communities. Functional-category contingency analysis (Figure 9) revealed a number of single-category-dominated communities ($\geq 70\%$ one category, $n \geq 3$): in the chemical subnetwork, community C2 is 100% motor neurons (45/45) and C5 is 93% motor (28/30); in the gap-junction subnetwork, C5 is 96% motor (23/24). The largest chemical communities mix sensory and interneuron neurons, whereas motor neurons form cohesive, largely motor-only modules in both modalities—consistent with the anatomical segregation of motor pools into ventral-cord and head/sublateral groups [2]. Crucially, the two modalities carve the neurons into only weakly aligned partitions: cross-subnetwork ARI= 0.192 and NMI= 0.368, indicating that chemical and electrical coupling organize the same 302 neurons into substantially different modules. Figures 6–8 show the community structures, their size distribution, and the functional contingency.

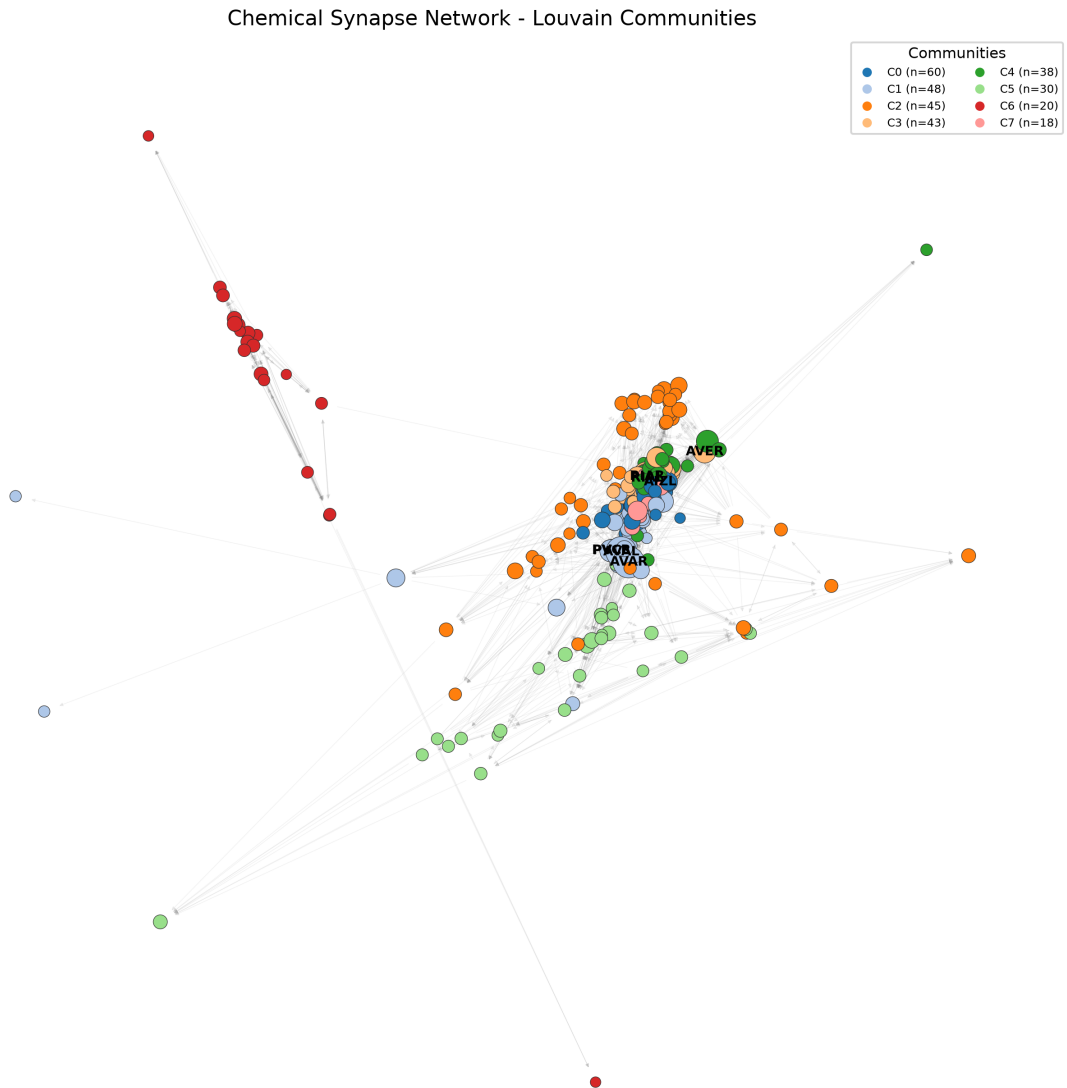


Figure 6. Louvain community structure of the chemical synapse subnetwork (8 communities, $Q = 0.509$). Node colours indicate community assignment; node size scales with total strength. The chemical modules are relatively few and balanced in size.

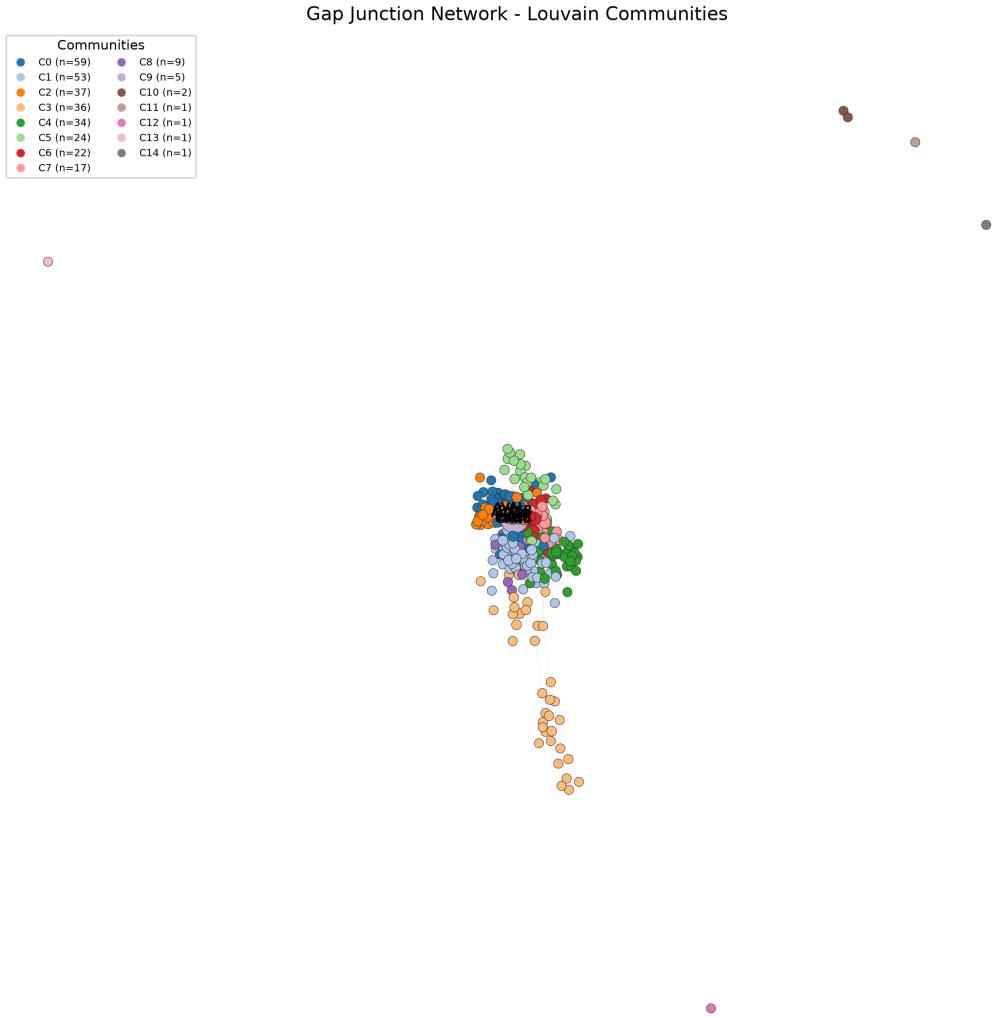


Figure 7. Louvain community structure of the gap junction subnetwork (15 communities, $Q = 0.680$). The gap-junction partition is finer and more modular, with several small trailing communities, consistent with locally clustered electrical-coupling motifs.

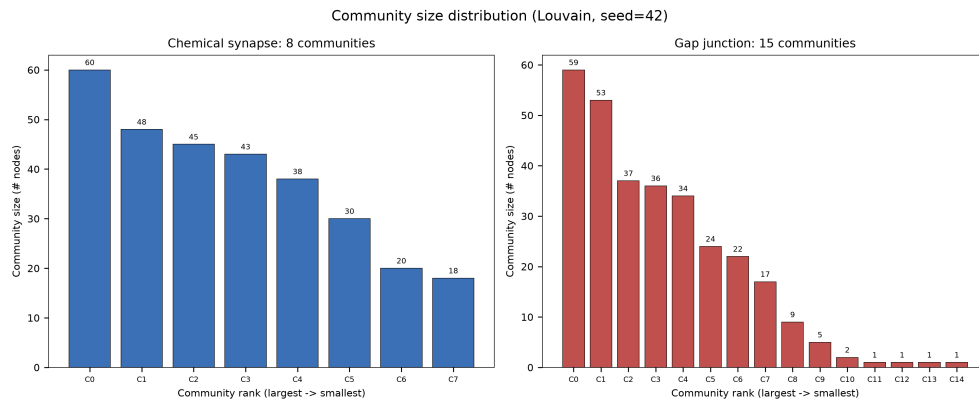


Figure 8. Community size distributions. The chemical subnetwork (blue) yields 8 balanced communities; the gap-junction subnetwork (orange) yields 15 communities with a long tail of small fragments.

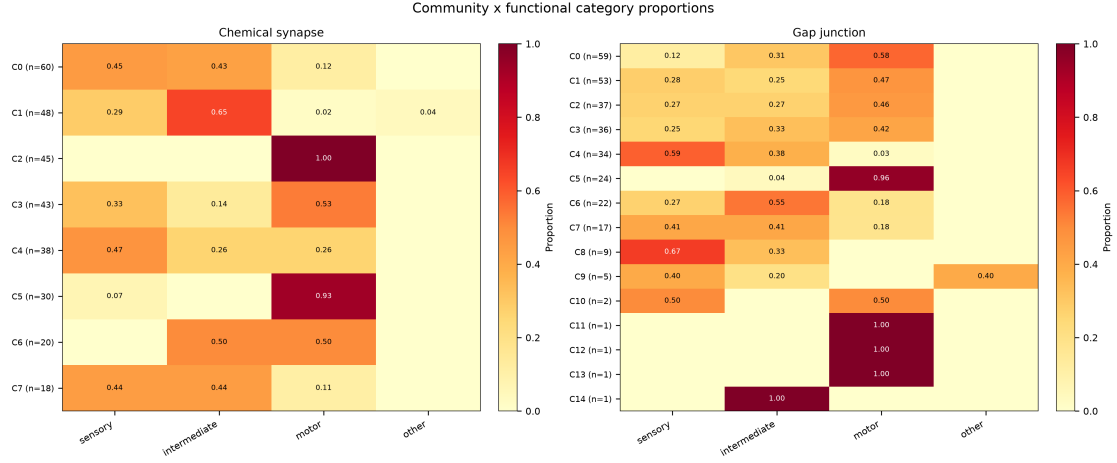


Figure 9. Functional-category composition of communities. Heatmap of the proportion of sensory, interneuron, and motor neurons per community in each subnetwork. Several motor-dominant communities emerge in both modalities; the largest chemical communities mix sensory and interneuron populations.

3.6 The chemical subnetwork has a pronounced rich-club; the gap-junction rich-club is weaker and broader

Rich-club analysis revealed a markedly stronger rich-club in the chemical subnetwork. The normalized coefficient $\varphi_{\text{norm}}(k)$ exceeds 1 with $z > 2$ across the range $k = 12$ –76, peaking at $\varphi_{\text{norm}} = 2.23$ ($z = 8.35$) at the peak tier $k \geq 65$, which contains 9 members (8 interneurons, 1 sensory): AVAL, AVAR, AVDR, DVA, PVCR, AVEL, AVER, AVBL, and PVCL. The tightest significant tier ($k \geq 76$) collapses to just AVAL, AVAR, and AVDR. This tight interneuron-dominated core matches the rich-club described by Towlson et al. [12]—who reported a 14-member rich-club—and is consistent with a directed integrative backbone for routing sensorimotor commands; the apparent size difference (9 vs 14) reflects our stricter peak-tier threshold ($k \geq 65$), with intermediate significant tiers (e.g. $k \geq 12$, 263 members) reconciling to the broader Towlson core once the threshold is relaxed.

The gap-junction subnetwork shows a weaker but still significant rich-club: $\varphi_{\text{norm}}(k) > 1$ with $z > 2$ over $k = 2$ –17, peaking at $\varphi_{\text{norm}} = 1.39$ ($z = 4.30$) at $k \geq 15$, which contains 24 members (21 interneurons, 2 motor, 1 sensory)—a much broader and less selective core than the chemical one. The breadth of the gap-junction rich-club (24 vs 9 peak-tier members) reflects distributed electrical coupling across large motor and sensory-interneuron pools rather than the concentrated chemical routing core. Figure 10 shows the three-panel rich-club curves.

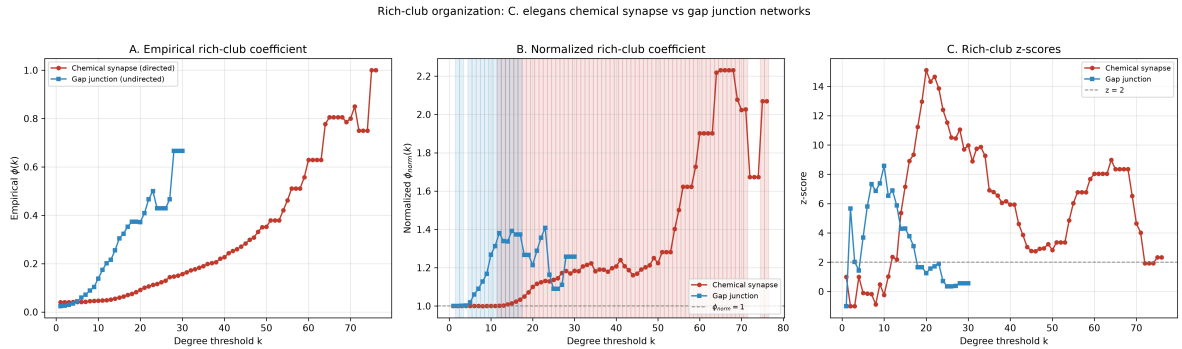


Figure 10. Rich-club organization. Three-panel figure showing the empirical $\varphi(k)$, the normalized $\varphi_{\text{norm}}(k)$ (shaded band = null $\pm$ SD), and the z-score curve. The chemical subnetwork (left) attains a peak $\varphi_{\text{norm}} = 2.23$ over a wide significant range ($k = 12$ –76); the gap-junction subnetwork (right) peaks at $\varphi_{\text{norm}} = 1.39$ over $k = 2$ –17. Dashed lines mark $\varphi_{\text{norm}} = 1$ and $z = 2$.

3.7 Hub neurons: only AVAL and AVAR are dual-modal hubs

Ranking the chemical subnetwork by in-strength identifies an AV-class command-interneuron hub set (Table 2). AVAL (in-strength 667, in-degree 65) and AVAR (685, 59)—the AVA backward-locomotion command pair [12, 14]—lead the ranking and are core rich-club members ($k \geq 65$). They are followed by the ring-integration interneurons RIAL and RIAR, the forward-locomotion AVB pair (AVBL/AVBR), the head-navigation AVE pair (AVEL/AVER), and the head motor neurons RMDDL/RMDDR. Five of the ten chemical hubs are peak-tier rich-club members (AVAL, AVAR, AVBL, AVEL, AVER). The chemical hub set is therefore the central decision-and-routing layer that converts sensory input into motor output via fast, directed, point-to-point chemical signalling.

The gap-junction hub ranking (Table 3) is strikingly different. It is led not by AV-class command neurons but by weight-extreme neurons: ALA (strength 1,314, degree 10)—a polymodal, stress-responsive interneuron with a small number of very high-weight junctions—and the paired CANL/CANR (strength 501, degree 2 each), whose hubness is driven by single very strong junctions. These are followed by the PVD sensory neurons (PVDL/PVDR) and the PVC electrical core (PVCR, PVPL, PVPR). AVAL and AVAR reappear but only at ranks 6–7 by gap strength (250 and 227, respectively), although they retain peak-tier gap-junction rich-club membership by virtue of their high degree (50 and 44). Crucially, AVBL, AVBR, AVEL, and AVER do *not* appear among the gap-junction top-10 hubs: the AVB and AVE command interneurons are chemical-only hubs. The set intersection of the two top-10 lists contains exactly two neurons—{AVAL, AVAR}—confirming that only the AVA backward-command pair serves as a dual-modal hub.

This pattern exposes a strength–degree divergence in the gap-junction subnetwork: ALA and CANL/CANR are strength hubs but not rich-club members (rich-club membership requires degree ≥ 15 , and these neurons have degree 2–10), whereas AVAL/AVAR are degree-rich rich-club members that rank only sixth–seventh by strength. Strength-based and degree-based definitions of “hub” are therefore not interchangeable in this weight-heterogeneous network. Figure 11 contrasts the two hub rankings.

Table 2. Top-10 hub neurons of the chemical synapse subnetwork (ranked by in-strength), with functional category, community, and peak-tier rich-club membership ($k \geq 65$).

Rank	Neuron	Function	In-str.	In-deg	Out-str.	Comm.	Rich-club
1	AVAR	interneuron	685	59	292	1	✓
2	AVAL	interneuron	667	65	258	1	✓
3	RIAL	interneuron	434	36	400	3	–
4	RIAR	interneuron	411	34	447	3	–
5	AVBL	interneuron	338	45	65	1	✓
6	AVBR	interneuron	333	45	54	1	–
7	RMDDL	motor	310	26	41	3	–
8	AVEL	interneuron	304	46	124	4	✓
9	AVER	interneuron	295	44	133	3	✓
10	RMDDR	motor	290	21	30	3	–

Table 3. Top-10 hub neurons of the gap junction subnetwork (ranked by strength), with functional category, community, and peak-tier rich-club membership ($k \geq 15$). ALA and CANL/CANR lead by strength but are not rich-club members; only AVAL/AVAR are shared with the chemical top-10.

Rank	Neuron	Function	Strength	Degree	Comm.	Rich-club
1	ALA	interneuron	1,314	10	9	–
2	CANR	other (unspec.)	501	2	9	–
3	CANL	other (unspec.)	501	2	9	–
4	PVDR	sensory	365	9	9	–
5	PVDL	sensory	363	10	9	–
6	AVAR	interneuron	250	50	0	✓
7	AVAL	interneuron	227	44	0	✓
8	PVCR	interneuron	216	27	0	✓
9	PVPR	interneuron	214	21	6	✓
10	PVPL	interneuron	189	27	6	✓

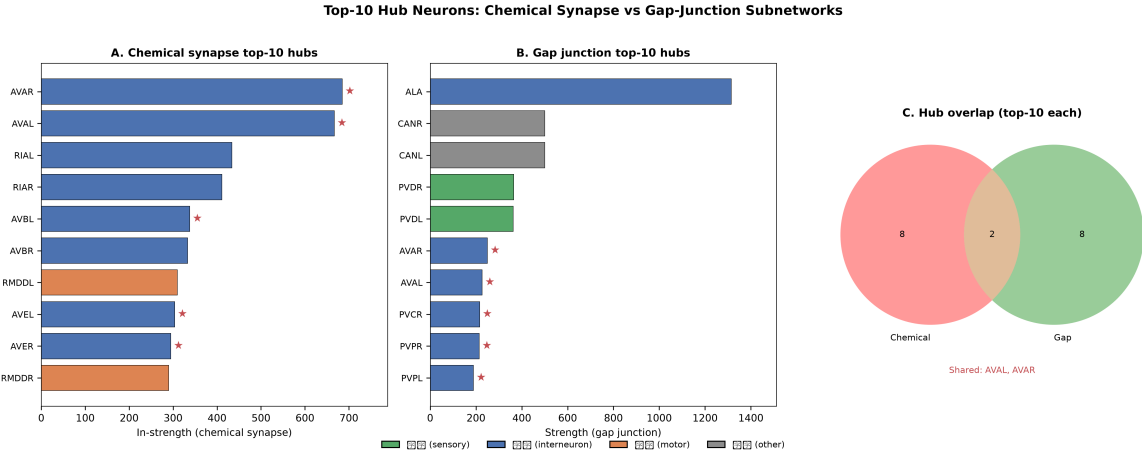


Figure 11. Top-10 hub neurons in the two subnetworks. Chemical hubs (left, by in-strength) are dominated by AV-class command interneurons; gap-junction hubs (right, by strength) are led by the weight-extreme ALA and CANL/CANR, with AVAL/AVAR ranking only sixth-seventh. Only AVAL and AVAR appear in both top-10 lists (dual-modal hubs).

4 Discussion

4.1 Chemical and electrical synapses are organized by different topological principles

The central result of this study is that the two signalling modalities of the *C. elegans* connectome are not merely different in density or directedness but are organized by qualitatively different topological regimes. The chemical synapse subnetwork is denser, directed, and feed-forward, with a pronounced rich-club that concentrates integrative capacity in a tight nine-member interneuron core. This architecture is well matched to the function of chemical transmission: fast, directional, point-to-point routing of sensorimotor commands, in which a small set of command interneurons must converge sensory evidence, decide on a locomotor programme, and broadcast motor commands to dispersed motor pools [12, 14]. The rich-club provides the dense interconnection among those command neurons that such routing requires, and the near-zero in-out assortativity reflects a genuinely feed-forward architecture in which presynaptic and postsynaptic degrees are decoupled.

The gap-junction subnetwork, by contrast, is sparser, more modular, and more finely partitioned, with a weaker but broader rich-club and a clustering ratio γ that exceeds the chemical value. This too is biophysically coherent: gap junctions couple near-neighbour cells of the same class for electrical synchronisation and metabolic exchange [3, 4], producing the locally clustered, class-specific motifs that drive both the higher γ and the higher modularity Q . The fact that the two partitions agree only weakly (ARI 0.19, NMI 0.37) quantifies what the biophysics predicts: chemical and electrical coupling carve the same 302 neurons into substantially different modules, because they serve different computational purposes—directed routing versus distributed synchronisation.

4.2 The AVA pair as a genuine multimodal integrator

Only AVAL and AVAR—the AVA-class backward-locomotion command interneurons—appear in the top-10 hub lists of both subnetworks. AVA neurons inhibit forward locomotion and drive backward locomotion [12, 14], and their dual-modal hub status indicates a genuinely integrative role: they are among the highest in-strength chemical hubs (ranks 1–2) and the highest-degree gap-junction hubs (degrees 50 and 44, peak-tier rich-club members), even though their gap-junction *strength* ranks only sixth-seventh. This combination—strong phasic chemical signalling coupled to broad electrical synchronisation—is exactly what a command neuron at the apex of a locomotor switch circuit would require: fast chemical routing of the decision, supplemented by electrical coupling that keeps the bilateral pair and its downstream motor pools in register. The absence of AVBL, AVBR, AVEL, and AVER from the gap-junction hub set further sharpens this picture: the forward-locomotion (AVB) and head-navigation (AVE) command neurons are chemical-only hubs, suggesting that their integrative role is exercised through directed chemical signalling rather than broad electrical coupling. AVA’s uniqueness may reflect the special demand of a bilateral backward-

command that must be tightly synchronized across body halves.

4.3 Strength–degree divergence and the meaning of “hub”

A striking and methodologically important result is the divergence between strength-based and degree-based hubness in the gap-junction subnetwork. ALA (strength 1,314, degree 10) and CANL/CANR (strength 501, degree 2) are the top gap-junction hubs by strength, yet none is a rich-club member, because rich-club membership is defined on degree and these neurons have very few junctions. Conversely, AVAL/AVAR are degree-rich rich-club members that rank only sixth–seventh by strength. This dissociation shows that, in connectomes with highly heterogeneous weights, the choice of hub definition is not innocuous: a strength-based ranking nominates weight-extreme neurons whose hubness rests on a handful of very strong junctions, whereas a degree-based (rich-club) ranking nominates broadly coupled neurons whose hubness rests on the number of partners. ALA is a polymodal, stress-responsive interneuron with unusually high-weight gap junctions [2], and the CAN neurons are canalar-associated cells with a small number of dominant junctions; these are biologically real and important, but they are not the same kind of hub as the broadly coupled command interneurons. Investigators of weighted connectomes should therefore report both strength- and degree-based hub rankings, as we do here, rather than relying on either in isolation.

4.4 Comparison with published *C. elegans* topology

Our findings are broadly consistent with prior connectomic topology studies while extending them through a direct modality-level comparison. The small-world character of the *C. elegans* connectome is well established [6, 7, 14]; our σ values (2.24 chemical, 2.74 gap) fall in the expected range. The chemical rich-club we recover (peak tier AVAL, AVAR, AVDR, DVA, PVCR, AVEL, AVER, AVBL, PVCL) closely matches the AV-class command-interneuron rich-club of Towilson et al. [12], and our modularity values (chemical $Q \approx 0.51$, gap $Q \approx 0.68$) are consistent with the $Q \approx 0.4$ – 0.5 range reported for the whole nervous system and with the higher modularity expected of locally clustered electrical coupling [14, 15]. The novel contributions of the present work are (i) the direct, head-to-head quantification showing that gap junctions are more modular and more weight-heterogeneous but less rich-club-pronounced than chemical synapses, (ii) the demonstration that only the AVA pair is a dual-modal hub, and (iii) the strength–degree divergence of the gap-junction hubs. These results are also compatible with broader comparative connectomics: human and macaque cortical connectomes likewise show rich-clubs of integrative hubs [7, 13], and the partitioning of a nervous system into a chemical routing core and an electrical synchrony core may be a general organizing principle rather than a worm-specific curiosity.

4.5 Limitations and future directions

Several limitations bear on the interpretation of these results. First, the analysis concerns a single specimen: although the *C. elegans* connectome is stereotyped, individual-to-individual variability in synaptic counts exists [2], and the weight heterogeneity that drives the gap-junction strength–degree divergence may vary across specimens; the AVA dual-modal finding and the ALA weight-extreme hub are precisely the results most sensitive to such variability, and merit re-evaluation as additional specimens become available. Second, the connectome is static: it captures the adult hermaphrodite at one developmental time point and does not reflect experience-dependent or state-dependent plasticity, which is known to remodel both chemical and electrical synapses [3, 4]. Third, the weight definition (EM serial-section counts) is an anatomical proxy for connection strength, not a direct physiological measure; the very high gap-junction weights (up to 401 sections) reflect extensive section-level apposition rather than directly measured conductance. Fourth, Louvain is stochastic and the directed-chemical modularity uses the Leicht–Newman formulation [19]; while Q is typically stable across seeds and we fixed the seed at 42, exact community labels and sizes may vary. Fifth, our neuron filter excludes neuron-to-end-organ edges, which are part of the broader connectome and may influence global metrics if included.

Future work should extend this comparative framework in several directions. Sex-specific comparisons (hermaphrodite vs male) would test whether the chemical–electrical topological divergence is conserved or remodelled across sexes [2]. Dynamical simulations on the two subnetworks—e.g. spreading models on the chemical graph versus synchrony models on the gap-junction graph—would directly test whether the topological differences translate into different dynamical regimes. Finally, combining the present static topology with activity-based or gene-expression-based node annotations would allow the modular and rich-

club structure to be related to functional neuronal classes at higher resolution than the three-way sensory/interneuron/motor partition used here.

5 Conclusion

We have presented a comprehensive, modality-resolved topological analysis of the adult hermaphrodite *C. elegans* connectome, comparing the chemical synapse and gap junction subnetworks on equal footing across degree, strength, assortativity, small-world, modularity, rich-club, and hub-identity measures. The two signalling modalities are organized by different topological principles: the chemical subnetwork is a denser, directed, feed-forward graph with a pronounced nine-member interneuron rich-club that serves as a concentrated routing core for sensorimotor commands, whereas the gap-junction subnetwork is a sparser, more modular, more weight-heterogeneous graph whose weaker but broader rich-club supports distributed electrical synchronisation. Only the AVA backward-command pair (AVAL/AVAR) functions as a dual-modal hub, bridging the chemical routing core and the electrical synchrony core. The strength–degree divergence of the gap-junction hubs (ALA, CANL/CANR as strength hubs but not rich-club members) demonstrates that strength- and degree-based definitions of “hub” are not interchangeable in weight-heterogeneous connectomes and should be reported together. These results provide a quantitative basis for understanding how a small nervous system can deploy two physically distinct signalling channels to achieve complementary—and only partially overlapping—organizational regimes.

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