Heterosynaptic plasticity rules induce small-world networks

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Abstract. Heterosynaptic plasticity is a form of 'off-target' synaptic plasticity where unstimulated synapses change strength. Although some theoretical work has explored its implications [7], its functions for brain learning remains unclear. Here we propose that one purpose of heterosynaptic plasticity is to encourage small-world connectivity [28]. Small-world topologies are ubiquitous in natural and biological networks, such as the brain [3], and have been shown to exhibit increased computational efficacy, efficiency, and robustness [28]. We used numerical and mathematical analysis to compare the evolution of fully-connected abstract weighted graphs under different plasticity rules (homosynaptic, competitive heterosynaptic, and cooperative heterosynaptic), and found that they yield distinct network architectures. In simple distributions of network activity patterns, heterosynaptic plasticity-based learning — in contrast to Hebbian-style homosynaptic learning — not only reduces the over-saturation of synaptic weights, but causes the networks to rapidly converge to small-world topologies. We find that under a variety of constant neural activities, different cooperative and competitive heterosynaptic rules can promote small-worldness, and we demonstrate the combinations of patterns of neural activity and specific heterosynaptic rules which promote the strongest measure of small-world quality. Finally, we implement more realistic and plausible network dynamics using weight-dependent activities, and show that in this context specific combinations of heterosynaptic rules continue to promote and maintain interesting small-world network structures.

Keywords: network structure, topology, small-world, heterosynaptic plasticity, neural activity distributions

1 Introduction

The link between structure and function in networks of complex systems is definitive, but a clear and comprehensive understanding of it is nevertheless elusive [22]. Network structures have been shown to have implications for the dynamics, behaviour, or functions of the network in question [23] [4], such as in efficiency and economy, memory capacity, enhanced signal-propagation speed, and resistance to potential damage [28] [20]. A structural feature that has been identified

as important for the function, efficiency, and robustness of networks is what is termed "small-world" characteristics [28], [3]. Small-world networks exhibit high degrees of local clustering and low average shortest path length. These features encourage efficient but effective information processing and computation. Small-world characteristics have been identified in biological neural networks [2] [3].

An issue of interest in the intersection between network structure and function is that of synaptic plasticity. Studies have demonstrated plasticity's involvement in networks, such as in homeostasis, hub formation, efficient information processing [27], improved network noise robustness and task performance [26], and maintenance of networks in health and disease [25] [1]. Synaptic plasticity, by dynamically altering the strength and efficacy of synaptic connections, plays a crucial role in the brain's ability to adapt and reorganise in response to various stimuli and experiences. This adaptability underpins critical processes like learning and memory, and it may enable the brain to maintain optimal functionality amidst changing internal and external environments. This research analysed heterosynaptic plasticity – a version of plasticity which operates on unstimulated synapses – and its implications for small-world network structure.

2 Background: Plasticity and Network Structure

Synaptic plasticity is a fundamental property of synapses and occurs in a variety forms [7]. It refers to a synapse's ability to change its size, function, activity, or efficiency in response to neural activity. Synaptic plasticity is believed to be the foundational mechanism underlying learning, memory, attention, and information processing in the brain [6]. In particular, it has been identified as a key player in the interplay of network structure and function [1] [25], and many aspects of its role in this area remain to be uncovered.

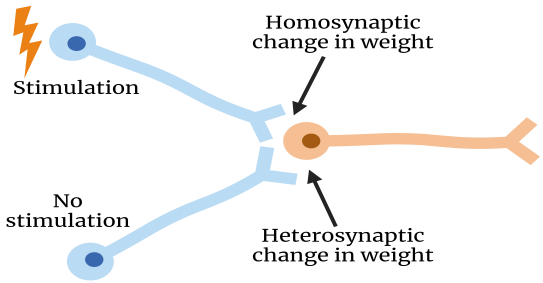

Fig. 1. Homosynaptic and heterosynaptic plasticity

There are two predominantly recognised forms of synaptic plasticity: homosynaptic and heterosynaptic (see Figure 1). Homosynaptic plasticity occurs at the

synapses that were active/stimulated and is primarily regulated by Hebbian-type learning [11]. This form of plasticity, often encapsulated in the adage "cells that fire together wire together", has received substantial theoretical and experimental support. Hebbian plasticity emphasises the necessity of concurrent activity in both pre- and postsynaptic neurons for plasticity induction, which strengthens the synaptic connections between co-active neurons, for instance by multiplicative or spike-timing-dependent plasticity rules [12] [18]. This version of synaptic plasticity is indubitably linked with network structure through its formation and regulation of weighted connections. However, despite its foundational role in learning and memory, several challenges persist with this mechanism.

Heterosynaptic plasticity refers to the ability of synapses that were not directly activated to undergo weight alterations, and may be understood as an "off-target" version of plasticity. This form of synaptic plasticity presents a promising solution to the deficiencies inherent in homosynaptic plasticity, and may provide additional insight into the brain's memory and signal processing capacities. Heterosynaptic plasticity has been experimentally observed [24] [15], and the neurobiological mechanisms whereby it acts are continuing to be uncovered — including intraneural molecular mechanisms, and interneural molecular and cellular mechanisms. This version of plasticity is posited to serve several critical functions, such as balancing synaptic changes, counteracting runaway dynamics and ensuring that synapses retain their specificity. Furthermore, it may enhance competition between synapses, which is vital for the selective strengthening and weakening of synaptic connections, thereby addressing the issues present in a solely Hebbian-based paradigm [29]. Other research has identified roles such as pattern separation, memory specificity, increased signal-to-noise ratio, homeostasis, functional clustering, and optimisation of network structure [6] [7].

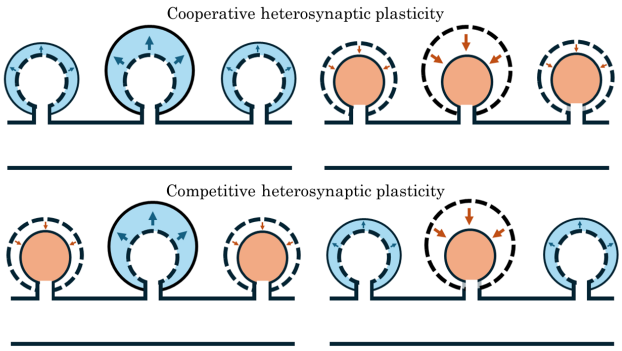

Fig. 2. The various directions of heterosynaptic plasticity weight changes; in all four cases, the central synapse is undergoing homosynaptic plasticity, while the two neighbouring synapses are being heterosynaptically altered.

Heterosynaptic plasticity may assume either a **cooperative** or **competitive** role in the alteration of synaptic weights. Figure 2 illustrates the multiple directions in which unstimulated synaptic weights may develop. Cooperative plasticity refers to the instances where the heterosynaptically altered synapses change in the same direction as the homosynaptically altered synapse, and competitive plasticity is when the directions of change are opposite. However, it is not clear what factors or protocols determine whether biological synapses will undergo competitive or cooperative heterosynaptic plasticity [6]. These differences in weight change may have fundamental implications for network structure and play vital roles in the optimising of function. Another noteworthy feature of heterosynaptic plasticity function is its operation over both fast/local and slow/global temporal and spatial scales. It can operate locally on single dendrites at neighbouring spines, or across neurons and whole networks [6] (see Figure 3).

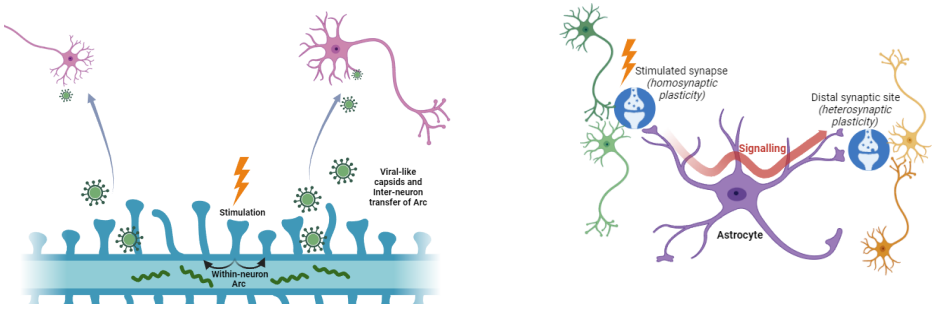

Fig. 3. Example possible biophysical mechanisms of intra-neuron, inter-neuron, and network-wide mediation of heterosynaptic plasticity through Arc protein (left) [21] and astrocytes (right) [9].

A vital aspect of synaptic plasticity is its role in shaping and maintaining network structure [25] [13]. Plasticity plays a large part in the organisation of neural networks, perhaps in response to experiences, learning, and stimuli, and possibly with a view to optimising functionality and processing capacities [8]. Synaptic plasticity, therefore, is a key player in the area of network structure and function. Much remains to be uncovered regarding heterosynaptic plasticity's part, in particular, in forging and maintaining optimal network topologies.

3 Methodology

In this section we outline the methodology adopted in this study. Firstly we discuss the simple plasticity model in abstract weighted graphs, the learning/update rules, and the network activity patterns based on probability distributions. We present the requisite graph theoretic measures required for the analysis. And

finally, we delineate an extension to the network dynamics, namely in a weight-dependent activity pattern paradigm, and develop a "hybrid" heterosynaptic plasticity rule, which incorporates elements of cooperative and competitive updates in the one network.

3.1 Model of Plasticity Rules

Given a weighted graph, we define three possible cases for the weights/edges while the network is in a state of activity. At any given time point, each edge is either

(1) between two active nodes,
(2) between one active and one inactive node, or
(3) between two inactive nodes.

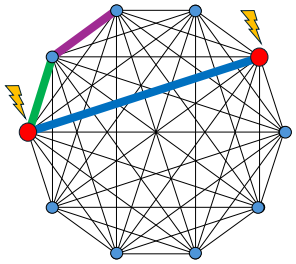

Fig. 4. Three cases for plasticity rules.

Based on these cases, we define the update/plasticity rules:

$$R_1 = \left\{ \begin{array}{ll} w_{i,j_{n+1}} = w_{i,j_n} + \eta_1(1 - w_{i,j_n}) & \text{Case (1)} \\ w_{i,j_{n+1}} = \eta_2 w_{i,j_n} & \text{otherwise} \end{array} \right\} \tag{1}$$

$$R_2 = \left\{ \begin{array}{ll} w_{i,j_{n+1}} = w_{i,j_n} + \gamma_1(1 - w_{i,j_n}) & \text{Case (1)} \\ w_{i,j_{n+1}} = \gamma_2 w_{i,j_n} & \text{Case (2)} \\ w_{i,j_{n+1}} = \gamma_3 w_{i,j_n}, & \text{Case (3)} \end{array} \right\} \tag{2}$$

$$R_3 = \left\{ \begin{array}{ll} w_{i,j_{n+1}} = w_{i,j_n} + \kappa_1(1 - w_{i,j_n}) & \text{Case (1)} \\ w_{i,j_{n+1}} = w_{i,j_n} + \kappa_2(1 - w_{i,j_n}) & \text{Case (2)} \\ w_{i,j_{n+1}} = \kappa_3 w_{i,j_n}, & \text{Case (3)} \end{array} \right\} \tag{3}$$

where R_1 is a homosynaptic rule (with potentiation at active synapses), and R_2 and R_3 are versions of competitive and cooperative heterosynaptic rules, respectively. The formulation of these rules ensures that weights are bounded between 0 and 1. The parameters η_i, γ_i and κ_i are the learning rates. We set these throughout the study to

$$\eta_1 = \gamma_1 = \kappa_1 = 0.2$$
$$\eta_2 = 1 - \eta_1 = 0.8 \qquad \gamma_2 = 1 - \gamma_1/2 = 0.9$$
$$\eta_2 = \gamma_3 = \kappa_3 = 0.8 \qquad \kappa_2 = \kappa_1/2 = 0.1$$

although, different values of update rates give similar qualitative results.

3.2 Activity Patterns on the Network

The activity of neural networks can often be described in terms of a distribution, whether that be a distribution of firings rates, interspike intervals, bursts, or network synchrony. These aspects of network activity are frequently seen to take the form of a log-normal distribution [5]. A distribution of firing rates, for example, may then be transformed into a distribution of probabilities; that is, instead of describing the average firing rate of every neuron, we can describe at every timestep the probability of that neuron being active. This enables us to define a set of "neural activity patterns" using probability distributions. We adopt the Beta distribution, which has compact support between 0 and 1, and allows us with varying parameters α and β to encapsulate a variety of possible activity pattern probability distributions. Figure 5 demonstrates some example Beta distributions.

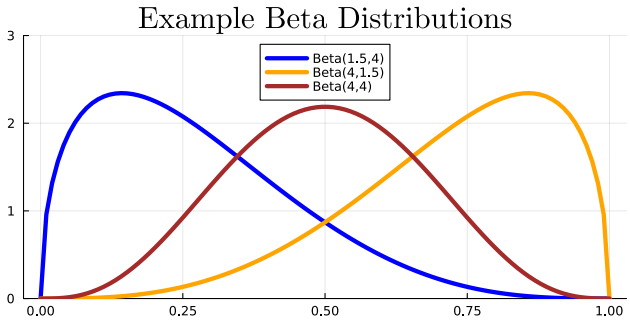

Fig. 5. Example Beta distributions which can be used to describe network activity probability distributions

3.3 Graph Theoretic Measures

We used the following measures on the networks: weighted clustering coefficient, average shortest path length, and small-world measure. The clustering coefficient is a measure of the degree to which nodes in a graph tend to cluster together. The weighted clustering coefficient [19] we used is:

$$\tilde{C} = \int_0^1 C_t \, dt \tag{4}$$

where $C_t = C(A_t)$ for $A_{ij}^t = 1$ if $w_{ij} \geq t$ and 0 otherwise. The local clustering measure C is given by [28]

$$C(i) = \frac{|\{e_{jk} : v_j, v_k \in N_i, e_{jk} \in E\}|}{k_i(k_i - 1)} \tag{5}$$

This is intuitively the proportion of the number of links between the vertices within a node's neighbourhood divided by the number of links that could possibly exist between them.

Average shortest path length is a network topology concept that measures the average number of (weighted) steps along the shortest paths for all possible pairs of nodes in the network. It is a way of measuring the efficiency of information or mass transport on a network. We utilise Dijkstra's algorithm [10] to find the path lengths d_{ij} and then compute:

$$L = \frac{1}{n(n-1)} \sum_{\substack{i,j \in V \\ i \neq j}} d_{ij} \tag{6}$$

These measures of clustering and average shortest path length are then used to find the measure of small-world characteristic [28]. This is a coefficient which seeks to capture the ratio of the clustering and average shortest path length of the graph of interest with an equivalent, random graph. It is given by:

$$\sigma = \frac{\tilde{C}/\tilde{C}_{\text{rand}}}{L/L_{\text{rand}}} > 1 \tag{7}$$

where $\tilde{C}, L$ denote the clustering and average shortest path length of the network in question, and $\tilde{C}_{\text{rand}}, L_{\text{rand}}$ represent the same measures of an equivalent, random graph.

3.4 Analytic Solutions

For the constant activity patterns we define with set probability distributions, given the probability distribution of activity, we can find a closed-form solution for the final resultant weight matrices:

$$\text{R1: } w_{i,j}^{\infty} \approx \frac{\eta_1 p_{ij}}{1 - (p_{ij}(1 - \eta_1 - \eta_2) + \eta_2)} \tag{8}$$

$$\text{R2: } w_{i,j}^{\infty} \approx \frac{\gamma_1 p_{ij}}{1 - (p_{ij}(1 - \gamma_1 - 2\gamma_2 + \gamma_3) + q_{ij}(\gamma_2 - \gamma_3) + \gamma_3)} \tag{9}$$

$$\text{R3: } w_{i,j}^{\infty} \approx \frac{(p_{ij}(\kappa_1 - 2\kappa_2) + \kappa_2 q_{ij})}{1 - (p_{ij}(-1 - \kappa_1 + 2\kappa_2 + \kappa_3) + q_{ij}(1 - \kappa_2 - \kappa_3) + \kappa_3)} \tag{10}$$

where $p_{i,j}$ is the probability of node i and node j being active, and $q_{i,j}$ is the probability of node i or node j being active. These allow us to calculate graph-theoretic measures on the final resulting weight matrices.

3.5 Weight Dependent Activity

In order to examine the effect of heterosynaptic plasticity rules on networks with non-constant activity, we alter the network probability to be dependent upon the neural weights. In this case, we define the probability of a node's activity/firing to be proportional to the accumulation of its total weights. This is given by

$$P(\text{node}_i \text{ active }) \propto \frac{\sum_{\substack{j=1 \\ j \neq i}}^{N} w_{ij}}{(N-1)} \tag{11}$$

3.6 Hybrid Heterosynaptic Rule

In order to test whether or not a specific combination of cooperative/competitive heterosynaptic plasticity might give even greater small-world measures, we introduced a "hybrid" rule. This rule induced cooperative plasticity when the neurons were relatively silent or sparse in activity (e.g. $P(\text{node}_i \text{ active}) < 0.5$), and competitive when the neurons were highly active (e.g. $P(\text{node}_i \text{ active}) > 0.5$). This was informed by insights from comparing the different activity patterns (see results in Section 4.3). We implemented this rule in the weight-dependent activity pattern, to investigate the dynamics of activity and weight change, as well as the resultant small-world structures.

4 Results

4.1 Evolution of Network Structures

We firstly implemented a pattern of activity with positively skewed heavy-tailed probability distribution (Beta(1.5,4)) in a network of 50 neurons. This mimics the statistics of log-normal firing rates [5]. Below is a simulation (across 100 trials) of how the network characteristics evolve in this activity under the homosynaptic ($R1$ left) and competitive/cooperative heterosynaptic ($R2$ middle, and $R3$ right) plasticity rules.

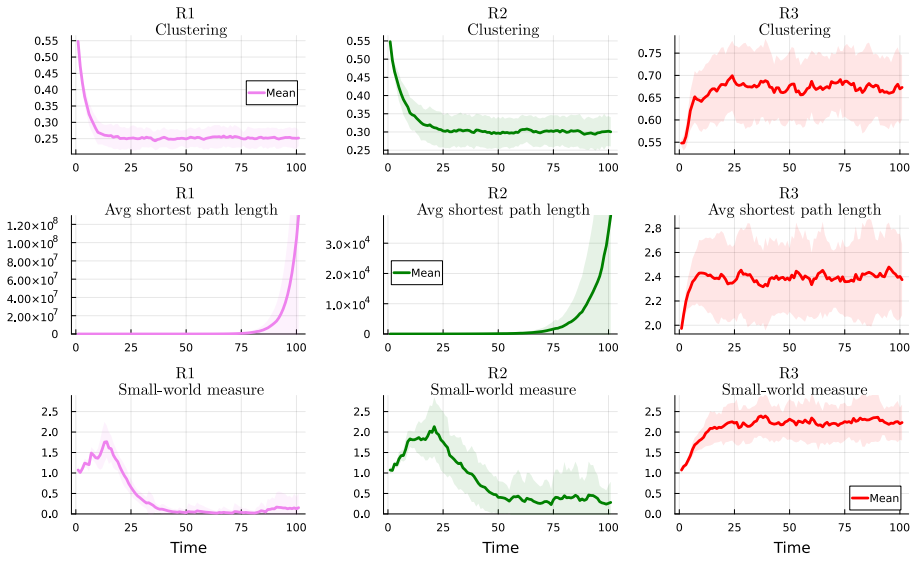

Fig. 6. Graph theory measures for the three plasticity rules (N = 50 nodes).

Rule 1 (left) and Rule 2 (middle) display similar qualitative characteristics: their clustering coefficients decrease, while their average shortest path lengths

rapidly and exponentially explode. The absolute values of clustering and shortest path length do not significantly matter here, but rather their values *relative* to equivalent random graphs. The small-world coefficient (bottom) row captures this. $R1$ and $R2$ show transient small-world qualities, but these decrease, indicating that their resultant topologies are not small-world in nature. On the other hand, Rule 3 (right) shows an increased clustering, and while the average shortest path length increases, it converges to a stable value. The small-world measure increases significantly beyond 1 and likewise stabilises, indicating that the cooperative heterosynaptic rule ($R3$) induced a small-world topology.

Another indicator of small-worldness is found in the distribution of node degree. Small-world networks contain a number of nodes that are highly interconnected, forming "hubs". We therefore examined the final distribution of the network weights as well as the weighted node degrees in the three plasticity rules under the Beta(1.5, 4) activity.

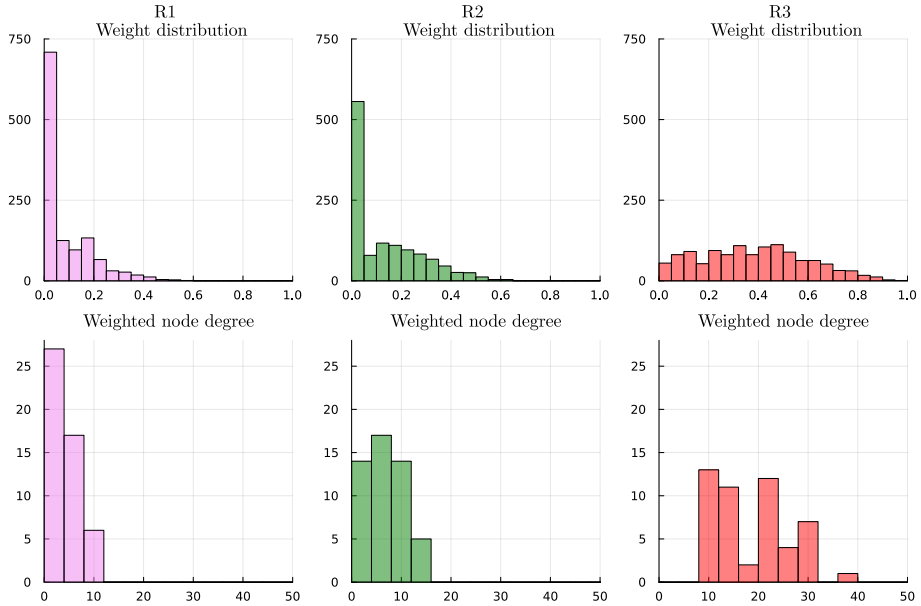

Fig. 7. Weight and weighted node degree distributions (N=50 nodes).

In $R1$ and $R2$, we found that the weights and node degrees saturate towards 0. However, the distribution of weights in $R3$ (Figure 7 top right) shows a preserving of a greater spread of weights, with the distribution approximating log-normal, which is observed in neural data for synaptic weights [16], [17] (see Figure 8). The presence of some highly weighted node degrees in Rule 3 (Figure 7 bottom right) gives further support to the fact that it possesses a small-world quality.

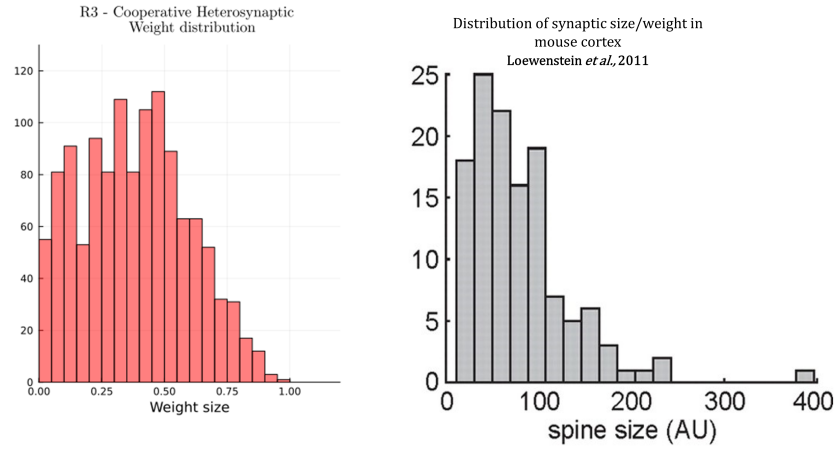

Fig. 8. A closer look at the weight distribution from Rule 3 (left); Example log-normal distribution of spine (synapse) size from mouse cortex (right)

4.2 Scaling the Network Size

We then tested the outcomes on larger networks with the Beta(1.5,4) activity pattern. $R1$ and $R2$ fail to exhibit small-world characteristics across increasing network size, whereas for $R3$ a strong small-world coefficient is consistently present.

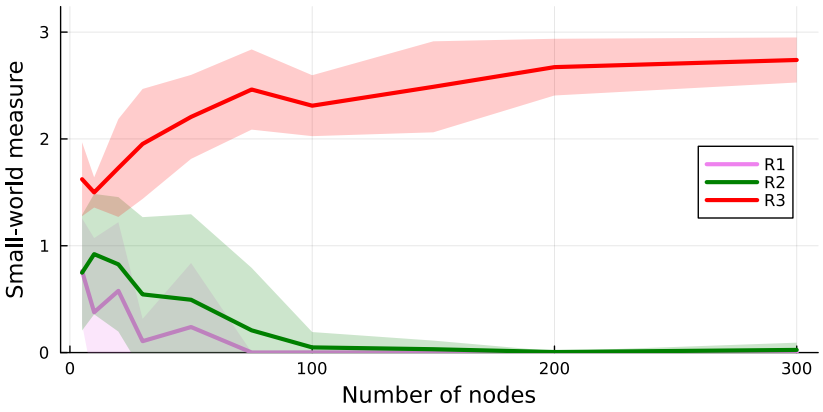

Fig. 9. Small-world measures across different sizes of networks.

4.3 Analysing Different Activity Patterns

We investigated the effects of the three plasticity rules in networks across *different* Beta activity pattern probability distributions in networks of 100 nodes, across 100 trials. These included the Beta(1.5,4) activity pattern already used, but also four more, namely: Beta(1,1), Beta(4,1.5), Beta(0.5,0.5), and Beta(4,4) (see Figure 10). These distributions ostensibly capture in a simple manner varying types of network activity.

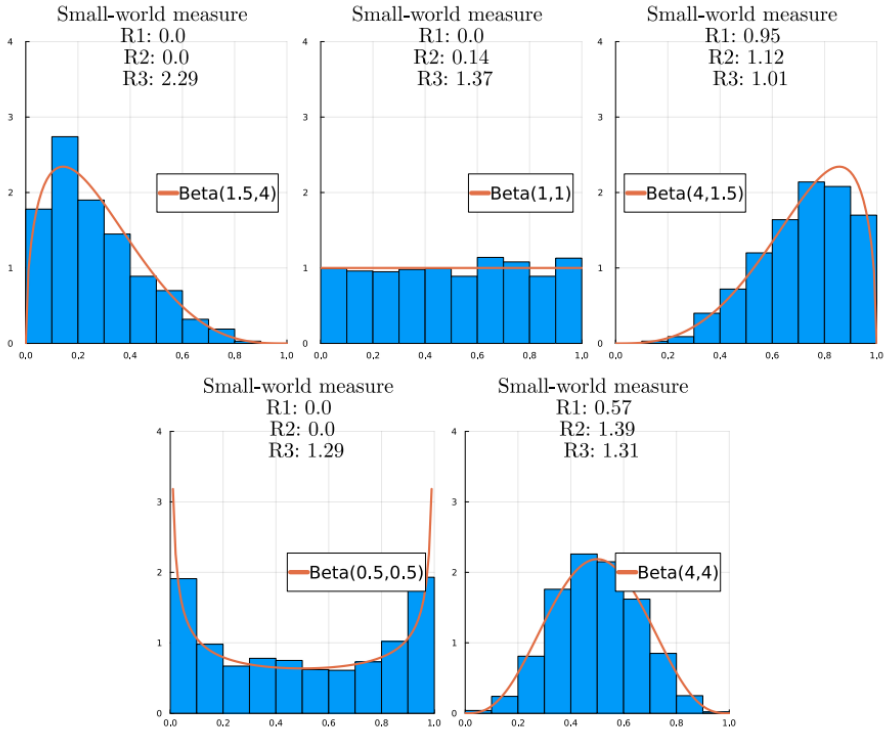

Fig. 10. Average small-world measures across different activity patterns (N=100 nodes).

In all cases of activity, the solely homosynaptic paradigm fails to promote small-world characteristics. On the other hand, the cooperative heterosynaptic plasticity rule (R3) yields small-world topologies in all activity patterns. Interestingly, in distributions where patterns are shifted toward the middle (Gaussian distribution) or shifted right (i.e. greater activity, negatively skewed distribution), such as with Beta(4,1.5) or Beta(4,4), the ***competitive*** heterosynaptic rule (R2) induces a greater degree of small-world qualities in resultant networks.

4.4 Weight-dependent Activity Pattern

Whenever we simulate the three rules with a network activity dependent on the weights, similar results emerge as with the pre-defined and constant activity patterns (see Figure 11). However, the most notable difference is that the small-world measure for the cooperative heterosynaptic plasticity rule is higher than in the case with constant pre-defined activity patterns. This may be due to the fact that basing the activity of the network proportional to the accumulations of weights on each node tends to create a positive feedback loop, where highly weighted nodes become more likely to be active, thus strengthening even further. This kind of activity is likely to encourage the formation of highly clustered hubs in the graph, thus yielding a high small-world coefficient.

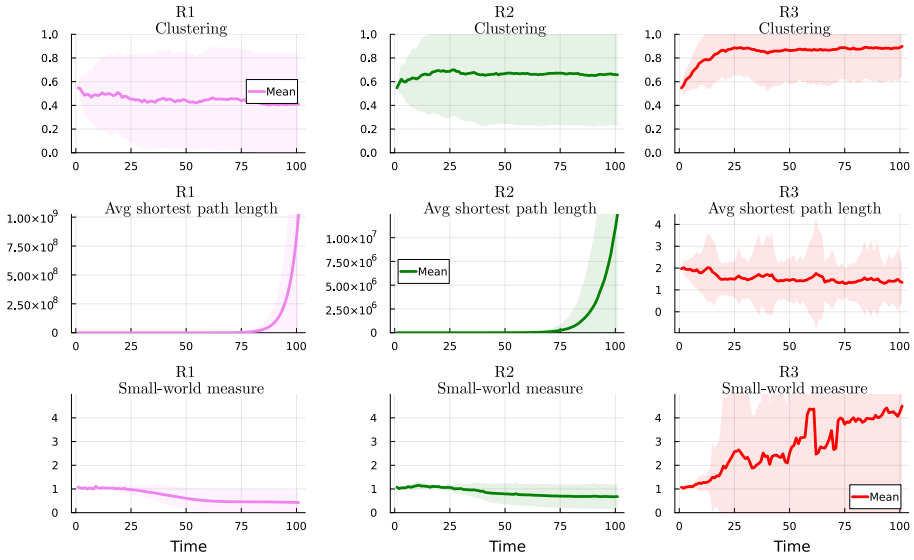

Fig. 11. Graph theory measures for the three plasticity rules where the network activity is variable, dependent on the network weights (N = 50 nodes).

Rule	Mean small-world measure
R1	0.3
R2	0.7
R3	4.0

Table 1. Average small-world coefficients for the 3 plasticity rules in variable weight-dependent network activity.

4.5 Hybrid Heterosynaptic Rule

We investigated the role of a "hybrid" heterosynaptic plasticity paradigm, where a combination of **cooperative** and **competitive** updates was present. From the results across different constant activity patterns, we hypothesised that cooperative plasticity might be optimal in patterns of sparse activity, while competitive plasticity might be optimal in patterns of higher activity (see Figure 10). We implemented this hybrid rule in a weight-dependent activity pattern, to examine the dynamics that would emerge, and the resulting structural characteristics.

We found that the hybrid heterosynaptic rule yields a higher measure of small-world characteristics than the solely cooperative and solely cooperative heterosynaptic rules (Figure 12 top row). We examined the costliness of the networks at each time step by summing the weights (Figure 12 bottom row); interestingly, the hybrid network not only gives a higher small-world coefficient, but also manages to maintain a more efficient or economical network, which is evident from the smaller sum of graph weights.

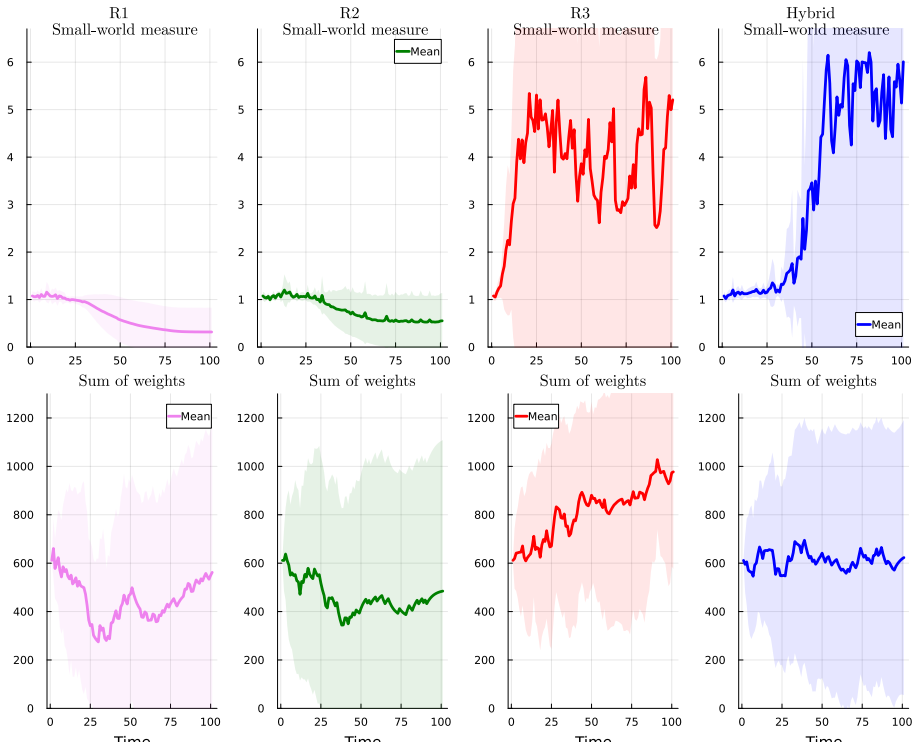

Fig. 12. Small-world measure (top row) and sum of network weights (bottom row) in the homosynaptic(R1), competitive heterosynaptic (R2), cooperative heterosynaptic (R3), and hybrid heterosynaptic rules (N=50 nodes).

5 Discussion

This research sought to investigate whether heterosynaptic plasticity has any role in encouraging and maintaining small-world topologies. In a baseline neural activity pattern (with a positively skewed, heavy tailed probability distribution), a **cooperative** heterosynaptic plasticity rule does indeed induce small-world characteristics (based on the measure proposed by [28]), across various network sizes (Figure 9). Homosynaptic and competitive heterosynaptic rules in this activity pattern show transient small-world properties, but these rapidly disappear (Figure 6). An examination of the distribution of weights and weighted node degrees of final resultant graphs (Figure 10) further lends support to the claim that the **cooperative** heterosynaptic rule creates small-world networks, owing to the presence of highly clustered hubs. These final weight distributions furthermore demonstrated that the cooperative heterosynaptic rule tends to produce a set of final weights and weighted nodes similar to that seen in real biological data (Figure 8).

Comparison of the resulting graph theoretic measures across several network activity patterns reveal some interesting facts. The homosynaptic rule always fails to give rise to small-world properties, while the **cooperative** heterosynaptic plasticity rule always produces small-worldness, albeit of differing magnitudes. Networks with the **competitive** heterosynaptic plasticity rule emerge with higher small-world measures in some instances. These cases occur when the activity of the network is shifted towards the middle (normally distributed probabilities, Beta(1,1)) or shifted right (negatively skewed distribution, Beta(4,1.5)). That is, whenever a greater proportion of the network is active, the **competitive** rules appears to induce a better small-world topology than the cooperative rule. This may offer insight into the various circumstances/protocols wherein neural networks in the brain implement a cooperative versus competitive heterosynaptic change. In activity patterns where the majority of firing rates are low, a cooperative heterosynaptic rule encourages a greater small-world property, but perhaps when network activity increases and a greater proportion of neurons become active, the competitive heterosynaptic rule may be implemented to stabilise the network properties and continue to maximise the small-world topology. This was tested with the hybrid heterosynaptic plasticity rule.

We investigated the role of the three plasticity rules where the activity of the network was variably dependent on the weights of nodes. This is arguably a more realistic scenario, where those neurons with greater accumulations of weights are more likely to be active, and those with few/weaker connections are more likely to be silent, or sparse in activity. We found that the homosynaptic and competitive heterosynaptic plasticity rules fail to produce small-world characteristics. However, the cooperative heterosynaptic rule induces distinctive small-worldness (even stronger than in the previous constant pre-defined activity patterns). This may be due to the fact that the framing of neural activity in this weight-dependent way tends to preferentially involve a small subset of nodes (which have higher weights) in the activity, generating a feedback

loop which encourages high degrees of clustering around these neurons, forming highly-interconnected hubs.

Finally, this study introduced a simple hybrid heterosynaptic plasticity rule which combines cooperative and competitive learning under different activity contexts. This resulted in graphs with higher small-world qualities than in any of the other rules ($R1, R2, R3$). Importantly, this hybrid rule also kept the cost of the network lower (i.e. more economical in terms of total network weights) than that of the next best small-world inducing rule ($R3$). This has promising implications for understanding not only the functions of heterosynaptic plasticity, but the neural protocols and contexts in which various versions of this plasticity are induced.

6 Conclusion

This research explored variants of plasticity rules in abstract weighted graphs with a view to understanding their impacts upon network structure. We utilised highly simplified versions of update rules and network activities, which allowed for a tractable examination of the roles of different plasticity paradigms in different network activity patterns. We demonstrated that heterosynaptic plasticity may be a key player in neural networks for promoting and maintaining small-world characteristics, and that competitive/cooperative aspects may have prioritised roles depending on the kind of network activity. We showed that a hybrid heterosynaptic plasticity rule may have the potential under certain constraints to optimise graph properties such as small-world qualities and economy. These insights may be useful for better understanding aspects of brain learning, as well as potentially optimising network structure for artificial intelligence and machine learning contexts.

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