

A selective diffusion model of brain network activity

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Abstract

Connectomics has made progress in elucidating the structure and functional significance of anatomic brain networks. Yet researchers are only beginning to consider design principles that support efficient routing on such networks. In engineered networks, packet switching was developed to efficiently support fast, asynchronous, sparse activity. However, little work has considered routing architectures that would be best suited to operational demands such as the need for reliability and to the constraints of sparse activity, low energy budgets, and small or non-existent node buffers. In this context, we constructed a selective diffusion model inspired by packet-switched architectures. We focus in particular on a model germane to visual system function, though we simulate activity on the entire macaque connectome. We use an agent-based system to address how the brain could trade off among sparseness, message loss, buffer size, and speed. We find that when nodes have no buffer, overall speed and population sparseness are maximal, but there is high message loss (>50%). Small buffers lead to modest reduction in speed, but drastically reduced message loss. However, population sparseness is comparable to physiological values across buffer size, suggesting that selective diffusion could be an efficient solution to brain-wide communication.

Keywords: connectome; sparseness; selective diffusion

Background

A fundamental fact about biological communication systems is that their basic scheme cannot be easily changed once a system is in place: they must be functional and stable for all nodes that can communicate with one another (Graham and Rockmore, 2011; Graham 2014; 2017). In the mammalian cortex, all neurons appear to have the capacity to communicate rapidly with essentially any other cortical neuron given the brain's small-world topology. Thus, we propose that there exist mechanisms for the selective routing of messages in the mammalian brain, which are fundamental to brain function. Numerous specific questions regarding functional and physiological phenomena in the brain can be

approached from this perspective. For example, how does the visual system achieve selectivity and invariance for object recognition? An early, detailed model of selective routing (Olshausen et al., 1993) addressed precisely this question, along with related ones (see also Wiskott, 2006). Indeed, many visual system functions such as attention and visual field remapping likewise appear to require these kinds of mechanisms, as first noted by Poggio (1984).

However, the need for fast, selective routing is also recognized in areas beyond the visual system, such as during imagination (e.g., “mental workspace” models). Functional tasks such as decision making—for which current models generally consider only the process of weighing evidence—can also be approached in terms of how a given neuron or group of neurons choose selectively among divergent output paths. In addition, it has long been suspected that brains quickly and selectively route signals from one path to another following lesion; functional reallocation could thus be conceived as a form of selective routing since reorganization has been observed within hours of lesion.

Current Models of Brain Network Dynamics

Connectomics has made progress in elucidating the structure and functional significance of anatomic brain networks (see, e.g., Bullmore and Sporns, 2012; Fornito et al., 2016). Recently, there has been increasing interest in the dynamics that could operate on such networks (Avena-Koenigsberger et al., 2018a,b; Misic et al., 2014a,b; 2018; Navlakha et al., 2015; 2017). However, a given topology can support a range of routing protocols. To date, little work has considered the kinds of routing architecture that would be best suited to the structure and functional demands of brain networks. In particular, previous models have largely ignored the need for fast, flexible, efficient, and reliable communication among widely distributed nodes.

Following Fornito et al. (2016), current models of network dynamics on brain-like networks fall into two general categories: *diffusion models* and *navigation models*. These models roughly reflect classical and alternative frameworks of neural communication, respectively. Diffusion models (e.g., Goñi et al., 2014) often assume that brain-wide communication is performed by an agglomeration of relatively simple, linearly summed elements. Summation is reasonable given that dynamics in isolated neurons can be predicted well. However, the dynamics of single neurons in

the brain in response to natural stimuli remain poorly understood (Olshausen and Field, 2005). While diffusion models may capture important aspects of spiking dynamics—and while brain networks undoubtedly perform some “broadcast”-like communications that resemble diffusion—we argue that existing models ignore critical features of brain dynamics that may be essential to efficient communication among dispersed, interconnected neurons. In particular, diffusion models of large scale activity—which have no active means for limiting the transmission of activity—would appear to be wastefully inefficient if employed globally given the highly constrained energy budget of the brain. Estimates for individual neurons over time, and for populations of neurons at a given time, activity must be less than 10% of the possible total (Attwell and Laughlin, 2001; Lennie, 2003). In contrast to diffusion models, efficient neural systems appear to require sparse activity both to conserve energy, and to take advantage of sparse inputs (see e.g., Graham and Field, 2006).

Given that canonical estimates of characteristic path length between any two cortical neurons is around 3 synapses, the potential for signals to travel considerable network distances to reach their destination is high, especially in brains with billions of neurons and trillions of synapses. For diffusion models, not only are signals usually subject to random path assignments, they are also highly redundant, since the same signal is propagated along many channels.

An alternative is navigation models, whereby messages are conveyed along a particular path. There is now substantial neurophysiological evidence that signals are propagated at great speed along selective paths, even without appealing to exotic routing protocols. Signals in lateral geniculate, for example, can travel to cortex and back to their origin in as little as 37 msec (Briggs and Usrey, 2007). Since thalamus is regarded as a central switchboard of the brain (Sherman, 2008), it thus appears that the brain’s fundamental dynamics may be built around selective path choice, as well as speed.

At the same time, diffusive processes have advantages in terms of communication reliability by dint of their redundancy, which have heretofore gone unrecognized. If signals diffuse, travel by random walks, or are more selectively routed, it may pay to have many copies of the same signal to ensure delivery. For example, though the goal of sensory coding appears to be in part to reduce redundancies in the input (Graham et al. 2006), it is clear that redundancies in sensory inputs are retained to a substantial extent in visual system activity. While the role of correlated activity has been debated in terms of the additional information throughput carried, such redundancies have not to our knowledge been considered as an error correction scheme for intra-brain communication.

Therefore, we introduce a *selective diffusion* model that aims to take advantage of the benefits of both diffusion and navigation. The model is inspired by engineered packet-switching communication systems, which are also a compromise between diffusion and navigation: they are selective in terms of pathfinding, but redundant because a

given message may utilize several paths. Such systems have established basic design principles for supporting fast, robust, efficient communication among billions of nodes on small-world networks (Graham and Rockmore, 2011; Graham, 2014). For example, packet-switched systems have allowed largely uninterrupted, exponential Internet growth, to the point where there are now more Internet hosts than there are neurons in the macaque cortex (Graham, 2017). In addition, engineered systems like the Internet highlight the critical need for error correction on networks. This need has gone mostly unrecognized in brains, and is salient given that brains are known to “lose” messages (due to synaptic failure, for example).

The Selective Diffusion Model

The purpose of this model is to capture the essential features of brain network *communication*, much as artificial neural networks (ANNs) such as the Perceptron attempt to capture the essential features of brain network *representation*. Our model, like most ANNs, is thus abstract compared to spiking neuron models, but seeks to capture fundamental activity dynamics and mechanisms.

At a conceptual level, messages are chopped into packets that each attempt to reach an intended target. Each packet potentially takes a different path, and each node requires the ability to buffer some number of packets in a queue. Such protocols were engineered for use in computer networks specifically to efficiently transmit sparse, asynchronous, directed signals; this stands in contrast to alternatives like circuit-switching (e.g., traditional telephony), which was designed to transmit dense, synchronous, bidirectional signals (Kleinrock, 1976). However, the selective diffusion model also considers the question of whether “packeting” in general improves reliability via redundancy of messages.

Model Design

We use whole-brain connectivity data queried from the CoCoMac 2.0 database (Bakker, Wachtler and Diesmann, 2012). All edges are directed, and reciprocal connections are treated as distinct edges. Edge weights were queried as connected or unconnected (0 or 1) and only fully connected nodes (i.e., those with an in-degree and out-degree of at least 1) were included (193 nodes total). It is assumed that viable paths are known to the system, a scheme that is plausible given the notion of “routing by synchrony.” Pathfinding in our simulations is accomplished via a fast matrix exponential method. In particular, for any n -vertex graph that can be represented by adjacency matrix A , the fastest way to find average path length (l_A) is to utilize the powers of A . Let $p(M)$ be the number of non-zero entries in any matrix M , and

$$S_k = \sum_{i=1}^k A^i$$

then

$$l_A = \frac{p(A) + \sum_{k=2}^n k \cdot [p(S_k) - p(S_{k-1})]}{n}$$

For a given message between sender and receiver, paths are chosen as follows: At each sending node, packets are distributed among N shortest paths in inverse proportion to network distance; thus, packets are likely to take short paths, but not necessarily the same short path.

Simulations of the Model: Parameters

Simulations of the model are agent-based: each autonomous node is assigned a decision vector that operates on network state variables such as message input, network topology, etc. The system employs first in-first out queuing and attempts to send the equivalent of 4000 total messages (5 packets per message). At each time step, 18 messages are injected with randomly chosen sender and receiver and message-passing occurs as a Poisson process. Messages are tracked across the network using a custom-designed “jam board” that tracks paths and message parts.

Buffer size b was uniform for all nodes and was varied over $[0, 5, \infty]$. The packeting parameter (set to 5) controls the number of packets each message is divided into, and the related number of initial paths they are sent on. Alternatively, this design allows us to consider number of redundant copies of a “message” sent on potentially different paths. Activity per node/timestep is measured as the sum over edges with buffered messages counted once per buffer.

Simulations of the Model: Results and Discussion

Results of the simulations illustrate the trade-offs among buffer size, speed, activity, message loss, and sparseness, and are shown in Fig. 1. We note first that the high level of activity on networks with $b > 0$ may be implausible given limits of around 10% activity or less in real brains.

Speed to completion is highest when $b = 0$ but there is very substantial message loss of 63.26%. Thus, there are clearly tradeoffs among buffer size, speed, activity, and message loss. However, if real neurons are truly as limited in buffering capacity as current neurophysiological models predict, we expect substantial message loss in brains. This could necessitate error correction strategies that resemble those used on the Internet (e.g., small receipt messages like “acks”).

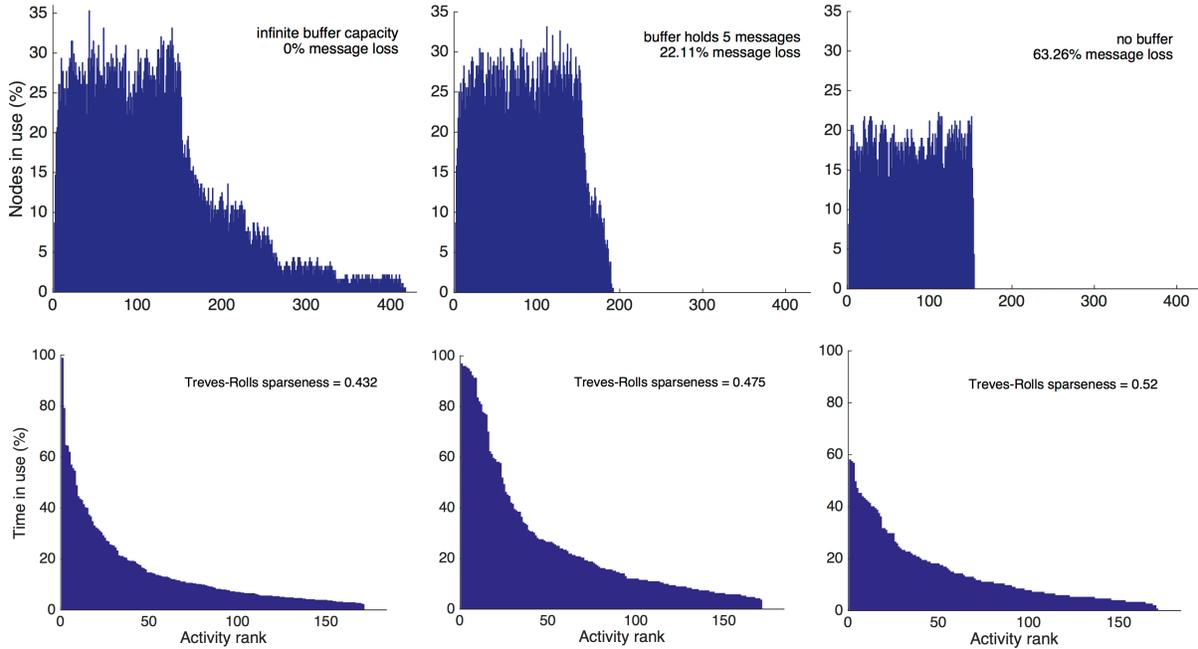


Figure 1: TOP: Activity of the network over time (x-axis in units of time steps), summed over nodes for three simulations that (from left to right) tested buffer sizes of ∞ , 5 total messages, and 0. Message loss (measured as a percentage of the total number of messages injected) is inset. BOTTOM: Rank order activity of the network per node, summed over time that tested buffer sizes as above (from left to right). Population sparseness is inset.

These results also suggest that systems with $b > 0$ tend to cause a smaller fraction of nodes to be active over the course of the simulation, which in turn results in higher population sparseness (as defined by Rolls and Tovee, 1995, population sparseness is 1 for Gaussian data, and maximum at 0; see also Graham and Field, 2006). However, all b values tested show

relatively high sparseness, and these values roughly match the range of empirical values in mammal visual cortex (0.36: Yoshida and Ohki, 2018; 0.60: Rolls and Tovee, 1995). We conclude that, as a general strategy in brain-like networks, selective diffusion may thus be advantageous as a compromise between diffusion and navigation models.

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