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Quasilinearization-based Controllability Analysis of Neuronal Rate Networks

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Abstract— **Recent interest has developed around the problem of assaying the controllability of networks in the brain. The analysis of such networks is highly nontrivial, owing to their overwhelming complexity. Thus, any controllability analysis must tradeoff against model complexity/explanatory power, and analysis tractability. Here, we consider a class of neuronal network models with nearly linear dynamics, whose primary complication arises due to a sigmoidal nonlinearity in the neuronal coupling. Exploiting the equivalence between the controllability gramian and the steady state covariance matrix of a linear system under white noise, we develop an approximate controllability analysis based on the method of stochastic linearization (quasilinearization). We show that for this relatively simple system, the quasilinear approach generates a significantly better characterization of controllability as compared with a Jacobian linearization. Our results provide a new tool for assessing controllability of networks with sigmoidal interactions, and, moreover, highlight the potential inaccuracy of linear characterizations of networks with even relatively mild nonlinearities.**

I. INTRODUCTION

An emerging line of research pertains to understanding the control properties, including controllability, of networks in the brain [1]–[4]. Understanding such propeties has intriguing implications for connecting brain network dynamics at multiple scales to information processing and function. Naturally, any approach to analyzing controllability of a system as complex as the brain must face the fundamental tradeoff between analytical tractability and model explanatory power. Characterization of brain network controllability has been carried out at macroscopic scales [1], via analysis of linear models fit to anatomical data; and at microscopic scales, via analysis of small networks of canonical spiking neuron models [3]. Reconciling these types of analysis across scale and interpreting them in the context of neurobiology is likely to be an active line of investigation over the next decade.

Several important frameworks for assessing controllability of nonlinear systems have been established in the latter half of the 20th century, most revolving around analysis of the Lie bracket (e.g., [5]–[7]). However, the depth of analysis associated with these methods makes their application to high-dimensional neural models challenging. More generally, the problem of tractably analyzing control properties of complex, nonlinear networked systems remains unresolved.

The goal of this paper is to develop an approximate controllability analysis for a class of firing rate models. Such models comprise an important class of dynamical systems models in computational neuroscience by providing a mean-field description of the spiking activity of neurons. They are appealing as they offer a relatively tractable description of neuronal activity, as compared to more detailed biophysical models, such as the classical Hodgkin-Huxley model that describe spiking processes. The main complexity in rate models is a sigmoidal nonlinearity that bounds the influence of neighboring neurons on each other. While relatively straightforward on the spectrum of possible nonlinearities, such functions nevertheless substantially complicate the deployment of exact analysis of controllability, particularly for large networks.

Here, we exploit the technique of stochastic linearization (or, quasilinearization) [2] to obtain an linear approximation of the rate network dynamics subject to a white noise input. The underlying concept behind this approach is the equivalence between the controllability gramian of a linear system and the steady-state covariance of such a system driven by white noise. We show that, indeed, quasilinearization can provide a highly accurate approximation of the fixed energy reachable sets of neuronal rate networks, thus enabling a characterization of network controllability. We verify that this approximation radically outperforms a simple Jacobian linearization in high variance (i.e., far from equilibrium) regimes.

This paper is organized in three parts: in the first part, we outline a methodology to approximate the controllability of a nonlinear neuronal network by introducing a vector of quasilinear gains, through which we linearize a set of nonlinear equations that govern the network dynamics. Then, we optimize the quasilinear gains stochastically based on the observation of how the responses of the neurons vary with the variances of white-noise input. This method enables us to approximate steady-state covariance of the nonlinear system. In the second part of this paper, we show that this approximation can serve as an accurate characterization of controllability. Finally, in the last part of this paper, we demonstrate the quality of the quasilinear approximation as compared with standard Jacobian linearization.

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II. PRELIMINARIES & METHODOLOGY

A. Neuronal Firing Rate Networks

We considered neuronal rate models, which describe the firing (spiking) rate ($spikes/time$, generally specified in Hz) of neurons in a population. Specifically, we considered rate models of the form:

$$\frac{dr_i}{dt} = \alpha_i r_i + \sum_{j=1}^{n} f_j(W_{ji} r_j) + I(t) \quad \text{for} \quad i = 1,2,3,...,n. \tag{1}$$

where r_i represents firing rate of the i-th neuron, α_i is the decay constant of the i-th neuron, f_i is a nonlinear function specific to the i-th neuron, and I is an external input to the system that is used to model background excitation, or noise. Here, we assume that I is common to all neurons, so that the same amount of external input current is injected to all neurons. The parameter W_{ji} describes the synaptic weight that couples neuron j to neuron i. Such a weight may be excitatory (positive) or inhibitory (negative). Typically, the non-linearity f_i is a sigmoid [8]. Such a sigmoid is important as it limits the influence of neighboring neurons, consistent with biological constraints.

B. Sigmoidal - Saturation Approximation

Typically, the sigmoid function f_i is modeled as a logistic sigmoid of the form:

$$f_i(x) = \frac{1}{1 + e^{-\alpha(x - x_{50})}} \tag{2}$$

where α determines how fast f_i increases as a function of x and x_{50} is the x for which f_i reaches 50% of its maximum value. Below, in the illustration of our methodology, we used a sigmoid with $\alpha = 4$ and $x_{50} = 1$ and replaced the sigmoidal nonlinearity (blue) with an odd piece-wise differentiable saturation function (red)

$$f_i(x) = \begin{cases} 0, & x < 0.5 \\ x - 0.5, & x \in [0.5, 1.5] \\ 1, & x > 1.5 \end{cases} \tag{3}$$

as shown in Figure 1. The nonlinearity (3) preserves the qualitative behavior of the function (2), while enabling a key analytical advantage due to its linear characteristic within the limits of saturation.

C. Approximate Controllability Analysis via Quasilinearization

1) Stochastic Linearization: The key methodology involves using stochastic linearization [9] to develop a linear approximation of the rate equations in the case of a white noise input. Briefly, stochastic linearization seeks, in essence, the expected value of the slope of $f_i(x)$, i.e. $E(\partial f/\partial x)$, the so-called '*quasilinear gain*'. In the case of a feedforward system, this expectation is the best linear approximation of $f_i(x)$ in the mean square sense [2], [9]. The method is referred to as 'quasilinearization' since, in constrast to standard Jacobian linearization, the linear approximation depends not simply on $f_i(x)$, but on all system parameters (via the expectation operation).

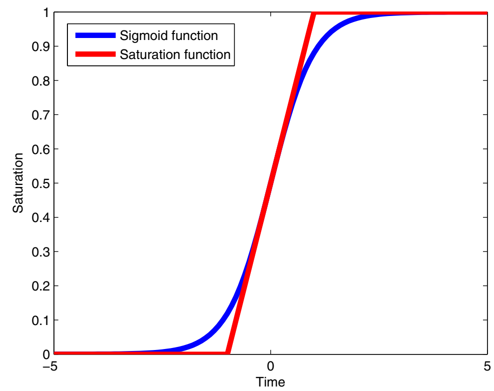

Fig. 1. Comparison of sigmoid function used in traditional model and saturation function used in our model.

Quasilinearization of the rate equations generates a vector $N \in \mathbb{R}^{(n\times 1)}$ of quasilinear gains. The general form of the quasilinear firing rate model is thus:

$$\frac{d\hat{r}_i}{dt} = -\alpha_i \hat{r}_i + \sum_{j=1}^{n} N_j W_{ji} \hat{r}_j + I(t) \quad \text{for} \quad i = 1,2,3,...,n, \tag{4}$$

where $\hat{r}_i$ are the approximate firing rates. The quasilinear gain N_j and the connection weight W_{ji} from the j-th to the i-th neuron are multiplied by the firing rate of each projecting neuron. Then, they are summed to represent the total post-synaptic input received by the i-th neuron in the network.

2) Converting (3) *to an Odd Nonlinearity:* As written, (3) is non-negative and, thus, prima facie our problem falls into the category of stochastic linearization with assymetric non-linearities [10], [11]. However, we can convert the problem to a more conventional quasilinear setup by assuming that the state variables r_i represent deviations from a nonzero baseline, so that $E(r_i) = 0$ under the assumption that $I(t)$ is zero mean white noise. In this case, x_{50} in (3) can be assumed to be zero, and the entire function is shifted to be centered at $x = 0$, i.e., (3) becomes an odd nonlinearity.

3) Computing the Optimal Quasilinear Gain: In order to find the optimal quasilinear gains, we need to determine the relationship between N_j and the distribution of $\hat{r}_j$. As described above, our goal is to approximate $f(r_j)$ with $N_j\hat{r}_j$ to minimize the following cost function [2].

$$\varepsilon(N_j) = E[(r_j(t) - \hat{r}_j(t))^2] \tag{5}$$

As developed in [2], when the input to the nonlinearity is zero mean and Gaussian, minimization of $\varepsilon(N)$ amounts to computing

$$N_j = E\left[\left. \frac{df(\hat{r}_j)}{d\hat{r}_j} \right|_{\hat{r}_j = \hat{r}_j(t)} \right] \tag{6}$$

which, under the quasilinear approximation of Gaussianity, reduces to

$$N_j = \int_{-\infty}^{\infty} E\left[\frac{d}{d\hat{r}_j} f(\hat{r}_j)\right] \frac{1}{\sqrt{2\pi\sigma_{\hat{r}_j}^2}} \exp\left(-\frac{\hat{r}^2}{2\sigma_{\hat{r}_j}^2}\right) d\hat{r} \tag{7}$$

where $\sigma_{\hat{r}_j}$ denotes the standard deviation of $\hat{r}$. In reality, r_j is not Gaussian, and thus, the formulation on the right hand side of (7) is the key point of the approximation. We notice that the above expression is equivalent to

$$N_j = erf(\frac{1}{\sqrt{2\sigma^2_{\hat{r}_j}}}) \tag{8}$$

A subtle, but absolutely crucial observation is that both the left *and* right sides of (8) depend on N_j. This is due to the fact that the distribution of $\hat{r}_j$, the approximate firing rate, itself depends on the quasilinear gain N_j. Thus, the final step is to solve (8) for all j.

4) Deriving Moment Equations of Stochastic Differential Equations: Finally, it is necessary to define the relationships between the variance of the input $I(t)$, denoted $\sigma_\eta{}^2$ and that of $\hat{r}$ in order to solve for the quasilinear gains. We accomplish this by computing the first and the second moments of the stochastic differential equations using Ito's formula. These moments can then be subtracted as shown below to determine the variance of the stochastic response.

$$Var(\hat{r}) = E[(\hat{r} - E(\hat{r}))^2] = E[\hat{r}^2] - (E[\hat{r}])^2 \tag{9}$$

We convert our quasilinear equations to stochastic differential equations of the form

$$d\hat{r} = a(\hat{r})dt + c(\hat{r})dBt \tag{10}$$

where $\hat{r} = \begin{bmatrix} \hat{r}_1 \\ \vdots \\ \hat{r}_n \end{bmatrix}$ for n neurons. Note that $c(\hat{r})$ is σ_η (from $I(t)$), while $a(\hat{r})$ will vary as a function of $\hat{r}$. We then use Ito's product rule to obtain expected values to get the second moment of the i-th neuron [12].

$$\frac{dE[(\hat{r}_i)^2]}{dt} = 2E[(\hat{r}_i)a_i(\hat{r})] + E[\sigma_\eta{}^2] \tag{11}$$

Thr cross term representing the second moment between two firing neurons, i and j, can be obtained by modifying the moment formula as

$$\frac{dE[(\hat{r}_i)(\hat{r}_j)]}{dt} = E[(\hat{r}_i)a_j(\hat{r})] + E[(\hat{r}_j)a_i(\hat{r})] + E[\sigma_\eta{}^2] \tag{12}$$

We then solve for

$$\frac{dE[(\hat{r}_i)^2]}{dt} = 0 \text{ for } i = 1,2,3,...,n. \tag{13}$$

$$\begin{aligned} &\frac{dE[(\hat{r}_i)(\hat{r}_j)]}{dt} = 0 \\ &\text{for } i = 1,2,3,...,n \quad j = 1,2,3,...,n \end{aligned} \tag{14}$$

When $I(t)$ is of zero mean, the variance of each approximate rate variable is simply the second moment, so that

$$\sigma^2_{\hat{r}_i}(\mathbf{N}) = E[(\hat{r}_1)^2], \tag{15}$$

where, here, we make the dependence on $\mathbf{N} = (N_1, N_2, ..., N_n)$ explicit. Substituting (15) into (8) generates n equations of the form

$$\begin{aligned} N_1 &= erf(\frac{1}{\sqrt{2\sigma^2_{\hat{r}_1}(\mathbf{N})}}) \\ N_2 &= erf(\frac{1}{\sqrt{2\sigma^2_{\hat{r}_2}(\mathbf{N})}}) \\ &\vdots \\ N_n &= erf(\frac{1}{\sqrt{2\sigma^2_{\hat{r}_n}(\mathbf{N})}}) \end{aligned} \tag{16}$$

In our results, we solved (16) numerically in MATLAB. It is important to note that these equations can, in some cases, produce multiple solutions for each N_j. However, it has been shown [9] that typically a unique solution can be expected. Below, we present results that highlight the veracity of this approach in characterizing rate network controllability.

III. RESULTS

A. Accurate Characterizations of Fixed-Energy Reachable Sets

We used the above methodology to assess the controllability of 1, 2 and 3-dimensional rate networks. For this, we characterized the fixed energy reachable set:

$$\hat{\mathbf{r}}^T \Sigma \hat{\mathbf{r}} = 1, \tag{17}$$

which corresponds to an ellipsoid in $n-$dimensions. This ellipsoid encompasses the unit-energy reachable set, where Σ is the inverse of the infinite-time controllability gramian, or, equivalently, the steady-state covariance of the system under white noise. The fixed energy reachable set provides a holistic quantification of controllability, and is the basis of many contemporary controllability metrics [13].

To highlight the utility of our results, we compared our characterization with one associated obtained from straightforward Jacobian linearization. Since, we considered sigmoidal nonlinearities with unit slope at the origin, a Jacobian linearization is equivalent to replacing $f(\cdot)$ in (1) with its argument. We simulated the original nonlinear system subject to white noise and recorded firing rate trajectories of all neurons. We then compared these trajectories from the nonlinear simulation and compared the output to the analytical predictions of the quasilinear and Jacobian linear approximations.

1) Two dimensional network analysis: Here, we use a specific example of 2-D network to demonstrate our methodology. Consider a nonlinear model defined as below:

$$\begin{aligned} \frac{dr_1}{dt} &= -\alpha_1 r_1 + f_1(r_1) + f_2(W_{21}r_2) + I(t) \\ \frac{dr_2}{dt} &= -\alpha_2 r_2 + f_2(r_2) + f_1(W_{12}r_1) + I(t) \end{aligned} \tag{18}$$

Its corresponding quasilinear model can be expressed as,

$$\begin{aligned} \frac{d\hat{r}_1}{dt} &= -\alpha_1 \hat{r}_1 + N_1\hat{r}_1 + N_2W_{21}\hat{r}_2 + I(t) \\ \frac{d\hat{r}_2}{dt} &= -\alpha_2 \hat{r}_2 + N_2\hat{r}_2 + N_1W_{12}\hat{r}_1 + I(t) \end{aligned} \tag{19}$$

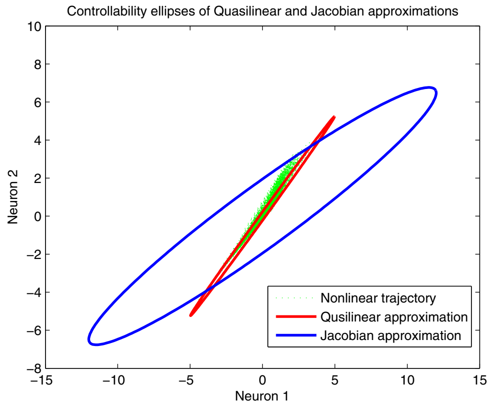

Fig. 2. Two dimensional unit-energy reachable ellipses of Quasilinear and Jacobian approximations compared with white-noise induced trajectory of the nonlinear system.

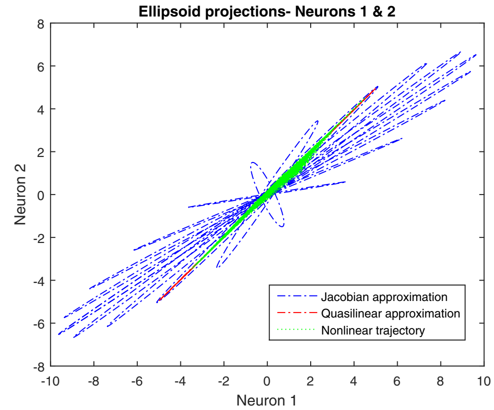

Fig. 3. Two dimensional projection (N1 vs. N2) of unit-energy reachable ellipsoids of Quasilinear and Jacobian approximations, with trajectory of nonlinear system overlaid. Each projection is depicted as a union of level sets of $N3$.

Following Ito's product rule and substitution of variances of firing rates resulted in the following expressions:

$$N_1 = erf\left(\frac{\sqrt{\alpha_1 - N_1}}{\sqrt{\frac{N_2[\alpha_1-\alpha_2-2(N_1-\alpha_1)(N_2-\alpha_2)]}{(N_1+N_2-\alpha_1-\alpha_2)[(N_1-\alpha_1)(N_2-\alpha_2)-N_1N_2]}} - 1\sigma_\eta}\right)$$
$$N_2 = erf\left(\frac{\sqrt{\alpha_2 - N_2}}{\sqrt{\frac{N_1[\alpha_1-\alpha_2-2(N_1-\alpha_1)(N_2-\alpha_2)]}{(N_1+N_2-\alpha_1-\alpha_2)[(N_1-\alpha_1)(N_2-\alpha_2)-N_1N_2]}} - 1\sigma_\eta}\right) \quad (20)$$

Next, we optimized the above two error functions to solve for N_1 and N_2.

We simulated the 2-D network with parameters as described in the Appendix. Figure 2 depicts unit energy reachable ellipses resulting from quasilinear and Jacobian approximations. Overlaid is the actual trajectory of the nonlinear system excited by white noise. Qualitatively, the figure reveals that the quasilinear ellipse provides a much closer approximation, in terms of shape and size, to the actual trajectory of the nonlinear system. The controllability Gramian of the Jacobian linearization encloses the actual trajectory, but is a highly conservative over-approximation.

2) Three dimensional network analysis: We considered a three-dimensional network with parameters as described in the Appendix, and followed the above procedure to obtain the quasilinear gains. Figures 3,4, and 5 depict the two-dimensional projections of unit-energy reachable sets generated from the quasilinear and Jacobian linearized systems. These projections are depicted as a union of level sets transverse to the projection plane. Overlaid on these ellipses are projections of the trajectory of the actual nonlinear system, obtained via simulation.

These figures again illustrate the stark over-approximation generated by Jacobian linearization, in contrast to the tight characterization afforded by the quasilinear approach.

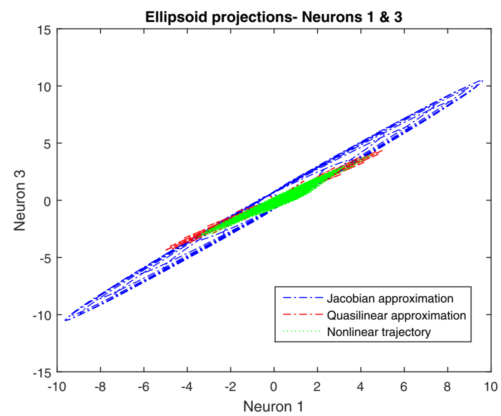

Fig. 4. Two dimensional projection (N1 vs. N3) of unit-energy reachable ellipsoids of Quasilinear and Jacobian approximations, with trajectory of nonlinear system overlaid. Each projection is depicted as a union of level sets of $N2$.

B. Monte-Carlo Analysis of 2- and 3-D Rate Networks

To assess the accuracy of our approach, we performed Monte-Carlo analysis of the two examples that we analyzed above. 100 and 651 simulations were performed for the two-dimensional and three-dimensional examples, respectively. Then, we computed the covariance mean ($2x2$ or $3x3$) across the total number of simulations and created error bars for each component in the covariance matrix in terms of percent error of Quasilinear and Jacobian approximations compared to the actual nonlinear response.

In Figure 3, the average covariance percent error of the quasilinear approach is close to zero with standard deviation less than 1%. This analysis applies to all four entries in the quasilinear covariance matrix. On the other hand, Jacobian approximation generates average covariance percent error at about -3% with standard deviation larger than approximately 5%. Hence, the results from the error bar chart confirms our qualitative results from Figures 2,3,4, and 5 in that quasilinear approach generates controllability Gramian that is a closer approximation to the actual controllability

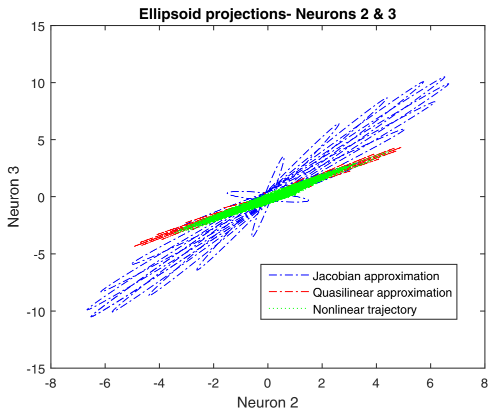

Fig. 5. Two dimensional projection (N2 vs. N3) of unit-energy reachable ellipsoids of Quasilinear and Jacobian approximations, with trajectory of nonlinear system overlaid. Each projection is depicted as a union of level sets of $N1$.

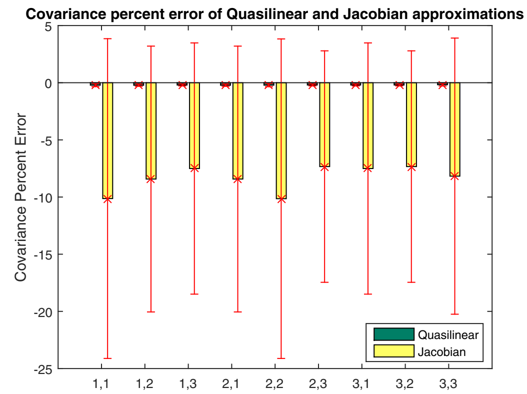

Fig. 7. Comparison of the error bars of Quasilinear and Jacobian approximations in a three dimensional motif. Nine sets of numbers labeled on the x-axis indicate the matrix element in the 3-by-3 covariance matrix.

Gramian.

Similarly, Figure 4 depicts the covariance percent errors of quasilinear and Jacobian approximations in the 3-D neural network. The nine elements in the covariance matrix of the Jacobian approximation show average percent errors ranging from 8% to 11% with standard deviations larger than 10%. Again, the error bar chart generated in the 3-D paradigm agrees with our results from the three projection figures (Figures 3,4, and 5) and our conclusion that our methodology produces a closer approximation in terms of controllability of the network than the local linearization approximation.

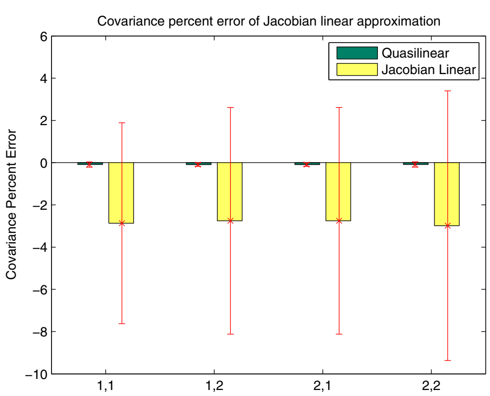

Fig. 6. Comparison of the error bars of Quasilinear and Jacobian approximations in a two dimensional motif. Four sets of numbers labeled on the x-axis indicate the matrix element in the 2-by-2 covariance matrix.

IV. CONCLUSIONS

In this paper, we utilize the technique of quasilinearization to approximate characterize the controllability of a rate network with sigmoidal nonlinearities in the coupling function. The techniques centers on obtaining a controllability gramian for a stochastically linearized version of the original nonlinear rate network. We illustrate the efficacy of our methdology for a neuronal firing rate model with sigmoidal nonlinearityWe convert the nonlinear equations into a set of linear equations by adopting a vector of quasilinear gains N, which we optimize stochastically by defining the relationships between the variance of the input and that of the variable response and solving for n error functions. The accuracy of our approach is demonstrated by means of simulation results qualitatively and quantitatively from two- and three-dimensional network examples.

The results indicate that a quasilinear approach may provide a more tractable alternative to direct nonlinear controllability analysis for these classes of networks. Moreover, they demonstrate that simple linearization risks generating significant overapproximation of the controllability of the nonlinear system. This latter result is, of course, not too surprising since Jacobian linearization is, by definition, a local approximation. Thus, the main utility of our approach is the ability to characterize high-variance regimes, in which the nonlinearity is activated.

Several nontrivial challenges remain to be resolved in the generalization of this method. Notable among them is scalability, since our approach involves high-dimensional optimization (i.e., finding zeros of the (16)). Thus, the principle immediate use-case of this research may be in the study of specific, small-scale network configurations. We note that an alternative formulation of this model involves absorbing the sum in (1) into the sigmoid (as opposed to the sum of sigmoids used herein). In this case, the overall methodology does not change, with appropriate modification to the right hand side of (8).

V. APPENDIX

In this section, we provide the exact parameter values that we used to simulate the results in III. All of our simulations lasted for the time duration of 500 msec. Simulation and quasilinear gain computations were implemented in MATLAB.

A. 2-D network parameters

In a 2-D paradigm, the decay constants, α_1 and α_2,were set to equal to 3.5, and connection weights W_{12} and W_{21} were randomly chosen from a normal distribution (mean=1, standard deviation=1). Next, fmincon MATLAB function was utilized to perform nonlinear optimization of two error functions. We minimized one of the equations while setting the other as a constraint, making the latter equal to zero. σ_η was chosen to equal 30 to solve for the two quasilinear gains N_1 and N_2.

B. 3-D network parameters

Similarly, a 3-D paradigm involved finding the optimal triple of quasilinear gains for the following parameters: $\alpha_1 = \alpha_2 = 3$ and $\alpha_3 = 4$, W_{ji} randomly chosen from a normal distribution(mean=1, standard deviation=1), and $\sigma_\eta = 20$. This time, we set two of the three error functions as our constraints and minimized the third equation using fmincon MATLAB function.

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