Designing the Dynamics of Spiking Neural Networks

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Precise timing of spikes and temporal locking are key elements of neural computation. Here we demonstrate how even strongly heterogeneous, deterministic neural networks with delayed interactions and complex topology can exhibit periodic patterns of spikes that are precisely timed. We develop an analytical method to find the set of all networks exhibiting a predefined pattern dynamics. Such patterns may be arbitrarily long and of complicated temporal structure. We point out that the same pattern can exist in very different networks and have different stability properties.

Repeated patterns of spikes with temporal precision in the millisecond range have been experimentally observed in different neuronal systems [1–4]. They correlate with internal and external stimuli and are thus discussed to be essential for neural information processing (see, e.g., [5]). Their dynamical origin, however, is unknown. One possible explanation for their occurrence is the existence of excitatorily coupled feed-forward structures, synfire chains [6–8], which are embedded in a network of otherwise random connectivity and receive a large number of random external inputs. Other studies point out that spike patterns can originate as attractors of deterministic recurrent networks if inhibitory interactions dominate [9,10]. These studies could already treat networks of complicated connectivities and successfully found one specific network solution for a given pattern. Yet it is still unclear which set of networks have the potential to realize a given spiking dynamics. Moreover, the recent studies considered interactions without delays. Delays, however, are known to be significant in biological neural systems [11] and to have a strong impact onto even the qualitative dynamics of neural networks (cf. [12–18]).

It is thus still an open question whether and how a deterministic network, despite simultaneously exhibiting delayed interactions and strong heterogeneities, can yet display precisely timed spiking dynamics. If so, what are the possible networks that generate a given dynamics?

In this Letter we study a class of spiking neural network models with delayed interactions. We provide a solution to an inverse problem for networks of arbitrary connectivity: We present an exact analytical method to find the set of all networks, by determining the coupling strengths, such that they exhibit a given periodic spike pattern of arbitrary temporal extent. The analysis shows that even arbitrarily large networks with complicated connection topologies and strong heterogeneities can yet display patterns of spikes that are timed precisely. The class of networks realizing a simple periodic pattern, i.e., one in which

each neuron fires exactly once before the sequence repeats, is derived and parameterized analytically. The network may have a mixture of both excitatory and inhibitory couplings, with the stability of a pattern depending on the particular coupling architecture.

Consider a network of $N \in \mathbb{N}$ oscillatory neurons that interact by sending and receiving spikes via directed delayed connections. One phaselike variable $\phi_l(t)$ specifies the state of each neuron $l \in \{1, \ldots, N\}$ at time t. A strictly monotonic increasing rise function U_l defines the membrane potential $U_l(\phi_l)$ of the neuron, representing its subthreshold dynamics [12]. In the absence of interactions, the phases increase uniformly obeying $d\phi_l/dt = 1$. When ϕ_l reaches its threshold, $\phi_l(t^-) = \Theta_l$, it is reset, $\phi_l(t) = 0$, and a spike is emitted. After a delay time τ_{ml} this spike signal reaches the postsynaptic neuron m, inducing an instantaneous phase jump

$$\phi_m(t + \tau_{ml}) = H_{\varepsilon_{ml}}^{(m)}(\phi_m([t + \tau_{ml}]^-)), \tag{1}$$

mediated by the transfer function $H_\varepsilon^{(m)}(\phi) = U_m^{-1}(U_m(\phi) + \varepsilon)$ that is strictly monotonic increasing both as a function of ε and of ϕ. Here, ε_{ml} denotes the strength of the coupling from neuron l to m. Sending and receiving of spikes are the only nonlinear events occurring in these systems. For simplicity of presentation, we here focus on nondegenerate events: We consider arbitrary periodic patterns in which (i) all spikes are sent at nonidentical times and (ii) received at nonidentical times, and (iii) neurons receiving a spike do not generate a new spike at the same time. We focus on networks of identical neurons $U_l(\phi) \equiv U(\phi)$ with the same intrinsic interspike intervals fixed by $\Theta_l \equiv 1$, on identical delays $\tau_{ml} \equiv \tau$, and patterns without silent neurons (that do not spike within a pattern due to sufficiently strong inibitory input). Below, we will explain the underlying ideas of how to find the set of all networks exhibiting a given pattern as an invariant solution for this class of systems. Nevertheless, based on

the analysis presented here, the developed method can be further extended [19] to cover also different types of neurons, heterogeneously distributed delays and thresholds, and complicated stored patterns that include degenerate spikes, multiple firings of the same neuron, and silent neurons that never fire. Figure 1 illustrates such a general case.

What characterizes a periodic pattern of precisely timed spikes? Let t_i, $i \in \mathbb{Z}$, be an ordered list of times at which a neuron emits the ith spike occurring in the network, such that $t_j > t_i$ if $j > i$. Assume a periodic pattern consists of M spikes. Such a pattern is then characterized by its period T, by the times $t_i \in [0, T)$ of spikes $i \in \{1, \ldots, M\}$, and by the indices $s_i \in \{1, \ldots, N\}$ identifying the neuron that spikes at t_i. To exclude technicalities in the presentation, we assume that for all pairs t_i and t_j of subsequent spike times of each neuron l, it receives at least one spike within the interval $(t_i, t_j) \cap (t_i, t_i + \Theta_l)$. Periodicity entails $t_i + nT = t_{i+nM}$ and $s_i = s_{i+nM}$ for all $n \in \mathbb{Z}$. This imposes conditions on the time evolution of the neurons' phases. Suppose a specific neuron l fires at $K(l)$ times $t_{i_k} \in [0, T)$, $k \in \{1, \ldots, K(l)\}$ within the first period. For the nondegenerate patterns considered, this implies

$$\phi_l(t_{i_k}^-) = 1, \qquad (2)$$

whereas at any other time $t \in [0, T)$, $t \neq t_{i_k}$ for all k,

$$\phi_l(t^-) < 1, \qquad (3)$$

to prevent untimely firing. The monotonicity of the transfer function implies that the periodicity of the pattern is necessary and sufficient [19] for the periodicity of the phases,

$$\phi_l(t) = \phi_l(t + nT), \qquad (4)$$

for all $n \in \mathbb{Z}$ and all $t \in [0, T)$. We therefore equivalently consider $\phi_l(t)$ for $t \in [0, T)$ with periodic boundary conditions. All times are measured modulo T and spike time labels i are reduced to $\{1, \ldots, M\}$ by subtracting a suitable integer multiple of M. Let $P(i) \in \{1, \ldots, M\}$ denote the spike arriving last before the firing time t_i such that $P(i) = \text{argmin}\{t_i - \theta_j | j \in \{1, \ldots, M\}\}$, where $\theta_j = t_j + \tau$ is the arrival time of the spike labeled j.
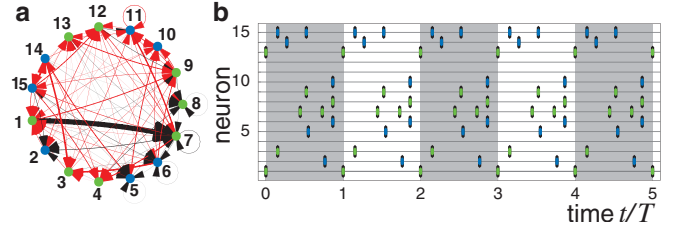

FIG. 1 (color).   Complicated spike pattern in a small network ($N = 15$). (a) Network of eight integrate-and-fire (green) and seven Mirollo-Strogatz (blue) neurons with distributed thresholds $\Theta_l \in [0.5, 2.0]$ and delays $\tau_{ml} \in [0.1, 0.9]$. Each directed connection between any two neurons is randomly chosen to be present with probability $p = 0.6$. Connections are either excitatory (black) or inhibitory (red) (thicknesses proportional to coupling strengths). (b) The spiking dynamics (green and blue bars according to neuron type) of the network shown in (a) perfectly agrees with the predefined pattern (period $T = 1.3$) of precisely timed spikes (black bars underlying the colored ones). The pattern includes several simultaneous spikes. Three neurons, $l \in \{4, 11, 12\}$, are switched off (nonspiking).

Moreover, let $\Delta_j = \theta_{j+1} - \theta_j$ be the time differences between two successive arrivals. We can now rewrite Eqs. (2) and (3) for neuron l as a set of conditions on the phases $\phi_l(\theta_i)$ at each spike-arrival time θ_i, in terms of the firing times t_{i_k} of that neuron and spike-arrival times θ_j,

$$\phi_l(\theta_{P(i_k)}) = 1 - (t_{i_k} - \theta_{P(i_k)}), \qquad (5)$$

$$\phi_l(\theta_j) < 1 - \Delta_j, \qquad (6)$$

where $k \in \{1, \ldots, K(l)\}$ and $j \in \{1, \ldots, M\}$, $j \neq P(i_k)$ for all k. The coupling strengths $\varepsilon_{ll'}$, $l, l' \in \{1, \ldots, N\}$ of a network realizing a given pattern are now restricted by a system of $\sum_{l=1}^{N} K(l) = M$ nonlinear equations and $\sum_{l=1}^{N}[M - K(l)] = (N - 1)M$ inequalities originating from (5) and (6): After a firing of neuron l at time t_i where its phase is zero, conditions (5) and (6) impose restrictions at each spike-arrival time while the time evolution proceeds towards the subsequent firing time t_j of neuron l, as illustrated in Fig. 2. As a result, we have

$$H_{\varepsilon_{ls_{P(i)+1}}}(\theta_{P(i)+1} - t_i) < 1 - \Delta_{P(i)+1},$$

$$H_{\varepsilon_{ls_{P(i)+2}}}[H_{\varepsilon_{ls_{P(i)+1}}}(\theta_{P(i)+1} - t_i) + \Delta_{P(i)+1}] < 1 - \Delta_{P(i)+2}, \qquad (7)$$

$$H_{\varepsilon_{ls_{P(j)}}}(\ldots H_{\varepsilon_{ls_{P(i)+2}}}[H_{\varepsilon_{ls_{P(i)+1}}}(\theta_{P(i)+1} - t_i) + \Delta_{P(i)+1}]\ldots + \Delta_{P(j)-1}) = 1 - (t_j - \theta_{P(j)}).$$

A particular solution [20] to the system (7), provides the coupling strengths $\varepsilon_{ll'}$, $l' \in \{1, \ldots, N\}$, of incoming connections to neuron l. Solutions to systems analogous to (7) for all neurons l define the coupling architecture of the entire network. Often (7) is an underdetermined system such that many solutions exist, implying that many different networks realize the same predefined pattern; cf. Fig. 3.

We can then require additional properties from the network. For instance, a connection from a neuron l to m can be absent (requiring the coupling strength $\varepsilon_{ml} = 0$), taken to be inhibitory ($\varepsilon_{ml} < 0$), excitatory ($\varepsilon_{ml} > 0$) or to lie within an interval. In particular, we can specify inhibitory and excitatory subpopulations. In certain cases, such as for networks of leaky integrate-and-fire neurons [21], $U(\phi) = U_\gamma(\phi) = [1 - \exp(-\gamma\phi)]/[1 - \exp(-\gamma)]$, $\gamma > 0$, or
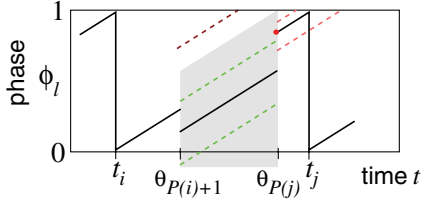
FIG. 2 (color). (color) Restriction of a neuron's dynamics between its firing events (7). In this example, two spikes arrive between the firing times t_i and t_j of neuron l. The solid line indicates one possible time evolution of the phase $\phi_l(t)$. Between the firing times, $\phi_l(t)$ may follow any path within a possibly semi-infinite polygon (gray shaded; green dashed lines show other possible trajectories). A too large phase at $\theta_{P(i)+1}$ contradicts (7) and will lead to early firing (dark red dashed line). The phase at $\theta_{P(j)}$ is fixed (red dot). Any other phase inconsistent with the equality in (7) would lead to a firing time earlier or later than predefined (light red dashed lines).

Mirollo-Strogatz neurons [12], $U(\phi) = U_b(\phi) = b^{-1}\ln(1 + [\exp(b) - 1]\phi)$, $b > 0$, a solution of (7) can be found in a simple way, because the system is then reducible to be linear in the couplings or polynomial in its exponentials.

Networks realizing a given pattern do not always exist. This can already be observed from a simple example: Consider a pattern with no spike arrival between two spikes sent by the same neuron. Because of its free evolution
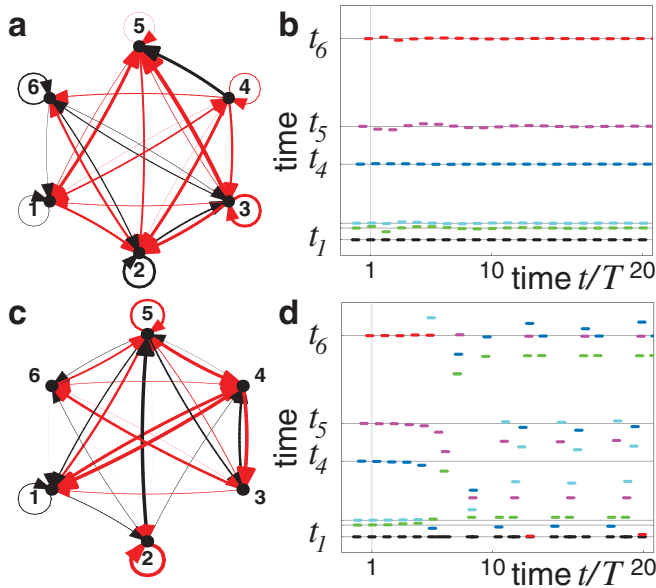

FIG. 3 (color). (color) Two different networks (a),(c) realize the same predefined pattern [(b),(d) gray lines]. A small random perturbation is applied at the beginning of the second period. The network dynamics (spike times relative to the spikes of neuron $l = 1$, color coded for each neuron), found by exact numerical integration [23] shows that in network (a) the pattern is stable and thus regained after a few periods (b); in network (c) it is unstable (d) and eventually another pattern will be assumed.

between the spiking times, their time difference must equal the free period; hence a predefined pattern with different interspike interval is not realizable by any network.

For a simple periodic pattern, the system (7) is guaranteed to have a solution, as long as basic requirements (e.g., the delays being smaller than the neurons' intrinsic interspike intervals) are obeyed. Without loss of generality the neuron firing at time t_l is labeled l, i.e., $s_l = l$ for $l \in \{1, \ldots, M \equiv N\}$. An analytic parameterization of all networks realizing such a pattern is then given by

$$\varepsilon_{lP(l)+1} = H^{-1}_{\phi_l(\theta_{P(l)+1})}(\theta_{P(l)+1} - t_l),$$

$$\varepsilon_{lP(l)+k} = H^{-1}_{\phi_l(\theta_{P(l)+k})}[\phi_l(\theta_{P(l)+k-1}) + \Delta_{P(l)+k-1}], \quad (8)$$

$$\varepsilon_{lP(l)} = H^{-1}_{1-(t_l-\theta_{P(l)})}[\phi_l(\theta_{P(l)-1}) + \Delta_{P(l)-1}],$$

in terms of the neurons' phases $\phi_l(\theta_i)$, $l, i \in \{1, \ldots, N\}$ at the spike-arrival times. Here $k \in \{2, \ldots, N-1\}$ and $H^{-1}_\psi(\phi)$ is the inverse of $H_\varepsilon(\phi)$ with respect to ε. The phases $\phi_l(\theta_i)$ are subject to the restrictions (6). This parameterization shows that an $N(N-1)$-dimensional submanifold of networks realizing the pattern exists in ε_{ij} space. Additional features entail additional conditions on the phases at the spike-arrival times: For instance, exclusion of self-interaction is guaranteed by the conditions $\phi_l(\theta_l) = \tau$ if there is no spike-arrival in (t_l, θ_l), and $\phi_l(\theta_l) - \phi_l(\theta_{l-1}) = \Delta_{l-1}$ otherwise, reducing the dimension of the submanifold of possible networks by N. Moreover, requiring the couplings to be purely inhibitory leads to the accessibility conditions

$$\phi_l(\theta_{P(l)+1}) \leq \theta_{P(l)+1} - t_l, \quad (9)$$

$$\phi_l(\theta_{j+1}) - \phi_l(\theta_j) \leq \Delta_j, \quad (10)$$

where $j \neq P(l)$. We can therefore successively choose $\phi_l(\theta_{P(l)+m})$, $m \in \{1, \ldots, N-1\}$, starting with $m = 1$. Inequalities (9) and (10) hold with reversed relations for purely excitatory coupling. Purely inhibitory realizations exist if a pattern has period $T > 1$ (larger than the neuron's intrinsic interspike interval); otherwise $\phi_l(t_l^-) = 1$ is not accessible from $\phi_l(t_l) = 0$. Similarly, purely excitatory realizations exist if a pattern has period $T < 1$.

Is a pattern emerging in a heterogeneous network stable or unstable? We numerically investigated patterns in a variety of networks and found that in general the stability properties of a pattern depend on the details of the network it is realized in; see Fig. 3 for an illustration. Depending on the network architecture, the same pattern can be exponentially stable or unstable, or exhibit oscillatory stable or unstable dynamics. For any specific pattern in any specific network, the linear stability properties can also be determined analytically, similar to the exact perturbation analyses for much simpler dynamics in more homogeneous networks [14,16]. More generally, in every network of neurons with congenerically curved rise functions and

with purely inhibitory (or purely excitatory) coupling, a nonlinear stability analysis shows that the possible non-degenerate patterns are either *all* stable or *all* unstable. For instance, in purely inhibitory networks of neurons with rise functions of negative curvature, such as integrate-and-fire neurons, every periodic nondegenerate spike pattern, no matter how complicated, is stable.

In summary, we presented a method to find the set of all networks realizing a predefined periodic pattern of spikes, and for imposing additional constraints, for instance specifying absent connections and choosing inhibitory or excitatory subpopulations. A predefined simple periodic pattern is particularly interesting because a network realizing it is guaranteed to exist; here we parameterized analytically all such networks.

In general, these results demonstrate that precise, reproducible dynamics arises even in high-dimensional heterogeneous complex systems where it might be unexpected. The design method of solving an inverse problem presented here, capable of finding all networks that exhibit a predefined dynamics, might thus be of interest in the theory of coupled oscillators and complex networks and contributes a novel perspective to theoretical neuroscience. The method can be extended to include heterogeneities in all parameters and nondegenerate patterns [19], hidden neurons outside a core network, as well as nonperiodic patterns, by dropping the periodicity constraint (4).

In particular, our results shed a new light on how patterns of precisely timed spikes may emerge in deterministic neural network dynamical systems, even for biologically realistic architecture. For instance, these networks may simultaneously exhibit strongly heterogeneous parameters, complicated topology, and substantial and distributed delays. However, future work still needs to fully answer how experimentally observed synchronization [2] as well as recurrent patterns of spikes [1,3,4] really arise. Important topics of theoretical research include, for instance, (i) the exact dynamics of networks of excitable neurons that are either excited by recurrent network inputs or by external stimuli [22], (ii) spike patterns that are not periodic but separated by intervals of irregular activity [24], as well as (iii) cortical songs which are sequences of patterns occurring repeatedly in the same order but varying in the timing between patterns [3,4]. Studies in these directions could further clarify mechanisms used for information processing in such networks. In particular, it will be exciting to see whether biological neural networks

rely on stochastic features of topology and input [8] or the exact wiring diagram and precise single neuron dynamics play a significant role in creating a temporal code.

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