Stochastic Interaction in Associative Nets

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Abstract

Spatio-temporal correlations in spike trains of simultaneously recorded neurons characterize stochastic interactions in neural networks. Information theoretic measures for "spatial" and "temporal stochastic interaction" can measure the total amount of dependence in a set of cells. In the present work we calculate these interaction measures for associative networks, the most prominent models for cortical gamma-oscillations and precisely repeating spike patterns (synfire chains). Stochastic interaction in these networks appears to be very high conflicting with the common belief that neurons are largely independent Poisson processes.

Key words: Spike correlations; Stochastic interaction; Associative memory models

1 Spike-correlations and Associative Models

Simultaneous recordings of multiple cortical units revealed various types of correlation patterns on the time-scale of single spikes [1,2,6,9]. Fig. 1F, for instance, displays the correlation function of two (artificially generated) spike trains and reveals a dominant peak at time zero indicative for frequent synchronous firings. The side-peaks at ± 20ms further relate to a preference of the cells to fire periodically around 50Hz. "Synchronized gamma-oscillations" of this type in real data have been proposed as expressing the binding of feature coding neurons into "coherent" object representations [9]. Figure 1G displays a correlation function for three units. The abscissa here counts spike-triplets, where the first unit fires at some time t, the second unit fires τ_1 ms later, and

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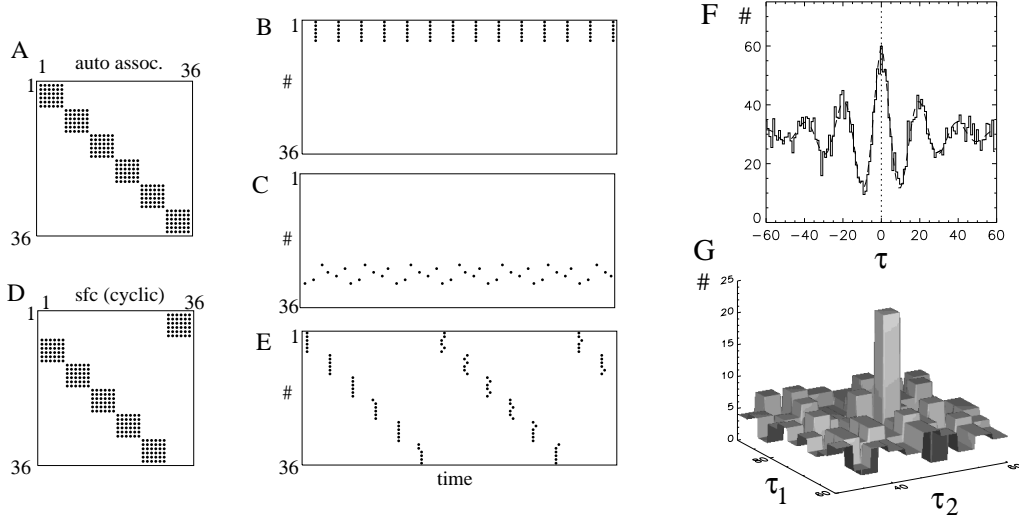
Fig. 1. A: Auto-associative synaptic coupling matrix storing six non-overlapping patterns of six neurons each. B: Persistent synchronized and C: asynchronous activity as raster plots. D: Hetero-associative matrix of six patterns (cyclic). E: Ordered retrieval of the stored sequence. F: Correlation function showing synchronized noisy oscillation of 2 neurons. G: Synfire pattern comprising 3 units, i.e., 2 time-shifts.

the third one τ_2 ms after the first. Most triplets occur at a low rate consistent with independent firing. The prominent peak in Fig. 1G, however, defines a certain pattern that appears significantly more often than expected by chance. Recordings from monkey prefrontal cortex [1] indicate that such "synfire patterns" occur behavior-dependent, but their functional role is unknown.

The above types of spatio-temporal correlations have been related to tentative network architectures. By far the most prominent networks used for that purpose are instances of associative memory models with more or less realistic artifical neurons and a synaptic connectivity matrix that stores a set of binary patterns using a Hebbian learning rule [8,11]. Realistic simulations with compartmental neurons can, e.g., be found in [10]. In the present paper we solely focus on firing patterns and not on how they are generated. Figure 1 displays some (non-exhaustive) prototypical types of firing patterns that can arise in associative networks. Figure 1A, e.g., shows an auto-associative synaptic matrix storing six non-overlapping patterns in a network of 36 units. Figures 1B and C reveal two modes of dynamic activity possible in an auto-associative net: In B all neurons of the first pattern fire periodically and synchronized. This example is the most simple one that explains the basic features of oscillatory synchronization as in Fig. 1F. In Fig. 1C the fifth pattern has been activated but now the neurons fire asynchronously though still periodically. Other types of behavior can be possible in concrete auto-associative networks. Thus, the observable spike patterns are not a unique function of connectivity.

Figure 1D shows a connectivity matrix, where six patterns have been stored

in cyclic order. Correspondingly, a sequence of firings of the whole patterns as in Fig. 1E can result. This principle basically constitutes the "synfire chain model" as proposed by Abeles [1] in order to explain precise repeating firing patterns as described in Fig. 1G. However, observe that also the cells in Fig. 1C fire in a fixed temporal order although they are homogeneously coupled. Thus, repeating patterns can occur in different architectures.

These simple examples show that the same architecture can lead to various types of firing correlations, and that different architectures can lead to spike patterns with comparable properties. Certainly, in real neural networks and complex neural simulations the relation between connectivity and correlation structure would be even more involved as in the simple example above (see, e.g., [2,6,10]). Therefore, one should carefully distinguish between the correlation structure in spike data –also called "functional couplings" [2]– and the underlying physical connectivity.

2   Spatial and Temporal Stochastic Interaction

Attempts have been made to characterize spike correlations and more general stochastic interactions in spike data mathematically [3–7]. For a stationary probability distribution p on the joint state space Ω of N units, *spatial (stochastic) interaction* can be defined in terms of Shannon-entropies as

$$I(p) \; := \; \sum_{v=1}^{N} H(p_v) - H(p) \;, \tag{1}$$

where the p_v are the marginals of p. $I(p)$ can be shown to measure the Kullback-Leibler distance from independence, whence, the name "interaction" [4]. Spatial interaction has been extended to stochastic processes by Ay [4]: Given a probability distribution p on the states of N units and a Markov kernel K for the probabilities of state transitions, *temporal (stochastic) interaction*, $I(p, K)$ can be represented analogous to (1) as

$$I(p, K) \; = \; \sum_{v=1}^{N} H(p_v, K_v) - H(p, K) \;, \tag{2}$$

where the *conditional entropy* of a Markov transition (p, K) is defined as $H(p, K) \; := \; - \sum_{\omega, \omega' \in \Omega} p(\omega) \, K(\omega' \,|\, \omega) \ln K(\omega' \,|\, \omega)$, and the p_v and K_v are marginal probabilities and Markov kernels for unit v, respectively. $I(p, K)$ is the KL-distance from a product of independent ("split") Markov chains [4]. Maximum values for $I(p)$ and $I(p, K)$ are $N \ln 2$. No system comprising N binary units can reveal stronger total interactions.
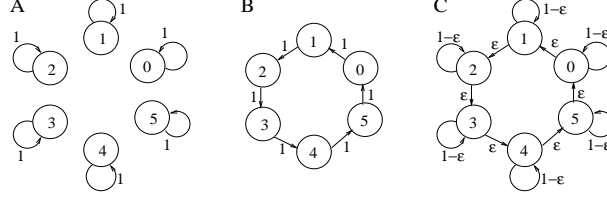
Fig. 2. Transition diagrams for (A) the auto-associative and (B) the synfire chain model and six stored patterns. Labels at edges denote one-step transition probabilities. Graph C contains A and B as limiting cases for $\epsilon = 0$ and 1.

Because associative memory models are the most prominent models proposed to explain stimulus-dependent synchronization and synfire patterns, we now study the stochastic interaction of firing patterns ideally observed in them. In order to map the time-continuous dynamics in real systems to time-discrete Markov chains, we assume a bin-size of the length of the firing-period in Fig. 2B and C and of the switching time between patterns in Fig. 2E. This perfectly leads to state-transition diagrams between activated patterns as depicted in Fig. 2A and B. Obviously, our simplifications neglect spike jitter, overlaps between patterns, and the different firing modes in Fig. 1B and C, but they enable a comparison of the prototypical modes in auto-associative and hetero-associative nets, i.e., attractor networks and synfire chain models.

Formally, we consider M patterns $s^i = (s_1^i, \ldots, s_N^i) \in \{0,1\}^N$, $i = 0, 1, \ldots, M-1$ such that for all units $v \in \{1, \ldots, N\}$: $|\{i : s_v^i = 1\}| \leq 1$ (i.e, each unit is in at most one pattern). We define the size of the patterns s^i as $N_i := |\{v : s_v^i = 1\}|$, and their average size as $\bar{N} := \frac{1}{M} \sum_{i=0}^{M-1} N_i$. Corresponding with Fig. 2C we use a parametric family of transition kernels: For $\varepsilon \in [0,1]$ we set $K^\varepsilon(s^i \,|\, s^j) := \varepsilon$ if $i = (j+1) \bmod M$, $K^\varepsilon(s^i \,|\, s^j) := 1 - \varepsilon$ if $i = j$, and $K^\varepsilon(s^i \,|\, s^j) := 0$ otherwise. The probability distribution $p := \frac{1}{M} \sum_{i=0}^{M-1} \delta_{s^i}$ is stationary for all kernels K^ε such that $I(p)$ results from (1) as

$$
\begin{aligned}
I(p) &= \left(\sum_{i=0}^{M-1} N_i \right) \cdot \left(-\frac{1}{M} \ln \frac{1}{M} - \frac{M-1}{M} \ln \frac{M-1}{M} \right) - \ln M \\
&= (\bar{N}M - 1) \ln M - \bar{N}(M-1) \ln(M-1) \,,
\end{aligned}
$$

which obviously is independent of ε. Now, we compute the temporal stochastic interaction. The marginal kernels K_v^ε are for all v

$$
K_v^\varepsilon(0|0) = \frac{M-1-\varepsilon}{M-1}, K_v^\varepsilon(1|0) = \frac{\varepsilon}{M-1}, K_v^\varepsilon(0|1) = \varepsilon, K_v^\varepsilon(1|1) = 1 - \varepsilon.
$$

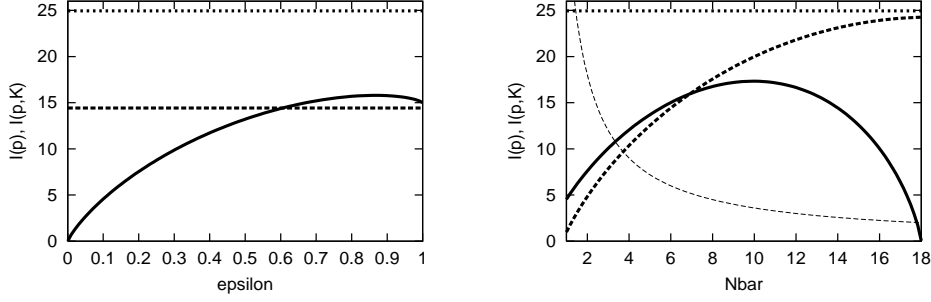Using these kernels and (2) the temporal stochastic interaction gets

Fig. 3. Temporal (solid) and spatial interaction (dashed) in the Willshaw associative memory; dotted line: maximally possible value, $N \ln 2 \approx 24.95$. Left: Interaction as function of ε with $N = 36$, $\bar{N} = 6.$, $M = 6$. Right: Interaction as a function of pattern size $\bar{N}$ with $N = 36$, $M = N/\bar{N}$, $\varepsilon = 1$. The thin dashed line represents the number of storable (non-overlapping, equal sized) patterns.

$$I(p, K^{\varepsilon}) = \bar{N}(M-1)\ln(M-1) - \bar{N}(M-1-\varepsilon)\ln(M-1-\varepsilon)$$
$$-(2\bar{N}-1)\,\varepsilon \ln \varepsilon - (\bar{N}-1)(1-\varepsilon)\ln(1-\varepsilon).$$

Figure 3 (left) displays $I(p)$ and $I(p, K)$ for $M = 6$ and $N_i = \bar{N} = 6$, $i = 0, \ldots, 5$ as in Fig. 1. Apparently, $I(p) = 14.4$ is constant at roughly 58 percent of the maximally possible value of $36 \ln 2 = 24.95$ for 36 independent binary units. So, the attractor and synfire chain dynamics have equal spatial interaction. Nonetheless, as Fig. 3 (left) shows, the attractor dynamics ($\varepsilon = 0$) has zero temporal interaction, whereas that of the synfire dynamics ($\varepsilon = 1$) is high. Figure 3 (right) displays interaction values as a function of pattern size for $\epsilon = 1$, i.e., the synfire chain model. Increasing pattern size decreases the number of storable (non-overlapping) patterns (thin dashed line). For $\bar{N} = N/2 = 18$ we can store just two patterns which must therefore alternate in each step ($\varepsilon = 1$). Then, the temporal interaction becomes zero. Conversely, for $\bar{N} = 1$, units are silent for $N - 1$ steps after firing also corresponding with a low interaction. Only for intermediate pattern sizes the temporal interaction can be large. In contrast, spatial interaction increases monotonically and obtains its optimal value at $\bar{N} = N/2 = 18$, where $M = 2$, such that the single unit entropies are maximal (each unit is 0 in one pattern and 1 in the other). These entropies decrease for smaller patterns such that $I(p)$ gets small for small $\bar{N}$. The picture remains basically the same for larger networks, but note, that storage of a reasonable number of patterns requires small pattern sizes. Then the interaction values may fall considerably below the maximum value of $N \ln 2$. Preliminary estimates show that *overlapping* patterns, e.g., random patterns, s^i, in that regime again result in interactions that reach a high fraction of the maximally possible values.

Correlations as in Fig. 1F and G derived from experiments are usually only small, synfire patterns are hardly observable at all (cf., [1]). This is often interpreted as suggesting that cortical neurons act largely as independent Poisson

processes. The spatial and temporal stochastic interaction measures for N independent Poisson processes, however, are zero (because these measures represent a Kullback-Leibler distance from independence). In contrast, we have shown here that the interaction measures for firing patterns expected in the most prominent models for synchronized gamma oscillations and synfire patterns, reach a moderate amount of the absolutely possible values for N binary units ($N \ln 2$): Such systems are therefore quite strongly interacting! As long as it is assumed that the models in principle cover aspects of cortical function, this seeming contradiction leaves as the only possibility that pair-wise and low-order correlations are not well suited measures to determine the dependence structure in multiple unit firing patterns. This would only show up in measurements from a large number of cells. Finally, note that temporal interaction is non-vanishing only in networks comprising hetero-associative propagation of activity. In [4,5] we argued that neural systems may try to maximize temporal interaction. In that case activity propagation along neural pathways should be the rule rather than persistent attractor states.

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