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Neuronal Information Encoding and Reduction of Dimension in Network Dynamics

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How is information stored and processed across different areas of the brain? This is a fundamental question in neuroscience; theoretical and computational efforts to answer it face significant challenges because of the vast hierarchy of spatial and temporal scales in brain dynamics. From a mathematical point of view, the issue is fundamentally one of dimension reduction—from very high-dimensional network dynamics to relatively low-dimensional dynamics in terms of relevant dynamical observables that capture/encode the essential information in sensory inputs.

For the visual cortex, information-theoretical methods indicate that neurons may respond almost independently, with little pairwise correlation. In some cases, then, a very low-dimensional representation of the visual information—namely, the firing rates of voltage spikes of individual neurons—is possible. It is difficult to understand, however, how any rate code, whether for a single neuron or a population of neurons, can decode/encode such complex perceptual phenomena as association, generalization, and contextual modulation.

In an alternative approach, proposed by Hebb, information is represented by synchronous activity distributed across many neurons; the propagation of information among the regions of the brain manifests itself as spatiotemporal patterns in the cortex. In temporal binding theory, this notion is elaborated to provide a framework for many perceptual phenomena, in which perceptually related features are linked through correlated firing among subpopulations of neurons.

On the level of rate coding, we have constructed an efficient representation of network dynamics in primary visual cortex (V1) with strongly fluctuating conductances and voltages. In the cat and monkey, cellular responses in V1, such as orientation preference, are arranged in regular patterns across the cortex. This suggests a coarse-grained construction: Some neuronal subpopulations can be effectively represented by coarse-grained patches that are sufficiently large to contain many neurons, yet sufficiently small that regular response properties of the individual neurons within a patch are approximately the same.

By extending concepts from nonequilibrium statistical physics to the network dynamics of V1, we have developed theoretical frameworks for studying these coupled homogenized, coarse-grained patches. We started with such "microscopic" networks of homogeneously coupled neurons within a coarse-grained patch. Without introducing any new parameters, we showed that, by *neglecting* correlations among neurons within the patch, it is possible to derive Boltzmann-like kinetic equations that govern the evolution of a one-particle (i.e., one-neuron) probability density function. As with derivations of hydrodynamic equations from the Boltzmann equation for molecular motion in fluids, further reduction to moment equations is possible via a moment closure based on the maximum-entropy principle. For example, for a network of excitatory neurons in the *small* synaptic time-constant limit $\sigma << 1$, the moment equations become

$$\begin{aligned} \partial_t \rho(v) &= \partial_v [U(\mu, v)\rho(v)], \\ \partial_t \mu(v) &= -\frac{1}{\sigma}[\mu(v) - \bar{g}] \\ &\quad + U(u,v)\partial_v \mu(v) \\ &\quad + \frac{\sigma_g^2}{\tau\rho(v)}\partial_v[(v-\varepsilon_E)\rho(v)], \end{aligned} \tag{1}$$

with $U(\mu,v) \equiv [(v - \varepsilon_r) + \mu(v)\,(v - \varepsilon_E)]\tau$, where $\rho(v)$ is the probability density function for finding a neuron whose membrane potential is v; $\mu(v)$ is the conditional moment of conductance; τ is the membrane time-constant; and ε_r and ε_E are constants representing the resting and reversal potentials for neurons, respectively. Here, $\bar{g}$ describes the mean activity of the network and σ_g^2 characterizes the fluctuation strength of the network response; $\bar{g}$, σ_g^2, and the firing rate $m(t)$ can be self-consistently determined in (1) by the total probability flux across the firing threshold V_T of the membrane potential.

We have demonstrated that this kinetic theory (extended to include inhibitory neurons and interactions amongst coarse-grained patches) captures very well the effects of large fluctuations in the dynamical response of neuronal networks, with high numerical efficiency and surprising accuracy. We have applied this kinetic theory to suggest that a *fluctuation-controlled criticality* underlies the orientation-tuning dynamics of V1, for which the near-criticality network dynamics is characterized by near-bistability and a rapid gain function induced by large synaptic fluctuations.

We have also considered how information can be encoded beyond simple rate coding. In our large-scale (~10^6 neurons) computational model of spatiotemporal dynamics of V1, it appears that correlated firing events of particular neuronal ensembles play a significant role in realistic dynamical regimes for phenomena in V1. The cortical phenomena we have examined are (a) spontaneous, ongoing coherent cortical activity and (b) the spatiotemporal patterns associated with the Hikosaka line-motion illusion (LMI)—the perception of motion induced by a static flashed stationary square cue quickly followed by a stationary bar.

Voltage-sensitive dye imaging has revealed intriguing similarities in the cortical spatiotemporal activity in response to the Hikosaka LMI stimulus and a small moving square. This similarity is believed to be associated with "pre-attentive illusory motion perception." In our model, we have revealed network mechanisms underlying the similarity in spatiotemporal patterns in response to these two stimuli. In our study, it appears that information is encoded in spatiotemporally coarse-grained *events* across many neurons or neuronal ensembles. An *event* could be said to occur whenever an ensemble of neurons attains a particular level of activity (e.g., a specified average subthreshold voltage or firing rate). This is a generalization of an event defined by a single spike of a single neuron. This generalization incorporates spatially and temporally averaged dynamical features. These cascading events are probabilistically robust and stable, and they can encode network inputs and can be used to discriminate fine dynamical features in the inputs, as shown in our numerical simulations.

Cascades of these events signify causal relationships and information flows among different neurons and have strong dynamic consequences for cortical activity. The next theoretical challenge is to characterize the probability structures of space–time event chains, which constitute a projection of high-dimensional, highly nonlinear, complex network activity to a backbone dynamics of critical space–time event chains on dynamically relevant spatial and temporal scales. The dynamics of space–time event chains hints at a path-integral-like language in capturing their potential for encoding information. These event chains of spatiotemporal activities are probably relevant to behavioral/cognitive dynamics. Animals don't sit counting spikes, to determine a rate, before taking action. Indeed, they can respond in $O(100)$ ms—not enough time to count many spikes. In our view, it is these distinct, critical spatiotemporal event chains in our brains that indicate that something has just happened. These chains of events are like lightning bolts: Once they flash in our brains, we have probably already attained a certain perception about the external world.

For Further Reading

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