
To signal the onset of salient sensory features or execute well-timed motor sequences, neuronal circuits must transform streams of incoming spike trains into precisely timed firing. To address the efficiency and fidelity with which neurons can perform such computations, we developed a theory to characterize the capacity of feedforward networks to generate desired spike sequences. We find the maximum number of desired output spikes a neuron can implement to be 0.1-0.3 per synapse. We further present a biologically plausible learning rule that allows feedforward and recurrent networks to learn multiple mappings between inputs and desired spike sequences. We apply this framework to reconstruct synaptic weights from spiking activity and study the precision with which the temporal structure of ongoing behavior can be inferred from the spiking of premotor neurons. This work provides a powerful approach for characterizing the computational and learning capacities of single neurons and neuronal circuits.

Pehlevan, C, Sompolinsky H. 2014 Selectivity and Sparseness in Randomly Connected Balanced Networks. PLOS ONE. 9(2)

Neurons in sensory cortex show stimulus selectivity and sparse population response, even in cases where no strong functionally specific structure in connectivity can be detected. This raises the question whether selectivity and sparseness can be generated and maintained in randomly connected networks. We consider a recurrent network of excitatory and inhibitory spiking neurons with random connectivity, driven by random projections from an input layer of stimulus selective neurons. In this architecture, the stimulus-to-stimulus and neuron-to-neuron modulation of total synaptic input is weak compared to the mean input. Surprisingly, we show that in the balanced state the network can still support high stimulus selectivity and sparse population response. In the balanced state, strong synapses amplify the variation in synaptic input and recurrent inhibition cancels the mean. Functional specificity in connectivity emerges due to the inhomogeneity caused by the generative statistical rule used to build the network. We further elucidate the mechanism behind and evaluate the effects of model parameters on population sparseness and stimulus selectivity. Network response to mixtures of stimuli is investigated. It is shown that a balanced state with unselective inhibition can be achieved with densely connected input to inhibitory population. Balanced networks exhibit the paradoxical effect: an increase in excitatory drive to inhibition leads to decreased inhibitory population firing rate. We compare and contrast selectivity and sparseness generated by the balanced network to randomly connected unbalanced networks. Finally, we discuss our results in light of experiments.


In many sensory systems, the neural signal splits into multiple parallel pathways. For example, in the mammalian retina, 20 types of retinal ganglion cells transmit information about the visual scene to the brain. The purpose of this profuse and early pathway splitting remains unknown. We examine a common instance of splitting into ON and OFF neurons excited by increments and decrements of light intensity in the visual scene, respectively. We test the hypothesis that pathway splitting enables more efficient encoding of sensory stimuli. Specifically, we compare a model system with an ON and an OFF neuron to one with two ON neurons. Surprisingly, the optimal ON-OFF system transmits the same information as the optimal ON-ON system, if one constrains the maximal firing rate of the neurons. However, the ON-OFF system uses fewer spikes on average to transmit this information. This superiority of the ON-OFF system is also observed when the two systems are optimized while constraining their mean firing rate. The efficiency gain for the ON-OFF split is comparable with that derived from decorrelation, a well known processing strategy of early sensory systems. The gain can be orders of magnitude larger when the ecologically important stimuli are rare but large events of either polarity. The ON-OFF system also provides a better code for extracting information by a linear downstream decoder. The results suggest that the evolution of ON-OFF diversification in sensory systems may be driven by the benefits of lowering average metabolic cost, especially in a world in which the relevant stimuli are sparse.
oscillator whose complete cycle generates a single movement segment. In order to demonstrate this hypothesis, we construct an oscillator-based model of movement generation. The model includes an oscillator that generates harmonic outputs whose frequency and amplitudes can be modulated by external inputs. The harmonic outputs drive a number of integrators, each activating a single muscle. The model generates muscle activation patterns composed of rectilinear and harmonic terms. We show that rectilinear and fundamental harmonic terms account for known properties of natural movements, such as the invariant bell-shaped hand velocity profile during reaching. We implement these dynamics by a neural network model and characterize the tuning properties of the neural integrator cells, the neural oscillator cells, and the inputs to the system. Finally, we propose a method to test our hypothesis that a neural oscillator is a central component in the generation of voluntary movement.

2010


We study the computational capacity of a model neuron, the tempotron, which classifies sequences of spikes by linear-threshold operations. We use statistical mechanics and extreme value theory to derive the capacity of the system in random classification tasks. In contrast with its static analog, the perceptron, the tempotron's solutions space consists of a large number of small clusters of weight vectors. The capacity of the system per synapse is finite in the large size limit and weakly diverges with the stimulus duration relative to the membrane and synaptic time constants.


Compressed sensing {{CS}} is an important recent advance that shows how to reconstruct sparse high dimensional signals from surprisingly small numbers of random measurements. The nonlinear nature of the reconstruction process poses a challenge to understanding the performance of {{CS}}. We employ techniques from the statistical physics of disordered systems to compute the typical behavior of {{CS}} as a function of the signal sparsity and measurement density. We find surprising and useful regularities in the nature of errors made by {{CS}}, a new phase transition which reveals the possibility of {{CS}} for nonnegative signals without optimization, and a new null model for sparse regression.


Neuronal activity arises from an interaction between ongoing firing generated spontaneously by neural circuits and responses driven by external stimuli. Using mean-field analysis, we ask how a neural network that intrinsically generates chaotic patterns of activity can remain sensitive to extrinsic input. We find that inputs not only drive network responses, but they also actively suppress ongoing activity, ultimately leading to a phase transition in which chaos is completely eliminated. The critical input intensity at the phase transition is a nonmonotonic function of stimulus frequency, revealing a "resonant" frequency at which the input is most effective at suppressing chaos even though the power spectrum of the spontaneous activity peaks at zero and falls exponentially. A prediction of our analysis is that the variance of neural responses should be most strongly suppressed at frequencies matching the range over which many sensory systems operate.
Humans can resolve the fine details of visual stimuli although the image projected on the retina is constantly drifting relative to the photoreceptor array. Here we demonstrate that the brain must take this drift into account when performing high acuity visual tasks. Further, we propose a decoding strategy for interpreting the spikes emitted by the retina, which takes into account the ambiguity caused by retinal noise and the unknown trajectory of the projected image on the retina. A main difficulty, addressed in our proposal, is the exponentially large number of possible stimuli, which renders the ideal Bayesian solution to the problem computationally intractable. In contrast, the strategy that we propose suggests a realistic implementation in the visual cortex. The implementation involves two populations of cells, one that tracks the position of the image and another that represents a stabilized estimate of the image itself. Spikes from the retina are dynamically routed to the two populations and are interpreted in a probabilistic manner. We consider the architecture of neural circuitry that could implement this strategy and its performance under measured statistics of human fixational eye motion. A salient prediction is that in high acuity tasks, fixed features within the visual scene are beneficial because they provide information about the drifting position of the image. Therefore, complete elimination of peripheral features in the visual scene should degrade performance on high acuity tasks involving very small stimuli.


Fluctuations in the temporal durations of sensory signals constitute a major source of variability within natural stimulus ensembles. The neuronal mechanisms through which sensory systems can stabilize perception against such fluctuations are largely unknown. An intriguing instantiation of such robustness occurs in human speech perception, which relies critically on temporal acoustic cues that are embedded in signals with highly variable duration. Across different instances of natural speech, auditory cues can undergo temporal warping that ranges from 2-fold compression to 2-fold dilation without significant perceptual impairment. Here, we report that time-warp-invariant neuronal processing can be subserved by the shunting action of synaptic conductances that automatically rescales the effective integration time of postsynaptic neurons. We propose a novel spike-based learning rule for synaptic conductances that adjusts the degree of synaptic shunting to the temporal processing requirements of a given task. Applying this general biophysical mechanism to the example of speech processing, we propose a neuronal network model for time-warp-invariant word discrimination and demonstrate its excellent performance on a standard benchmark speech-recognition task. Our results demonstrate the important functional role of synaptic conductances in spike-based neuronal information processing and learning. The biophysics of...
temporal integration at neuronal membranes can endow sensory pathways with powerful time-warp-invariant computational capabilities.


We consider a threshold-crossing spiking process as a simple model for the activity within a population of neurons. Assuming that these neurons are driven by a common fluctuating input with gaussian statistics, we evaluate the cross-correlation of spike trains in pairs of model neurons with different thresholds. This correlation function tends to be asymmetric in time, indicating a preference for the neuron with the lower threshold to fire before the one with the higher threshold, even if their inputs are identical. The relationship between these results and spike statistics in other models of neural activity is explored. In particular, we compare our model with an integrate-and-fire model in which the membrane voltage resets following each spike. The qualitative properties of spike cross-correlations, emerging from the threshold-crossing model, are similar to those of bursting events in the integrate-and-fire model. This is particularly true for generalized integrate-and-fire models in which spikes tend to occur in bursts, as observed, for example, in retinal ganglion cells driven by a rapidly fluctuating visual stimulus. The threshold-crossing model thus provides a simple, analytically tractable description of event onsets in these neurons.

2008


To perform nontrivial, real-time computations on a sensory input stream, biological systems must retain a short-term memory trace of their recent inputs. It has been proposed that generic high-dimensional dynamical systems could retain a memory trace for past inputs in their current state. This raises important questions about the fundamental limits of such memory traces and the properties required of dynamical systems to achieve these limits. We address these issues by applying Fisher information theory to dynamical systems driven by time-dependent signals corrupted by noise. We introduce the Fisher Memory Curve \{(FMC)\} as a measure of the signal-to-noise ratio \{(SNR)\} embedded in the dynamical state relative to the input \{SNR\}. The integrated \{FMC\} indicates the total memory capacity. We apply this theory to linear neuronal networks and show that the capacity of networks with normal connectivity matrices is exactly 1 and that of any network of N neurons is, at most, N. A nonnormal network achieving this bound is subject to stringent design constraints: It must have a hidden feedforward architecture that superlinearly amplifies its input for a time of order N, and the input connectivity must optimally match this architecture. The memory capacity of networks subject to saturating nonlinearities is further limited, and cannot exceed square root N. This limit can be realized by feedforward structures with divergent fan out that distributes the signal across neurons, thereby avoiding saturation. We illustrate the generality of the theory by showing that memory in fluid systems can be sustained by transient nonnormal amplification due to convective instability or the onset of turbulence.


In the brain, mutual spatial alignment across different sensory representations can be shaped and maintained through plasticity. Here, we use a Hebbian model to account for the synaptic plasticity that
results from a displacement of the space representation for one input channel relative to that of another, when the synapses from both channels are equally plastic. Surprisingly, although the synaptic weights for the two channels obeyed the same Hebbian learning rule, the amount of plasticity exhibited by the respective channels was highly asymmetric and depended on the relative strength and width of the receptive fields \{(RFs)\}: the channel with the weaker or broader \{RFs\} always exhibited most or all of the plasticity. A fundamental difference between our Hebbian model and most previous models is that in our model synaptic weights were normalized separately for each input channel, ensuring that the circuit would respond to both sensory inputs. The model produced three distinct regimes of plasticity dynamics (winner-take-all, mixed-shift, and no-shift), with the transition between the regimes depending on the size of the spatial displacement and the degree of correlation between the sensory channels. In agreement with experimental observations, plasticity was enhanced by the accumulation of incremental adaptive adjustments to a sequence of small displacements. These same principles would apply not only to the maintenance of spatial registry across input channels, but also to the experience-dependent emergence of aligned representations in developing circuits.

2007


In this work, we studied the adaptation of H1, a motion-sensitive neuron in the fly visual system, to the variance of randomly fluctuating velocity stimuli. We ask two questions. 1) Which components of the motion detection system undergo genuine adaptational changes in response to the variance of the fluctuating velocity signal? 2) What are the consequences of this adaptation for the information processing capabilities of the neuron? To address these questions, we characterized the adaptation of H1 by estimating the changes in the parameters of an associated Reichardt motion detection model under various stimulus conditions. The strongest stimulus dependence was exhibited by the temporal kernel of the motion detector and was parametrized by changes in the model's high-pass time constant \{(tau(H))\}. This time constant shortened considerably with increasing velocity fluctuations. We showed that this adaptive process contributes significantly to the shortening of the velocity response time-course but not to velocity gain control. To assess the contribution of time-constant adaptation to information transmission, we compared the information rates generated by our adaptive model motion detector with model simulations in which \{tau(H)\} was held fixed at its unadapted value for all stimulus conditions. We found that for intermediate stimulus conditions, fixing \{tau(H)\} at its unadapted value led to higher information rates, suggesting that time-constant adaptation does not optimize total information rates about velocity trajectories. We also found that, over the wide range of stimulus conditions tested here, H1 information rates are dependent on the amplitude of velocity fluctuations.


Humans can distinguish visual stimuli that differ by features the size of only a few photoreceptors. This is possible despite the incessant image motion due to fixational eye movements, which can be many times larger than the features to be distinguished. To perform well, the brain must identify the retinal firing patterns induced by the stimulus while discounting similar patterns caused by spontaneous retinal activity. This is a challenge since the trajectory of the eye movements, and consequently, the stimulus position, are
unknown. We derive a decision rule for using retinal spike trains to discriminate between two stimuli, given that their retinal image moves with an unknown random walk trajectory. This algorithm dynamically estimates the probability of the stimulus at different retinal locations, and uses this to modulate the influence of retinal spikes acquired later. Applied to a simple orientation-discrimination task, the algorithm performance is consistent with human acuity, whereas naive strategies that neglect eye movements perform much worse. We then show how a simple, biologically plausible neural network could implement this algorithm using a local, activity-dependent gain and lateral interactions approximately matched to the statistics of eye movements. Finally, we discuss evidence that such a network could be operating in the primary visual cortex.

2006


The timing of action potentials in sensory neurons contains substantial information about the eliciting stimuli. Although the computational advantages of spike timing-based neuronal codes have long been recognized, it is unclear whether, and if so how, neurons can learn to read out such representations. We propose a new, biologically plausible supervised synaptic learning rule that enables neurons to efficiently learn a broad range of decision rules, even when information is embedded in the spatiotemporal structure of spike patterns rather than in mean firing rates. The number of categorizations of random spatiotemporal patterns that a neuron can implement is several times larger than the number of its synapses. The underlying nonlinear temporal computation allows neurons to access information beyond single-neuron statistics and to discriminate between inputs on the basis of multineuronal spike statistics. Our work demonstrates the high capacity of neural systems to learn to decode information embedded in distributed patterns of spike synchrony.


In many cortical and subcortical areas, neurons are known to modulate their average firing rate in response to certain external stimulus features. It is widely believed that information about the stimulus features is coded by a weighted average of the neural responses. Recent theoretical studies have shown that the information capacity of such a coding scheme is very limited in the presence of the experimentally observed pairwise correlations. However, central to the analysis of these studies was the assumption of a homogeneous population of neurons. Experimental findings show a considerable measure of heterogeneity in the response properties of different neurons. In this study, we investigate the effect of neuronal heterogeneity on the information capacity of a correlated population of neurons. We show that information capacity of a heterogeneous network is not limited by the correlated noise, but scales linearly with the number of cells in the population. This information cannot be extracted by the population vector readout, whose accuracy is greatly suppressed by the correlated noise. On the other hand, we show that an optimal linear readout that takes into account the neuronal heterogeneity can extract most of this information. We study analytically the nature of the dependence of the optimal linear readout weights on the neuronal diversity. We show that simple online learning can generate readout weights with the appropriate dependence on the neuronal diversity, thereby yielding efficient readout.

A persistent change in neuronal activity after brief stimuli is a common feature of many neuronal microcircuits. This persistent activity can be sustained by ongoing reverberant network activity or by the intrinsic biophysical properties of individual cells. Here we demonstrate that rat and guinea pig cerebellar Purkinje cells in vivo show bistability of membrane potential and spike output on the time scale of seconds. The transition between membrane potential states can be bidirectionally triggered by the same brief current pulses. We also show that sensory activation of the climbing fiber input can switch Purkinje cells between the two states. The intrinsic nature of Purkinje cell bistability and its control by sensory input can be explained by a simple biophysical model. Purkinje cell bistability may have a key role in the short-term processing and storage of sensory information in the cerebellar cortex.


Many sensory systems adapt their input-output relationship to changes in the statistics of the ambient stimulus. Such adaptive behavior has been measured in a motion detection sensitive neuron of the fly visual system, H1. The rapid adaptation of the velocity response gain has been interpreted as evidence of optimal matching of the H1 response to the dynamic range of the stimulus, thereby maximizing its information transmission. Here, we show that correlation-type motion detectors, which are commonly thought to underlie fly motion vision, intrinsically possess adaptive properties. Increasing the amplitude of the velocity fluctuations leads to a decrease of the effective gain and the time constant of the velocity response without any change in the parameters of these detectors. The seemingly complex property of this adaptation turns out to be a straightforward consequence of the multidimensionality of the stimulus and the nonlinear nature of the system.


Ongoing spontaneous activity in the cerebral cortex exhibits complex spatiotemporal patterns in the absence of sensory stimuli. To elucidate the nature of this ongoing activity, we present a theoretical treatment of two contrasting scenarios of cortical dynamics: (1) fluctuations about a single background state and (2) wandering among multiple “attractor” states, which encode a single or several stimulus features. Studying simplified network rate models of the primary visual cortex (V1), we show that the single state scenario is characterized by fast and high-dimensional Gaussian-like fluctuations, whereas in the multiple state scenario the fluctuations are slow, low dimensional, and highly non-Gaussian. Studying a more realistic model that incorporates correlations in the feed-forward input, spatially restricted cortical interactions, and an experimentally derived layout of pinwheels, we show that recent optical-imaging data of ongoing activity in V1 are consistent with the presence of either a single background state or multiple...
attractor states encoding many features.


Abstract

Theoretical and experimental studies of distributed neuronal representations of sensory and behavioral variables usually assume that the tuning of the mean firing rates is the main source of information. However, recent theoretical studies have investigated the effect of cross-correlations in the trial-to-trial fluctuations of the neuronal responses on the accuracy of the representation. Assuming that only the first-order statistics of the neuronal responses are tuned to the stimulus, these studies have shown that in the presence of correlations, similar to those observed experimentally in cortical ensembles of neurons, the amount of information in the population is limited, yielding nonzero error levels even in the limit of infinitely large populations of neurons. In this letter, we study correlated neuronal populations whose higher-order statistics, and in particular response variances, are also modulated by the stimulus. We ask two questions: Does the correlated noise limit the accuracy of the neuronal representation of the stimulus? and, How can a biological mechanism extract most of the information embedded in the higher-order statistics of the neuronal responses? Specifically, we address these questions in the context of a population of neurons coding an angular variable. We show that the information embedded in the variances grows linearly with the population size despite the presence of strong correlated noise. This information cannot be extracted by linear readout schemes, including the linear population vector. Instead, we propose a bilinear readout scheme that involves spatial decorrelation, quadratic nonlinearity, and population vector summation. We show that this nonlinear population vector scheme yields accurate estimates of stimulus parameters, with an efficiency that grows linearly with the population size. This code can be implemented using biologically plausible neurons.


Neurons in macaque primary visual cortex (V1) show a diversity of orientation tuning properties, exhibiting a broad distribution of tuning width, baseline activity, peak response, and circular variance (CV). Here, we studied how the different tuning features affect the performance of these cells in discriminating between stimuli with different orientations. Previous studies of the orientation discrimination power of neurons in V1 focused on resolving two nearby orientations close to the psychophysical threshold of orientation discrimination. Here, we developed a theoretical framework, the information tuning curve, that measures the discrimination power of cells as a function of the orientation difference, deltatheta, of the two stimuli. This tuning curve also represents the mutual information between the neuronal responses and the stimulus orientation. We studied theoretically the dependence of the information tuning curve on the orientation tuning width, baseline, and peak responses. Of main interest is the finding that narrow orientation tuning is not necessarily optimal for all angular discrimination tasks. Instead, the optimal tuning width depends linearly on deltatheta. We applied our theory to study the discrimination performance of a population of 490 neurons in macaque V1. We found that a significant fraction of the neuronal population exhibits favorable tuning properties for large deltatheta. We also studied how the discrimination capability of neurons is distributed and compared several other measures of the orientation tuning such as CV with Chernoff distances for normalized tuning curves.

We study the ability of linear recurrent networks obeying discrete time dynamics to store long temporal sequences that are retrievable from the instantaneous state of the network. We calculate this temporal memory capacity for both distributed shift register and random orthogonal connectivity matrices. We show that the memory capacity of these networks scales with system size.

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