Supplementary Material: Adaptation Reduces Variability of the Neuronal Population Code

A State-Dependent Hazard Function

We define a limiting probability density to an event, given the state variable x, as

$$h_x(x,t) := \lim_{\epsilon \to 0} \frac{\Pr(N[t, t+\epsilon] > 0 | x(t))}{\epsilon}, \tag{A.1}$$

where $N[t, t+\epsilon]$ is a right continuous integer-valued function that jumps 1 at each event time and is constant otherwise. Thus, $N[t, t+\epsilon]$ counts the number of events in the interval $(t, t+\epsilon]$, and x is a general state variable of the system. Here, we assume a shot noise dynamics as described by Eq. (1) in the main text governs the state variable x.

The hazard function for neuronal ensembles can be derived from a field master equation of the system as it is stated in Eq. (B.1) [13]. Generally, a full master equation assumes an infinite reservoir of entities and sparse interaction among them (the underling assumptions of mean-field theory). Therefore, it results that the fluctuation in the inputs are incoherent and sufficiently uncorrelated. This allows to apply the method of elimination of fast variables [6] given the slow state variable x [13]. Indeed, it can be shown that the hazard function is the response function of a neuron in the presence of noise, which can be derived by the Fokker-Planck approximation of the mean field master equation [16, 2] as described in [9] for the mean-adaptation theory.

In [13] it is shown that the Kramer rate function [5]

$$\hat{h}_x(x,t) = a_t \exp(-b_t x) \tag{A.2}$$

provides an excellent agreement with the mean field calculation of the response function, where a_t and b_t are fit parameters and hat indicates the approximation nature of the hazard function to the full model of a neuron including voltage dynamics and conductance-based synapses. In a dynamic input setting a_t and b_t are respectively determined by interpolating the mean excitatory and inhibitory synaptic conductance to the neuron (see section 3 and 4 in [13]). In a static case, a_t and b_t denote as a and b, respectively. Moreover, the effect of input statistics and varying noise strength on Eq. (A.2) and the resulting inter-event distribution is studied in [14]. In summary, a corresponds to firing rate of a neuron given the

statistics of input parameters, where $x = 0$, and b is the adaptation coefficient otherwise and can be derived using adaptation self-consistency in Eq. (13) in the main text. This relationship allows to construct the rate model as in the main text (last argument in Section *Benefits for Neural coding*), where a and b are derived using the fit provided in NeuroTools [1]. It is clear from Eq. (A.2) that without adaptation a is the firing rate of the Poisson rate model. In order to allow comparison, we normalized both processes to have the same initial firing rate (Fig. 2) by assuming that there exists some constant regulation $0 < \mathcal{N} < 1$ that maintains rate equality in the steady-state such that

$$r_{eq} = a\mathcal{N} = \mathcal{W}(abq\tau)/(bq\tau). \tag{A.3}$$

Thereafter, we assumed a change ϵ in the mean conductance on the order of $0.01\,\mathrm{nS}$ and recompute a^ϵ and b^ϵ, thus the rate model new equilibrium rate is $\bar{r}^\epsilon_{eq} = a^\epsilon\mathcal{N}$. The new equilibrium rate of the adaptive process is obtained by $r^\epsilon_{eq} = \mathcal{W}(a^\epsilon b^\epsilon q\tau)/(b^\epsilon q\tau)$. This construction leads to Fig. 2 (Left) in the main text.

A violation of the mean-field theory assumptions, such as a finite size of reservoir, in the network bring about "coherent" fluctuations in addition to "incoherent" fluctuations, both can be used to derive the response function of the system [11, 1], which implicates an alternative form for the hazard function which includes a stochastic element [11]. However, under the condition that the correlation time course of the interactions is short compared to adaptation time scale, namely on the order of the synaptic time constant, interactions can be treated as fast variables and, in the presence of slow adaptation, will vanish by the method of elimination of fast variables.

The hazard function has been derived for many physical systems. We mention the examples of models for earthquake events [4], financial risk modeling in econophysics [8]. It is also plausible to apply the adiabatic elimination technique for quantum dissipative system to obtain a matching hazard model as suggested in [3].

B   Serial Correlation: Process memory

The history dependency of the slow dynamic shot-noise in Eq. (1) of the main text, results in a state-dependent reset mechanism ψ which makes the process non-renewal. Since the state variable $x(t)$ when an event occurs, makes a jump $x(t + dt) = x(t) + q$ defining the reset mapping $\psi(\eta(x))$, such that the reset condition become $\eta(x) \mapsto \eta(x + q)$, it follows that

$$\psi(t_x) = \eta(\eta^{-1}(t_x) + q) = -\tau \ln(\exp(-t_x/\tau) + 1) \tag{B.1}$$

with its inverse given by

$$\psi^{-1}(t_x) = -\tau \ln(\exp(-t_x/\tau) - 1). \tag{B.2}$$

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[1] http://neuralensemble.org/trac/NeuroTools

It is clear that at the time of event, state variable remapping condition deviates from $t_x \mapsto 0$. However, if we assume $q = 0$, it results second and third terms in right hand side of Eq. (2) canceling each other, which makes the master equation follows a renewal theory and non-locality due to q vanishes.

Therefore, the state-dependent reset ψ indicates the memory of the process in the terms of serial correlation between consecutive inter-event intervals. Here, we shall now relate the interval correlation coefficient to the probability of observing n events in the time window T, $P(n, T)$, using the relationships derived in [12]. Hence, the correlation of two back to back intervals is

$$\int_0^\infty P(1, T)dT = \lim_{s \to 0} \tilde{P}(1, s) = E[\Delta_0 \Delta_1]/\mu_1 \qquad (B.3)$$

and similarly for k lagged intervals, we have $\tilde{P}(k, 0) = E[\Delta_0 \Delta_k]/\mu_1$ [12].

Here, we show that serial correlations between inter-events are negative for phenomenological model of adaptation, following the ISI distribution given in Eq. (4) and its corresponding counting process $P(n, T)$, for a given hazard function as Eq. (A.2) and defined ψ in the main text for a static firing rate: We know ψ only operates on the current state and the reset at the kth interval before has a vanishing effect on the current state of t_x, we have $\lim_{k \to \infty} \rho(\Delta_0, \Delta_k) = \rho(\Delta_0)\rho(\Delta_k)$ [13]. Therefore, applying Lemma (6.5) in [12] $\lim_{k \to \infty} \tilde{P}(k, 0) = \mu_1$. Additionally, for the defined ψ in the main text we have $\psi : \mathbb{R} \mapsto \mathbb{R}^-$; it follows that all trajectories are reinserted at negative pseudo-ages, and we have $\partial_{t_x} \psi < 0$, therefore "younger" event trajectories are reinserted at more negative values and hazard function that explicitly defined in Eq. (A.2) is an increasing $\partial_{t_x} \hat{h}_x(\eta(x)) > 0$. Hence, for a given μ_1 it follows that neuronal adaption model here has the property $\mu_1^2 \geq E[\Delta_0 \Delta_k]$. Thus, the correlation coefficient ξ_k between two intervals separated by lag k is negative and dies out for large values of k.

Generally, following the same argument, if ψ and h are monotonous and

$$\partial_{t_x} \psi(t_x) \partial_{t_x} h(t_x) < 0 \qquad (B.4)$$

then the intervals exhibit a negative serial correlation. The condition on the Eq. (B.4) also indicates that if $\partial_{t_x} \psi(t_x) \partial_{t_x} h(t_x) = 0$ the process is renewal and under the condition of

$$\partial_{t_x} \psi(t_x) \partial_{t_x} h(t_x) > 0 \qquad (B.5)$$

process produces positive serial correlation.

C   Serial Correlations Beyond the Neuronal Systems

In this letter, we show that the negativity of serial correlation in neural adaptation enhances the signal transmission. Moreover, it has been argued that a sub-Poissonian statistics ($C_v^2 < 1$) is superior for light communication systems because it exhibits reduced variability the count statistics as compared to the Poisson statistics [15, 7]. The phenomenon of negative serial correlations

Tab. 1: Neuron model parameters as it is used for simulations of the full model neuron including voltage dynamics, adaptation and conductance-based synapses [13] as it is illustrated in Fig.1(Left) for comparsion to the master equation approch. The simulation is performed in PyNEST.

Parameter	Description	Value
v_{th}	Threshold voltage	-57mV
v_{reset}	Rest voltage	-70mV
c_m	Membrane capacitance	289.5pF
g_l	Membrane leak conductance	28.95pS
E_l	Membrane reversal potential	-70mV
q_{rr}	RELREF quantal conductance increase	3214nS
τ_{rr}	RELREF conductance decay time	1.97ms
E_{rr}	RELREF reversal potential	-70mV
q_s	SFA quantal conductance increase	14.48nS
τ_s	SFA conductance decay time	110ms
E_s	SFA reversal potential	-70mV
$E_{e,i}$	Reversal potential of excitatory and inhibitory synapses, respectively	0 mV, -75mV
$q_{e,i}$	Excitatory and inhibitory synaptic quantal conductance increase	2nS
$\tau_{e,i}$	Excitatory and inhibitory synaptic decay time	1.5ms , 10ms
$\lambda_{e,i}$	Excitatory and inhibitory input rate	6Hz, 11.4Hz

(Eq. (B.4)) is also observed in multi-level quantum systems [17] where $\mathcal{M}$ measures the serial correlation between consecutive inter-photon times. According to our results, a superposition of non-renewal photon emitters could enhance reliable information transmission and signal discrimination in photo detecting devices.

The condition in Eq. (B.5) might be of interest for event emitting systems that exhibit a self-exciting feedback and thus depart from renewal assumption by positive serial correlations between adjacent inter-event intervals. For example, it has been shown in [10] that after major earthquakes the rate of the aftershocks decreases in time by the Omori law. This decreasing rate generates a memory of inter-events where small (large) recurrence intervals follow small (large) ones, implying positive correlations among inter-event times.

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