How Noise Affects the Synchronization Properties of Recurrent Networks of Inhibitory Neurons

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GABAergic interneurons play a major role in the emergence of various types of synchronous oscillatory patterns of activity in the central nervous system. Motivated by these experimental facts, modeling studies have investigated mechanisms for the emergence of coherent activity in networks of inhibitory neurons. However, most of these studies have focused either when the noise in the network is absent or weak or in the opposite situation when it is strong. Hence, a full picture of how noise affects the dynamics of such systems is still lacking. The aim of this letter is to provide a more comprehensive understanding of the mechanisms by which the asynchronous states in large, fully connected networks of inhibitory neurons are destabilized as a function of the noise level. Three types of single neuron models are considered: the leaky integrate-and-fire (LIF) model, the exponential integrate-and-fire (EIF) model and conductance-based models involving sodium and potassium Hodgkin-Huxley (HH) currents. We show that in all models, the instabilities of the asynchronous state can be classified in two classes. The first one consists of clustering instabilities, which exist in a restricted range of noise. These instabilities lead to synchronous patterns in which the population of neurons is broken into clusters of synchronously firing neurons. The irregularity of the firing patterns of the neurons is weak. The second class of instabilities, termed oscillatory firing rate instabilities, exists at any value of noise. They lead to cluster state at low noise. As the noise is increased, the instability occurs at larger coupling, and the pattern of firing that emerges becomes more irregular. In the regime of high noise and strong coupling, these instabilities lead to stochastic oscillations in which neurons fire in an approximately Poisson way with a common instantaneous probability of firing that oscillates in time.
1 Introduction

Of the various patterns of synchronous oscillations that occur in the brain, episodes of activity during which local field potentials display fast oscillations with frequencies in the range 40 to 200 Hz have elicited particular interest. Such episodes have been recorded in vivo in several brain areas, in particular in the rat hippocampus (Buzsáki, Urioste, Hetke, & Wise, 1992; Bragin et al., 1995; Csicsvari, Hirase, Czurko, Mamiya, & Buzsáki, 1999a, 1999b; Siapas & Wilson, 1998; Hormuzdi et al., 2001). During these episodes, single-neuron firing rates are typically much lower than local field potential (LFP) frequencies (Csicsvari et al., 1999a), and single-neuron discharges appear very irregular. Although a detailed analysis of the single-cell firing statistics during these episodes is lacking, this irregularity is consistent with findings of high variability in interspike intervals of cortical neurons in various contexts (see, e.g., Softky & Koch, 1993; Compte et al., 2003), and the observation of large fluctuations in membrane potentials in intracellular recordings in cortex in vivo (see, e.g., Destexhe & Paré, 1999; Anderson, Lampl, Gillespie, & Ferster, 2000).

Recent theoretical studies have shown that fast synchronous population oscillations in which single-cell firing is highly irregular emerge in networks of strongly interacting inhibitory neurons in the presence of high noise. Brunel and Hakim (1999) investigated analytically the emergence of such oscillations in networks of sparsely connected leaky integrate-and-fire neurons activated by an external noisy input. They showed that the frequency of the population oscillations increases rapidly when the synaptic delay decreases and that it can be much larger than the firing frequency of the neurons. For instance, a network of neurons firing with an average rate of 10 Hz can oscillate at frequencies that can be on the order of 200 Hz when synaptic delays are on the order of 1 to 2 msec (Brunel & Hakim, 1999; Brunel & Wang, 2003). Tiesinga and Jose (2000) found similar collective states in numerical simulations of a fully connected network of inhibitory conductance-based neurons activated with a noisy external input. However, the frequency of the population oscillations in their model was smaller (in the range 20–80 Hz), and the variability of the spike trains was weaker than in the leaky integrate-and-fire (LIF) network for similar synaptic time constants and average firing rates of the neurons. Following the terminology of Tiesinga and Jose (2000), we will call this type of state a stochastic synchronous state.

Stochastic synchrony occurs in the presence of strong noise, in contrast to so-called cluster states, which are found when noise and heterogeneities are weak. In the simplest cluster state, all neurons tend to spike together in a narrow window of time; they form one cluster. In such a state, the population oscillation frequency is close to the average frequency of the neurons (Abbott & van Vreeswijk, 1993; Tsodyks, Mit’kov, & Sompolinsky, 1993; Hansel, Mato, & Meunier, 1995; White, Chow, Soto-Treviño, & Kopell,
Clustering in which neurons are divided into two or more groups can also occur (Golomb, Hansel, Shraiman, & Sompolinsky, 1992; Golomb & Rinzel, 1994; Hansel et al., 1995; van Vreeswijk, 1996). Within each of these groups, neurons fire at a similar phase of the population oscillation, but different groups fire at different phases. Thus, the frequency of the population oscillations can be very different from the neuronal firing rate, as in stochastic synchrony. However, in contrast to stochastic synchrony, in cluster states the population frequency is always close to a multiple of the neuronal firing rate. Moreover, single-neuron activity in cluster states is much more regular than in stochastic synchronous states.

In this letter, we examine the dynamics of networks of inhibitory neurons in the presence of noisy input. For simplicity, we consider a fully connected network; similarities and differences with more realistic randomly connected networks will be mentioned in the discussion. We consider three classes of models: the LIF model (Lapicque, 1907; Tuckwell, 1988), the exponential integrate-and-fire model (EIF) (Fourcaud-Trocmé, Hansel, van Vreeswijk, & Brunel, 2003), and simple conductance-based (CB) models (Hodgkin & Huxley, 1952) with two active currents, a sodium and a potassium current. In these models, we study the instabilities of the asynchronous state. In this state, the population-averaged firing rate becomes constant in the large $N$ limit, and correlations between neurons vanish in this limit. We investigate in particular how the instability responsible for stochastic synchrony relates to other types of instabilities of the asynchronous state.

Section 2 is devoted to the LIF model. We fully characterize the spectrum of the instabilities of the asynchronous state and explore in what ways these instabilities depend on the noise amplitude, the average firing rate of the neurons, and the synaptic time constants (latency, rise, and decay time). This can be performed analytically, due to the simplicity of the LIF model and the simplified all-to-all architecture.

The LIF neuron has the great advantage of analytical tractability, but it often exhibits nongeneric properties. For instance, the frequency-current relationship that characterizes the response of the neuron to a steady external current exhibits a logarithmic behavior near current threshold, while generic type I neurons have a square root behavior. LIF and standard Hodgkin-Huxley (HH) models may also display substantially different synchronization behaviors in the low-noise regime (Pfeuty, Golomb, Mato, & Hansel, 2003; Pfeuty, Mato, Golomb, & Hansel, 2005). Crucially, LIF neurons respond in a nongeneric way to fast oscillatory external inputs (Fourcaud-Trocmé et al., 2003). This motivates an investigation of synchronization properties in models with more realistic dynamics. In section 3, we combine analytical calculations with numerical simulations to study a network of EIF neurons. In this model, single-neuron dynamics depend on a voltage-activated current that triggers action potentials. This framework allows us to make predictions regarding the way sodium currents
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affect the emergence of fast oscillations. In section 4 we simulate several conductance-based network models to compare their behaviors with those of the LIF and the EIF. We conclude that although quantitative aspects of the phenomenology of stochastic synchrony depend on the details of the neuronal dynamics, the occurrence of this type of collective state is a generic feature of large neuronal networks of strongly coupled inhibitory neurons.

2 Networks of Leaky Integrate-and-Fire Neurons

2.1 The Model. We consider a fully connected network of \( N \) inhibitory LIF neurons. The membrane potential, \( V_i \), of neuron \( i \) (\( i = 1, \ldots, N \)) evolves in the subthreshold range \( V_i(t) \leq V_t \) where \( V_t \) is the firing threshold, according to

\[
\tau_m \dot{V}_i(t) = -V_i(t) + I_{rec}(t) + I_{i,ext}(t),
\]

where \( \tau_m \) is the membrane time constant, \( I_{i,ext}(t) \) is an external input, and \( I_{rec}(t) \) is the recurrent input due to the interactions between the neurons. When the voltage reaches threshold \( V_t \), a spike is emitted and the voltage is reset to \( V_r \).

The external input is modeled as a current,

\[
I_{i,ext}(t) = I_0 + \sigma \sqrt{\tau_m} \eta_i(t),
\]

where \( I_0 \) is a constant DC input, \( \sigma \) measures the fluctuations around \( I_0 \), and \( \eta_i(t) \) is a white noise that is uncorrelated from neuron to neuron, \( \langle \eta_i(t) \rangle = 0 \), \( \langle \eta_i(t) \eta_j(t') \rangle = \delta_{ij} \delta(t - t') \).

Since the network is fully connected, all neurons receive the same recurrent synaptic input. It is modeled as

\[
I_{rec}(t) = -\frac{J}{N} \sum_{j=1}^{N} \sum_{k} s(t - t_j^k),
\]

where the postsynaptic current elicited by a presynaptic spike in neuron \( j \) occurring at time \( t_j^k \), is denoted by \( s(t - t_j^k) \), and \( J \), which measures the strength of the synaptic interactions, has the dimension of a voltage. The first sum on the right-hand side in this equation represents a sum over synapses; the second sum is over spikes.

For the function \( s(t) \), we take

\[
s(t) = \begin{cases} 
0 & t < \tau_l \\
A(\exp[-(t - \tau_l)/\tau_d] - \exp[-(t - \tau_l)/\tau_r]) & t \geq \tau_l
\end{cases}
\]
where $\tau_l$ is the latency, $\tau_r$ is the rise time, $\tau_d$ is the decay time of the postsynaptic current, and $A = \tau_m / (\tau_d - \tau_r)$ is a normalization factor that ensures that the integral of a unitary postsynaptic current remains independent of the synaptic time constants. With this normalization, $\int s(t)dt = \tau_m$. Such kinetics are obtained from the set of differential equations,

\begin{align}
\tau_d \dot{s}(t) &= -s(t) + x(t) \\
\tau_r \dot{x}(t) &= -x(t) + \tau_m \delta(t - \tau_l)
\end{align}

where $x$ is an auxiliary variable.

In the following we assume that all the neurons are identical, and we take $\tau_m = 10$ ms (McCormick, Connors, Lighthall, & Prince, 1985), $V_l = 20$ mV, $V_r = 14$ mV (Troyer & Miller 1997).

### 2.2 The Asynchronous State.

The dynamics of the LIF network can be studied using a mean-field approach (Treves, 1993; Abbott & van Vreeswijk, 1993; Brunel & Hakim, 1999; Brunel, 2000). In the thermodynamic limit $N \to \infty$, the recurrent input to the neurons can be written up to corrections of order $1/\sqrt{N}$:

\begin{align}
I_{rec}(t) &= -J s(t) \\
\tau_d \dot{s} &= -s + x \\
\tau_r \dot{x} &= -x + \tau_m \nu(t - \tau_l)
\end{align}

where $\nu(t)$ is the instantaneous firing rate of the neurons at time $t$ averaged over the network. The dynamical state of the network can then be described by a probability density function (PDF) for the voltage, $P(V, t)$, which satisfies the Fokker-Planck equation,

\begin{equation}
\tau_m \frac{\partial P}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2 P}{\partial V^2} + \frac{\partial}{\partial V} [(V - I_{rec}(t) - I_0)P].
\end{equation}

with the boundary conditions

\begin{align}
P(V_l, t) &= 0 \\
\frac{\partial P}{\partial V}(V_l, t) &= -\frac{2\nu(t)\tau_m}{\sigma^2} \\
\lim_{\epsilon \to 0} (P(V_r + \epsilon, t) - P(V_r - \epsilon, t)) &= 0 \\
\lim_{\epsilon \to 0} \left( \frac{\partial P}{\partial V}(V_r + \epsilon, t) - \frac{\partial P}{\partial V}(V_r - \epsilon, t) \right) &= -\frac{2\nu(t)\tau_m}{\sigma^2}.
\end{align}
Finally, $P(V, t)$ must obey $\int P(V, t) dV = 1$ at all times $t$.

In the stationary state of the network, the PDF of the membrane potential as well as the population average of the firing rate, $\nu(t) = \nu_0$, are constant in time, and the neurons fire asynchronously. Integrating equation 2.10 together with the condition $\partial P / \partial t = 0$ and the boundary conditions, equation 2.14, one can show that the stationary firing rate $\nu_0$ is given by Ricciardi (1977), Amit and Tsodyks (1991), and Amit and Brunel (1997),

$$\frac{1}{\nu_0 \tau_m} = \sqrt{\pi} \int_{-\infty}^{y_h} e^{x^2} \left[ 1 + \text{erf}(x) \right] dx$$ (2.15)

where erf is the error function (Abramowitz & Stegun, 1970),

$$y_h = \frac{V_l + J \nu_0 \tau_m - I_0}{\sigma}$$ (2.16)

$$y_r = \frac{V_r + J \nu_0 \tau_m - I_0}{\sigma}.$$ (2.17)

The coefficient of variation of the interspike interval distribution, which measures the irregularity of single-neuron firing, can also be computed in the asynchronous state. This yields (Brunel, 2000; Tuckwell, 1988)

$$\text{CV}^2 = 2\pi (\nu_0 \tau_m)^2 \int_{y_h}^{y_r} e^{x^2} dx \int_{-\infty}^{x} e^{y^2} \left[ 1 + \text{erf}(y) \right] dy.$$

Figure 1 shows how the coefficient of variation (CV) increases with noise level $\sigma$, for several values of the average firing rate.

### 2.3 Stability Analysis of the Asynchronous State.

The asynchronous state is stable if any small perturbation from it decays back to zero. To study the instabilities of the asynchronous state, one approach is to diagonalize the linear operator, which describes the dynamics of small perturbations from the asynchronous state (see appendix A). A specific eigenmode, with eigenvalue $\lambda$, is stable (resp. unstable) if $\text{Re}(\lambda) < 0$ (resp. $\text{Re}(\lambda) > 0$). The frequency at which the mode oscillates is $\omega/(2\pi)$ where $\omega = \text{Im}(\lambda)$. The asynchronous state is stable if the real part of the eigenvalue is negative for all the eigenmodes.

Here we present an alternative approach that directly provides the equation that determines the critical manifolds in parameter space on which eigenmodes change stability (see also Brunel & Wang, 2003).

The derivation proceeds in two steps. The first step is to compute the recurrent current, assuming that the population firing rate of the network is weakly modulated and oscillatory with a frequency
Figure 1: Coefficient of variation as a function of the noise level, $\sigma$, for $V_l = 20$ mV, $V_r = 14$ mV, $\tau_m = 10$ ms, and several values of the average firing rate $v_0$, indicated on the graph.

$\omega : v(t) = v_0 + v_1 \exp(i\omega t)$ with $v_1 \ll 1$ (for notational simplicity, we use complex numbers in the following linear analysis). At leading order, the recurrent current is also oscillatory at the same frequency, and its modulation can be written as

$$I_1 = -J v_1 \tau_m \exp(-i\omega \tau_l)/(1 + i\omega \tau_d)(1 + i\omega \tau_r) \equiv J v_1 \tau_m A_S(\omega) \exp[i\pi + i \Phi_S(\omega)],$$

(2.18)

where

$$A_S(\omega) = \frac{1}{\sqrt{(1 + \omega^2 \tau_d^2)(1 + \omega^2 \tau_r^2)}},$$

(2.19)

$$\Phi_S(\omega) = \omega \tau_l + \tan(\omega \tau_r) + \tan(\omega \tau_d).$$

(2.20)

The phase shift of the synaptic current with respect to the oscillatory presynaptic firing rate modulation is the sum of four contributions. Three of them, on the right-hand side of equation 2.20, depend on the latency, the rise time, and the decay time of the synapses and vary with $\omega$. The fourth contribution, which does not depend on $\omega$, is due to the factor $\exp(i\pi)$ in equation 2.18. It results from the inhibitory nature of the synaptic interactions.
The second step is to compute the firing rate in response to an oscillatory input, equation A.3. It is given by (Brunel & Hakim, 1999; Brunel, Chance, Fourcaud, & Abbott, 2001),

\[ \nu_1 = \frac{I_1 \nu_0}{\sigma(1 + i \omega \tau_m)} \frac{\partial U}{\partial y}(y_t, i \omega) - \frac{\partial U}{\partial y}(y_r, i \omega). \]  

(2.21)

where \( y_t, y_r \) are given by equations 2.16 and 2.17 and the function \( U \) is defined in appendix A, equation A.5. The modulation \( \nu_1 \) can also be written as

\[ \nu_1 = \frac{I_1 \nu_0}{\sigma} A_N(\omega) \exp[i \Phi_N(\omega)], \]  

(2.22)

where \( (I_1 \nu_0/\sigma) A_N(\omega) \) is the amplitude of the firing rate modulation and \( \Phi_N(\omega) \) is the phase shift of the firing rate with respect to the oscillatory input current. A negative (resp. positive) phase shift means that the modulation of the neuronal response is in advance (resp. delayed) compared to the modulation of the input.

Since in the network, the modulation of the firing rate and the modulation of the recurrent current must be consistent, combining equations 2.18 and 2.21, the following self-consistent condition must be satisfied:

\[ 1 = J \frac{\nu_0 \tau_m}{\sigma} A_N(\omega) A_S(\omega) \exp[i \pi + i \Phi_S(\omega) + i \Phi_N(\omega)]. \]  

(2.23)

This equation is a necessary and sufficient condition for the existence of self-sustained oscillations of the population firing rate with vanishingly small amplitude and frequency \( \omega \). Therefore, it is identical to the condition that an eigenmode of the linearized dynamics, oscillating at frequency \( \omega \), has marginal stability (i.e., the real part of its eigenvalue vanishes). Note that \( A_N \) depends on \( \nu_0, \sigma, V_t, \) and \( V_r \), whereas \( A_S \) depends on synaptic time constants \( \tau_i, \tau_r, \) and \( \tau_d \).

The complex equation 2.23 is equivalent to two real equations. The first of these equations is

\[ \Phi_S(\omega) + \Phi_N(\omega) = (2k + 1)\pi, \quad k = 0, 1, 2, \ldots \]  

(2.24)

Equation 2.24 does not depend on the coupling strength \( J \) \( > 0 \). It determines the frequency spectrum of the eigenmodes with marginal stability.

The second equation is

\[ 1 = J \frac{\nu_0 \tau_m}{\sigma} A_N(\omega) A_S(\omega). \]  

(2.25)
It determines the coupling $J_c(\omega)$,

$$J_c(\omega) = \frac{\sigma}{\nu_0 \tau_m A_N(\omega) A_S(\omega)},$$

at which a mode with frequency $\omega$ has marginal stability.

In the following, we study the instability of the asynchronous state in the $J$-$\sigma$ plane, at a fixed firing rate $\nu_0$. When $J$ and $\sigma$ are varied, $\nu_0$ is kept fixed by a suitable adjustment of $I_0$. The effect of the firing rate $\nu_0$ on instabilities is then studied separately in section 2.4.4. For given $\nu_0$ and $\sigma$, one expects the asynchronous state to be stable when $J$ is sufficiently small. The first eigenmode to lose stability when $J$ increases determines the stability boundary of the asynchronous state. Therefore, this boundary is given by

$$\tilde{J}_c = \min_{\{\omega|\Phi_1^S(\omega) + \Phi_1^N(\omega) = (2k+1)\pi\}} \frac{\sigma}{\nu_0 \tau_m A_N(\omega) A_S(\omega)},$$

where the minimum is computed over all the solutions to equation 2.24.

2.4 The Spectrum of Instabilities. Inspection of the qualitative properties of the synaptic and neuronal phase lag helps us to understand how the instabilities of the asynchronous state occur and how they depend on the noise level (see also Fuhrmann, Markram, & Tsodyks, 2002, Brunel & Wang, 2003, for similar considerations).

2.4.1 The Solutions to Equation 2.24. The synaptic phase lag $\Phi_1^S(\omega)$ is an increasing function of frequency. For low and high frequencies, it behaves like $\Phi_1^S(\omega) \sim \omega (\tau_l + \tau_r + \tau_d)$ and $\Phi_1^S(\omega) \sim \pi + \omega \tau_l$, respectively. The function $\Phi_1^S(\omega)$, which does not depend on the noise level, is plotted in Figure 2A.

The neuronal phase lag, $\Phi_1^N(\omega)$, depends markedly on the noise level. For low noise levels, $\Phi_1^N(\omega)$ has a sawtooth profile with peaks and very sharp variations at frequencies $\omega = 2\pi f_n$, where $f_n$ are in the limit of zero noise integer multiples of the firing rate of the neurons, $f_n = n \nu_0$, $n = 1, 2 \ldots$ (see Figure 2B). Provided the latency is strictly positive, $\tau_l > 0$, the function $\Phi_1^N + \Phi_1^S$ goes to infinity with a sawtooth profile in the large $\omega$ limit (see Figure 2C). Since the frequencies of the eigenmodes with marginal stability are solutions to equation 2.24, they can be determined graphically by looking at the intersections of the graph of the function $\Phi_1^N + \Phi_1^S$ with the horizontal lines at ordinates $(2k+1)\pi$. For $\tau_l > 0$, one can show that an odd number, $2p + 1$, of such intersections exists for any $k$. For instance, for the parameters of Figure 2C, there are for $k = 0$, 13 intersections for $\sigma = 0.01 \text{ mV}$, 3 intersections for $\sigma = 0.05 \text{ mV}$, and only 1 intersection for $\sigma \geq 0.1 \text{ mV}$. Out of these $2p + 1$ intersections, $p + 1$ are for frequencies close to $f_n$ for values of $n$ in a range that depends on the noise level and also on the synaptic
Figure 2: Interpretation of equation 2.24 in terms of synaptic and neuronal phase lags. (A) Synaptic phase lag for $\tau_l = 1$ ms, $\tau_r = 1$ ms, $\tau_d = 6$ ms. (B) Neuronal phase lag for $V_l = 20$ mV, $V_r = 14$ mV, $\nu_0 = 30$ Hz, $\tau_m = 10$ ms, and five noise levels: 0.01 mV (dot-dashed), 0.05 mV (dashed), 0.1 mV (thin solid), 1 mV (medium solid), and 10 mV (thick solid). Note the sharp variations at integer multiples of the firing rate $\nu_0$ (30, 60, 90, ... Hz) for low noise levels, which disappear as noise becomes stronger. (C) Total phase lag (sum of synaptic and neuronal phase lags, for the same noise levels as in B). Solutions to equation 2.24 for a given noise level are at the intersection of the curve representing the total phase lag and the horizontal dotted line at 180 degrees. Note the large number of intersections for low noise levels that disappear as noise increases until a single intersection is left.

kinetics, as will be shown later. For instance, $n = 3, \ldots, 9$ for $\sigma = 0.01$ mV, $n = 4, 5$ for $\sigma = 0.05$ mV, as shown in Figure 2C. The remaining $p$ intersections are at intermediate frequencies $n\nu_0 < \omega/(2\pi) < (n + 1)\nu_0$. 
Figure 2B shows that the amplitude of the peaks in \( \Phi_N(\omega) \) decreases, and the peaks themselves become less sharp and broader when the noise increases. As a result, pairs of intersections with the 180 horizontal line coalesce and disappear. For example, in Figure 2C, a pair of intersections—one near 60 Hz and the other at a frequency between 60 and 90 Hz—disappears when the noise is increased from \( \sigma = 0.01 \) (dot-dashed curve) to 0.05 mV (dashed curve). Eventually, for sufficiently large noise, all the intersections except one have disappeared, and the neuronal phase \( \Phi_N \) becomes a monotonously increasing function of \( \omega \) (see Figure 2C, for \( \sigma \geq 0.1 \) mV). For the parameters of Figure 2C, this single intersection is between 90 Hz (for \( \sigma = 10 \) mV) and 120 Hz (for \( \sigma = 0.1 \) mV), three to four times larger than the average firing rate of the neurons, \( v_0 = 30 \) Hz. In general, the value of \( \omega \) at this intersection depends not only on \( v_0 \) but also on the synaptic time constants, \( \tau_l, \tau_r, \) and \( \tau_d \) as will be discussed below.

A similar picture holds for the intersections with horizontal lines at \((2k + 1)\pi\) with \( k \geq 1 \), although they occur at much larger frequencies. For example, intersections with the line at 540 degrees \((k = 1)\) occur around 1000 Hz for the parameters of Figure 2.

Once the frequencies of the marginal modes have been obtained from equation 2.24, the corresponding critical couplings are determined by solving equation 2.26. The results can be represented in the plane \( J-\sigma \).

2.4.2 The Instability Spectrum in the \( J-\sigma \) Plane. We start by describing the structure of the instability spectrum in the case where the synaptic time constants are \( \tau_r = 1 \) ms, \( \tau_d = 6 \) ms, and \( \tau_l = 1 \) ms. What happens when these parameters change is briefly discussed in section 2.5.

We first consider the case \( v_0 = 30 \) Hz. The lines on which eigenmodes are marginal are plotted in the \( \sigma-J \) plane in Figure 3A. The frequencies of the marginal modes are plotted as a function of noise in Figure 3B.

Figure 3A shows that there are several families of lines. Each family corresponds to the set of solutions to the phase equation, 2.24, for a given \( k = 0, 1, 2, 3, \ldots \) (from low \( J \) to high \( J \); for clarity, only lines belonging to \( k = 0, 1 \) families are shown) as \( \sigma \) varies. As discussed in the previous section, an odd number \( 2p + 1 \) of solutions to the phase condition exist for any \( k \). These \( 2p + 1 \) solutions can be divided into \( p \) pairs of solutions that coalesce at some level of noise and one solution that exists at any noise level.

We first discuss the \( p \) lines corresponding to the \( 2p \) solutions that disappear as the noise level increases. Each line is composed of an upper and a lower branch that approach each other as the noise level increases and subsequently meet at a critical value of the noise. The area enclosed by the line is the region in which the corresponding eigenmode is unstable (i.e., the region to the left of the curve). The frequency of the mode on the lower part of this line is very close to an integer multiple of the average neuronal firing rate \( n v_0 \), while on the upper part of the line, the frequency is between
Figure 3: (A) Lines on which eigenmodes become unstable, obtained from equations 2.24 and 2.25, in the plane $J - \sigma$, for the parameters of Figure 2. The asynchronous state is stable below the lowest line (region marked “asynchronous state stable”). Only lines corresponding to families of solutions at $k = 0$ and $k = 1$ (marked in the figure) are indicated. Each family is composed of individual branches labeled by integer values of $n$ (indicated only for $k = 0$).

(B) Frequency of marginal modes. The thick curve in A is the stability boundary of the asynchronous state. The thick curve in B is the frequency of the unstable mode on this boundary plotted against the noise.
$n \nu_0$ and $(n+1)\nu_0$ or $(n-1)\nu_0$ (see Figure 3B). These two parts of the line meet each other for the noise level at which the eigenmode becomes stable for any value of the coupling. Hence, we can index all eigenmodes and the lines on which they have marginal stability in the $\sigma - J$ plane by the integer $n$. This index is the number of clusters that emerge via the instability on the lower part of the line. If $n = 1$, one cluster emerges, and all the neurons in the network tend to fire simultaneously. For $n \geq 2$, they tend to split into groups of neurons that fire in synchrony one after the other (see Figure 4B).

Thus, the frequency of the population oscillations can be significantly larger than the average firing rate of the neurons, $\nu_0$, if $n$ is large. All these instabilities exist only in a limited range of noise amplitude. For example, in Figures 3A and 3B, the $n = 2$ curve exists for $\sigma < 0.005$ mV, $n = 3$ exists for $\sigma < 0.04$ mV, and so forth. This reflects the sensitivity of clustering to noise. As noise increases, neurons are less able to maintain their phase locking to the population oscillation. Clustering cannot emerge since neurons would skip more and more between clusters and spend less time bound to a specific cluster. The instabilities corresponding to these $p$ eigenmodes are called clustering instabilities.

An additional solution to the phase condition differs from the other solutions by the fact that it survives even for large noise. As noise increases, it generates a single-valued curve in the $J - \sigma$ plane. On this line, the desynchronizing effect of the noise that would suppress the instability can be compensated for by increasing the coupling strength (see Figure 3A). The mode that has marginal stability on this line can also be indexed by an integer $n$ since in the limit of weak noise, its frequency goes to one of the integer multiples of the firing rate $f_n$ ($n = 4$ in Figure 3).

Hence, at low noise levels, this instability, like the clustering instabilities described above, leads to a cluster state in which the neurons fire in a regular manner. When the noise becomes strong, it leads to a state in which individual neurons fire in a highly irregular way while the population activity oscillates—a stochastic synchronous state. In this state, the neurons increase their firing probability together with the oscillatory population activity, that is, they display “rate oscillations” (see Figure 4D). To distinguish this instability from those described above, we term it an oscillatory rate instability.

2.4.3 Stability Boundary of the Asynchronous State. For each value of $\sigma$, the asynchronous state is stable for $J < \tilde{J}_c$ where $\tilde{J}_c$ is given by equation 2.27. Typically, $\tilde{J}_c = J(\omega_1)$ where $\omega_1$ is the smallest solution of equation 2.24. This is because if $\omega_1 < \omega_2 < \cdots$ are solutions to equation 2.24, we have $A_5(\omega_1) > A_5(\omega_2) > \cdots$, and likewise $A_5(\omega_1) > A_5(\omega_2) > \cdots$. The bold lines in Figure 3A indicate the boundary of the region in which the asynchronous state is stable.

When the noise is weak, the stability boundary coincides with one of the lines where a clustering instability occurs ($n = 2$ for $\sigma < 0.005$ mV, $n = 3$ for
Figure 4: Simulations of a network of 1000 LIF neurons. All four panels show spike trains of 20 selected neurons (rasters) and instantaneous population firing rate, computed in 1 ms bins. (A, B) Low coupling–low noise region. In A, the asynchronous state is stable ($I = 1 \text{ mV, } \sigma = 0.04 \text{ mV}$). In B, the noise is decreased ($\sigma = 0.02 \text{ mV}$). The network now settles in a three-cluster state, as predicted by the analytical results. (C, D) Strong coupling–strong noise region. C: $I = 100 \text{ mV, } \sigma = 10 \text{ mV}$; the asynchronous state is stable. Decreasing $\sigma$ to $\sigma = 4 \text{ mV}$ leads to a stochastic oscillatory state, as predicted by the analytical results. See appendix C for more details on numerical simulations.
0.005 < \sigma < 0.04 \text{ mV}) and the CV of the firing is smaller than 0.04. When the noise is sufficiently large (\sigma > 0.04 \text{ mV}), the stability boundary coincides with the oscillatory rate instability. On this part of the boundary, the CV increases from 0.04 to about 1 for \sigma \sim 5 \text{ mV} (see Figure 1).

The frequency of the marginal mode on the stability boundary of the asynchronous state is shown in Figure 3B. At low noise levels, the index of the marginal mode is \( n = 2 \), and the frequency is about \( 2\nu_0 = 60 \text{ Hz} \). It increases discontinuously when \( \sigma \approx 0.005 \text{ mV} \) to about \( 3\nu_0 = 90 \text{ Hz} \), as the index changes from \( n = 2 \) to \( n = 3 \). A second discontinuity occurs for \( \sigma \approx 0.04 \text{ mV} \), and the marginal mode on the boundary becomes the oscillatory rate mode. The index \( n \) changes from 3 to 4, and the frequency jumps to 120 Hz. For further increases of \( \sigma \), the frequency changes smoothly with the noise and remains significantly larger than \( \nu_0 \).

The two regions of the stability boundary (clustering and rate oscillation) are characterized by different relationships between \( \tilde{J}_c \) and \( \sigma \). At low noise levels, in the clustering region, \( \tilde{J}_c \sim \sigma^2 \) (Abbott & van Vreeswijk 1993), while at high noise levels, in the rate oscillation region, \( \tilde{J}_c \sim \sigma/\sqrt{\ln \sigma} \) (see appendix B for details of the derivation).

### 2.4.4 How the Stability Boundary Depends on the Firing Rate \( \nu_0 \)

The instabilities that occur on the asynchronous state stability boundary depend on \( \nu_0 \), as shown in Figure 5. For \( \nu_0 = 10 \text{ Hz} \), clustering instabilities with \( n = 7, 8, 9, 10, 11 \) occur at very low noise levels. For \( \sigma \approx 10^{-4} \), the instability becomes an oscillatory rate instability with \( n = 12 \). As \( \nu_0 \) increases, the asynchronous state loses stability at smaller \( J \) and \( \sigma \). Intuitively, this is because the inhibitory feedback responsible for the destabilization of the asynchronous state increases with \( \nu_0 \). Moreover, clustering instabilities occur in a larger range of noise, the number of emerging clusters becomes smaller, and the transition to the oscillatory rate instability moves toward larger noise level. The last effect is a consequence of the fact that as the firing rate increases, the spike trains become more regular. For \( \nu_0 = 30 \text{ Hz} \), this transition occurs around \( \sigma = 0.04 \text{ mV} \), whereas for \( \nu_0 = 50 \text{ Hz} \), it is at about \( \sigma = 0.3 \text{ mV} \). For all these values of \( \nu_0 \), the CV is in the range 0.01 to 0.1 at this transition.

### 2.5 The Effect of Synaptic Kinetics

The synaptic time constants and delay have a strong effect on the asynchronous state instability spectrum and asynchronous state stability boundary. Three qualitatively different situations can occur.

First, when the latency and the rise time are both zero, the synaptic phase, \( \Phi_{\tilde{S}}(\omega) \), is bounded by \( \pi/2 \). Since the neuronal phase is smaller than \( \pi/2 \) (see Figure 2), equation 2.24 has no solutions. Hence, the asynchronous state is stable for any \( J, \sigma \).

Second, when there is no latency (\( \tau_l = 0 \)) but the rise time is finite, the synaptic phase is bounded by \( \pi \). Hence, solutions to equation 2.24 exist
Figure 5: Instabilities of the asynchronous state versus firing rate. (A) Stability boundary of the asynchronous state in the $\sigma - J$ plane. (B) Frequency of the marginal mode on this boundary. In both panels, curves for three firing rates are shown: $\nu_0 = 10$ Hz (thin curves), 30 Hz (intermediate curves), 50 Hz (thick curves). Dashed lines indicate cluster state instabilities; the solid line indicates the oscillatory rate instability.
Figure 6: Influence of the shape of the inhibitory synaptic currents on the location of instabilities in the $\sigma - J$ plane and on the frequencies of the eigenmodes with marginal stability. (A) Instantaneous synaptic currents ($\tau_r = \tau_d = 0$) and latency $\tau_l = 2$ ms. The rate oscillation mode has an index $n = 8$ (frequency about 180 Hz at $\sigma = 10$ mV). When noise decreases, there is a succession of transitions to cluster modes with lower $n$. (B) Synaptic currents with $\tau_r = 2$ ms, $\tau_d = 6$ ms, and no latency ($\tau_l = 0$). The oscillatory rate instability has a large index $n$ ($n \sim 25$). The rate oscillations have a frequency of about 120 Hz for $\sigma = 10$ mV. The critical coupling $J_c$ varies in a nonmonotonic way when $\sigma$ increases. Note the different scales in ordinate of the top panels of A and B.

only for $k = 0$. An example of such a case is shown in Figure 6B. Note that in this case, the oscillatory rate instability has a very large index $n$, and there is a range of $J$ in which the stability of the asynchronous state varies nonmonotonically as the noise level increases. The asynchronous state is
first unstable due to clustering instabilities, then becomes stable, becomes unstable again due to the oscillatory rate instability, and finally becomes stable as the noise increases.

Third, with a finite latency, the synaptic phase is unbounded as $\omega$ increases. Hence, solutions to equation 2.24 exist for any $k$, leading to families of eigenmodes associated with each integer $k$ as in Figure 3, for any value (zero or nonzero) of rise and decay times. For example, the families of lines on which eigenmodes have marginal stability in the $\sigma - J$ plane and the frequencies of the marginal modes are shown in Figure 6A for $k = 0$ and $k = 1$. However, the region of stability of the asynchronous state is larger for nonzero decay time and/or rise time, as seen by comparing Figure 6A and Figure 3A (note that the scale of the ordinates is 10 times larger in Figure 3A than in Figure 6A).

The number of clusters emerging on the asynchronous state stability boundary (i.e., the index $n$ of the corresponding instability mode) in the weak noise region depends on the amplitude of noise, but also on all synaptic time constants (latency, rise time, decay time): the shorter the synaptic time constants, the larger the number of clusters. This is shown in Figure 7, where the number of clusters is plotted as a function of $\sigma$ and a scaling factor, $\alpha$, for all three synaptic time constants ($\tau_l = \alpha \times 1$ ms, $\tau_r = \alpha \times 1$ ms, $\tau_d = \alpha \times 6$ ms). The solid lines in this figure show the boundary between regions in which the instability mode has frequency $\sim n\nu_0$, for example, the corresponding instability leads to $n$-cluster states (number of clusters $n$ marked in each region) in the $\sigma - J$ plane. The number of clusters can vary from 1 for slow synaptic currents (for example with $\tau_l = 3$ ms, $\tau_r = 3$ ms, $\tau_d = 18$ ms) to infinity as synaptic currents become infinitely fast (van Vreeswijk, 1996).

These lines delineate open stripes in the $\sigma - J$ plane; upon crossing such lines, a pair of solutions to equation 2.24 either appears or vanishes, one of which corresponds to the stability boundary of the asynchronous state. For example, for $\alpha = 1$, the instability line on the stability boundary of the asynchronous state is $n = 3$ for $\sigma = 0.01$; increasing $\alpha$, the pair of solutions corresponding to $n = 3$ disappears, and the instability line becomes the $n = 4$ line.

The dotted line separates the region where the number of solutions to equation 2.24 is strictly larger than one (on the left of the line) from a region where a single solution exists (on the right of the line)—hence, a pair of solutions vanishes when crossing the line from left to right. The difference between the dotted line and the solid lines is that on a dotted line, none of the solutions corresponds to the stability boundary of the asynchronous state. Taking again the case where $\alpha = 1$ as an example, crossing the dotted line marks the point where the $n = 5$ pair coalesces (see Figure 3). The set of lines that marks the boundary of the open, large noise region (composed of a set of alternating solid and dotted lines) can be defined as the boundary of the stochastic synchrony region. For the LIF neuron, this set of lines remains...
Figure 7: The nature of the unstable modes on the stability boundary of the asynchronous state as a function of noise and a global scaling factor of the synaptic kinetics $\alpha$. The synaptic time constants are $\tau_r = \alpha$ ms, $\tau_d = 6\alpha$ ms, and $\tau_l = \alpha$ ms. The solid lines are the boundaries between regions in which the instability mode has a frequency $\sim n\nu_0$, for example, the corresponding instability leads to $n$-cluster states, where $n$ is indicated in each region. The dotted line separates a weak noise regime where the number of solutions to equation 2.24 is strictly larger than 1, from a strong noise regime where there is only one solution left. In the weak noise regime, the instabilities are cluster-type instabilities, while in the strong noise regime, the instability is the oscillatory rate instability.

confined to a range of values of $\sigma$, which is between 0.05 and 0.2 mV, for the range of $\alpha$ shown in the figure.

3 Networks of EIF Neurons

3.1 The Model. In the following we consider a network of $N$ inhibitory fully connected exponential integrate-and-fire neurons (EIF, Fourcaud-Trocmé et al., 2003) receiving noisy external inputs. In the EIF, the fixed threshold condition of the LIF neuron is replaced by a spike-generating
current that depends exponentially on voltage. In this model, the voltage of neuron \( i \) is described by

\[
\tau_m \dot{V}_i(t) = -V_i(t) + \Delta_T \exp\left( \frac{V - V_T}{\Delta_T} \right) + I_{\text{rec}}(t) + I_{i,\text{ext}}(t),
\]

where the external and the recurrent currents are modeled as in the LIF network. The parameter \( V_T \) is the highest voltage at which the membrane potential can be maintained injecting a steady external input, and the slope factor \( \Delta_T \) measures the sharpness of the action potential generation. When the external current is large enough, the voltage diverges to infinity in finite time, due to the exponential term in the right-hand side of equation 3.1. This divergence defines the time of the spike. At that time, the voltage is reset to a fixed voltage \( V_r \), where it remains during an absolute refractory period \( \tau_{\text{ARP}} \). Unless specified otherwise, the results presented below were obtained for the following set parameters: \( \tau_m = 10 \) ms, \( V_T = 5.1 \) mV, \( V_r = -3 \) mV, \( \tau_{\text{ARP}} = 1.7 \) ms, and \( \Delta_T = 3.5 \) mV (Fourcaud-Trocmé et al., 2003).

The EIF model is a good compromise between the simplified LIF neuron, which has an unrealistic spike generation mechanism, and more realistic HH-type models. It is simple enough that analytical techniques can be applied to study its dynamics. Moreover, simple HH models, can be mapped onto EIF models, as shown in Fourcaud-Trocmé et al. (2003).

In the following, we study the stability properties of the asynchronous state in this model and compare them to those of the LIF model, which can be thought of as an EIF neuron with infinitely sharp spike initiation (\( \Delta_T = 0 \)). More generally, we investigate how the synchronization properties of the EIF network depend on the sharpness of the spike initiation.

### 3.2 Stability of the Asynchronous State

The approach described in section 2 can be applied to study the stability of the asynchronous state of the EIF network. Marginal modes are still determined by equations 2.24 to 2.27, but \( A_N(\omega) \) and \( \Phi_N(\omega) \) now represent the amplitude and the phase shift of the instantaneous firing rate modulation of a single EIF neuron in response to an oscillatory input at frequency \( \omega \). Fourcaud-Trocmé et al. (2003) computed these functions in the low- and the high-frequency limits. Obtaining these functions analytically at any \( \omega \) is a difficult task. Hence, we compute them for various noise levels using numerical simulations. Examples are shown in Figure 8. Once \( \Phi_N(\omega) \) and \( A_N(\omega) \) are known, we solve equations 2.24 to 2.26 to find the frequency of the unstable modes at the onset of instabilities, together with the critical coupling strength where these instabilities appear. The instability spectrum derived using this approach is plotted in the \( \sigma - J \) plane in Figure 9A for \( \nu_0 = 30 \) Hz, \( \tau_l = 1 \) ms, \( \tau_r = 1 \) ms, \( \tau_d = 6 \) ms. In this figure, only the lines corresponding to \( k = 0 \) and \( n = 1, 2, 3 \) are shown. This instability spectrum bears some resemblance to the one obtained in the LIF
Figure 8: (A) Single-neuron phase shift for low noise (small circles, $\sigma = 0.5$ mV) and high noise (large circles, $\sigma = 5$ mV). Note that for low noise, the phase shift increases sharply when the frequency is close to integer multiples of the stationary frequency (here, 30 Hz), and decreases in between two successive integer values, while for high noise, the phase increases monotonically with frequency. (B) Total phase shifts (neuronal + synaptic, left-hand side of equation 2.24) for the same two noise levels as in A. The intersection of curves with the horizontal dotted line at 180 degrees gives the frequencies of oscillatory instabilities. Note that for low noise, these intersections are close to integer multiples of the firing rate ($\sim 30, 60, 90$ Hz) and intermediate frequencies ($\sim 45, 75$ Hz), while for high noise, there is a single intersection around 50 Hz that is unrelated to the single-cell firing frequency.
Figure 9: Oscillatory instabilities in the EIF model (circles and solid lines) and in the simulations of the Wang-Buzsáki model (stars and dashed lines; see the details in section 4.) (A) Frequency of oscillatory instabilities versus noise. (B) Critical lines on which eigenmodes become unstable in the $\sigma - J$ plane. In both panels, cluster instabilities with $n = 1, 2, 3$, corresponding to the resonances at 30, 60, 90 Hz (see Figure 8), are shown. Note that the frequency and the critical coupling strength on the stability boundary of the asynchronous state are very close in the two models.
model for the same parameters (see Figure 3A). However, there are several significant differences between the two figures. One is that in the LIF model, the marginal modes for $k = 0$ have indices $n \geq 3$, whereas the first mode to be unstable is for $n = 1$ in the EIF model. Moreover, in the EIF network, the oscillatory rate instability for $k = 0$ has an index $n = 1$, whereas it is $n = 4$ in the LIF network for the same parameters. As a consequence, the oscillations that emerge from the rate instability are slower in the EIF model than in the LIF model (40–70 Hz versus 90–120 Hz; compare Figure 9B with Figure 3B). Another difference is that the noise level at which all instabilities but the oscillatory rate instability have disappeared is to times greater in the EIF than in the LIF.

These differences can be understood by comparing the functions $\Phi_N(\omega)$, and $\Phi_N(\omega) + \Phi_S(\omega)$ in the two models. These functions are plotted in Figure 8 for the EIF neuron (same parameters are in Figure 9A) for weak and strong noise.

For low noise levels, the neuronal phase shift, $\Phi_N(\omega)$, displays sharp variations close to integer multiples of the average firing frequency $\nu_0$. This is similar to what happens in the LIF model. However, in contrast to the LIF model, where at the peaks $\Phi_N(\omega)$ is close to 90 degrees, here it is close to 180 degrees. Hence, for fixed synaptic time constants, solutions to equation 2.24 exist for lower values of $n$ in the EIF model than in the LIF model. In particular, in the EIF model, solutions to equation 2.24 exist for $k = 0$, $n = 1$, and $n = 2$, while this is not the case in the LIF model.

Similarly, one can understand why for high noise levels, the frequency of the oscillatory rate mode is typically smaller in the EIF than in the LIF. This is because the function $\Phi_N(\omega)$ monotonously increases from 0 to 90 degrees in the EIF, whereas in the LIF, it is smaller than 45 degrees (Fourcaud-Trocmé et al., 2003; Geisler, Brunel, & Wang, 2005).

Finally, the sharp variations of $\Phi_N(\omega)$ at integer multiples of the frequency $\nu_0$ are more resistant to noise in the EIF neuron—they disappear at larger values of the noise—than in the LIF neuron. As a matter of fact, the clustering instabilities persist until the noise level is in the range 1 to 2 mV, which is much larger than in the LIF model.

The effects of changing the synaptic time constants or the spike sharpness parameter $\Delta T$ on the stability of the asynchronous state are depicted in Figure 10. This figure shows how the nature of the instability on the asynchronous state stability boundary depends on the noise level and a global scaling factor of the synaptic time constants, $\alpha$. Three values of $\Delta T$ are considered: $\Delta T = 3.5$ mV, $\Delta T = 1$ mV, and $\Delta T = 0$ (the LIF model, already shown in Figure 7, is shown for comparison). At low noise levels for fixed $\alpha$, clustering instabilities occur with an index $n$, which increases when $\Delta T$ decreases. This reflects the fact that the amplitude of the peaks of $\Phi_N(\omega)$ decreases with $\Delta T$, and hence solutions with small $n$ of equation 2.24 disappear. This effect can be compensated for by increasing $\alpha$, that is, making the synapses slower. The $n = 1$ cluster instability for $\Delta T = 0$ requires
Figure 10: The nature of the unstable modes on the stability boundary of the asynchronous state as a function of noise and a global scaling factor of the synaptic kinetics $\alpha$. The results are displayed for three values of $\Delta T$: $\Delta T = 0$ (LIF model, thin lines and labels, see Figure 7); $\Delta T = 1$ mV (intermediate lines and labels); $\Delta T = 3.5$ mV (thick lines and labels). For clarity, the dotted line for $\Delta T = 3.5$ mV is truncated for $\sigma < 1$ mV.

synapses three times slower than for $\Delta T = 3.5$ mV. The cluster instabilities are more resistant to noise when $\Delta T$ increases (for the $n = 1$ instability, up to about 0.2 mV for $\Delta T = 0$, 1 mV for $\Delta T = 1$ mV, 2 mV for $\Delta T = 3.5$ mV), reflecting the fact that peaks in $\Phi_N(\omega)$ are more resistant to noise for larger $\Delta T$. Finally, the frequency of the firing rate oscillations that appear in the high noise region also depends on $\Delta T$: as $\Delta T$ increases, the frequency of these oscillations decreases. Frequencies in such a regime range from 40 to 70 Hz for $\Delta T = 3.5$ mV, from 60 to 90 Hz for $\Delta T = 1$ mV, and from 90 to 120 Hz for $\Delta T = 0$ (LIF model).

4 Network of Conductance-Based Neurons

In this section, we study networks of conductance-based neurons in which action potential dynamics involve sodium and potassium currents. Using numerical simulations, we characterize the instabilities by which
synchronous oscillations emerge in these models and compare the results with those we have presented above for the EIF and the LIF. In particular, we examine whether the fact that in the EIF, the frequency of rate oscillations increases with the sharpness of the spike initiation is also valid in simple conductance-based models.

4.1 The Models. We consider single-compartment conductance-based models in which the membrane potential, $V$, of a neuron obeys the equation

$$C \frac{dV}{dt} = I_L - \sum_{\text{ion}} I_{\text{ion}} + I_{\text{rec}}(t) + I_{\text{ext}}(t), \quad (4.1)$$

where $C$ is the capacitance of the neuron, $I_L = -g_L(V - V_L)$ is the leak current, and $\sum_{\text{ion}} I_{\text{ion}}$ is the sum over all voltage-dependent ionic currents, $I_{\text{ext}}$ is the external current, and $I_{\text{rec}}$ denotes the recurrent current received by the neuron. The voltage-dependent currents are an inactivating sodium current,

$$I_{Na} = g_{Na} m_\infty^3 h (V - V_{Na}),$$

and a delayed rectifier potassium current,

$$I_K = g_K n^4 (V - V_K).$$

As in Wang and Buzsáki (1996) the activation of the sodium current is assumed instantaneous,

$$m_\infty(V) = \frac{\alpha_m(V)}{\alpha_m(V) + \beta_m(V)},$$

while the kinetics of the gating variable $h$ and $n$ are given by (see, e.g., Hodgkin & Huxley, 1952)

$$\frac{dx}{dt} = \alpha_x(V)(1 - x) - \beta_x(V)x, \quad (4.2)$$

with $x = h, n$. The functions $\alpha_x$ and $\beta_x$ for the three models we consider are given in appendix D.

For simplicity, we neglect the driving force in the synaptic interactions. Hence, the recurrent current has the form

$$I_{\text{rec}}(t) = -\frac{G}{N} \sum_{j=1}^{N} \sum_{k} s(t - t^k_j), \quad (4.3)$$
where the function $s(t)$ is given by equation 2.4 (in which $\tau_m = C / g_L$), and $G$, which has the dimension of a current density (mA/cm$^2$), measures the strength of the synapses.

The external input is also modeled as a noisy current,

$$I_{\text{ext}}(t) = I_0 + \sigma \sqrt{C g_L} \eta(t), \quad (4.4)$$

where $I_0$ is a constant DC input, $\eta(t)$ is a white noise with zero mean and unitary variance, and $\sigma$, which has the dimension of a voltage, measures the amplitude of the temporal fluctuations of the external input.

### 4.2 Characterization of the Instability of the Asynchronous State.

To characterize the degree of synchrony in the network, we define the population-averaged membrane potential,

$$\bar{V}(t) = \frac{1}{N} \sum_{i=1}^{N} V_i(t). \quad (4.5)$$

and the variance

$$\sigma_V^2 = \langle [\bar{V}(t)]^2 \rangle_t - [\langle \bar{V}(t) \rangle_t]^2 \quad (4.6)$$

of its temporal fluctuations, where $\langle \cdots \rangle_t$ denotes time averaging. After normalization of $\sigma_V$ to the average over the population of the variance of single-cell membrane potentials,

$$\sigma_{V_i}^2 = \langle [V_i(t)]^2 \rangle_t - [\langle V_i(t) \rangle_t]^2,$$

one defines $\chi(N)$ (Hansel & Sompolinsky, 1992, 1996; Golomb & Rinzel 1993, 1994; Ginzburg & Sompolinsky, 1994),

$$\chi(N) = \sqrt{\frac{\sigma_V^2}{\frac{1}{N} \sum_{i=1}^{N} \sigma_{V_i}^2}}, \quad (4.7)$$

which varies between 0 and 1. The central limit theorem implies that in the limit $N \to \infty$, $\chi(N)$ behaves as

$$\chi(N) = \chi_\infty + \frac{\delta \chi}{\sqrt{N}} + O \left( \frac{1}{N} \right), \quad (4.8)$$

where $\chi_\infty$ is the large $N$ limit of $\chi(N)$ and $\delta \chi$ measures the finite size correction to $\chi$ at the leading order. For a given strength of the coupling,
the network is in the asynchronous state for sufficiently large noise. This means that \( \chi_\infty = 0 \). When the noise level decreases, the asynchronous state loses stability via a Hopf bifurcation, and synchrony appears: \( \chi_\infty > 0 \). Near the bifurcation, \( \chi_\infty \) behaves at the leading order as

\[
\chi_\infty = A (\sigma_c - \sigma)^\gamma \quad \text{for} \quad \sigma < \sigma_c \tag{4.9}
\]

\[
= 0 \quad \text{for} \quad \sigma > \sigma_c, \tag{4.10}
\]

with an exponent \( \gamma = 1/2 \) (Kuramoto, 1984; van Vreeswijk, 1996).

To locate the noise level where the instability of the asynchronous state occurs for a given value of the synaptic coupling, we simulate networks of various sizes \( N \). Comparing the values of \( \chi(N) \) for the different \( N \), we estimate \( \delta \chi \), and \( \chi_\infty \) as a function of \( \sigma \). The obtained values of \( \chi_\infty \) are subsequently fitted according to equation 4.10. In a network of LIF neurons, in which the stability boundary of the asynchronous state can be computed analytically, we show in appendix C that this method gives an accurate prediction of such a boundary for network sizes on the order of 1000.

The results of this analysis for the Wang-Buzsáki network and two values of the synaptic coupling, \( G = 2 \text{ mA/cm}^2 \) and \( G = 12 \text{ mA/cm}^2 \), are plotted in Figure 11. For \( G = 2 \text{ mA/cm}^2 \), \( \delta \chi(\sigma) \) can be reliably estimated from simulations with \( N = 800 \) and \( N = 3200 \). For \( G = 12 \text{ mA/cm}^2 \), the finite size effects are larger because the coupling is stronger, and a substantially better account of these effects requires simulations of larger networks \( (N = 1600 \) and \( N = 3200) \). This is shown in Figures 11B and 11C. Still, the estimates of \( \sigma_c \) obtained in the fits in these two figures are very close.

Once the instability has been located, we compute the frequency of the population oscillations at the onset of the instability. To this end, we simulate the network for a noise level \( \sigma \approx \sigma_c \). A good estimate of the oscillation frequency is provided by looking at the autocorrelation of the population average of the membrane potentials of the neurons. If the bifurcation at \( \sigma_c \) is supercritical, the frequency estimates on the two sides of the transition are similar. If the bifurcation is subcritical, they may differ significantly. In that case, the frequency of the unstable mode has to be determined in the vicinity of the transition, but on the side where the asynchronous state is still stable. In fact, in the simulation reported below, the bifurcations were found to be supercritical. We checked using several examples that the frequency estimates thus obtained were only weakly sensitive to the size of the network for \( N > 800 \). Hence, in the results displayed below, the population frequency was estimated from simulations of networks with \( N = 800 \). The traces of two neurons, the membrane potential of the neurons averaged over all the network and its autocorrelation in the vicinity of the asynchronous state instability onset, are shown in Figure 12 for \( G = 12 \text{ mA/cm}^2 \). The oscillations present in the population activity are not clearly reflected in the spiking activity at the single-cell level, which is highly
Figure 11: The measure of synchrony $\chi$ as a function of the noise in the Wang-Buzsáki model for two values of the coupling. In each panel, the finite size correction $\delta \chi$ is estimated by comparing the simulation results (circles and crosses) for two sizes of the network. Subtracting the finite size correction leads to estimates for $\chi_\infty$ (squares) as a function of $\sigma$, which are fitted using equation 4.10 (solid lines). (A) $G = 2$ mA/cm$^2$, crosses: $N = 800$; circles: $N = 3200$. Fit: $\sigma_c = 1.61$ mV; $A = 0.84$ mV$^{-1/2}$. (B) $G = 12$ mA/cm$^2$, crosses: $N = 800$; circles: $N = 3200$. Fit: $\sigma_c = 7.68$ mV; $A = 0.48$ mV$^{-1/2}$. (C) $G = 12$ mA/cm$^2$, crosses: $N = 1600$; circles: $N = 6400$. Fit: $\sigma_c = 7.62$ mV; $A = 0.5$ mV$^{-1/2}$. In all these simulations, $\tau_l = 1$ ms, $\tau_r = 1$ ms, $\tau_d = 6$ ms. The DC part of the external input, $I_0$, was tuned to get an average firing rate of the neuron of 30 Hz ±0.5 Hz near the onset of synchrony.

irregular. In contrast, the population average of the membrane potentials (or on the population activity, not shown) and its autocorrelation reveals the existence of population oscillations at a frequency that is about 70 Hz, compared to an average firing rate of the neurons of 29.5 Hz.
Figure 12: The Wang-Buzsáki network near the onset of instability of the asynchronous state. \( N = 800, G = 12 \text{ mA/cm}^2, \sigma = 7.75 \text{ mV}. \) Synaptic time constants and delay as in Figure 11. The average firing rate of the neurons is 29.5 Hz. The coefficient of variation of the interspike interval distribution is 0.72. (A) Membrane potential of two neurons in the network. The noise masks the fast oscillations of the subthreshold membrane potential. (B) The fast oscillations of the membrane potential are revealed on averaging over many neurons (here over all the neurons in the network.) (C) Autocorrelation of the population average membrane potential (averaging over 2 s). The frequency of the oscillations is 66 Hz.

4.3 The Stability Boundary of the Asynchronous State. We performed simulations for the three models described in appendix D. These models differ in the sharpness of the activation function of their sodium current. In each model, we varied the synaptic coupling strength and looked for the critical noise level, \( \sigma_c \), at which the asynchronous state becomes unstable. The external input was also changed with \( G \) so that for \( \sigma \) near \( \sigma_c \), the average firing rate of the neurons was \( 30 \pm 0.5 \text{ Hz} \). Once the transition was located, the frequency of the population oscillations emerging at this transition was estimated, as explained above.

The results obtained for the Wang-Buzsáki model are summarized in Figure 9. The agreement with the predictions from the EIF model (see
In the EIF model, the frequency of the unstable mode at instability onset depends on the parameter $\Delta_T$, which characterizes the sharpness of the spike initiation driven by the sodium current. In fact, we found in section 3 that the frequency increases when $\Delta_T$ decreases. We have also shown that the index $n$ of the rate oscillatory instability increases when $\Delta_T$ decreases. To test whether the spike initiation sharpness had similar effects in the conductance-based models, we simulated networks of neurons that differ from the WB model only for the function $m_{\infty}$. The activation functions of these models are given in appendix D and are plotted in Figure 13. The slopes at half-height are $2.01 \times 10^{-2}$ mV$^{-1}$ (dashed line, model 1) and $3.4410^{-2}$ mV$^{-1}$ (dotted line, model 2), compared to the $2.64 \times 10^{-2}$ mV$^{-1}$ in the WB model (solid line; see Figure 14A). The change in the activation curve has a substantial effect on the threshold of the f-I curve (see Figure 13B) and on the shape of the spikes (see Figure 13C).
The stability boundary of the asynchronous state and the frequency of the population oscillations on this boundary are plotted for the three models in the $\sigma - J$ plane in Figure 14. In all the models, for sufficiently weak noise or sufficiently weak coupling, the frequency is close to the average firing rate of the neurons, $\nu_0 = 30$ Hz. This indicates that in this limit, the index of the instability mode is $n = 1$ (with $k = 0$) for the three models. The frequency
increases with the noise. In the Wang-Buzsáki model and in model 1, the increase is smooth. Hence the index of instability remains \( n = 1 \) at large coupling, and the destabilization of the asynchronous state always occurs via the \( n = 1 \) rate oscillatory instability. At \( \sigma \approx 3 \text{ mV} \left( G \approx 5 \text{ mA/cm}^2 \right) \), the frequencies of the oscillations in the Wang-Buzsáki model and in model 1 begin to differ. The frequency of the oscillation is smaller in model 1 than in the Wang-Buzsáki model. This is consistent with our analysis of the EIF model which predicts that in the high-noise regime, the frequency of the rate oscillatory mode should decrease with the sharpness of the spike initiation (\( \Delta_T \) larger).

In model 2, the population frequency jumps to a value close to 60 Hz for \( \sigma \approx 1 \text{ mV} \left( G \approx 2.5 \text{ mV/cm}^2 \right) \). Beyond this value, it increases smoothly with \( \sigma \). This indicates that the index of the instability changes from \( n = 1 \) to \( n = 2 \) as the coupling (or equivalently the noise) increases and that the index of the rate oscillatory instability is \( n = 2 \). Just after the change in \( n \), the instability leads to a two-cluster state. This is confirmed in Figure 15 where the membrane potentials of two neurons are plotted together with the population average of the membrane potential for \( G = 3 \text{ mV/cm}^2 \). However, because of the local noise, neurons do not belong to the same cluster all the time, but rather switch between the two clusters. Still, on average, at any time, each cluster comprises half of the neurons in the network (not shown). This behavior and the fact that in the high-noise
Figure 16: The effect of synaptic kinetics on the pattern of synchrony near the onset of instability of the asynchronous state in model 2. The coupling strength is $G = 1 \text{ mA/cm}^2$. The size of the network is $N = 1600$. The average frequency of the neurons is about 30 Hz. (Left) The control case: The synaptic rise time and decay time are $\tau_1 = 1 \text{ ms}$ and $\tau_2 = 6 \text{ ms}$, respectively. The synaptic delay is $\delta = 1 \text{ ms}$. The spikes of the two neurons are well synchronized, and both fire at almost every cycle of the oscillations of the population averaged voltage. Noise: $\sigma = 0.66 \text{ mV}$. (Right) Fast synapses: $\tau_1 = 0.5 \text{ ms}$, $\tau_2 = 3 \text{ ms}$, $\tau_f = 0.5 \text{ ms}$. The pattern of synchrony corresponds to a smeared two-cluster state. The two neurons fire in alternate periods in which they are nearly in-phase and nearly in antiphase (spikes indicated by a star). The maxima of the voltage population average coincide with the action potential of at least one of the two neurons. Noise: $\sigma = 0.57 \text{ mV}$.

5 Discussion

Our study sheds new light on the instabilities of the asynchronous state in networks of inhibitory neurons in presence of noisy external input. Previous...
studies investigated synchronization properties of networks of inhibitory neurons in fully connected networks at zero noise or in the weak noise regime (Abbott & van Vreeswijk 1993; Treves, 1993; van Vreeswijk, 1996; Gerstner, van Hemmen, & Cowan, 1996; Wang & Buzsáki, 1996; White et al., 1998; Neltner, Hansel, Mato, & Meunier, 2000), in sparsely connected networks in absence of noise (Wang & Buzsáki 1996; Golomb & Hansel, 2000) or in sparsely connected networks in the strong noise–strong coupling region (Brunel & Hakim 1999; Tiesinga & Jose, 2000; Brunel & Wang, 2003). These studies had found qualitatively distinct types of instabilities of the asynchronous state in weak and strong noise regimes. This article shows how the two types of instabilities are related when the noise level is varied and investigates for the first time stochastic synchrony in the simpler framework of fully connected networks.

5.1 The Two Types of Eigenmodes in Large Neuronal Networks of Inhibitory Neurons. Our main result is the existence of two types of eigenmodes of the linearized dynamics around the asynchronous state that differ in terms of the effect of noise on their stability. One type of mode can be unstable only if the noise is sufficiently small. Such an instability occurs when the neurons resonantly lock with the oscillatory synaptic input. When the noise is too high, resonant locking is destroyed and the modes are stable. We termed these eigenmodes clustering modes because when destabilized, they lead to clustering. Eigenmodes of the second type can be destabilized at weak noise and weak coupling, leading to clustering, but also at strong noise provided the coupling is sufficiently strong, leading to coherent modulation of the firing probability of the neurons. In this regime, the network displays stochastic synchrony. We termed the eigenmodes undergoing this instability oscillatory rate modes.

Which of the clustering eigenmodes or oscillatory rate modes becomes unstable first, when the coupling strength increases, depends on the noise level, the synaptic kinetics, and the intrinsic properties of the neurons. However, as a general rule, clustering eigenmodes are the first to be unstable, for low noise levels and fast synapses. At sufficiently large noise, the oscillatory rate mode is the only remaining unstable mode. The transition between these two regimes of synchrony and the frequency of the stochastic oscillations depends on the synaptic and single cell properties, as briefly discussed below. In particular, if the synapses are sufficiently fast, the frequency of the emerging oscillations can be significantly faster than the firing rate of the individual neurons (Brunel & Hakim, 1999; Brunel & Wang, 2003).

Previous studies have shown that in networks of integrate-and-fire inhibitory neurons, a discrete spectrum of eigenmodes exists at zero noise (Abbott & van Vreeswijk, 1993; Treves, 1993; van Vreeswijk, 1996; Hansel & Mato, 2003). Abbott and van Vreeswijk (1993) showed that such eigenmodes become stable at very low values of noise, in a model with
phase noise and no latency. However, the existence of specific eigenmodes that display instabilities robust to noise has not been reported in those studies.

5.2 Beyond the Instability Line of the Asynchronous State. We also used numerical simulations to explore the dynamics of both LIF and Wang-Buzsáki networks in the synchronous regime beyond the stability boundary of the asynchronous state. A detailed description of the dynamics of the various synchronized states of the LIF networks is presented in appendix C. Using numerical simulations, we showed that the bifurcation leading to the stochastic synchronous state is supercritical, consistent with the results of Brunel and Hakim (1999). We also showed multistability between different types of cluster states in the low-noise, low-coupling region, with cluster states disappearing one after the other as the noise level increases.

5.3 On the Role of Intrinsic Properties in Stochastic Synchrony. Theoretical studies have shown that intrinsic properties of neurons have a strong influence on the stability of the asynchronous state in large neuronal networks at weak noise (Hansel et al., 1995; van Vreeswijk & Hansel, 2001; Ermentrout, Pascal, & Gutkin, 2001; Pfeuty et al., 2003, 2005). A key concept in grasping this influence is the phase response function, which characterizes the way a tonically firing neuron responds to small perturbations (Kuramoto, 1984; Ermentrout & Kopell, 1986; Hansel, Mato, & Meunier, 1993; Rinzel & Ermentrout, 1988). The shape of the phase response function depends on the intrinsic properties of the neurons. In conductance-based models, it is determined by the sodium, calcium, and potassium currents involved in the neuronal dynamics (Hansel et al., 1993, 1995; van Vreeswijk, Abbott, & Ermentrout, 1994; Ermentrout et al., 2001). Hence, the single-neuron dynamics can be related to network dynamics. This idea has been applied in the framework of simple integrate-and-fire models as well as in conductance-based models (for reviews, see Golomb, Hansel, & Mato, 2001; Mato, 2005). In the strong noise–strong coupling region, the phase response function is no longer relevant, and other approaches, such as the one used in this article, are required.

5.3.1 The Effect of Spike Initiation and Repolarization. Besides the synaptic time constants, we showed that the sharpness of the spike initiation is an important parameter that affects the quantitative features of stochastic synchronous oscillations at their onset (see also Geisler et al., 2005). In the EIF model, the frequency of the stochastic oscillations and the transition between the clustering and rate oscillation regions are strongly affected by the parameter $\Delta T$. The sharpness of spike initiation greatly influences the amplitude of the noise where the transition between the two modes of synchrony occurs. For LIF neurons ($\Delta T = 0$), this transition occurs at very
low noise levels (below 0.1 mV). When the parameter $\Delta_T$ increases, the transition moves to higher noise levels. For instance, it is larger than 1 mV when $\Delta_T = 3.5$ mV. Similarly, in the conductance-based model, we found a significant influence of the shape of the function $m_\infty$ on the frequency of the stochastic synchronous oscillations and the noise level required for their appearance.

In contrast to the role of the spike initiation dynamics, our work suggests that the membrane potential repolarization dynamics following an action potential is much less critical for stochastic synchronous oscillations. In fact, for the quantitative features of the stochastic synchronous oscillation instability in the Wang-Buzsáki and the EIF models to be similar, it is sufficient to choose the parameter $\Delta_T$ to match the spike initiation dynamics of the EIF to those of the Wang-Buzsáki model.

5.3.2 The Effect of Subthreshold Active Currents on Stochastic Oscillations. We have focused on inhibitory networks of integrate-and-fire neurons and of specific HH-type neurons. In particular, the panoply of ionic currents in the conductance-based model we studied is limited to the standard fast sodium current and the delayed-rectifier potassium current. Synchronization properties of neurons with additional types of ionic currents, including those significantly activated in the sub-threshold range, remain to be explored in the high-noise regime. However, we believe that the stochastic synchronous state should be robust to the addition of such additional currents because such currents do not substantially affect the discharge modulation of neurons in response to oscillatory inputs at high frequency (Fourcaud-Trocèmé et al., 2003).

5.4 The Effect of Temporal Correlations in the External Noisy Input. In this article, we have considered white noise. Colored noise modifies the phase of LIF neurons at high frequencies. In this limit, the phase is 0 degrees for colored noise compared to 45 degrees in case of white noise (Brunel et al., 2001). One consequence is a larger population frequency in the stochastic synchronous state (Brunel & Wang, 2003). Note that in the particular case of synaptic currents with no latency, such a change in the properties of noise can lead to a drastic change in the synchronization properties of the network. Indeed, with white noise, the network displays the stochastic synchronous instability in the high-noise regime, whereas for sufficiently colored noise, no such instability can be found, because in this case, the sum of synaptic and neuronal phase lag is bounded by 180 degrees. In the case of EIF and CB neurons, differences of the neuronal firing rate response between white and colored noise are much less important (Fourcaud-Trocèmé et al., 2003), and therefore the synchronization properties of networks of such neurons should only weakly depend on the nature of the noise.
For simplicity, we have also considered current-based inputs rather than conductance-based inputs. Conductance-based inputs are expected to yield qualitatively similar results, though the frequency of the stochastic oscillation is known to increase as the input conductance of neurons increases (Geisler et al., 2005).

5.5 Perspectives. In the models studied here, all the neurons have the same intrinsic properties and the connectivity is all-to-all. The addition of heterogeneities in cellular properties and in the external inputs would contribute to stabilize the modes leading to clustering instabilities (Neltner et al., 2000; Hansel & Mato, 2001, 2003). If the heterogeneities are too strong, these modes are stable for any value of the coupling. This fragility of cluster states to heterogeneity is due to the fact that the appearance of such states is dependent on neuronal resonances at integer multiples of the firing rate, and therefore any heterogeneity leading to pronounced cell-to-cell variability of firing rates will destroy such states. In contrast, we conjecture that the instability of the rate oscillatory mode is very robust to heterogeneities, although the coupling strength at which it occurs is likely to depend on the level of heterogeneities. This robustness would be due to the fact that the synchrony in this regime is no longer dependent on resonant peaks at integer multiples of the single-cell firing rate. More work is required to confirm this conjecture.

Brunel and Hakim (1999) found stochastic synchrony in a network of $N$ LIF neurons, connected at random with an average of $C \gg 1$ synapses in the limit $N \to \infty$ but $C/N \ll 1$. Their analytical approach and the one used in this article are similar in spirit. However, an important difference is that when the connectivity is random, an additional noise term contributes to the synaptic inputs. The study of the stability of the asynchronous state then requires knowing how oscillations in the variance of the inputs to a neuron affect the single-cell firing rate. This analysis can be performed when synaptic interactions are modeled as a delta function, and presynaptic neurons fire approximately as Poisson processes, as in Brunel and Hakim (1999). Unfortunately, this analysis does not generalize easily to situations in which a finite rise and decay time are present (Fourcaud & Brunel, 2002) and/or neurons fire in a significantly non-Poissonian fashion. Still, we expect that if the connectivity is very large, these fluctuations will not destroy the oscillatory rate instability. In contrast, if the connectivity is too sparse, the spatial fluctuations in the synaptic inputs that increase with the synaptic strength can prevent the oscillatory rate instability from occurring (see, e.g., Golomb & Hansel, 2000). This will happen if the connectivity $C$ is smaller than some critical number that depends on the synaptic kinetics, the average firing rate of the neurons, and their intrinsic properties. The exact conditions for existence of the oscillatory rate instability in such sparse networks should also be clarified in future work.
Synchronization Properties of Inhibitory Networks

Appendix A: Linear Stability Analysis of the Asynchronous State in LIF Networks

The asynchronous state described by equations 2.15 to 2.17 is stable if any small perturbation from it decays back to zero. In the mean field framework, a perturbation of the asynchronous state can be described by its effect on the average firing rate, on the PDF, and on the recurrent current, as follows:

\[ \nu(t) = \nu_0 + \varepsilon \nu_1(t) \]  
\[ P(V, t) = P_0(V) + \varepsilon P_1(V, t) \]  
\[ I_{\text{rec}}(t) = J \tau_m \nu_0 + \varepsilon I_1(t) \]

where \( \varepsilon \ll 1 \), and \( \nu_1(t), P_1(V, t) \) are finite. Inserting these expression in equations 2.9, 2.10, and 2.14 and keeping only the leading order in \( \varepsilon \) and looking for solutions \( P_1, \nu_1, I_1 \propto \exp \lambda t \) with \( \lambda \) a complex number yields

\[ \frac{1}{\sigma} = -\int \nu_0 \tau_m \exp(-\lambda \tau_f) \left( \frac{\partial U(y_f, \lambda)}{\partial y} - \frac{\partial U(y_r, \lambda)}{\partial y} \right) \frac{\partial U(y_f, \lambda) - U(y_r, \lambda)}{U(y_f, \lambda) - U(y_r, \lambda)} . \]  

where \( y_f \) and \( y_r \) are given in equations 2.16 and 2.17 and the function \( U(y, \lambda) \) is given in terms of combinations of hypergeometric functions (Abramowitz & Stegun, 1970):

\[ U(y, \lambda) = \frac{e^{y^2}}{\Gamma \left( \frac{1 + \lambda \tau_m}{2} \right)} M \left( \frac{1 - \lambda \tau_m}{2}, \frac{1}{2}, -y^2 \right) \]

\[ + \frac{2ye^{y^2}}{\Gamma \left( \frac{\lambda \tau_m}{2} \right)} M \left( \frac{1 - \lambda \tau_m}{2}, \frac{3}{2}, -y^2 \right) . \]

The asynchronous state is stable if for all the solutions to this equation, \( \text{Re}(\lambda) < 0 \). Conversely, the existence of at least one solution with \( \text{Re}(\lambda) > 0 \) signals that the asynchronous state is unstable. Thus, an onset of instability of the asynchronous state in parameter space is determined by setting \( \lambda = i \omega \) in equation A.4. At this onset, a Hopf bifurcation occurs, and \( \omega \) is the frequency of the oscillation of the network activity in the corresponding unstable mode. In cases where the Hopf bifurcation is supercritical, \( \omega \) is also the frequency of the synchronous oscillations that emerge at the instability onset.
Appendix B: Scaling of the Critical Coupling Strength with Noise for Large Noise

When \( \sigma \) goes to infinity, an expansion of equation 2.15 yields

\[
\frac{1}{\nu_0 \tau_m} = \frac{V_t - V_r}{\sigma} \Psi(y_r) + \frac{(V_t - V_r)^2}{2\sigma^2} \Psi'(y_r) + \ldots
\]

(B.1)

where \( \Psi(x) = \sqrt{\pi} \exp(x^2)(1 + \text{erf}(x)) \). To keep a finite rate \( \nu_0 \) as \( \sigma \) goes to \( \infty \), \( y_r \) must go to \( -\infty \) as

\[ y_r \sim -\sqrt{\ln(\sigma)}. \]

In addition,

\[
\left( \frac{\frac{\partial U}{\partial y}(y_t, \lambda)}{\frac{\partial U}{\partial y}(y_l, \lambda)} - \frac{\partial U}{\partial y}(y_t, \lambda) \right) \sim |y_r|
\]

in the limit \( y_r \to -\infty \). Equation 2.23 then implies that the critical coupling strength goes as

\[ J_c \sim \frac{\sigma}{\sqrt{\ln(\sigma)}} \]

for large \( \sigma \).

Appendix C: Numerical Simulations of LIF Networks

Simulations of LIF networks were performed at various levels of \( J \) and \( \sigma \) close to the predicted stability boundary of the asynchronous state for different network sizes (\( N = 1000, 2000, 4000 \)). The methods are as described in section 4.2. We show in Figure 17 the resulting phase diagram for \( \nu_0 = 30 \) Hz, \( \tau_l = 1 \) ms, \( \tau_r = 1 \) ms, and \( \tau_d = 6 \) ms. At low-coupling levels (\( J < 2 \) mV), the asynchronous state destabilizes through a subcritical bifurcation. There is a small parameter range where the asynchronous state coexists with the \( n = 3 \) cluster state. At low-noise levels, at least three types of cluster states coexist (with 1, 2, 3 clusters). The state that is selected by the network depends on initial conditions. These states destabilize successively through discontinuous transitions (for \( J = 1 \) mV, \( n = 1 \) destabilizes at \( \sigma = 0.16 \) mV, \( n = 2 \) destabilizes at 0.25 mV, \( n = 3 \) at 0.32 mV). Above a coupling level of about 2 mV, the asynchronous state destabilizes through a supercritical Hopf bifurcation to the stochastic synchronous state. The stochastic synchronous state coexists with the other cluster states in some range of noise amplitudes. As the coupling strength increases, the stochastic...
synchronous state merges successively with the $n = 3$ cluster state (around 8 mV), the $n = 2$ cluster state (above 12 mV), and finally the $n = 1$ cluster state (above 30 mV). Thus, at high coupling strengths (see top panel for a coupling strength of 100 mV), there is a single synchronous state that varies continuously from the fully synchronized state at $\sigma = 0$ mV (population frequency equal to firing rate) to the stochastic synchronous state close to the bifurcation at $\sigma = 5$ mV (population frequency about 90 Hz, much larger than single-cell firing rate, CV close to 1). The phase diagram
shown in Figure 17 is representative of networks with short synaptic time constants, when the population firing rate in the high-noise region is larger than the single-cell firing rate, though the specifics of which cluster states are obtained depend on parameters. On the other hand, for large synaptic time constants, when the population frequency at high noise is on the same order or smaller than the single-cell firing rate, and the destabilization of the asynchronous state occurs exclusively on the $n = 1$ instability line, the phase diagram simplifies drastically: the asynchronous state destabilizes at any $J$ through a supercritical bifurcation, a scenario similar to high-coupling strengths in Figure 17.

Appendix D: The Conductance-Based Models

In all the three conductance-based models dealt with in this work, the inactivation functions of the potassium and the sodium currents are as in the model of Wang and Buzsáki (1996):

\[
\alpha_m(V) = \frac{0.1(V + 35)}{1 + e^{-(V+35)/10}} 
\]
\[
\beta_m(V) = 4e^{-(V+60)/18} 
\]
\[
\alpha_n(V) = 0.03\frac{(V + 34)}{1 - e^{-(V+34)/10}} 
\]
\[
\beta_n(V) = 0.375e^{-(V+44)/80} 
\]
\[
\alpha_h(V) = 0.21 e^{-(V+58)/20} 
\]
\[
\beta_h(V) = \frac{3}{1 + e^{-(V+28)/10}}. 
\]

In order to study how the activation of the sodium affects the instability of the asynchronous state and the frequency of the population oscillations at synchrony onset we also considered two other models that differ from the Wang-Buzsáki model in the sharpness of the sigmoidal function $m_\infty(V)$ (see also Figure 13).

In model 1:

\[
\alpha_m(V) = \frac{0.1(V + 30)}{1 + e^{-(V+30)/10}} 
\]
\[
\beta_m(V) = 4e^{-(V+55)/12}. 
\]

Hence, the slope of the activation curve at the inflexion point of the sigmoid is smaller in model 1 than in the Wang-Buzsáki model (see also Figure 13A, dashed line).
In model 2:

\[
\alpha_m(V) = \frac{0.1(V + 35)}{1 + e^{-(V+35)/20}} \tag{D.9}
\]

\[
\beta_m(V) = 4e^{-(V+47.4)/18} \tag{D.10}
\]

In this model the activation curve is sharper than in the Wang-Buzsáki model (see also Figure 13A, dotted line).

In all three models \( g_{Na} = 35 \text{ mS/cm}^2 \), \( V_{Na} = 55 \text{ mV} \), \( V_K = -90 \text{ mV} \), \( g_L = 0.1 \text{ mS/cm}^2 \), \( V_L = -65 \text{ mV} \), and \( C = 1 \text{ µF/cm}^2 \). In particular, the passive membrane time constant of the neuron is \( \tau_m = C/g_L = 10 \text{ msec} \) as in Wang and Buzsáki (1996).

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References


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