Oscillatory background activity implements a backbone for sampling-based computations in spiking neural networks

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Abstract

Various data suggest that the brain carries out probabilistic inference. Models that perform inference through sampling are particularly appealing since instead of requiring networks to perform sophisticated mathematical operations, they can simply exploit stochasticity in neuron behavior. However, sampling from complex distributions is a hard problem. In particular, mixing behavior is often very sensitive to the temperature parameter which controls the stochasticity of the sampler. We propose that background oscillations, an ubiquitous phenomenon throughout the brain, can mitigate this issue and thus implement the backbone for sampling-based computations in spiking neural networks. We first show that both in current-based and conductance-based neuron models, the level of background activity effectively defines the sampling temperature of the network. This mechanism allows brain networks to flexibly control the sampling behavior, either favoring convergence to local optima or promoting mixing. We then demonstrate that background oscillations can in this way structure stochastic computations into discrete sampling episodes. In each such episode, solutions are first explored at high temperatures before annealing to low temperatures favors convergence to a good solution.

1 Introduction

Behavioral data show that humans act in a probabilistically optimal way in many scenarios, suggesting that the brain performs probabilistic inference (Pouget et al., 2013; Körding and Wolpert, 2004). This observation has inspired neural network models capable of carrying out probabilistic inference computations. Sampling-based models are especially attractive as they have a number of functional advantages (Fiser et al., 2010) as well as experimental support (Berkes et al., 2011).

Sampling-based computations in neural networks necessitate stochasticity of neuronal activity. In networks of idealized spiking neuron models with stochastic spiking behavior, the network’s stationary distribution can be exactly characterized mathematically (Buesing et al., 2011). Although such a characterization is not possible for more biologically realistic models of neural networks, it has been shown that most networks do have a stationary distribution, as long as they are stochastic in some way (Habenschuss et al., 2013).

One source of stochasticity on the level of individual neurons is the large number of inputs that cortical neurons typically receive, resulting in membrane potential fluctuation which give rise to stochastic firing behavior. Theoretical models often assume the limit of infinitely large background firing rates to arrive at Gaussian noise currents (Gerstner et al., 2014). However, firing rates in the brain as well as the number of presynaptic partners of individual neurons are limited. Moreover, activity levels in the brain are rarely constant, and often show cyclic behavior in different frequency bands (Buzsáki, 2006).
We investigate in this work the effect of limited, varying levels of background input on networks of leaky integrate-and-fire (LIF) neurons. We show that the level of background input shapes the network activity by defining the sampling temperature, an important parameter of sampling models controlling the shape of the distribution of network states. High temperatures flatten the distribution, allowing the network to easily traverse the state space, while low temperatures lead to more pronounced maxima, resulting in more time being spent there. If background activity is oscillatory, then phase-dependent stationary distributions emerge (Habenschuss et al., 2013).

We show how its effect on the temperature allows oscillatory background activity to structure sampling-based computations in spiking neural networks (SNNs) into discrete episodes, in which a high-temperature search phase is followed by a low-temperature phase of convergence to a good solution, which also provides a reference time at which solutions can be read out. These observations establish a novel link between the findings of the experimental neurosciences and the understanding of brain computations with theoretical models.

2 Background

2.1 Sampling temperature in neural sampling

Several SNN models for probabilistic inference have been proposed. The neural sampling model by Buesing et al. (2011) considers idealized stochastic spiking neurons with rectangular post-synaptic potentials (PSPs) of length $\tau$, spiking with instantaneous firing intensity

$$p_k(t) = \frac{1}{\tau} \exp \left( \frac{1}{T} u_k(t) \right).$$

(1)

Here, $u_k(t)$ is the membrane potential of neuron $k$ and $T$ is the "temperature", a parameter that scales the stochasticity of the neuron. Using exponential functions as firing intensity functions (also called escape rate functions) has been shown to fit the behavior of cortical neurons very well (Jolivet et al., 2006). Let $z(t)$ denote the state vector of the network at time $t$, where the state $z_k(t)$ of a neuron $k$ is 1 if the neuron has spiked within $[t - \tau, t]$, and 0 otherwise. Let $p(z)$ denote the distribution over states that are visited by the network over time. Buesing et al. (2011) proved that under certain conditions on the membrane potentials, recurrent networks of such neurons generate samples from a Boltzmann distribution

$$p(z) = \frac{1}{Z} \exp \left( \frac{1}{T} (z^T W z + b^T z) \right).$$

(2)

where $Z$ is the normalization constant and $W$ and $b$ are synaptic weights and neuronal biases. Clearly, the temperature $T$ influences the sampled distribution. At high values of $T$, the distribution is flatter (i.e., the probability differences between different states decrease), and mixing is easier,
while at low values of $T$, energy maxima are more pronounced and the state will tend to stay around modes. Hence, in this model (Eq. 1), any factor that multiplicatively scales $u(t)$ directly sets the sampling temperature (see Fig. 1a for the effect of $T$ on $\rho_k(t)$). The temperature changes the network behavior (see Fig. 1b for an example with a small network), controlling the energy landscape (see Fig. 1c).

In this work, we use more realistic LIF neurons instead of the abstract neuron model used by Buesing et al. (2011). In these neuron models, there is no explicit temperature parameter that scales the exponent in a probability distribution (but see Petrovici et al., 2016, for a way of relating LIF neuron spiking to sampling from Boltzmann distributions). We next discuss how multiplicative scaling similar to the $\frac{1}{T}$ factor in Eq. 1 arises for LIF neurons when background input is present.

2.2 Membrane potential fluctuations influence stochasticity of current-based neuron models

For a given input current, cortical neurons are thought to behave rather deterministically (Mainen and Sejnowski, 1995). However, when subject to large numbers of inputs as is the case in vivo, they exhibit stochastic behavior necessary for networks to carry out sampling tasks (Jolivet et al., 2006). This synaptic bombardment causes fluctuations of the membrane potential. The relation between stochastic input and resulting membrane fluctuations with the firing behavior of current-based neuron models has been investigated in different ways.

Mensi et al. (2011) fitted a stochastic spike response model (SRM) to a current-based adaptive exponential integrate-and-fire (AdEx) neuron using colored noise current as simulated background input. The resulting SRM can reproduce the AdEx behavior with high accuracy using an escape rate function of the form $\rho_k(t) = \rho_0 \exp \left( (u_k(t) - u_T) / \Delta u \right)$, where $\rho_0$ is a scaling parameter, $u_T$ sets the (soft) threshold of the SRM and $\Delta u$ defines the degree of stochasticity. Both of the latter parameters are functions of $\sigma$, the standard deviation of the white noise input current used to drive the neuron. For increasing levels of $\sigma$, both $u_T$ and $\Delta u$ monotonically increase (Mensi et al., 2011, Fig. 4). Hence, the level of stochastic background input influences the stochasticity of the neuron model.

Analytical expressions for the escape rate function of current-based LIF neurons have also been developed, e.g. by Plesser and Gerstner (2000). Their results show that the variance of the membrane potential fluctuations multiplicatively scales the membrane potential within the escape rate function. As these fluctuations can be caused by fluctuations of the input current, this similarly suggest an influence of the background input on the stochastic behavior of the neuron.

3 Results

Given that background activity can influence neuronal stochasticity, we first asked whether background activity does in fact change the sampling behavior of spiking neural networks in a way similar to the influence of the temperature $T$ in idealized neural sampling networks. It is expected that the linear relationship between the input currents and membrane potential leads to a more direct and more pronounced effect in current-based neuron models (which were also considered in the studies discussed in Sec. 2.2). We therefore first discuss the effect of background activity on networks of LIF neurons with current-based synapses before moving to the more realistic conductance-based case.

3.1 Effects of background input on temperature in networks of current-based neurons

Assume that neurons receive background input via exponential current-based synapses (see Methods 5.1) from Poisson processes with rates $\nu_e$ (excitatory input) and $\nu_i$ (inhibitory input). Changes of this background input may have a strong effect on a neuron’s behavior, potentially placing it in drastically different regimes. To avoid this, it is often assumed that the input is balanced, i.e. changing rates do not alter the mean membrane potential. In current-based models, such a
Figure 2: Background input rate sets the sampling temperature in networks of current-based LIF neurons. Excitatory and inhibitory background firing rates (a), mean membrane potential (u) (b), and variance (u^2) of the membrane potential (c) for different levels of background input α. d) Illustrative sampling task showing the effect of background input (see Methods 5.5). Four neurons receiving different input currents I_0, . . . , I_5 (bottom: values of input currents) are connected with lateral inhibition in a winner-take-all (WTA) fashion. Additionally, all neurons receive spiking input from a fifth neuron (f = 75 Hz). e) Probability of each neuron being exclusively active for low (α = 1) and high (α = 5) temperatures (see Methods 5.5). The probability of mixed states is shown in gray. At high temperatures, the energy landscape becomes flatter. f) Probability of each neuron being exclusively active as α increases. g) Normalized energy landscape: at each value of α, the probabilities are divided by the maximum occurring value to offset overall activity changes. Towards high temperatures, response become more similar. h) Neuron firing rate in response to stimulus used for fitting (see Methods 5.6). i) Temperature values resulting from fitting an SRM to the LIF neuron at various α. j) Soft threshold values from fitting. k) Firing intensity curves ρ(u) resulting from fitting for α ∈ {1, 3, 5}. With increasing background input rate, the firing intensity becomes flatter.

Balanced state can easily be achieved if both excitatory and inhibitory input rates change in a linear fashion, i.e.

ν_e = αν_{e,0} \quad \text{and} \quad ν_i = αν_{i,0}, \quad (3)

where ν_{e,0} and ν_{i,0} are some excitatory and inhibitory base rates, and α is a factor scaling the background input. In this case, a balanced state can be achieved for arbitrary firing rates and synaptic time constants by appropriately setting the weights for excitatory and inhibitory inputs (see Methods 5.5 for details). Ignoring the firing threshold, this results in fluctuations of the membrane potential u(t) with zero mean over time (i.e. ⟨u⟩ = E_L, where E_L is the resting potential) and with variance

⟨u^2⟩ = α \left( \frac{c_e}{ν_{e,0}} + \frac{c_i}{ν_{i,0}} \right), \quad (4)

where c_e and c_i are constants (see Methods 5.5). We see that the variance linearly increases with the background input rates, and an arbitrarily high variance can be reached if the background input rates are high enough (Fig. 2a-c shows firing rates, mean u, and variance of u as functions of α for a LIF neuron with ν_{e,0} = ν_{i,0}). As ⟨u^2(t)⟩ has been shown to determine neuron stochasticity, this suggests that linearly increasing background activity rates (i.e. α) results in linearly increasing temperatures in networks of such neurons.

To show that this is indeed the case, we investigated how the behavior of a network with lateral inhibition (Fig. 2f, see Methods 5.5 for details) changes with increasing background frequency. We find that for high background activity rates, the energy landscape is flatter than for low rates.
This trend (Fig. 2) is particularly visible if the state probabilities are compared in a normalized way, offsetting the change of the maximum state probability (Fig. 2)).

To quantify the change of the sampling temperature, we fitted an SRM model to the LIF neuron for different values of $\alpha$ using the fitting method by Jolivet et al. (2006) (see Methods 5.6). We used an SRM model that was identical to the LIF neuron model except for a stochastic firing criterion with instantaneous firing intensity

$$\rho(u) = \frac{1}{\Delta t} \exp \left( \frac{u - u_T}{T} \right),$$

where $T$ is the temperature, $u_T$ is the soft threshold (i.e. the value of $u$ where the firing intensity reaches $1/\Delta t$), and $\Delta t$ is the resolution of the discrete-time simulation. Fig. 2j shows the firing rate of the neuron in response to the stimulus. As the input is balanced, the firing rate does not change with the level of background activity. The temperature values resulting from the fitting procedure (see Methods 5.6 for details) are shown in Fig. 2. We find that the temperature increases linearly with increasing levels of background activity. The soft threshold $u_T$ shows a slightly increasing linear trend (Fig. 2i). The resulting firing intensity curves are well-aligned, as in the theoretical model (Fig. 2k, cf. Fig. 1a). This shows that balanced background activity can control the sampling temperature without altering the overall level of neuronal responses in current-based models.

### 3.2 Effects of background input on temperature in networks of conductance-based neurons

The effect of background input on neuron behavior is much more complicated in conductance-based neuron models. In particular, since input currents depend on the membrane potential, background currents can only be balanced at a particular voltage. Nevertheless, the impact of background input on membrane potential fluctuations of conductance-based LIF neurons can be calculated (Zerlaut et al. 2018) (see Methods 5.3). Generally, both the mean $\langle u \rangle = \mu_u(\nu_e, \nu_i)$ and the variance $\langle u^2 \rangle = \sigma_u^2(\nu_e, \nu_i)$ are bounded and converge towards a finite value as $\alpha$ increases. This suggests a more complex relationship between background rates and the sampling temperature.

To see whether background input can still control sampling temperature over a reasonable range, we investigated four different scenarios (Fig. 3, see Methods 5.3). These scenarios arise from different choices of synaptic conductances for background inputs and different ways of changing the background activity levels:

**Unbalanced**: In this scenario, we do not care about the balance of background input. This can result from many parameter settings, for simplicity, we choose $\nu_e = \nu_i$. As a result, both $\mu_u$ and $\sigma_u^2$ increase with $\alpha$ (Fig. 3a–c, first column).

**Balanced at the resting potential $E_L$**: As in the current-based case, we can balance the input at $\mu_u(\nu_e, \nu_i) \equiv E_L$ for $\nu_e = \nu_i$ (Fig. 3a–c, second column) using the same parameters as in the previous case except for a specifically chosen inhibitory synaptic input conductance (see Methods 5.3).

**Balanced at $-55 \text{ mV}$**: This mimicks the regime of cortical up-states, where neurons have membrane potentials close to the firing threshold (here: $u_{th} = -50 \text{ mV}$). For a given choice of synaptic input conductances, this results from a special way of increasing $\nu_i$ with $\alpha$ (i.e. $\nu_i \neq \nu_e$ here, see Methods 5.3). Note that balancing here requires some minimal background input level (Fig. 3a–c, third column).

**Approximately balanced with high variance**: A different regime results from choosing larger synaptic conductances. This regime is approximately balanced (small change of $\mu_u$), but differs from the previous scenarios in two significant ways: the overall variance is much higher, and the variance decreases with $\alpha$ (Fig. 3a–c, last column). Such a regime might lead to different temperature behavior (e.g. $T$ might decrease with increasing $\alpha$ if the variance defines the temperature).

The different behaviors of membrane potential mean and variance raise the question whether (and what kind of) temperature effects can be seen in these cases. We performed the same analysis as before, now using conductance-based neurons (see Methods 5.1), for the four cases described above. The resulting state probabilities (Fig. 3d) show that temperature effects are indeed present. The effect is strong in the unbalanced and the exactly balanced cases. In the approximately
balanced case, the effect is small but shows the same trend (flatter distribution with increasing $\alpha$, see Fig. 3b), which is surprising as the variance of $u$ here decreases as $\alpha$ is increased. This can be explained as follows: even as the variance decreases, the overall synaptic conductance evoked by background input grows. Therefore, as $\alpha$ increases, the effect of the background input grows stronger relative to the input from the recurrent network connections, thus leading to more equal responses.

These results suggest that conductance-based models show temperature effects similar to current-based models. To quantify the effect, we repeated the fitting procedure described above. Again, we solely replaced the firing mechanism (see Methods 5.1) without changing the integration of inputs. The resulting model is not an SRM, but rather a conductance-based LIF neuron with stochastic firing.

We again performed the fitting for different values of $\alpha$. The results (Fig. 4) confirm the temperature effect in conductance-based models, with some differences to the current-based case. Fig. 4a shows the neuronal firing rates in response to the stimulus used for fitting. In the unbalanced case, the mean membrane potential increases with $\alpha$, resulting in increased firing rates. In the balanced and approximately balanced cases, however, the firing rates decrease even though the mean membrane potential stays constant. This marks an important difference to the current-based case. Fig. 4b shows the temperature values resulting from fitting. In all four scenarios, $T$ increases with $\alpha$, as expected by the responses in the sampling network (cf. Fig. 3b). Fig. 4c shows the soft threshold values. In contrast to the current-based case, $u_T$ here significantly changes over the range of $\alpha$ values in all cases (as expected from the changing firing rates, Fig. 4a). This shows
Figure 4: Fitting stochastic models to conductance-based LIF neurons with background input. a) Firing rate in response to stimulus used for fitting. Even if the input is balanced or approximately balanced, the firing rates change substantially for different values of $\alpha$. b) Temperature values resulting from fitting stochastic models to the LIF neurons. Temperatures increase with increasing $\alpha$ in all cases. c) Soft thresholds resulting from fitting. Values change substantially in some cases. d) Firing intensity values $\rho(u)$ resulting from fitting for $\alpha \in \{1, 3, 5\}$. Behavior is different in each scenario, but the exponentials are never aligned as in the current-based case.

that even in balanced regimes, increased background activity changes the level of neuronal activity in the conductance-based case. This is also visible when comparing the resulting firing intensity functions (Fig. 4d) to those from the current-based case (Fig. 2). Here, the intensity functions for different values of $\alpha$ do not seem aligned at first glance. However, as both $T$ and $u_T$ increase in a linear fashion with $\alpha$, there always is a voltage value where all curves meet (see Methods 5.7), as in the theoretical neural sampling model by Buesing et al. (2011). By interpolating between the unbalanced scenario and the scenario balanced at $E_L$ (which only differ in the synaptic conductance for inhibitory background input), we can find parameter values in which the intensities are aligned in a similar point as in the current-based case (see Methods 5.8).

3.3 Background oscillations structure sampling-based computations

To summarize, we found that the strength of background activity can control the sampling behavior of neural networks. Since background activity levels exhibit oscillatory changes across many different brain areas (Buzsaki, 2006), this effect could have profound implications for the organization of computations in the brain. The proposed link between activity levels and sampling temperature suggests that brain networks alternate between sampling at high temperatures, allowing rapid traversing of the state space for good mixing, and low temperatures, promoting convergence to states of high probability. We next describe possible functional advantages of such oscillatory sampling networks.

We considered a network consisting of 15 assemblies, each consisting of 3 strongly recurrently connected neurons (Fig. 5a). These assemblies were organized in three groups of five assemblies each (blue, green, and red group in Fig. 5a). Assemblies within a group were connected through inhibitory connections, i.e. each group implements a winner-take-all (WTA) motif of five assemblies. In addition, the $n^{th}$ assembly in group 2 was linked with excitatory connections to the $n^{th}$ assembly in group 1 and group 3 (Fig. 5a). Hence, the network distribution consists of five high-probability states where one interlinked assembly-triple is active — we term such a high-probability state a solution of the sampling problem. This triple will then inhibit other assemblies due to the WTA
Figure 5: Background oscillations structure computations into sampling episodes. a) Network setup. Three winner-take-all groups contain five recurrently connected assemblies, defining a sampling task with five equal solutions (see text). b) Network activity with oscillating background input. Top: background activity scaling factor $\alpha$ is varied in $[0.5, 5]$ at $f = 10$ Hz. Middle: spikes from each assembly in 500 ms of a simulation. Bottom: number of distinct solutions the network has visited. Green bars show times when the network state defines a valid solution. c) Probability of network state encoding a solution depending on oscillation phase, estimated over $t = 100$ s. Gray horizontal lines show estimated probability for constant $\alpha$ values. Inset shows change of $\alpha$. d) Mean time until the network has visited all five solutions for oscillating and constant background activity ($\alpha \in \{0.5, 2.5, 5\}$) for $N = 100$ runs (whiskers denote SD). Significance $** \equiv p < 10^{-20}$ (Wilcoxon ranksum test). e) Time between choosing distinct solutions (see Methods 5.9) for $t = 100$ s. $* \equiv p < 10^{-9}$.

structures. We say that the network has found a valid solution if one linked assembly triple is active (>50% of neurons per assembly fired within the last 10 ms) while all other assemblies remain silent (<50% of neurons fired; see Methods 5.9 for details). As the recurrent connectivity within each assembly is rather strong, the network tends to lock into one such solution, making mixing hard. However, the goal of the sampling process is to visit all solutions in a reasonable amount of time.

We compared the behavior of the network when $\alpha$ was oscillating in the range considered before ($\alpha \in [0.5, 5]$, i.e., total background rates in [2500, 25000] Hz, network activity shown in Fig. 5b) with the behavior when $\alpha$ was constant. To obtain similar levels of activity for low and high background activity, we chose a parameter set between the first and second scenario from above (Fig. 3) which resulted in minimal change of the neurons’ firing rates for any value of $\alpha$ (see Methods 5.8).

Fig. 5 shows that background oscillations structure sampling-based computations by defining times when good solutions can be read-out from the network. We quantified this by the probability that the current state is a valid solution over the phase of the oscillation (Fig. 5c). At times of low temperature, oscillating networks are much more likely to provide a solution compared to high (dotted line) or medium (dashed line) temperature networks. Networks with constant low temperature provide higher probabilities for valid solutions (dashed-dotted line). However, these networks tend to converge to one solution and stay there for a long time, thus they exhibit much worse mixing behavior. We quantified mixing by measuring (i) the time it takes the network to
visit each solution at least once (Fig. 5d), and (ii) the time it takes on average to move from one solution to another one (Fig. 5e). On both measures, best performance is achieved with oscillatory background activity or intermediate constant background activity levels. In summary, oscillatory network activity structures sampled-based computations in spiking neural networks. This oscillatory structure can provide good solutions with high probability while inheriting the good mixing properties of high temperature networks.

4 Discussion

We have shown that background input effectively sets the sampling temperature in networks of LIF neurons in both current-based and in more realistic conductance-based models, and how this effect leads to functional advantages in sampling networks when oscillatory background input is present. Cyclic background activity thus structures sampling-based computations in spiking neural networks by allowing the network to alternate between periods of high and low temperature, performing a kind of annealing process [Kirkpatrick et al., 1983]. High temperatures allow traversing the state space rapidly, giving rise to good mixing behavior, while low temperatures promote momentary convergence to good solutions. Such a form of computing in discrete steps in brain networks has previously been suggested based on phased-lock shifts of attention in the visual stream [Buschman and Miller, 2010]. Low temperature periods furthermore provide a reference time for reading out good network solutions with high probability, reminiscent of phase-based neural codes in which firing at particular phases conveys information [O’Keefe and Recce, 1993].

Habenschuss et al. [2013] have previously shown that in the presence of periodic input, spiking networks have a phase-specific stationary distribution which is influenced by the network parameters and the properties of the inputs. We have identified in this work the specific nature of the phase-dependent distributions by showing that changing background input levels result in temperature changes without otherwise altering responses.

The general functional benefits of background oscillations shown in this work are intriguing as cyclic activity is prevalent throughout the brain. It has recently been suggested that although cyclic activity is routinely separated into distinct frequency bands, oscillations in fact have a similar function throughout the cortex [Lundqvist et al., 2020]. We have used a modulation frequency of 10 Hz, corresponding to high theta-band or low alpha-band oscillations, but in principle, cyclic sampling episodes can take place at any frequency (e.g. beta-band oscillations, prominent in the frontal lobe).

A number of functional roles have been proposed for oscillations [Lengyel et al., 2005]. Aitchison and Lengyel [2016] showed how oscillations between excitatory and inhibitory populations implement Hamiltonian Monte Carlo. Such excitatory-inhibitory oscillations are usually quite fast (i.e. gamma-band). We focus here on activity on longer time scales. It has furthermore been suggested on theoretical grounds that during the hippocampal theta cycle, modulation of GABA_B synapses performs a process similar to simulated annealing in a model of population dynamics [Sohal and Hasselmo, 1998]. Such a mechanism was shown to be advantageous for sequence disambiguation [Sohal and Hasselmo, 1998a]. In this work we propose that temperature control takes place on the level of individual neurons via input regardless of the synapse type, thus, the mechanism we propose has a much more general scope.

The benefit of providing a particular time window for reading out good solutions suggests that using temperature oscillations might enhance any-time computations with neuromorphic computing platforms, which often use sampling-based computations. There, while theory guarantees that spiking networks converge towards a stationary distribution [Habenschuss et al., 2013] which is shaped so that solution states have a high probability [Jonke et al., 2016], it is not clear at any given point in time whether the current state is a solution candidate or a transitional state. Temperature oscillations, e.g. provided by activity oscillations, could enhance such networks by mitigating this problem.
5 Methods

5.1 Neuron models

In the current-based LIF model the membrane potential \( u(t) \) is updated according to

\[
C_m \frac{du}{dt} = -g_L (u - E_L) + I_c + I_i + I_{\text{ext}} ,
\]

where \( C_m \) is the membrane capacitance, \( g_L \) is the leak conductance, \( E_L \) is the leak reversal potential, and \( I_c(t) \) and \( I_i(t) \) are the synaptic currents from excitatory and inhibitory input at time \( t \) (\( I_{\text{ext}} \) is externally injected current). The synaptic currents are modeled as exponentials and updated from synaptic input via

\[
\frac{dI_c}{dt} = -\frac{I_c}{\tau_c} + \sum_{j \in \text{PRE}_e} w_j S_j(t) \quad \frac{dI_i}{dt} = -\frac{I_i}{\tau_i} + \sum_{j \in \text{PRE}_i} w_j S_j(t)
\]

where \( S_j(t) = \sum_f \delta \left( t - t_{j(f)} \right) \) is the spike train of the presynaptic neuron \( j \), \( w_j \) is the synaptic weight from the presynaptic neuron \( j \), and \( \tau_c \) and \( \tau_i \) are the time constants of excitatory and inhibitory synapses, respectively. The sums run over sets of all excitatory and inhibitory presynaptic partners. The LIF neuron generates spikes every time \( u(t) \) reaches a threshold \( u_\text{th} \), this also triggers a reset

\[
\text{if } u(t) \geq u_\text{th} \quad u \leftarrow u_\text{reset} .
\]

After spiking, neurons are clamped to \( u_\text{reset} \) for the duration of an absolute refractory period \( \Delta_{\text{abs}} \).

The stochastic model we fitted to data generated from such a LIF neuron is identical to the LIF neurons except for the deterministic spike generation mechanism, which is replaced by a stochastic spike criterion using an instantaneous firing intensity of

\[
\rho(t) = \frac{1}{\Delta t} \exp \left( \frac{u(t) - u_T}{T} \right)
\]

where \( u_T \) and \( T \) are parameters (temperature and soft threshold) obtained from the fitting method. Spikes drawn from a Poisson process with this instantaneous intensity. In our discrete-time simulations, we calculate the probability of a spike within each simulation time step \( \Delta t \), which is

\[
\Pr \left( \text{spike in } [t, t + \Delta t] | u(t) \right) = 1 - \exp \left( -\rho(t) \Delta t \right) ,
\]

and draw spikes accordingly. The neuron parameters are given in Tab. 1.

In the conductance-based LIF model, \( u(t) \) evolves according to

\[
C_m \frac{du}{dt} = -g_L (u - E_L) - g_e (u - E_e) - g_i (u - E_i) + I_{\text{ext}} ,
\]

where \( g_e(t) \) and \( g_i(t) \) are the excitatory and inhibitory conductances at time \( t \), and \( E_e \) and \( E_i \) are the excitatory and inhibitory reversal potentials, respectively. The conductances are modeled as exponentials and updated from synaptic input via

\[
\frac{dg_e}{dt} = -\frac{g_e}{\tau_e} + \sum_{j \in \text{PRE}_e} g_j S_j(t) \quad \frac{dg_i}{dt} = -\frac{g_i}{\tau_i} + \sum_{j \in \text{PRE}_i} g_j S_j(t)
\]

where \( g_j \) is the synaptic conductance of the synapse with the presynaptic neuron \( j \) (other terms as in Eq. 7). Spike generation in the deterministic conductance-based model was identical to the deterministic current-based model (Eq. 6), and the stochastic model similarly only replaces the spike generation mechanism with stochastic firing (Eq. 9). The neuron parameters are given in Tab. 1.

Background activity was provided to each deterministic LIF neuron via Poisson input at excitatory rate \( \nu_e \) and inhibitory rate \( \nu_i \). In the current-based case, the input rates are \( \nu_e = \nu_i = \alpha \nu_0 \) with \( \nu_0 = 5000 \text{ Hz} \), and the input is scaled by synaptic weights \( w_e \) and \( w_i \) (see below, Methods 5.2). In the conductance-based case, the input rates \( \nu_e \) and \( \nu_i \) and synaptic conductances of \( g_{\text{e},bg} = g_{\text{e},bg} g_L \) and \( g_{\text{i},bg} = g_{\text{i},bg} g_L \) depend on the scenario (see below, Methods 5.3 and 5.4).
Table 1: neuron parameters.

| parameter       | $C_m$ | $g_L$ | $E_L$ | $E_e$ | $E_i$ | $\tau_e$ | $\tau_i$ | $w_0$ | $u_{th}$ | $u_{reset}$ | $\Delta_{abs}$ |
|-----------------|-------|-------|-------|-------|-------|-----------|-----------|-------|----------|-------------|---------------|
| unit            | pF    | nS    | mV    | mV    | mV    | ms        | ms        | pA    | mV       | mV          | ms            |
| current-based   | 250   | 25    | -65   | 2     | 3     | 500       | -50       | -65   | 3        |              |               |
| conductance-based | 250   | 25    | -65   | 0    | -80   | 2         | 3         | -50   | -65      | 3           |               |

5.2 Balancing input to current-based LIF neurons

Assume a LIF neuron receives background Poisson input in the form of an excitatory spike train $S_e(t)$ and an inhibitory spike train $S_i(t)$, with rates of $\nu_e$ (excitation input) and $\nu_i$ (inhibitory input). The inputs are scaled by synaptic weights $w_e$ (excitation) and $w_i$ (inhibition). The resulting input current to the neuron is

$$I_{bg}(t) = w_e \int_0^\infty \epsilon_e(s) S_e(t-s) \, ds + w_i \int_0^\infty \epsilon_i(s) S_i(t-s) \, ds$$

(13)

where $\epsilon_e(t)$ and $\epsilon_i(t)$ are the unweighted responses to a single excitatory and inhibitory spike, respectively. Applying Campbell’s theorem [Papoulis and Pillai 2002] gives the expected value of this current

$$\langle I_{bg}(t) \rangle = w_e \nu_e \bar{\epsilon}_e + w_i \nu_i \bar{\epsilon}_i,$$

(14)

where $\bar{\epsilon}_e$ and $\bar{\epsilon}_i$ are the integrals over a single unweighted excitatory and inhibitory synaptic response, respectively. If the excitatory and inhibitory background input rates are both linearly scaled versions of some base firing rate, i.e.

$$\nu_e = \alpha \nu_{e,0} \quad \text{and} \quad \nu_i = \alpha \nu_{i,0},$$

(15)

we get a balanced state by setting

$$w_e = \frac{w_0}{\nu_e \bar{\epsilon}_e} \quad \text{and} \quad w_i = -\frac{w_0}{\nu_i \bar{\epsilon}_i},$$

(16)

where $w_0$ is some scalar.

We are interested in the effect of such background input for different input rates. A linear change of both excitatory and inhibitory rate, i.e. an increase or decrease of $\alpha$, adds no offset to the membrane potential $u(t)$ (as the mean current is always zero). To calculate the variance of the membrane potential fluctuations, we assume exponential synapses (as in Eq. 7) with time constants $\tau_e = \bar{\epsilon}_e$ (excitation) and $\tau_i = \bar{\epsilon}_i$ (inhibition). In this case, the postsynaptic current and the effect of leaky integration by the LIF neuron can be combined into a single filter describing the postsynaptic potential (with double exponential shape). This filter can be used to calculate the membrane potential fluctuations resulting from the background input (again using Campbell’s theorem) for a passive membrane, i.e. a neuron without a spike generation mechanism. It is given by

$$\langle u^2 \rangle = \frac{\alpha}{2} \left( \frac{w_0}{g_L} \right)^2 \left( \frac{1}{\nu_e \tau_m + \tau_e} + \frac{1}{\nu_i \tau_m + \tau_i} \right),$$

(17)

for the choice of $w_e$ and $w_i$ described above (here, $\tau_m = C_m/g_L$). This can be written in the form of $\langle u^2 \rangle = \alpha (c_e/\nu_{e,0} + c_i/\nu_{i,0})$ (see text), where

$c_e = \left( \frac{w_0}{g_L} \right)^2 \frac{1}{2(\tau_m + \tau_e)}$  and  $c_i = \left( \frac{w_0}{g_L} \right)^2 \frac{1}{2(\tau_m + \tau_i)}$.

5.3 Balancing input to conductance-based LIF neurons

The impact of input in the form of excitatory and inhibitory Poisson spikes on conductance-based LIF neurons has been investigated by Zerlaut et al. [2018], who have derived approximations of
we used a simple sampling task (see Fig. 2d). The SNN consisted of 4 neurons receiving bias 
which features high variance due to larger values of both excitatory and inhibitory background 
we balance the input at a value

5.4 Conductance-based input scenarios

Table 2: background input parameters for conductance-based background input scenarios.

| scenario            | parameter | \( \nu_e \)  | \( \nu_i \) | \( \tilde{g}_{e, bg} \) | \( \tilde{g}_{i, bg} \) | \( g_{stim, max} \) |
|---------------------|-----------|--------------|------------|-------------------------|-------------------------|---------------------|
| unbalanced          | \( \alpha \cdot 5000 \) | \( \alpha \cdot 5000 \) | 0.02       | 0.02                    | 10                      |
| balanced at \( E_L \) | \( \alpha \cdot 5000 \) | \( \alpha \cdot 5000 \) | 0.02       | from Eq. 21              | 50                      |
| balanced at \( \bar{\mu}_u = -55 \text{ mV} \) | \( \alpha \cdot 5000 \) | from Eq. 20 | 0.02       | 0.02                    | 10                      |
| approximately balanced | \( \alpha \cdot 5000 \) | \( \alpha \cdot 5000 \) | 0.1        | 0.15                    | 30                      |

the resulting membrane potential mean and variance. The former is given by

\[
\mu_u (\nu_e, \nu_i) = \frac{\nu_e \tau_e \tilde{g}_{e, bg} E_e + \nu_i \tau_i \tilde{g}_{i, bg} E_i + g_i E_L}{\mu_G (\nu_e, \nu_i)}
\]  

with \( \mu_G (\nu_e, \nu_i) = \nu_e \tau_e \tilde{g}_{e, bg} + \nu_i \tau_i \tilde{g}_{i, bg} + g_i \). Here, \( \tilde{g}_{e, bg} \) and \( \tilde{g}_{i, bg} \) are the synaptic conductances of synapses for excitatory and inhibitory background input, respectively. The variance of the membrane potential fluctuations is

\[
\sigma_u^2 (\nu_e, \nu_i) = \nu_e \left( \frac{g_{e, bg}}{\mu_G (\nu_e, \nu_i) \tau_e} (E_e - \mu_u (\nu_e, \nu_i)) \right)^2 + \nu_i \left( \frac{g_{i, bg}}{\mu_G (\nu_e, \nu_i) \tau_i} (E_i - \mu_u (\nu_e, \nu_i)) \right)^2
\]

In this work, we use \( \nu_e = \alpha \nu_{e,0} \) for the excitatory rate. The inhibitory rate is \( \nu_i = \alpha \nu_{i,0} \) unless we balance the input at a value \( \neq E_L \). In this case, we set \( \mu_u \) to some target value \( \bar{\mu}_u \). Assuming

\[
\nu_i = \nu_e \frac{\tau_e \tilde{g}_{e, bg} (E_e - \bar{\mu}_u)}{\tau_i \tilde{g}_{i, bg} (\bar{\mu}_u - E_i)} + \frac{g_i (E_L - \bar{\mu}_u)}{\tau_i \tilde{g}_{i, bg} (\bar{\mu}_u - E_i)}
\]

If we wish to balance the input at \( \bar{\mu}_u = E_L \), we can again choose \( \nu_i = \alpha \nu_{i,0} \) and balance the input by choosing the conductance to inhibitory background input depending on the other parameters by setting

\[
\tilde{g}_i = \frac{g_e}{\tau_i (E_i - E_L)}
\]

5.5 Illustrative sampling task

To illustrate the effect of the background input activity on the sampling behavior of an SNN, we used a simple sampling task (see Fig. 2d). The SNN consisted of 4 neurons receiving bias input by injecting currents of amplitudes \( I_{\text{ext}} = [40, 60, 80, 40] \text{ pA} \), respectively. Each neuron
additionally received input from an external neuron (Poisson spiking at $f = 75$ Hz, synaptic weight $w_{\text{in}} = 3000$ pA; current-based case; conductance-based case: synaptic conductance $g_{\text{in}} = g_{\text{stim, max}}$, see Tab. 2 and Methods 5.6). Neurons had inhibitory lateral connections (weight $w_{\text{inh}} = -3w_{\text{in}}$ or conductance $g_{\text{inh}} = 3g_{\text{in}}$).

We ran this network for 100 s. From the spikes of each neuron, we computed network states as proposed by Berkes et al. (2011) by setting the state $z_j$ of each neuron $j$ to 1 if the neuron fired within the last 5 ms and otherwise to 0. This allowed us to estimate the fraction of time in which one neuron was exclusively active (i.e. $z_j = 1$ for some $j = j_0$ and $z_k = 0$ for all $k \neq j_0$) and in which the state was mixed (i.e. $z_j = 1$ for more than one $j$).

5.6 Stimulus and fitting procedure

To fit neuron models with stochastic spike generation to data from deterministic neurons, we followed the method for fitting escape rate functions described by Jolivet et al. (2006). We estimated the spiking probability given the membrane $u$ using a stimulus consisting of 100 inputs (80% excitatory), each firing according to a Poisson process with $f_{\text{stim}} = 5$ Hz. Each input had a synaptic weight drawn from a uniform distribution in $[0, 3000]$ pA (current-based model) or $[0, g_{\text{stim, max}}]$ (conductance-based case, given for each scenario in Tab. 2). This stimulus was presented to the deterministic LIF models, recording the resulting spike times. It was then presented to a passive version of the stochastic neurons (i.e. no firing mechanism) which were reset at every spike of the deterministic model. Binned histograms of $u$ of the passive model at all times and at spike times of the original model allow estimating the firing probability $p(\text{spike}|u)$ (see Jolivet et al. 2006).

To fit the model, we insert Eq. 9 into Eq. 10 and reformulate the result to get

$$\frac{u - u_T}{T} = \log \left( -\log \left( 1 - p(\text{spike}|u) \right) \right), \quad (22)$$

where we perform linear regression on the right-hand side to get values of $T$ and $u_T$. The shape of $p(\text{spike}|u)$ is approximately Gaussian. We found that the best fits result from using only the values of $p(\text{spike}|u)$ from $u < \arg \max_u p(\text{spike}|u)$ for fitting, except for the case in which we balance at $E_L$, where we used all values of $p(\text{spike}|u)$ until they were no longer convex (starting from low values of $u$).

The stochastic models were evaluated by simulating 1000 deterministic and 1000 stochastic versions of the model for 1 s using a new stimulus. From these runs, the time-varying firing intensities $\nu_{\text{LIF}}(t)$ and $\nu_{\text{fit}}(t)$ were estimated. A criterion measuring the quality of fit used to assess how well the fitted models match the originals, it was calculated as

$$M_d = \frac{2 \int \nu_{\text{LIF}}(t)\nu_{\text{fit}}(t)dt}{\int \nu_{\text{LIF}}^2(t)dt + \int \nu_{\text{fit}}^2(t)dt}. \quad (23)$$

for every model. This similarity criterion, which determines how well the firing intensities match, is inspired by Mensi et al. (2011)\footnote{The $M_d$ criterion as stated by Mensi et al. (2011) Eq. 16) seems to contain an error, therefore, it is slightly adapted here so its properties match those discussed by Mensi et al., i.e. a value of 1 indicates a perfect match, while a value of 0 indicates no match (e.g. if $\nu_{\text{fit}}(t) = 0$).}. We found that the stochastic models were generally capable of reproducing the LIF behavior reasonably well (i.e. $M_d > 0.5$ in most scenarios, Fig. 6). The fitting method has difficulties (and the quality of fit decreases) if either the variance is high (large $\alpha$ in all scenarios, all models in the approximately balanced scenario) or if the mean membrane potential is far from the threshold (scenario balanced at $E_L$). We used the results from fitting only for elucidating the temperature effect in networks of LIF neurons with background input, so any errors resulting from imperfect fits did not carry over to the experiments showing the functional advantages of background oscillations (where we again used LIF neurons and spiking background input for our simulations).
5.7 Firing intensities are always aligned for linear relationships of $T$ and $b$

In the theoretical model of Buesing et al. (2011), the firing intensities $\rho(u)$ are aligned in some point $\rho_0$ regardless of the temperature value $T$. We show here that the same is true for the intensity curves of conductance-based LIF neurons as the temperature $T$ and the soft threshold $u_T$ both scale linearly with $\alpha$ (cf. Fig 4).

Assume that the relationship between $\alpha$ and both $T$ and $u_T$ is linear, i.e.

$$T(\alpha) =: T_1 \alpha + T_0 \quad \text{and} \quad u_T(\alpha) =: u_{T,1} \alpha + u_{T,0} \ .$$

Then, for firing intensities of the form

$$\rho(u; \alpha) = \frac{1}{\Delta t} \exp \left( \frac{u - u_T(\alpha)}{T(\alpha)} \right) = \frac{1}{\Delta t} \exp \left( \frac{u - u_{T,1} \alpha - u_{T,0}}{T_1 \alpha + T_0} \right)$$

the intensities are always aligned in some intensity value $\rho_0 := \rho(u_0; \alpha)$ at some constant $u_0$ for all values of $\alpha$. This point is given by

$$\rho_0 = \frac{1}{\Delta t} \exp \left( \frac{u_{T,1}}{T_1} \right) \quad \text{and} \quad u_0 = -u_{T,1} \frac{T_0}{T_1} + u_{T,0} \ .$$

Note that $\rho_0$ might be very small or large depending on the slope of $T(\alpha)$ and $u_T(\alpha)$.

5.8 Conductance-based scenario with constant firing rate

The unbalanced and balanced at $E_L$ scenarios differ only in the inhibitory conductance $g_{i,bg}$. We see in Fig. 4 that in the former case, increasing $\alpha$ leads to an offset of the $\rho$-curves towards smaller values of $u$, while in the latter, larger values of $\alpha$ correspond to $\rho$-curves shifted towards larger $u$ values. This suggests that there are scenarios in between where the $\rho$-curves overlap in a similar fashion to the current-based case. When interpolated between these two conditions, linearly changing $g_{i,bg}$ as well as $g_{stim,max}$, it is possible to obtain scenarios where the $\rho$-curves align at a point of $\rho_0 \approx 1 \text{ms}^{-1}$, or any other value. It is also possible to choose parameters resulting in (almost) constant $u_T$, resulting in alignment around $\rho_0 = \frac{\Delta t}{\Delta t}$.

For the sampling task described below (Methods 5.9), we found it was advantageous to minimize the change of the firing frequency over the range of $\alpha$. This ensures that when comparing oscillating background input to constant background levels, the latter show similar firing rates for all scenarios.
Figure 7: Parameters used for sampling task with background oscillations, tuned to have similar firing rates for any value of $\alpha$. a) Background input rates per $\alpha$. b) Mean membrane potential. c) Variance of membrane potential fluctuations. d) Firing rate in response to stimulus used for fitting. e) Temperature values resulting from fitting, as well as linear fit (gray). f) Soft threshold values resulting from fitting, as well as linear fit (gray). g) Firing intensities resulting from fitting. Due to noise in the fitting procedure (resulting in a too large value of $u_T$ at $\alpha = 5$), the curves do not seem aligned. h) Firing intensities using linear fits of the values of $T$ and $u_T$ (see gray lines in panels e and f), showing good alignment.

(i.e. leading to fair conditions for comparing the behavior; for the proposed computational function of oscillations, it is not problematic if there is no or almost no network activity during at some part of the cycle). For the stimulus used above (for fitting), this was the case for a scaling factor of $g_{\text{bg}} = 0.02646$ with $g_{\text{stim, max}} = 17 \text{nS}$ (see Fig. 7).

5.9 Sampling with background oscillations

To illustrate the advantage of oscillatory background input, we constructed a sampling task with several equal solutions which are far apart in the state space, thus making mixing hard. The circuit consisted of 3 winner-take-all (WTA) groups (Fig. 5a). Each group contained 5 assemblies, each formed by 3 neurons with strong recurrent connectivity (all neuron pairs bidirectionally connected) and lateral inhibition (bidirectional connections between all neuron pairs that not part of the same assembly). Between groups, the $n^{th}$ assemblies were bidirectionally linked in the form of a chain: one neuron of the $n^{th}$ assembly in the first group was connected to one neuron of the $n^{th}$ assembly in the second group, a different neuron in this assembly was connected to one neuron of the $n^{th}$ assembly of the third group (see Fig. 5a). Synapse parameters are given in Tab. 3. As there are no input units providing activity to the network, it was necessary to inject a current of $I_{\text{ext}} = 400 \text{pA}$ into each neuron so neurons did not remain silent. The other neuron parameters used for this task are described above (Methods 5.8).

This circuit defines a sampling task with 5 equally probable solutions. A network state is defined to encode the $n^{th}$ solution if the $n^{th}$ assembly in each group is simultaneously active, and all other assemblies are inactive. An assembly is regarded as active if $50\%$ of its neurons fired within the last $10 \text{ms}$, otherwise, it is regarded as inactive. This definition allows to characterize the network state at each time step of the discrete-time simulation as either a solution state (with

| connection | $g$ | $E_{\text{syn}}$ | delays |
|------------|-----|----------------|--------|
| unit       | nS  | mV            | ms     |
| recurrent  | 8.5 | 0             | $\sim U(1,3)$ |
| inhibitory | -17 | -80           | 0.1    |
| link       | 8.5 | 0             | $\sim U(1,3)$ |

Table 3: Connection parameters for oscillation experiment. Excitatory connections have random synaptic delays ($U(a,b)$ denotes a uniform distribution in $[a, b]$).
Figure 8: Comparison of network activity for different background input conditions (as in Fig. 5b). See Fig. 5c-e for statistics over many runs. 

- **a)** Oscillating background activity with $\alpha \in [0.5, 5]$.
- **b)** Constant background activity with $\alpha = 0.5$.
- **c)** Constant background activity with $\alpha = 2.5$.
- **d)** Constant background activity with $\alpha = 5$.

Background input was provided to the network via Poisson spikes. Each neuron received independent background input, with rates scaled by $\alpha$ as in previous experiments. The scaling factor $\alpha$ was sinusoidally modulated over time, with $\alpha(t) \in [0.5, 5]$ and modulation frequency $f = 10$ Hz (see Fig. 5b top). We compare the results in this case to the results when $\alpha$ is kept constant ($\alpha \in \{0.5, 2.5, 5\}$). Fig. 8 shows sample behavior for the different cases, highlighting the different behavioral regimes (e.g. locking into one solution for $\alpha \equiv 0.5$, see text).

To estimate the probability of the network state encoding a solution, we ran the network for 100 s in each case. For the constant $\alpha$ cases, we report the fraction of network states that encode one of the 5 solutions. For the oscillatory case, we estimated the phase-aligned fractions of solution states (Fig. 5c).

We tested the mixing behavior in two ways. First, we estimated the time it took to switch between solutions over 100 s of simulation time. Switching times were defined as the difference between the time the network state changed to any solution state and the time the network state next changed to a solution state for a different solution (i.e. difference between solution state onset times, Fig. 5e shows mean and SD). We also estimated the time it took to find all solutions by running the network $N = 100$ times for 20 s for each of the four background input setups. We recorded how long it took for the network state to visit each of the 5 solutions in each of these simulations (Fig. 5d shows mean and SD). In some rare cases, the simulation time was not enough
for the network to visit all solutions, these runs were discarded. Significance values were calculated using the Wilcoxon rank-sum test.

5.10 Simulations

All simulations were performed with Brian2 (Stimberg et al., 2019) with a resolution of $\Delta t = 0.05$ ms.

5.11 Acknowledgements

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