1 Analytical derivations

In this section we assume $D = \bar{D}$. The generalization to the case $D \neq \bar{D}$ is straightforward but lengthy. Numerical results for $D \neq \bar{D}$ are presented in section 4.

1.1 Activity of a single population in the oscillatory regime

The firing rate of a single population in the oscillatory regime was derived in [1]. For sufficiently large $K_0$, the total input current is negative in a range $[0, T_1]$ where $T_1 > D$, and positive in a range $[T_1, T]$ where $D < R = T - T_1 < 2D$ (see Fig. A).

The firing rate is:

$$m(t) = \begin{cases} 
    M e^{-t} & t \in [0, T_1] \\
    M e^{-t} + M K_0 e^D \left[ e^{-t} - e^{-T_1} + e^{-t}(t - T_1) \right] & t \in [T_1, T_1 + D] \\
    M e^{-t} + M K_0 e^D \left[ e^{-t} - e^{-T_1} + e^{-t}(t - T_1) \right] + M K_0^2 e^{2D} \left[ e^{-t} - e^{-D-T_1} + e^{-t}(t - T_1 - D + \frac{(t-T_1-D)^2}{2}) \right] & t \in [T_1 + D, T]
\end{cases}$$

in which $M$ is a positive constant which depends linearly on $h_{ext}$, and $T_1$ and $R = T - T_1$ are given by the following coupled equations:

$$e^R = 1 + K_0 e^D (1 + R - D - e^{R-D})$$

$$e^T = 1 + K_0 e^D (1 - e^R + R) + K_0^2 e^{2D} \left( 1 - e^{R-D} + R - D + \frac{(R-D)^2}{2} \right)$$

The temporal evolution of the total input current and of the firing rate is shown in Fig. A.

1.2 Phase response curve

The phase response curve (PRC) is obtained by computing the response of the firing rate to the injection of a small current $M h_p \delta(t - T_p)$. This perturbation induces a phase shift $Z(T_p)M h_p$ of the limit cycle, compared with the unperturbed trajectory. The PRC $Z(T_p)$ is given by:

$$Z(T_p) = \begin{cases} 
    0 & T_p \in [0, T_1] \\
    -e^{T_p-T} (1 + K_0 e^D (T - T_p - D)) & T_p \in [T_1, T - D] \\
    -e^{T_p-T} & T_p \in [T - D, T]
\end{cases}$$

in which $R = T - T_1$ and $D < R < 2D$. Numerical results for $D \neq \bar{D}$ are presented in section 4.
Figure A: Input current and firing rate of an isolated population as a function of time, in the oscillatory region, $K_0 = -100$, $D = 0.1$.

Figure B: Phase response curves for $K_0 = -50$ and $K_0 = -100$. The PRCs are zero in the range $[0, T_1]$ and there are pronounced discontinuities at $T_1$, $T - D$, and $T$. 
Two examples for different values of \( k_0 \) are shown in Fig. B. Increasing \( k_0 \), the phase range \([0, T_1/T]\) in which the oscillation is unaffected by the applied perturbation becomes more extended. Positive and negative phase-shifts occur in the phase interval corresponding to the supra-threshold total input current part of the limit cycle.

1.3 Phase shift between two populations in the weak coupling limit

In the weak coupling limit, the phase shift \( \Delta \phi \) between the two populations evolves according to

\[
\frac{d \Delta \phi}{dt} = \Gamma(\Delta \phi)
\]

where

\[
\Gamma(\Delta \phi) = \int_0^T Z(t)m(t + \Delta \phi - D)dt - \int_0^T Z(t)m(t - \Delta \phi - D)dt
\]

The phase shifts between the two populations in the stable phase-locked states are therefore given by the zeroes of \( \Gamma \) such that \( \Gamma' < 0 \).

The integrals in Eq. (3) can be computed using Eqs. (1) and (2). Six different intervals of \( \Delta \phi \) need to be considered to compute:

\[
C(\Delta \phi) = \int_0^T Z(t)m(t + \Delta \phi - D)dt
\]
The result is:

\[
C(\Delta \phi) = \begin{cases}
C_{00}(T_1, T) + C_{10}(T_1, T - D) & \Delta \phi \in [D - T_1, T_1 + D - T] \\
C_{00}(T_1, T) + C_{10}(T_1, T - D) + C_{01}(T_1 + D - \Delta \phi, T) & \Delta \phi \in [T_1 + D - T, T_1 + 2D - T] \\
C_{00}(T_1, T) + C_{10}(T_1, T - D) + C_{01}(T_1 + D - \Delta \phi, T) + C_{12}(T_1 + 2D - \Delta \phi, T - D) & \Delta \phi \in [T_1 + 2D - T, D] \\
C_{00}(T_1, T) + C_{10}(T_1, T - D) + C_{01}(T_1 + D - \Delta \phi, T) + C_{12}(T_1 + 2D - \Delta \phi, T - D) & \Delta \phi \in [D, T_1 - T + 3D] \\
C_{00}(T_1, T) + C_{10}(T_1, T - D) + C_{01}(T_1 + D - \Delta \phi, T) + C_{11}(T_1, T + D - \Delta \phi) & \Delta \phi \in [T_1 + T - 3D, 2D] \\
C_{00}(T_1, T) + C_{10}(T_1, T - D) + C_{01}(T_1 + D - \Delta \phi, T) + C_{11}(T_1, T + D - \Delta \phi) & \Delta \phi > 2D
\end{cases}
\]

where

\[
C_{00}(a, b) = -(b-a)\epsilon^{-T-\Delta \phi + D} \\
C_{10}(a, b) = K_0 \epsilon^{2D-T-\Delta \phi} \left[ \frac{(t + D - T)^2}{2} \right]_a \\
C_{01}(a, b) = -K_0 \epsilon^{D-T} \left[ (b-a) \epsilon^{D-\Delta \phi} + \epsilon^{-T_1} (\epsilon^b - \epsilon^a) + \epsilon^{-\Delta \phi} \left[ \frac{(t + \Delta \phi - D - T_1)^2}{2} \right]_a \right] \\
C_{02}(a, b) = -K_0^2 \epsilon^{2D-T} \left[ (b-a) \epsilon^{D-\Delta \phi} - \epsilon^{-D-T_1} (\epsilon^b - \epsilon^a) + \epsilon^{-\Delta \phi} \left[ \frac{(t + \Delta \phi - 2D - T_1)^2}{2} + \frac{(t + \Delta \phi - 2D - T_1)^3}{6} \right]_a \right] \\
C_{11}(a, b) = K_0^2 \epsilon^{2D-T} \left[ \epsilon^{D-\Delta \phi} \left( \frac{b^2}{2} - \frac{a^2}{2} + (D - T)(b - a) \right) - \epsilon^{-T_1} \left[ (t - 1)\epsilon^c + (D - T)\epsilon^c \right]_a + \epsilon^{-\Delta \phi} \left[ \frac{(t + D - T)^3}{3} + (t + \Delta \phi - 2D - T_1) \frac{(t + D - T)^2}{2} \right]_a \right] \\
C_{12}(a, b) = K_0^3 \epsilon^{3D-T} \left[ \epsilon^{D-\Delta \phi} \left( \frac{b^2}{2} - \frac{a^2}{2} + (D - T)(b - a) \right) - \epsilon^{-D-T_1} \left[ (t - 1)\epsilon^c + (D - T)\epsilon^c \right]_a + \epsilon^{-\Delta \phi} \left[ \frac{(t + D - T)^3}{3} + (T + \Delta \phi - 3D - T_1) \frac{(t + D - T)^2}{2} + \frac{(t + D - T)^4}{8} \right]_a + (T + \Delta \phi - 3D - T_1) \frac{(t + D - T)^3}{3} + (T + \Delta \phi - 3D - T_1) \frac{(t + D - T)^2}{4} \right]_a \right]
\]

Two examples of the function are shown in Fig. C, where the qualitative difference between strong and weaker \(K_0\) can be easily seen looking at the number of zeroes. The inset of Fig. 1 in the paper is obtained evaluating the \(\Gamma\) function from Eq. (3) in a range of \(K_0\) including the bifurcation point \(K_0^*(D)\) from anti-phase locking to out-of-phase lockings.
2 Feigenbaum scenario for $|K_0| > |K_0^c|$

When $|K_0| > |K_0(D)|$, the transition to chaos according to the Feigenbaum scenario is validated by analyzing the bifurcation diagram of the laggard population. Fig. D shows the relevant geometric parameters.

2.1 First Feigenbaum constant

The critical couplings $K_1 = r_n$ where the number of fixed points changes from $2^{n-1}$ to $2^n$ scale like:

$$r_n - r_\infty \propto \delta^{-n}$$

The first Feigenbaum constant approximants are given by:

$$\delta = \lim_{n \to \infty} \delta_n = \lim_{n \to \infty} \frac{r_{n+1} - r_n}{r_{n+2} - r_{n+1}}$$

Accurate simulations (4th order Runge-Kutta integrator, time-step up to $10^{-6} \tau$) yield the following results for $K_0 = -250$:
which provide an estimate $\delta_7 = 4.669(2) \pm 0.0002$ to be compared with the universal value $\delta = 4.6692016\ldots[2]$.

### 2.2 Second Feigenbaum constant

At each bifurcation point, two new "forks" are generated in the bifurcation diagram, one more narrow than the other. For $n > 1$ the ratios of the widths of homologous forks— i.e., $n$-th wide (narrow) fork to $(n + 1)$-th wide (narrow) fork— converge to a universal ratio:

$$\alpha = \lim_{n \to \infty} \alpha_n = \lim_{n \to \infty} \frac{d_{n-1}}{d_n}$$

Considering the widths of large forks:

<table>
<thead>
<tr>
<th>$n$</th>
<th>$d_{n-1}/d_n$</th>
<th>$\alpha_n - \alpha_{n-1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>2.4565</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>2.4792</td>
<td>0.0226</td>
</tr>
<tr>
<td>4</td>
<td>2.49197</td>
<td>0.0128</td>
</tr>
<tr>
<td>5</td>
<td>2.50109</td>
<td>0.00912</td>
</tr>
<tr>
<td>6</td>
<td>2.502585</td>
<td>0.00149</td>
</tr>
<tr>
<td>7</td>
<td>2.502791</td>
<td>0.000206</td>
</tr>
<tr>
<td>8</td>
<td>2.502891</td>
<td>0.000100</td>
</tr>
</tbody>
</table>

These data provide an estimate $\alpha_8 = 2.502(9) \pm 0.0001$ to be compared with the universal value $\alpha = 2.502907875\ldots[2]$.

### 3 Role of entrainment in the transition to chaos for $|K_0| > |K^c_0|$ 

For $|K_0| > |K^c_0|$, the population permutation symmetry is spontaneously broken. The fluctuations in the oscillation amplitudes for the laggard activity are indeed more important than for the leader activity, despite the excitatory feedback among the two populations. We compare here the behavior of this symmetrically coupled system with another architecture in which the excitatory coupling is taken to be unidirectional (Fig. E). In this latter case, a population (driver) entrains the other (driven) by construction. Bifurcation diagrams for both bidirectional and unidirectional excitatory couplings are shown in Fig. F. In virtue of the spontaneous symmetry breaking, the leader population in the feedback architecture (bidirectional) plays the same role than the driver population in the entrainment architecture (unidirectional).
Figure E: Network architectures. Left: excitatory feedback between leader and laggard. Right: a driver population entrains the other.

Figure F: Bifurcation diagrams for bidirectional excitatory feedback and for unidirectional excitatory coupling ($K_0 = -250$).
On the other hand, phase-locked states which are symmetric under permutation of the two populations go to chaos according to a quasi-periodic scenario. This is true not only for the anti-phase periodic

5.1 Single neuron dynamics

When \( D \neq \bar{D} \), more than two phase-locked oscillatory regimes may exist in the weak \( K_1 \) limit depending on the strength of local inhibition \( K_0 \). In numerical simulations, stable in-phase, anti-phase and out-of-phase oscillations are observed for different ranges of \( K_0 \). Fig. I shows the phase-shift between the two populations for a weak coupling \( K_1 = 0.1, \bar{D} = 0.1 \) and varying \( D \).

Increasing \( K_1 \), a series of bifurcations leads to chaos, according to a scenario depending on \( K_0 \). Out-of-phase oscillatory states undergo a period doubling cascade leading to asymmetric chaotic states. On the other hand, phase-locked states which are symmetric under permutation of the two populations go to chaos according to a quasi-periodic scenario. This is true not only for the anti-phase periodic oscillations analyzed in the paper, but also for the in-phase periodic regimes. Fig. J shows the route to chaos for such an in-phase oscillatory state.

5 Simulations of networks of conductance-based neurons

5.1 Single neuron dynamics

We simulate networks of Wang-Buzsáki (WB) conductance-based neurons [3]. The WB model is described by a single compartment endowed with sodium and potassium currents. The membrane potential
Figure H: Phase diagrams for $D = \bar{D} = 0.3$ (left) and $D = \bar{D} = 0.5$ (right).

Figure I: Weak coupling limit phase-shifts for $D = 0.1$ and various $\bar{D}$. 
Figure J: In-phase quasi-periodic route to chaos \((D = 0.1, \dot{D} = 0.3, K_0 = -40)\). Panels: in-phase periodic \((K_1 = 0.5)\), in-phase quasi-periodic \((K_1 = 6.5)\), in-phase chaotic \((K_1 = 8)\).
is given by:

\[ C \frac{dV}{dt} = -I_L - I_{Na} - I_K + I_{ext} + I_{rec} \]

where \( C \) is the capacitance of the neuron, \( I_L = g_L(V - V_L) \) is the leakage current, \( I_{ext} \) is an external driving current and \( I_{rec} \) is due to recurrent interactions with other neurons in the network (see Section 5.2). Sodium and potassium currents are voltage-dependent and given by:

\[ I_{Na} = g_{Na}m^3h(V - V_{Na}) \] 
\[ I_K = g_Kn^4V - V_K \]

The activation of the sodium current is instantaneous:

\[ m^\infty(V) = \frac{\alpha_m(V)(1 - x)}{\alpha_m(V) + \beta_m(V)} \]

Sodium current inactivation and potassium current activation evolve according to:

\[ \frac{dx}{dt} = \phi(\alpha_x(V)(1 - x) - \beta_x(V)x) \]

where \( x = h, n \) and \( \alpha_x(V) \) and \( \beta_x(V) \) are non-linear functions of the membrane potential given by:

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

Other parameters are \( g_{Na} = 35 \text{ mS/cm}^2 \), \( V_{Na} = 55 \text{ mV} \), \( g_K = 9 \text{ ms/cm}^2 \), \( V_K = -90 \text{ mV} \), \( g_L = 0.1 \text{ mS/cm}^2 \), \( C = 1 \mu\text{F/cm}^2 \) and \( \phi = 5 \).

### 5.2 Two-populations network architecture

The network architecture discussed in the paper is illustrated schematically in Fig. K (left). We consider two populations, \( I_1 \) and \( I_2 \), each one including \( N \) WB neurons. Local inhibitory connections between neurons within a same population are established randomly with homogeneous probability \( p^I \). In
addition, neurons in different populations interact directly via excitatory synapses with homogeneous probability $p^E$.

The synaptic current induced by a single action potential fired by a presynaptic cell in population $I_t$ in a postsynaptic neuron in population $I_k$ ($k,l = 1,2$) is given by $I_{\text{spike}}(t) = -g^{kl}\delta(t) (V - V_\delta)$, where $V$ is the potential in the postsynaptic neuron; the reversal potential $V_\delta$ of the synapse is 0 mV if $k \neq l$ (inter-population excitatory synapses), -80 mV for $k = l$ (intra-population inhibitory synapse).

The time-course of the postsynaptic conductance is described by:

$$s_{\text{spike}}(t) \propto \left( \exp \left(-\frac{t + d - t^*}{\tau_1} \right) - \exp \left(-\frac{t + d - t^*}{\tau_2} \right) \right)$$

for $t > t^*$, 0 otherwise, where $t^*$ is the time of the presynaptic spike, $d$ is the latency, $\tau_1$ the rise-time and $\tau_2$ the decay-time. The total recurrent current $I_{\text{rec}}(t)$ is the sum of time-dependent contributions $I_{\text{spike}}(t)$ from all the presynaptic spikes fired to time $t$. The normalization constant of $s_{\text{spike}}(t)$ is chosen such as the peak value of $s_{\text{spike}}$ is equal to 1.

For simplicity, we take only two possible peak conductances, $g^I$ for inhibitory synapses within a population ($k = l$) and $g^E$ for excitatory synapses between populations ($k \neq l$).

The external input to each neuron is modeled as a Poisson train of excitatory currents having the same functional form as the recurrent currents, a firing rate $\nu_{\text{ext}}$ and a peak conductance $g_{\text{ext}}$.

In the simulations shown in Fig. 4 of the paper (strong local inhibition), we take $\nu_{\text{ext}} = 5$ kHz, $g_{\text{ext}} = 5 \mu$S/cm$^2$. In the simulations shown in Fig. 5 of the paper (weaker local inhibition), we take $\nu_{\text{ext}} = 3$ kHz, $g_{\text{ext}} = 3 \mu$S/cm$^2$. The peak excitatory conductance $g^E$ was taken to be equal to $g_{\text{ext}}$ in both cases. Finally, in all the simulations shown in Figs. 4 and 5 in the paper, $\tau_1 = 1$ ms, $\tau_2 = 3$ ms and $d = 1.5$ ms.

5.3 Four-populations network architecture

A more realistic architecture is shown in Fig. K (right). Each local network $k$ ($k = 1,2$) contains a population $E_k$ of $N$ excitatory WB neurons and a population $I_k$ of $N$ inhibitory WB neurons.

Short range connections within a local network $k$ from population $\beta_k$ to population $\alpha_k$ are established with probability $p^{\alpha\beta}_{kk}$ ($\alpha = E,I, k = 1,2$). The excitatory populations $E_k$ are allowed also to establish connections toward the populations $E_l$ and $I_l$ in the remote local network ($k \neq l, k,l = 1,2$). Such long-range connections are established with a probability $p^{\alpha\beta}_{kl}$ ($\alpha = E,I, k,l = 1,2$).

Synaptic currents have the same functional form as in the recurrent case. The recurrent current due to an action potential fired by a neuron in population $\beta$ in the local network $l$ toward a neuron in population $\alpha$ in the local network $k$ ($\alpha = E,I, k,l = 1,2$) is given by $I_{\text{spike}} = -g^{\alpha\beta}_{ij}\delta(t) (V - V_\beta)$, where $V$ is the potential in the postsynaptic neuron, $V_\beta$ is the reversal potential of the synapse (0 mV for $\beta = E$, -80 mV for $\beta = I$). For simplicity we assume that $g^{\alpha\beta}_{ij} = g^\beta$, depending only on the excitatory or inhibitory character of the presynaptic cell.

We performed simulations choosing $p^{II}_{kk} = p^{EI}_{kk} = p^I$ and $p^{EE}_{kk} = p^{IE}_{kk} = p^{IE}_{kl} = p^{EE}_{kl} = p^E$. Delay in the interactions is $d = 0.7$ ms, rise-time is $\tau_1 = 1$ ms and the decay-time is $\tau_2 = 3$ ms. We take the same peak-conductances as in the two-population architecture case. Under these conditions, the four-population model simulations yield dynamical states equivalent to the two-population model (compare the rasters in Figs. 3 and 4 in the paper and Fig. L).

In normal conditions in vivo, the firing-rate of excitatory neurons is smaller than the firing-rate of interneurons. Our model can easily be modified to account for this firing-rate difference, by introducing different external driving rates $\nu_k$ and $\nu_l$ for excitatory and inhibitory populations. Two example rasters are shown in Fig. M (strong and weak local inhibition regime).

The properties of the rhythm are not qualitatively modified by the introduction of different feed-forward excitatory driving rates, since the oscillation is induced by inhibitory to inhibitory interactions. The excitatory cells fire in synchrony with the rhythm imposed by inhibitory cells (Fig. N). For the
Figure L: Raster plots for the four-populations model. $N = 12000$, synaptic delay set to $d = 0.7$ ms, rise time $\tau_1 = 1$ ms, decay-time $\tau_2 = 3$ ms. Left column: strong local inhibition regime. Parameters: $p^I = 0.6, g^I = 89 \mu S/cm^2; \nu = 5$ kHz, $g_{out} = g^E = 5 \mu S/cm^2$. From bottom to top: asymmetric out-of-phase periodic ($p^E = 0.01$); asymmetrically irregular ($p^E = 0.10$); symmetrically irregular ($p^E = 0.14$). Right column: weaker local inhibition regime. Parameters: $p^I = 0.1, g^I = 19 \mu S/cm^2; \nu = 3$ kHz, $g_{out} = g^E = 3 \mu S/cm^2$. From bottom to top: anti-phase ($p^E = 0.008$); regular doublets ($p^E = 0.035$); irregular doublets ($p^E = 0.06$).
Figure M: Raster plots for the four-populations model (different driving rates for excitatory and inhibitory populations). $N = 12000$, synaptic delay set to $d = 0.5$ ms, rise time $\tau_1 = 1$ ms, decay-time $\tau_2 = 3$ ms. Left: strong local inhibition regime. Parameters: $p^I = 0.6$, $g^I = 89 \mu S/cm^2$; $p^E = 0.02$, $g_{ext} = g^E = 5 \mu S/cm^2$; $\nu_I = 5$ kHz, $\nu_E = 4$ kHz. Right: weaker local inhibition regime. Parameters: $p^I = 0.08$, $g^I = 19 \mu S/cm^2$; $p^E = 0.02$, $g_{ext} = g^E = 4 \mu S/cm^2$; $\nu_I = 4$ kHz, $\nu_E = 2.7$ kHz.

Figure N: Typical traces of individual neurons in the four-population model (different driving rates for excitatory and inhibitory populations). Parameters as in Fig. M (left).
strong local inhibition regime shown in Fig. N (left), the frequency of the collective population rhythm is approximately 65 Hz, the average firing rate of individual inhibitory interneurons is 6.3 Hz, and the average firing rate of excitatory neurons is 0.7 Hz (rates evaluated over multiple simulations of duration $10^4$ ms).

Smaller average firing rates result also in a smaller overall synchronization among excitatory cells than among inhibitory cells. The ratio between the synchronization factor $\chi_E$ for the excitatory populations and $\chi_I$ for the inhibitory populations varies for increasing difference in the driving rate. In the shown simulations, the excitatory synchronization factor is tenfold smaller than $\chi_I$ for a relative difference of approximately 20 percent in the driving excitatory rates.

References