From quasiperiodic partial synchronization to collective chaos in populations of inhibitory neurons with delay

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Collective chaos is shown to emerge, via a period-doubling cascade, from quasiperiodic partial synchronization in a population of identical inhibitory neurons with delayed global coupling. This system is thoroughly investigated by means of an exact model of the macroscopic dynamics, valid in the thermodynamic limit. The collective chaotic state is reproduced numerically with a finite population, and persists in the presence of weak heterogeneities. Finally, the relationship of the model’s dynamics with fast neuronal oscillations is discussed.

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Electrical measurements of brain activity display a broad spectrum of oscillations, reflecting the complex coordination of spike discharges across large neuronal populations [1]. A particularly fruitful theoretical framework for investigating neuronal rhythms is to model networks of neurons as populations of heterogeneous oscillators [2–4]. These models exhibit a prevalent transition from incoherence to partial coherence, when a fraction of the oscillators becomes entrained to a common frequency. As a result a macroscopic oscillatory mode appears with the same frequency as that of the synchronized cluster [2, 5].

Yet, even populations of globally coupled identical oscillators are capable of exhibiting a much wider diversity of complex oscillatory states, see [6] for a recent survey. In general, this is due to the complexity of the coupling functions and of the individual oscillators. A relevant example is the so-called quasiperiodic partial synchronization (QPS), which has been extensively investigated in networks of excitable leaky integrate-and-fire (LIF) neurons [7–11], as well as in populations of limit-cycle oscillators and phase oscillators [12–18]. In QPS, the network sets into a nontrivial dynamical regime in which oscillators display quasiperiodic dynamics while the collective observables periodicity. Remarkably, the period of these oscillations differs from the mean period of the individual oscillators. As pointed out recently [17], this interesting property of QPS is shared by the collective chaos observed in populations of globally coupled limit-cycle oscillators [19–25]. Here, the collective chaotic mode is typically accompanied by microscopic chaotic dynamics at the level of the individual oscillators. However, as noticed in [20], populations of limit-cycle oscillators may also display pure collective chaos without trace of orbital instability at the microscopic level. In this state the coordinates of the oscillators fall on a smooth closed curve and no mixing occurs, what points to the existence of collective chaos in populations of oscillators governed by a single phase-like variable.

In this Letter we uncover the spontaneous emergence of pure collective chaos from QPS, via a cascade of period-doubling bifurcations. Notably, this is found in a simple population of identical integrate-and-fire oscillators with time-delayed pulse coupling, which is thoroughly analyzed within the framework of the so-called Ott-Antonsen theory [26–29]. Moreover, we show that pure collective chaos persists when weak heterogeneities are considered. This suggests that certain forms of irregular collective motion observed in large networks of heterogeneous LIF neurons with delay [30] may be already found for identical neurons.

We investigate a model consisting of a population of \(N \gg 1\) neurons, with membrane potentials \(\{V_j\}_{j=1,...,N}\). The evolution of \(V_j\) is governed by the so-called quadratic integrate-and-fire (QIF) model, which obeys the nonlinear differential equation [31–33]

\[
\tau \dot{V}_j = V_j^2 + I_j, \tag{1}
\]

where \(\tau\) is the neuron’s membrane time constant. When \(V_j\) reaches the value \(V_p\), the QIF neuron emits a spike, and \(V_j\) is reset to \(V_r\). Thereafter we consider \(V_p = -V_r = \infty\) [34]. In this case the model (1) can be exactly transformed to a phase model called theta-neuron [31, 33]. The external inputs \(I_j\) have the form

\[
I_j = \eta_j + J s_D, \tag{2}
\]

where parameters \(\eta_j\) determine the dynamics of each uncoupled neuron, \(J = 0\): Those neurons with \(\eta_j < 0\) are excitable, whereas neurons with \(\eta_j > 0\) behave as self-sustained oscillators with period, or interspike interval \(\text{ISI}_j = \pi\tau/\sqrt{\eta_j}\). In Eq. (2), the delayed mean activity \(s_D \equiv s(t - D)\) is defined summing the spikes of all neurons:

\[
s_D = \frac{\tau}{N\tau_s} \sum_{j=1}^N \sum_k \int_{t-D}^{t-D+D} \delta(t' - t'_k) \, dt', \tag{3}
\]

In this equation, \(t'_k\) is the time of the \(k\)th spike of \(j\)th neuron, and \(\delta(t)\) is the Dirac delta function. We assume the thermodynamic limit \(N \to \infty\), so that a second limit in the temporal window \(\tau_s \to 0\) leads to the relationship \(s_D = \tau r_D\), where \(r_D \equiv r(t-D)\) is the time-delayed firing rate, i.e. the population-averaged number of spikes per unit time. The strength of the interactions is controlled in Eq. (2) by the...
in Eq. (4), without lack of generality \[37\].

Figures 1(b,d) and 2(a,c) display FREs in Fig. 2(b,d,f) is in perfect agreement with the global dynamics in the infinite network, which exactly describe the macroscopic dynamics of the system and its first order kinetics, the firing order of the neurons is preserved (i.e. neuron \( j \) always fires just before neuron \( j + 1 \)) and mixing is not possible.

Where and how QPS and collective chaos emerge is investigated next. To this aim, we follow \[29\] and using the Ott-Antonsen theory (by means of a Lorentzian ansatz) derive the mean-field character of the model and its first order kinetics, the firing order of the neurons is preserved (i.e. neuron \( j \) always fires just before neuron \( j + 1 \)) and mixing is not possible.

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We start performing numerical simulations of an inhibitory (\( J < 0 \)) population of identical neurons with \( \eta_j = \bar{\eta} > 0 \). In panels (a) and (c) of Fig. 1, showing raster plots for two values of \( J \), the system exhibits QPS. In fact, the return plots in panels (b,d) show a closed line indicating quasiperiodic single-neuron dynamics, see \[7\]. Remarkably, for certain values of the time delay \( D \), see Fig. 1(e,f), increasing inhibition leads to a different macroscopic state, where neurons exhibit irregular dynamics whereas the macroscopic dynamics is chaotic, as shown below.

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As parameters are varied, the reflection symmetry of the limit cycle breaks down at a period-doubling bifurcation. Moreover, the inset of Fig. 3 shows that this bifurcation is followed by a period-doubling cascade as parameter \( J \) is varied, giving rise to a state of collective chaos as that of Fig. 2(f). Remarkably, though the collective dynamics is chaotic, the single-neuron evolution is not. Indeed, as a consequence of the mean-field character of the model and its first order kinetics, the firing order of the neurons is preserved (i.e. neuron \( j \) always fires just before neuron \( j + 1 \)) and mixing is not possible.

In the following, we analyze the FREs (4) in detail, what permits to elucidate why collective chaos is found only in a certain range of delays, and only for inhibitory coupling. For identical neurons, \( \Delta = 0 \), the only fixed point is \( (r_s, v_s) = ((J + \sqrt{J^2 + 4\pi^2})/(2\pi^2), 0) \), corresponding to an incoherent state. Its stability can be determined linearizing around the fixed point \( r(t) = r_s + \delta r e^{\lambda t} \) and \( v(t) = \delta v e^{\lambda t} \), and imposing the condition of marginal stability: \( \lambda = i\Omega \). We find a family of Hopf instabilities at

\[
J_H^{(n)} = \pi(\Omega_n^2 - 4) \times \begin{cases} 
(6\Omega_n^2 + 12)^{-1/2} & \text{for odd } n \\
(2\Omega_n^2 - 4)^{-1/2} & \text{for even } n 
\end{cases}
\]
with associated frequencies \( \Omega_n = n\pi/D \). The line with several cusps depicted in Fig. 3 correspond to the boundaries of incoherence given by Eq. (6). The blue and red colors indicate the sub- and super-critical character of the bifurcation, respectively, and have been calculated perturbatively [38]. The stability region of incoherence (shaded) closely resembles that of the Kuramoto model of coupled oscillators, with alternating domains at positive and negative \( J \) values as time delay is increased [39–42]. However, the presence of supercritical Hopf bifurcations in some ranges of the inhibitory part of the diagram is a distinct and important feature of model (1)-(2), as we show below.

We also calculated the stability boundaries of the fully synchronized states, \( V_j(t) = v(t) \), which are given by the family of functions

\[
J_c^{(m)} = 2 \cot \left( \frac{D}{m} \right), \quad \text{with } m = 1, 3, 5, \ldots \quad (7)
\]

and by evenly spaced vertical lines at \( D = n\pi \), with \( n = 1, 2, \ldots \) [44]. Accordingly, the regions of unstable full synchrony correspond to the hatched regions of the phase diagram Fig. 3. Note that for weak coupling, i.e. close to the \( J = 0 \) axis, the phase diagram in Fig. 3 is fully consistent with that of the Kuramoto model with delay [39], as it can be proven applying the averaging approximation to model (1) with \( \Delta = 0 \), see [5, 28]. Specifically, we observe three qualitatively different regions at small \( |J| \): Incoherence (shaded-hatched), one or more fully synchronized states (white-unhatched), and coexistence between incoherence and full synchrony (shaded-unhatched).

Away from the weak coupling regime, the system displays collective phenomena unseen in the Kuramoto model. Inside the unshaded-hatched region, located below the Hopf curve \( J_H^{(1)} \), both incoherence and synchronization are simultaneously unstable. Moreover, due to the supercritical character of the Hopf boundary \( J_H^{(1)} \) in the range \( 2.250 < D < 3.684 \) [45], QPS emerges as a stable, small-amplitude oscillatory solution—as that of Fig. 2(a)—bifurcating from incoherence with period \( T = 2D \).

Additionally, QPS can also emerge via the destabilization of full synchronization at \( J_c^{(1)} \). The simulation of the FREs confirms the prediction of Eq. (7), and allows to complete a somewhat peculiar picture: The fully synchronous state is a degenerate, infinitely long trajectory along the \( \nu \)-axis, and the limit cycle corresponding to QPS emanates from it with an unbounded size—see Fig. 2(d), for a situation not far away from the bifurcation point. In Fig. 4(a), a sketch of the bifurcation diagram (valid for \( J < -2.54 \) and \( D \) around \( \pi \)) is depicted. Stable QPS bifurcates from the fully synchronous state at \( D_c^{(1)} = \arctan(2/J) < \pi \), through a transcritical bifurcation of limit cycles. Then, in a second transcritical bifurcation at \( D = \pi \) (involving unstable QPS), the synchronized state recovers its stability. This scenario implies the existence of a region of bistability between QPS (or collective chaos) and full synchronization for \( D > \pi \)—in consistence, again, with the supercritical character of the Hopf bifurcation \( J_H^{(1)} \) for \( D < 3.684 \).

So far, we have concentrated on identical QIF neurons. Our final results concern the robustness of QPS and collective chaos against heterogeneity. In the presence of heterogeneity full synchronization and QPS cannot be observed, but states reminiscent of them persist, as sketched in Fig. 4(b). Indeed, as the transcritical bifurcation is fragile, the bifurcation originally located at \( D = \pi \) is replaced by a saddle-node bifurcation, whereas the other bifurcation at \( D = D_c^{(1)} \) vanishes.

Regarding collective chaos, Fig. 5(a-c) shows numerical simulations of the heterogeneous QIF neurons (1), with parameter values close to those of Fig. 1(e). We observe in Fig. 5(c) synchronized clusters at different average ISIs. Using the FREs (4) we checked that (i) the macroscopic infinite-
A frequency heterogeneity. However, our conclusion is quite the opposite: dynamics is stable as revealed by the Lyapunov exponents obtained from ciliations in the gamma and fast frequency ranges (30-200 Hz) emphasized. A large body of data demonstrate that brain oscillations. This is in agreement with the frequency of the oscillations displayed by heuristic firing rate models with fixed time delays and inhibitory coupling [49–52]. Exactly the same range of frequencies is also observed in networks of identical, noise-driven inhibitory neurons with synaptic delays, in the so-called sparsely synchronized state [49, 53–55]. Remarkably, sparse synchronization also displays a macroscopic/microscopic dichotomy, similar to that of the QPS and collective-chaos states analyzed here.

The analysis of the thermodynamic limit of the model (1)-(2) by means of the firing-rate equations (4), permits to dissect macroscopic from microscopic dynamics in that limit. This strategy seems to be particularly useful for investigating collective chaos [19–25] as well as irregular activity states in heterogeneous neuronal ensembles [30, 56].

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[35] See Supplementary Material [url] for the exact derivation of the FRES corresponding to Eqs. (1)-(2).
[36] For identical neurons the dynamics of the model is degenerate (and described by the Watanabe-Strogatz theory [57]), but the presence of a tiny amount of noise attracts the dynamics to the Lorentzian manifold, making Eq. (4) with \( \Delta = 0 \) asymptotically correct [58]. Accordingly, the initial conditions for the numerical simulations in Figs. 1 and 2 are taken to represent a Lorentzian density with arbitrary values of the center \( \nu \) with half-width \( \pi \nu \): \( V_j(0) = \nu + \pi \nu \tan[(\pi/2)(2j - N - 1)/(N + 1)] \).
[37] This can always be achieved (for \( \bar{\eta} > 0 \)) under rescaling of time \( \bar{t} = t\sqrt{\bar{\eta}}/\tau \), the variables \( \bar{t} = \tau t/\sqrt{\bar{\eta}}, \bar{v} = v/\sqrt{\bar{\eta}} \) and the parameters \( \bar{J} = J/\sqrt{\bar{\eta}}, \bar{D} = D/\sqrt{\bar{\eta}}/\tau, \bar{\Delta} = \Delta/\bar{\eta} \).
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