

Chaos via Shilnikov's Saddle-Node Bifurcation in a Theory of the Electroencephalogram

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We study the bifurcation diagram of a mesoscopic model of the human cortex. This model is known to exhibit robust chaotic behavior in the space of parameters that model exterior forcing. We show that the bifurcation diagram has an unusual degree of organization. In particular, we show that the chaos is spawned by a codimension-one homoclinic bifurcation that was analyzed by Shilnikov in 1969 but has never before been found in a physical application.

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Introduction.—Modern approaches to understanding brain function have become increasingly concerned with the dynamics of neurons and neuronal populations [1,2]. In an attempt to formally understand these dynamics and their relationship to the brain's ongoing behavior, a range of theoretical approaches have been developed to mathematically model the essential physiological features of such activity [3,4]. Of particular relevance to understanding brain function are those approaches that scale to the whole brain, are associated with some form of noninvasive experimental measurement, and have a time scale commensurate with that of cognition. In this regard, theories of the brain's scalp recordable electrical activity, or electroencephalogram (EEG), which evolves on a millisecond time scale, have been of particular interest. Because a single EEG electrode records the simultaneous activity of many thousands of weakly connected cortical neurons, the modeling of the EEG is particularly amenable to a mean field spatially continuous approach [5–7]. The resulting formulations enable the theoretical investigation of neuronal population dynamics using a range of methods drawn from dynamical systems and bifurcation theory. These models therefore offer the possibility of characterizing and explaining the qualitative changes, or bifurcations, in cortical spatiotemporal dynamics that have been inferred to occur in cognition [3] and in a range of central nervous system disease processes such as epilepsy [8]. Using a local version of a physiologically specific mean field theory of the mammalian EEG [9,10] we explain the emergence of robust, physiologically plausible, chaos through an unusual sequence of bifurcations. The route to chaos that we find was proposed by Shilnikov as early as 1969 [11] but has, to our best knowledge, never been found before in a physical model. We show that it leads to a bifurcation diagram with an unusually high degree of organization in the physiologically admissible part of parameter space. The analysis of the local model points to the existence of invariant dynamical structures in the full partial differential equation model. As a number of generic

and thus easily detectable bifurcations are organized about the Shilnikov saddle-node bifurcation an experimental strategy suggests itself in which the parametric organization of these bifurcations, in, e.g., cortical slice preparations, can be used to experimentally infer whether real mammalian cortex is capable of supporting chaos. This may provide an alternative to the largely unsuccessful attempts [12] to identify chaotic activity directly from noisy and nonstationary time series.

The mesoscopic EEG model.—The cortical activity is locally described by the mean soma membrane potentials of the excitatory neuron population, h_e , and the inhibitory neuron population, h_i , along with the mean synaptic activities I_{ee} , I_{ie} , I_{ei} , I_{ii} , each modeling the interaction between two populations as indicated by the subscripts. The connection with physiological measurement is through h_e , which, on the basis of extensive experimental evidence [7,13], is assumed to be linearly related to the EEG. The dynamical equations are

$$\tau_e \frac{d}{dt} h_e = h_{er} - h_e + \frac{h_{eeq} - h_e}{|h_{eeq} - h_{er}|} I_{ee} + \frac{h_{ieq} - h_e}{|h_{ieq} - h_{er}|} I_{ie}, \quad (1)$$

$$\tau_i \frac{d}{dt} h_i = h_{ir} - h_i + \frac{h_{ieq} - h_i}{|h_{ieq} - h_{ir}|} I_{ei} + \frac{h_{iieq} - h_i}{|h_{iieq} - h_{ir}|} I_{ii}, \quad (2)$$

where h_{er} and h_{ir} are the resting potentials and h_{eeq} and h_{ieq} are the equilibrium potentials. Following [10] we set $h_{er} = h_{ir} = -70$ mV, $h_{eeq} = 45$ mV, and $h_{ieq} = -90$ mV. The relaxation time scales are set to $\tau_e = 9$ ms and $\tau_i = 39$ ms. These two equations describe, respectively, the response of the mean soma membrane potential of excitatory and inhibitory neuronal populations to synaptic current. In the local case considered here these synaptic currents can be traced to a single essential source: local feedforward and feedback excitatory (I_{ee} , I_{ei}) and

inhibitory (I_{ie} , I_{ii}) synaptic activity. The time course of such activity, based on extensive experimental evidence [7], is modeled by a critically damped oscillator driven by the mean rate of incoming excitatory or inhibitory axonal pulses. Thus, for the synaptic activity we have

$$\frac{d^2}{dt^2}I_{ee} + 2a\frac{d}{dt}I_{ee} + a^2I_{ee} = Aae[N_{ee}S_e(h_e) + p_{ee}], \quad (3)$$

$$\frac{d^2}{dt^2}I_{ie} + 2b\frac{d}{dt}I_{ie} + b^2I_{ie} = BbeN_{ie}S_i(h_i), \quad (4)$$

$$\frac{d^2}{dt^2}I_{ei} + 2a\frac{d}{dt}I_{ei} + a^2I_{ei} = Aae[N_{ei}S_e(h_e) + p_{ei}], \quad (5)$$

$$\frac{d^2}{dt^2}I_{ii} + 2b\frac{d}{dt}I_{ii} + b^2I_{ii} = BbeN_{ii}S_i(h_i), \quad (6)$$

where A and B are the postsynaptic potential peak amplitudes and a and b the synaptic rate constants. We set $A = 0.81$ mV, $B = 4.85$ mV, $a = 490$ s⁻¹, and $b = 592$ s⁻¹. Excitatory (inhibitory) neurons receive a total of N_{ee} (N_{ei}) synapses from nearby excitatory neurons and N_{ie} (N_{ii}) synapses from nearby inhibitory neurons, where $N_{ee} = N_{ei} = 3034$ and $N_{ie} = N_{ii} = 536$. The functions S_q convert the mean membrane potential of the neuron populations to an equivalent mean firing rate, and are given by

$$S_q(h_q) = m_q\{1 + \exp[-\sqrt{2}(h_q - \theta_q)/s_q]\}^{-1}, \quad (7)$$

where $q = e, i$. For the firing thresholds we have $\theta_e = \theta_i = -50$ mV, and for the associated standard deviations $s_e = s_i = 5$ mV. The maximal firing rates are fixed to $m_e = m_i = 500$ s⁻¹. Our main bifurcation parameters

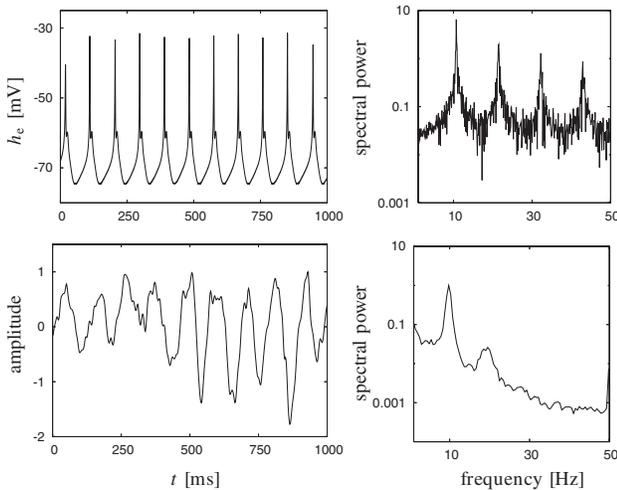


FIG. 1. Top row: Chaotic time series of the mesoscopic EEG model along with its power spectrum. Bottom row: Experimental data from a single occipital electrode measurement of human EEG along with its power spectrum (normalized, arbitrary units). Note the dominant alpha peak around 11 Hz.

are p_{ee} and p_{ei} , the excitatory input from distant excitatory cortical and subcortical neurons.

Parameter values were chosen to be physiologically admissible and to give rise to dynamical activity similar in its spectral features to spontaneous local field potential and EEG recordings. Equations (1)–(6) and their extensions [14] are capable of reproducing the main features of spontaneous human EEG [9]. In particular, autonomous limit cycle and chaotic oscillatory activity in the alpha band (8–13 Hz) can be easily produced. An example of chaotic alpha is illustrated in Fig. 1.

Bifurcation analysis.—If excitatory input to inhibitory neurons (p_{ei}) is much larger than that to excitatory neurons (p_{ee}) a stable equilibrium is the unique limit state of the EEG model (1)–(6). If we increase p_{ee} , this equilibrium loses stability in a Hopf bifurcation and periodic motion sets in with a frequency of about 11 Hz. For larger p_{ee} the fluctuations can become irregular; i.e., the limiting behavior of the model is governed by a chaotic attractor. We can distinguish between the different kinds of limiting behavior by computing the largest Lyapunov exponent (LLE), which is negative, zero, or positive for equilibria, (quasi)-periodic fluctuations, and chaotic fluctuations, respectively. Dafilis *et al.* [10] computed the LLE on a fine grid of parameter values p_{ee} and p_{ei} . They found that a chaotic attractor exists for a set of parameters which is fractal and of positive measure.

Bifurcation analysis indicates that the boundary of the chaotic parameter set is formed by infinitely many saddle-node and period-doubling bifurcations. In Fig. 2 we have superimposed a two-parameter continuation of a number of

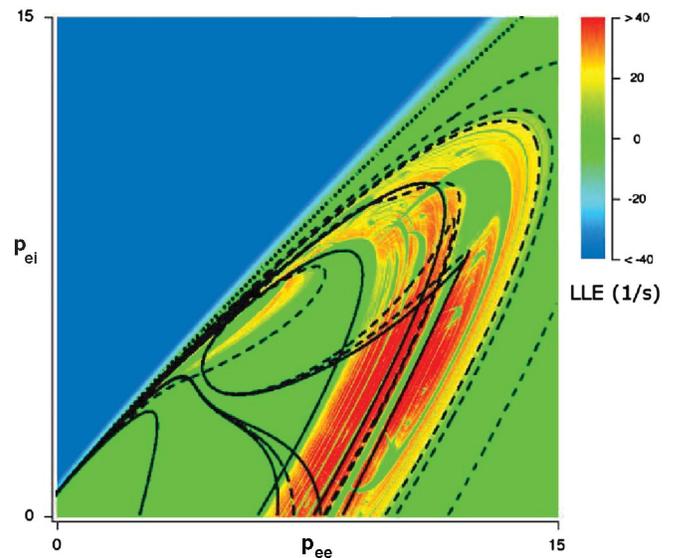


FIG. 2 (color). The largest Lyapunov exponent in color, reproduced from [10], with a superimposed two-parameter continuation of saddle-node and period-doubling bifurcations. The leftmost wedge of chaos terminates for negative values of the exterior forcings, p_{ee} and p_{ei} . Numerical continuations were performed using AUTO97 [20].

these bifurcations on the LLE computations. Indeed, these curves largely form the boundaries between periodic behavior (green) and chaotic behavior (red). A remarkable feature of the bifurcation curves is that they all converge to a narrow wedge with its tip close to the origin. Thus, as will become evident, they literally point to the crucial part of the bifurcation diagram.

Figure 3(a) shows a schematic blowup of the bifurcation diagram at the tip of the wedge. The blue line with the cusp point c separates regions with one and three equilibria. The line of Hopf bifurcations terminates on this line at the Bogdanov-Takens point BT . The green line which emanates from BT denotes a homoclinic bifurcation. On an open interval it coincides with the blue line of saddle-node bifurcations. On this interval it denotes an orbit homoclinic to a saddle node. The point GH is a generalized Hopf point, where the Hopf bifurcation changes from sub- to super-critical. From it emanates a line of saddle-node bifurcations of periodic orbits. The wedge delimited by a solid and a dashed line denotes the tip of the chaotic tongue (yellow-red areas in Fig. 2).

The quintessence of bifurcation analysis is that we can vary an increasing number of parameters to detect singularities of higher codimension, which organize the quali-

tative dynamics in a larger part of parameter space. Such singularities are called *organizing centers*. In the EEG model, we encounter such an organizing center when we vary the time scale τ_i as a third parameter. At $(p_{ee}, p_{ei}, \tau_i) = (-1.81 \text{ ms}^{-1}, -2.21 \text{ ms}^{-1}, 17.4 \text{ ms})$ the codimension-two points c , BT , and GH collapse onto a degenerate Bogdanov-Takens point of codimension three. It is known that the qualitative behavior near this singularity can be of three different possible types, called the saddle, focus, and elliptic case [15]. Following Ref. [16] we computed the normal form and found the singularity to be of the focus type. The qualitative dynamics for this case agrees largely with Fig. 3(a). There is, however, one essential difference, which lies in the interval on which the saddle-node and homoclinic bifurcations coincide. In the normal form, this interval is bounded by the points n_1 and n_2 , at which the homoclinic orbit is noncentral; i.e., it does not lie in the local center manifold. The normal form is two dimensional and allows only for one orbit homoclinic to the saddle-node equilibrium. In contrast, the high-dimensional EEG model allows for several coexisting orbits. In order to see the difference in the bifurcation diagrams, consider the continuation of the homoclinic orbit along the saddle-node curve, starting from n_1 , as shown in Fig. 3(b). Instead of terminating at n_2 , it overshoots this point and folds back at t_1 , where the center-stable and center-unstable manifolds of the saddle node have a tangency. In fact, the curve of homoclinic orbits folds several times before it terminates at n_2 , thereby creating an interval, bounded by t_1 and t_2 , in which up to four homoclinic orbits coexist.

Shilnikov proved that the coexistence of two or more orbits homoclinic to a saddle node leads to the existence of infinitely many periodic orbits, the hallmark of chaos [11]. In contrast to the homoclinic bifurcation of a saddle focus, commonly referred to as the Shilnikov bifurcation, this route to chaos has not been reported before in the analysis of a physical model. In fact, Glendinning posed the identification of a model which produces Shilnikov's saddle-node bifurcation as an open problem in 1988 [17]. Since then two studies have appeared in which models with the desired properties are constructed [18,19]. The configuration we find here is similar to that in Ref. [19], in which the unfolding of a tangency like t_1 is studied. In that paper it is also proved that the bifurcation structure of the infinitely many periodic orbits is the same as that of the fixed points of a perturbation of the Hénon map. Thus, we can expect to find period-doubling cascades, infinitely many coexisting attractors and other complex dynamics.

The route to chaos through Shilnikov's saddle-node bifurcation has codimension one; i.e., it takes place along a line segment in two-parameter space as indicated in Fig. 3(a). This line segment lies at the tip of the chaotic tongue that is visualized in Fig. 2. As can be seen in Fig. 3(b), this segment is rather short, too short in fact to be visible on the scale of Fig. 2, and lies at small, negative values of the forcing parameters p_{ee} and p_{ei} . Yet it organ-

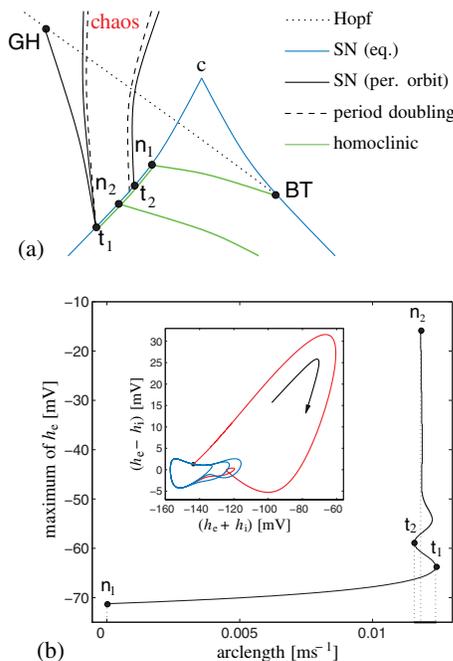


FIG. 3 (color). (a) Schematic bifurcation diagram at the tip of the chaotic wedge. The abbreviations stand for Bogdanov-Takens (BT), generalized Hopf (GH), and saddle node (SN). (b) Continuation of the homoclinic orbit along the saddle-node line, i.e., the blue line in (a). The horizontal axis shows the arc length measured from n_1 . Between t_1 and t_2 multiple homoclinic orbits coexist and Shilnikov's saddle-node bifurcation takes place. The inset shows a projection of four such orbits at n_2 . The blue orbits lie in the center manifold, and the red orbit is noncentral. The arrow shows the direction of the flow.

izes the bifurcation diagram, and thus the qualitative behavior of the EEG model, globally. The outer boundaries of the chaotic tongue are formed by period-doubling and saddle-node bifurcations of infinitely many periodic orbits. These codimension-one bifurcations extend globally into parameter space and form the boundaries between regular and chaotic behavior.

We have performed extensive continuations of the pivotal bifurcations in Fig. 3(a) in the additional parameters of the model. The organization of the bifurcation diagram does not depend critically on these parameters in the larger part of their physiological range, and thus we can conclude that Shilnikov's saddle-node bifurcation organizes the relevant part of parameter space.

Conclusion.—Physiological models often have large numbers of parameters, each with their natural range of variability and uncertainty in measurement. Qualitative behavior can vary wildly from one set of parameters to another. Bifurcation analysis provides a way of unraveling the organization of this complicated parameter space. The study of boundaries (bifurcations) between different types of behavior is a prerequisite both for the understanding of brain function and for the application of control techniques. Control can be aimed at preventing the brain from entering an undesirable, pathological state such as a seizure.

We have shown that the parameter space of a realistic local model of EEG activity is organized by Shilnikov's saddle-node bifurcation, which gives rise to robust chaotic behavior. To our best knowledge this is the first time this route to chaos has been found in any application or physical theory. One may wonder why, when this is a codimension-one phenomenon and should be as generic in models with parameters, as Shilnikov's saddle-focus bifurcation is. One possible answer is that is hard to detect, as a one-parameter bifurcation analysis does not give enough information. A two-parameter analysis shows bifurcation curves of periodic orbits converging to a line of saddle-node equilibria as the period diverges. Alternatively, one can continue orbits homoclinic to a saddle node and look for a tangency like t_1 .

It is interesting that this route to chaos occurs in the vicinity of a degenerate Bogdanov-Takens point. The normal form of the latter is two dimensional and thus does not admit chaotic behavior. Its unfolding, however, includes orbits homoclinic to saddle nodes. How the bifurcation diagram changes qualitatively as we move away from the codimension three point in parameter space is the subject of future research.

In order to study spatiotemporal cortical dynamics we need to analyze the global EEG model [9]. The spatially homogeneous modes of that model again display the bifurcations of Fig. 3 for physiologically interesting parameter sets, implicating the route to chaos described in this Letter to the time and space resolved model EEG.

Empirical EEG evidence will depend upon experimental attempts to identify the cusp and Hopf bifurcations. The results of our analysis suggest the need to look outside normal physiological ranges, as parameter space searches to date reveal most examples of plausible EEG dynamics are associated with only one equilibrium point [14]. The challenge for experimentalists will be to systematically manipulate p_{ee} and p_{ei} to assume both positive and negative (unphysiological) values. In cortical slices this might be achieved using M -type current (a slowly activating persistent inward ionic membrane current) antagonists (e.g., carbachol) and agonists (e.g., retigabine).

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