Nonlinear Dyn (2017) 88:1493–1500
DOI 10.1007/s11071-016-3325-9

ORIGINAL PAPER

Can Lyapunov exponent predict critical transitions in biological systems?

Fahimeh Nazarimehr · Sajad Jafari · Seyed Mohammad Reza Hashemi Golpayegani · J. C. Sprott

Received: 15 July 2016 / Accepted: 27 December 2016 / Published online: 7 January 2017

Abstract Transitions from one dynamical regime to another one are observed in many complex systems, especially biological ones. It is possible that even a slight perturbation can cause such a transition. It is clear that this can happen to an object when it is close to a tipping point. There is a lot of interest in finding ways to recognize that a tipping point (in which a bifurcation occurs) is near. There is a possibility that in complex systems, a phenomenon known as "critical slowing down" may be used to detect the vicinity of a tipping point. In this paper, we propose Lyapunov exponents as an indicator of "critical slowing down."

Keywords Critical transition · Early-warning signal · Lyapunov exponent · Chaos

1 Introduction

Transitions from one dynamical regime to another one are observed in complex systems such as dynamical disease, brain response to flickering light, climate, and financial markets [1–3]. Such "regime shifts" can be the result of a massive external shock, or a stepwise change in the conditions. However, it is also possible that a slight perturbation can invoke a massive shift to a contrasting and lasting state. It is clear that this can happen to an object when it is close to a tipping point. As tipping points can have large consequences and make major changes to the system's behavior, there is much interest in finding ways to recognize that a bifurcation is near. There is a possibility that in complex systems, a phenomenon known as "critical slowing down" can be used to detect the vicinity of a tipping point [1–4]. Close to the tipping point, the return to equilibrium from small perturbations will become slower because the basin of attraction becomes shallower. Recent studies suggest that critical slowing down typically causes an increase in the variance and temporal autocorrelation of fluctuations in the system states [4]. Figure 1 shows the variation of variance and autocorrelation at lag-1.

Chaos is a common feature in complex dynamical systems. Many systems from fields such as biology and economics exhibit chaos, and the study of such systems and their signals has progressed in recent decades. There has been an increasing interest in analyzing neurophysiology from a nonlinear and chaotic systems viewpoint in recent years [6–16]. It has been claimed that many biological systems, including the brain (both in microscopic and macroscopic aspects) [17–23] and the heart [24,25], have chaotic properties. This is true as well for the atmosphere [26], voice sig-

F. Nazarimehr · S. Jafari (✉) ·
S. M. R. Hashemi Golpayegani
Biomedical Engineering Department, Amirkabir University of Technology, Tehran 15875-4413, Iran
e-mail: sajadjafari@aut.ac.ir

J. C. Sprott
Department of Physics, University of Wisconsin - Madison, Madison, WI 53706, USA

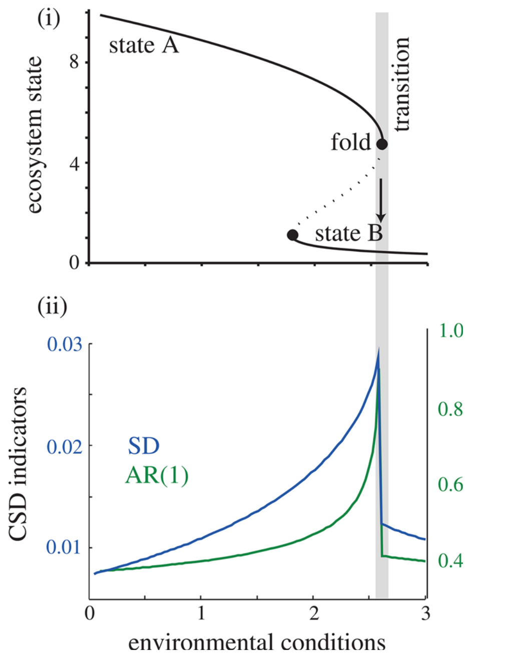


Fig. 1 **i** Bifurcation diagram in a bistable system. **ii** SD (*blue plot*) and autocorrelation at lag-1 (*green plot*) [5]. (Color figure online)

nals [27], and electronic circuits [28,29]. For a dynamical system, sensitivity to initial conditions is quantified by Lyapunov exponents. Lyapunov exponents show the intrinsic instability of trajectories in a system and are computed as the average rate of exponential convergence or divergence of trajectories that are nearby in the phase space. In two trajectories with nearby initial conditions on an attracting manifold, when the attractor is chaotic, the trajectories diverge, on average, at an exponential rate characterized by the largest Lyapunov exponent. A discrete-time system with all negative Lyapunov exponents will have an attracting fixed point or periodic cycle and will not present chaotic behavior [30–33]. Lyapunov exponents can determine the flexibility of attractors in response to external perturbations. In other words, calculation of Lyapunov exponents locally along the attractor shows where a system ignores an external signal and where it responds to it [34–39]. For illustrating the mathematical definition of Lyapunov exponent, consider two points in a space, X_0 and $X_0 + \Delta X_0$. It is useful to study the mean exponential rate of divergence of two initially close orbits using the formula,

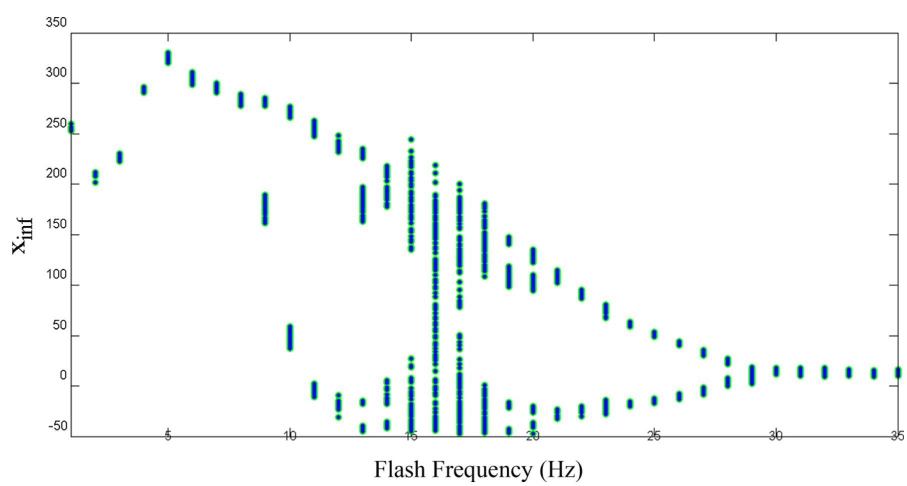
$$\lambda = \lim_{\substack{t\to\infty \\ |\Delta X_0 \to 0|}} \frac{1}{t} \ln \frac{|\Delta X(X_0, t)|}{|\Delta X_0|} \tag{1}$$

This number is the Lyapunov exponent "λ" and is used for distinguishing between the various types of orbits [40]. To illustrate the properties of nonlinear dynamical systems, the Lyapunov exponent has a crucial role [32]. Many approaches have been proposed to compute this measure based on system equations and time series [33, 40–42]. In this paper, we suggest the largest Lyapunov exponent as an indicator of tipping points. We show how sensitivity to initial conditions and recovery rate from small perturbations are connected.

2 Lyapunov exponent as a prominent early-warning signal

In this paper, Lyapunov exponent is proposed as a prominent early-warning signal for predicting critical

Fig. 2 Bifurcation diagram of the salamander ERG by changing flash frequency at contrast $c = 1$ [49]



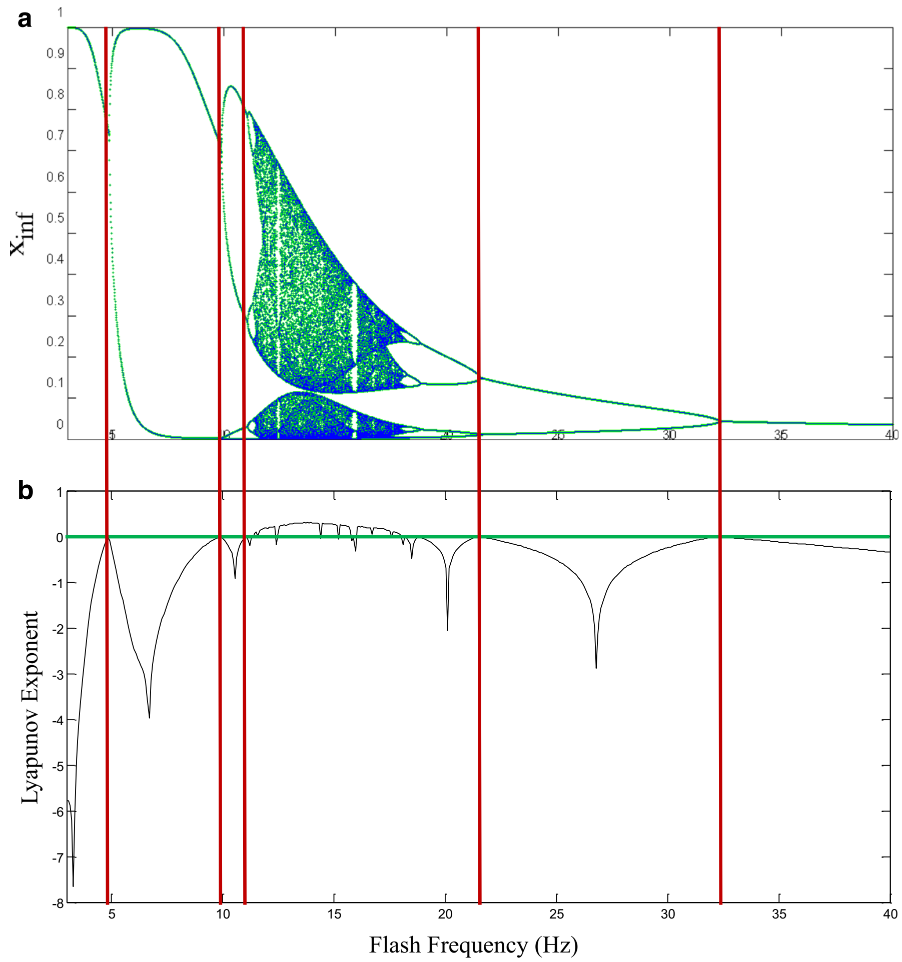


Fig. 3 **a** Bifurcation diagram and **b** Lyapunov exponent as a prominent early-warning signal for predicting critical transitions in brain response to flickering light ($\tau = .058$, $B = 35$, $C = 1$)

transitions. However, there are some major challenges that make this indicator hard to use. Computing Lyapunov exponents based on observed signals is difficult. It requires a long time series that is as clean as possible (noise is a serious problem for calculating Lyapunov exponents) [25,43,44]. The first step in calculating Lyapunov exponent is reconstruction of phase space from a time series. Then, Lyapunov exponents can be calculated using this reconstructed phase space [45–48]. In the rest of this section, the idea of anticipating tipping points is illustrated by two biological models and one ecological model.

2.1 Brain response to flickering light

The first example is the model of brain response to flickering light described in [49]. Periodic flashes of light can be used to investigate dynamical properties of the visual system. Crevier and Meister in 1998 proposed a simple iterative model that can show the same bifurcation as was observed in flicker vision of a salamander [49]. Figure 2 shows a bifurcation diagram of the salamander ERG with respect to changing flash frequency.

This model, proposed in [49], is given by

$$y_{k+1} = e^{-\frac{1}{f\tau}} \left(\frac{BC}{1 + y_k^4} + y_k \right)$$
$$x_{k+1} = \frac{C}{1 + y_{k+1}^4} \tag{2}$$

where f is the flash frequency, τ is the time constant of exponential decay, B is an amplification constant, C is the stimulus contrast, y is the feedback variable, and x is the amplitude of response to a flash. The model uses nonlinear feedback to account for period doubling in

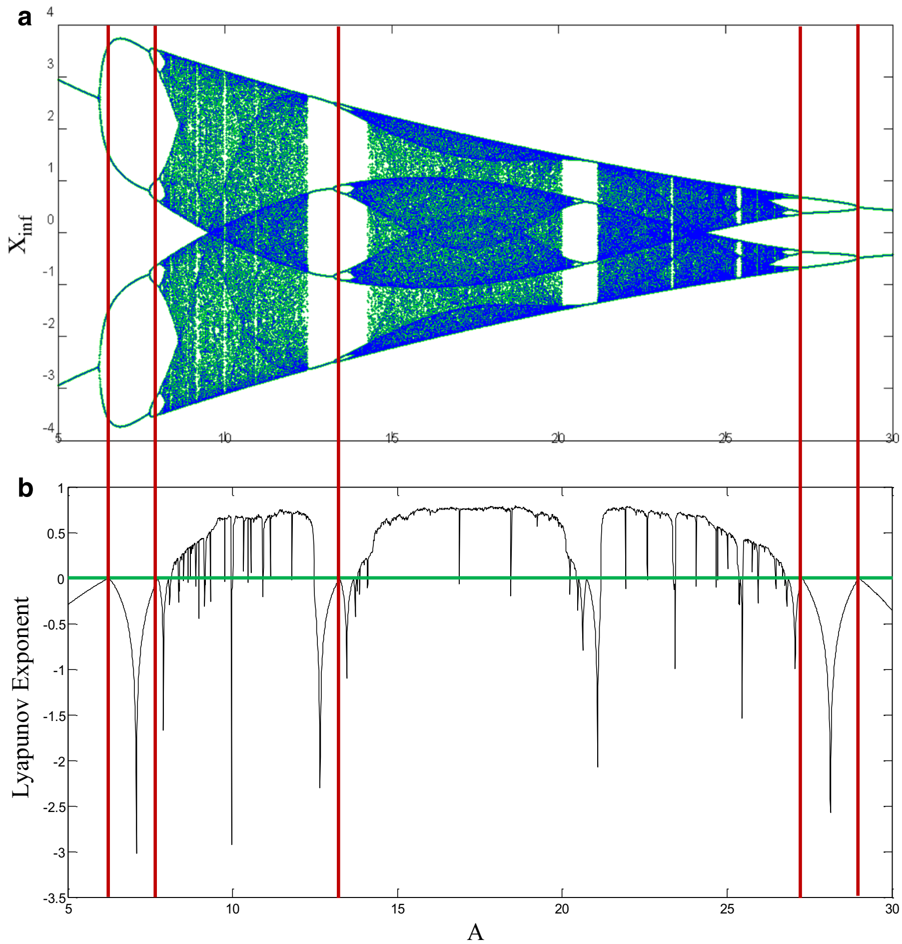


Fig. 4 **a** Bifurcation diagram and **b** Lyapunov exponent as a predictor of tipping points in ADD attention model with respect to changing A parameter ($B = 5.821$, $w_1 = 1.487$, $w_2 = 0.2223$)

the ERG response to periodic flashes. For more detail about the model, see [49]. Figure 3 shows when the Lyapunov exponent reaches zero, there is a critical transition. Red lines identify some tipping points and their Lyapunov exponents. Thus, we propose the Lyapunov exponent as a prominent early-warning signal for predicting critical transitions.

2.2 Attention deficit disorder

The second example is an attention deficit disorder (ADD) model proposed in [50]. Dopamine deficiency is one of the causes of this disorder. The model uses a simple nonlinear neuronal network which represents the interactions of inhibitory and excitatory parts of brain action and is given by

$$x_{k+1} = B \times \tanh(w_1 x_k) - A \times \tanh(w_2 x_k) \quad (3)$$

The Lyapunov exponent of this model demonstrates that this measure can be a good predictor for tipping points (Fig. 4).

2.3 Consumption of resources

The third example is a continuous model of logistic growth and consumption of resources with a control variable grazing rate which is familiar from investigation of critical slowing down dynamics [5,51,52]. In this model, resource biomass x grows logistically and is harvested according to

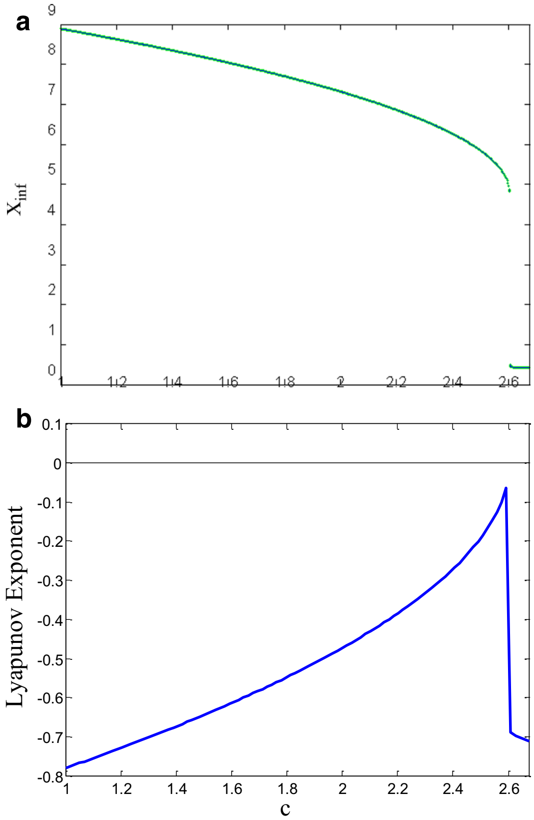


Fig. 5 **a** Bifurcation diagram of ecological model of growing resource under harvesting. **b** Lyapunov exponent of the model

$$\mathrm{d}x = \left(rx \left(1 - \frac{x}{k} \right) - \frac{cx^2}{x^2 + h^2} \right) \mathrm{d}t \tag{4}$$

where r is the growth rate, K is the population's carrying capacity, h is the half-saturation constant, and c is the grazing rate. When c reaches the value $c = 2.904$, the ecosystem goes to an alternate state (critical transition) through a fold bifurcation. Part a of Fig. 5 depicts a bifurcation diagram of the model. Application of Lyapunov exponent as an early warning of critical transitions in the continuous model of growing resource under harvesting is investigated in part b of Fig. 5. The Lyapunov exponent goes close to zero as the bifurcation approaches the tipping point.

In dynamical systems, sensitivity to initial conditions is an important feature that shows complexity of a system. Lyapunov exponents measure sensitivity to initial conditions. If a small perturbation is assumed as a change in initial conditions of a system, Lyapunov exponents determine the rate of divergence or convergence. The results show that the Lyapunov exponent is a prominent predictor of critical transitions.

3 Discussion

In order to show the ability of Lyapunov exponent in predicting tipping points, we compare it with the entropy method. Entropy is a measure of unpredictability [53]. In changing from one fixed point to another one, irregularity of the state of the system increases because of critical slowing down. Thus, the entropy measure shows a meaningful change. However, in many other bifurcation points like changing from period two to period four, the entropy does not show any monotonic change before the tipping point. Figure 6 shows the entropy of ADD model. Comparison of Figs. 4 and 6 describes that the entropy measure only finds transitions from one fixed point to another one, but the Lyapunov exponent depicts any transitions. On the other hand, Lyapunov exponent approaches zero before the parameter reaches the critical values. This property makes Lyapunov exponent a very good indicator of tipping points.

It is believed that Kolmogorov–Sinai entropy is the sum of the positive exponents Lyapunov exponents, which for a low-dimensional chaotic system is just the largest LE since the others are zero or negative [44,54]. This measure can be considered in future works.

4 Conclusion

In this paper, we proposed Lyapunov exponents as prominent early-warning signals for predicting critical transitions. However, computing Lyapunov exponents based on observed signal needs long enough time series, which should be as clean as possible.

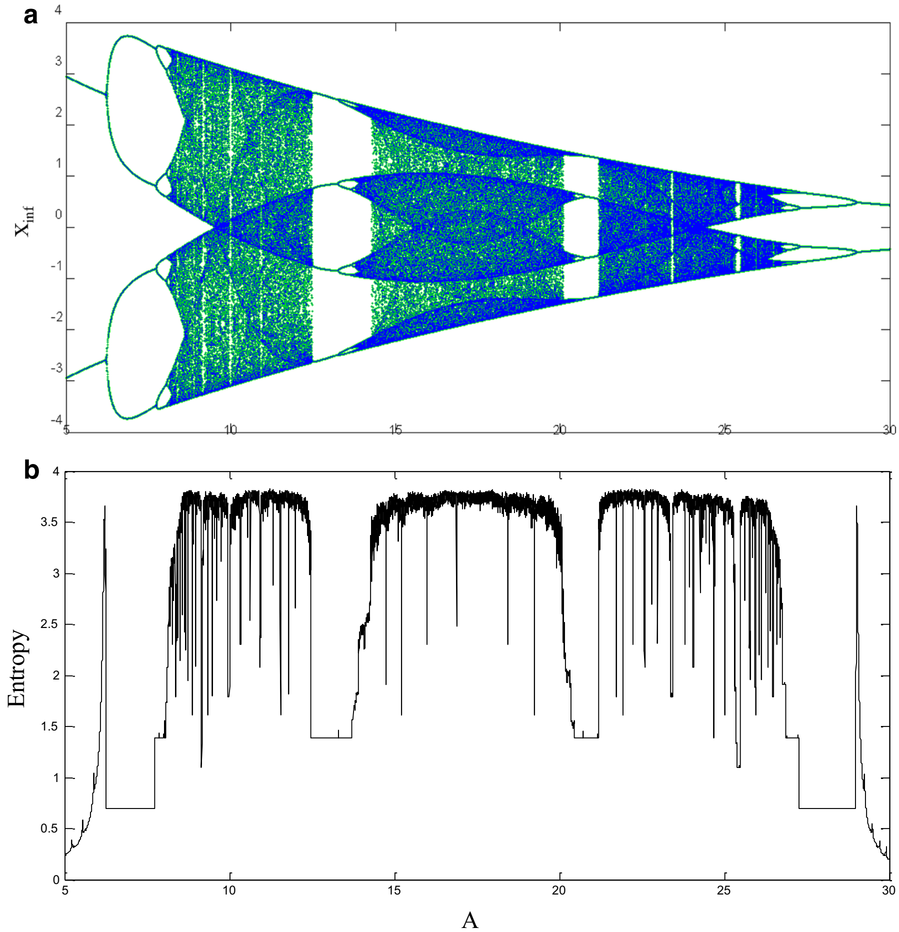


Fig. 6 **a** Bifurcation diagram and **b** entropy measure in ADD attention model with respect to changing A parameter ($B = 5.821$, $w_1 = 1.487$, $w_2 = 0.2223$)

Application of Lyapunov exponent for anticipating tipping points is illustrated by two biological models and one ecological model. The results show that Lyapunov exponents can be good predictors in different critical transitions.

Acknowledgements The authors would like to thank Dr. Leslie Samuel Smith for the help and edits.

References

1. Veraart, A.J., Faassen, E.J., Dakos, V., van Nes, E.H., Lürling, M., Scheffer, M.: Recovery rates reflect distance to a tipping point in a living system. Nature **481**, 357–359 (2012)
2. van de Leemput, I.A., Wichers, M., Cramer, A.O., Borsboom, D., Tuerlinckx, F., Kuppens, P., et al.: Critical slowing down as early warning for the onset and termination of depression. Proc. Natl. Acad. Sci. **111**, 87–92 (2014)
3. Dakos, V., Bascompte, J.: Critical slowing down as early warning for the onset of collapse in mutualistic communities. Proc. Natl. Acad. Sci. **111**, 17546–17551 (2014)
4. Scheffer, M., Carpenter, S.R., Lenton, T.M., Bascompte, J., Brock, W., Dakos, V., et al.: Anticipating critical transitions. Science **338**, 344–348 (2012)
5. Dakos, V., Carpenter, S.R., van Nes, E.H., Scheffer, M.: Resilience indicators: prospects and limitations for early warnings of regime shifts. Philos. Trans. R. Soc. B: Biol. Sci. **370**, 20130263 (2015)
6. Christini, D.J., Collins, J.J.: Controlling nonchaotic neuronal noise using chaos control techniques. Phys. Rev. Lett. **75**, 2782 (1995)
7. Sarbadhikari, S., Chakrabarty, K.: Chaos in the brain: a short review alluding to epilepsy, depression, exercise and lateralization. Med. Eng. Phys. **23**, 447–457 (2001)
8. Hadaeghi, F., Hashemi Golpayegani, M.R., Moradi, K.: Does “crisis-induced intermittency” explain bipolar disorder dynamics? Front. Comput. Neurosci. **7**, 116 (2013)
9. Jafari, S., Baghdadi, G., Golpayegani, S., Towhidkhah, F., Gharibzadeh, S.: Is attention deficit hyperactivity disorder a kind of intermittent chaos? J. Neuropsychiatry Clin. Neurosci. **25**, E2 (2013)
10. Mattei, T.A.: Nonlinear (chaotic) dynamics and fractal analysis: new applications to the study of the microvascularity of gliomas. World Neurosurg. **79**, 4–7 (2013)

11. Elbert, T., Ray, W.J., Kowalik, Z.J., Skinner, J.E., Graf, K.E., Birbaumer, N.: Chaos and physiology: deterministic chaos in excitable cell assemblies. Physiol. Rev. **74**, 1–47 (1994)
12. Jafari, S., Ansari, Z., Hashemi Golpayegani, S.M.R., Gharibzadeh, S.: Is attention a " period window" in the chaotic brain? J. Neuropsychiatry Clin. Neurosci. **25**, E05 (2013)
13. Jafari, S., Baghdadi, G., Hashemi Golpayegani, S.M.R., Towhidkhah, F., Gharibzadeh, S.: Is attention deficit hyperactivity disorder a kind of intermittent chaos? J. Neuropsychiatry Clin. Neurosci. **25**, E2 (2013)
14. Jafari, S., Hashemi Golpayegani, S.M.R., Gharibzadeh, S.: Is there any geometrical information in the nervous system?. Front. Comput. Neurosci. **7** (2013)
15. Molaie, M., Falahian, R., Gharibzadeh, S., Jafari, S., Sprott, J.C.: Artificial neural networks: powerful tools for modeling chaotic behavior in the nervous system. Front. Comput. Neurosci. **8** (2014)
16. Falahian, R., Mehdizadeh Dastjerdi, M., Molaie, M., Jafari, S., Gharibzadeh, S.: Artificial neural network-based modeling of brain response to flicker light. Nonlinear Dyn. **81**, 1951–1967 (2015)
17. Kowalik, Z.J., Elbert, T.: Changes of chaoticness in spontaneous EEG/MEG. Integr. Physiol. Behav. Sci. **29**, 270–282 (1994)
18. Kowalik, Z.J., Wróbel, A., Rydz, A.: Why does the human brain need to be a nonlinear system? Behav. Brain Sci. **19**, 302–303 (1996)
19. Mühlnickel, W., Rendtorff, N., Kowalik, Z.J., Rockstroh, B., Miltner, W., Elbert, T.: Testing the determinism of EEG and MEG. Integr. Physiol. Behav. Sci. **29**, 262–269 (1994)
20. Rabinovich, M.I., Varona, P., Selverston, A.I., Abarbanel, H.D.: Dynamical principles in neuroscience. Rev. Mod. Phys. **78**, 1213 (2006)
21. Korn, H., Faure, P.: Is there chaos in the brain? II. Experimental evidence and related models. C. R. Biol. **326**, 787–840 (2003)
22. Gong, Y., Ren, W., Shi, X., Xu, J., Hu, S.: Recovering strange attractors from noisy interspike intervals of neuronal firings. Phys. Lett. A **258**, 253–262 (1999)
23. Elbert, T., Rockstroh, B., Kowalik, Z.J., Hoke, M., Molnar, M., Skinner, J.E., et al.: Chaotic brain activity. Electroencephalogr. Clin. Neurophysiol./Suppl. **44**, 441–449 (1995)
24. Signorini, M.G., Marchetti, F., Cirigioni, A., Cerutti, S.: Nonlinear noise reduction for the analysis of heart rate variability signals in normal and heart transplanted subjects. In: Engineering in Medicine and Biology Society, 1997. Proceedings of the 19th Annual International Conference of the IEEE, pp. 1402–1405 (1997)
25. Kantz, H., Schreiber, T.: Nonlinear Time Series Analysis, vol. 7. Cambridge University Press, Cambridge (2004)
26. Patil, D., Hunt, B.R., Kalnay, E., Yorke, J.A., Ott, E.: Local low dimensionality of atmospheric dynamics. Phys. Rev. Lett. **86**, 5878 (2001)
27. Herzel, H., Holzfuss, J., Kowalik, Z., Pompe, B., Reuter, R.: Detecting bifurcations in voice signals. In: Kantz, H., Kurths, J., Meyer-Kress, G. (eds.) Nonlinear Analysis of Physiological Data. pp. 325–344. Springer, Berlin (1998)
28. d'Humieres, D., Beasley, M., Huberman, B., Libchaber, A.: Chaotic states and routes to chaos in the forced pendulum. Phys. Rev. A **26**, 3483 (1982)
29. Cumming, A., Linsay, P.S.: Quasiperiodicity and chaos in a system with three competing frequencies. Phys. Rev. Lett. **60**, 2719 (1988)
30. Meador, C.-E.E.: Numerical calculation of Lyapunov exponents for three-dimensional systems of ordinary differential equations. Master's thesis. Marshall University (2011)
31. Medio, A., Lines, M.: Nonlinear Dynamics: A Primer. Cambridge University Press, Cambridge (2001)
32. Kowalik, Z., Schnitzler, A., Freund, H.-J., Witte, O.: Local Lyapunov exponents detect epileptic zones in spike-less interictal MEG recordings. Clin. Neurophysiol. **112**, 60–67 (2001)
33. Wolf, A., Swift, J.B., Swinney, H.L., Vastano, J.A.: Determining Lyapunov exponents from a time series. Phys. D: Nonlinear Phenom. **16**, 285–317 (1985)
34. Marhl, M., Perc, M.: Determining the flexibility of regular and chaotic attractors. Chaos Solitons Fractals **28**, 822–833 (2006)
35. Perc, M., Marhl, M.: Sensitivity and flexibility of regular and chaotic calcium oscillations. Biophys. Chem. **104**, 509–522 (2003)
36. Perc, M., Marhl, M.: Local dissipation and coupling properties of cellular oscillators: a case study on calcium oscillations. Bioelectrochemistry **62**, 1–10 (2004)
37. Perc, M., Marhl, M.: Synchronization of regular and chaotic oscillations: the role of local divergence and the slow passage effect–A case study on calcium oscillations. Int. J. Bifurc. Chaos **14**, 2735–2751 (2004)
38. Gosak, M., Stožer, A., Markovič, R., Dolenšek, J., Marhl, M., Rupnik, M.S., et al.: The relationship between node degree and dissipation rate in networks of diffusively coupled oscillators and its significance for pancreatic beta cells. Chaos: Interdiscip. J. Nonlinear Sci. **25**, 073115 (2015)
39. Perc, M., Marhl, M.: Detecting and controlling unstable periodic orbits that are not part of a chaotic attractor. Phys. Rev. E **70**, 016204 (2004)
40. Rosenstein, M.T., Collins, J.J., De Luca, C.J.: A practical method for calculating largest Lyapunov exponents from small data sets. Phys. D: Nonlinear Phenom. **65**, 117–134 (1993)
41. Elert, G.: The chaos hypertextbook. http://hypertextbook.com/chaos (1999)
42. Fernández Rodríguez, F., Sosvilla Rivero, S., Andrada Félix, J.: A new test for chaotic dynamics using Lyapunov exponents. FEDEA working paper no. 2003–09. https://ssrn.com/abstract=390380 (2003)
43. Abarbanel, H.D.: Introduction. In: Analysis of Observed Chaotic Data, pp. 1–12. Springer (1996)
44. Sprott, J.C.: *Chaos and Time-Series Analysis*, Oxford University Press, Oxford (2003)
45. Kodba, S., Perc, M., Marhl, M.: Detecting chaos from a time series. Eur. J. Phys. **26**, 205 (2004)
46. Perc, M.: Visualizing the attraction of strange attractors. Eur. J. Phys. **26**, 579 (2005)
47. Perc, M.: Introducing nonlinear time series analysis in undergraduate courses. FIZIKA A-ZAGREB- **15**, 91 (2006)
48. Perc, M.: The dynamics of human gait. Eur. J. Phys. **26**, 525 (2005)
49. Crevier, D.W., Meister, M.: Synchronous period-doubling in flicker vision of salamander and man. J. Neurophysiol. **79**, 1869–1878 (1998)

50. Baghdadi, G., Jafari, S., Sprott, J.C., Towhidkhah, F., Hashemi Golpayegani, S.M.R.: A chaotic model of sustaining attention problem in attention deficit disorder. Commun. Nonlinear Sci. Numer. Simul. **20**, 174–185 (2015)
51. Noy-Meir, I.: Stability in simple grazing models: effects of explicit functions. J. Theor. Biol. **71**, 347–380 (1978)
52. Dakos, V., Carpenter, S.R., Brock, W.A., Ellison, A.M., Guttal, V., Ives, A.R., et al.: Methods for detecting early warnings of critical transitions in time series illustrated using simulated ecological data. PloS ONE **7**, e41010 (2012)
53. Cover, T.M., Thomas, J.A.: Elements of Information Theory. Wiley, New York (2012)
54. Hilborn, R.C.: Chaos and Nonlinear Dynamics: An introduction for Scientists and Engineers. Oxford University Press on Demand, Oxford (2000)