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Network attractors and nonlinear dynamics of neural computation

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Abstract
The importance of understanding the nonlinear dynamics of neural systems, and the relation to cognitive systems more generally, has been recognised for a long time. Approaches that analyse neural systems in terms of attractors of autonomous networks can be successful in explaining system behaviours in the input-free case. Nonetheless, a computational system usually needs inputs from its environment to effectively solve problems, and this necessitates a non-autonomous framework where typically the effects of a changing environment can be studied. In this review, we highlight a variety of network attractors that can exist in autonomous systems and can be used to aid interpretation of the dynamics in the presence of inputs. Such network attractors (that consist of heteroclinic or excitable connections between invariant sets) lend themselves to modelling discrete-state computations with continuous inputs, and can sometimes be thought of as a hybrid model between classical discrete computation and continuous-time dynamical systems. Bibliographic info here.

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Nonlinear dynamics of computation

Neurobiological systems with cognitive features, in particular those that can successfully perform computational tasks, can often be usefully viewed through the lens of nonlinear dynamical systems. For example [28,24,29,2], consider a range of systems that are modelled by nonlinear dynamical systems. In fact, the so-called 'Dynamical Hypothesis' [58] proposes that the best way to analyse and understand cognitive systems is in dynamical systems terms. Beer and colleagues [11,16] have produced a large body of work developing and analysing cognitive models consisting of CTRNNs (continuous time recurrent neural networks) using dynamical systems techniques. There are also many results on universal approximation of dynamical systems by neural networks [26,59].

A key concept from nonlinear dynamics is that the set of actually observed states (the attractor) is typically a subset of the set of possible states (the phase space). While the latter is high dimensional and typically simple in geometry (e.g., if there are two variables of interest, the phase space is simply an infinite plane, and if there are more variables, the phase space is simply a higher dimensional analogue of a plane), the former can be low dimensional yet quite complex in geometry (e.g., in the case of chaotic attractors).

The tools of nonlinear dynamics have been used for many years to model a wide range of tasks in neural computation. This includes the pioneering works of Hopfield for storing patterns [30] and using simple neural networks to solve complex optimisation problems such as the travelling salesman problem [31]. More recent work includes modelling associative memory [55,13,33], pattern recognition [53,43], and storage and recall with partial and degraded cues [55]. Even quite simple neural systems with no input can exhibit a wide range of attracting nonlinear dynamics and bifurcation behaviour — see for example [12,34,50].

Generalising these ideas to understand the 'dynome' [38] of larger-scale neural systems is a challenge, not only because of the high dimensionality of realistic neural models but also because of the issues of input-dependence of the system state. In this review, we highlight some attempts to develop dynamical systems paradigms that are able to explain the response of a system to a changing but unknown input from the environment. These use the idea of a 'network' in phase space that allows one to model both the (discrete) states of the system and the allowable transitions between them.

A notion that has been explored in recent years is that of *heteroclinic network attractors* [60], also called 'winnerless competition' dynamics [52,47]. In contrast to 'winner takes all' dynamics [49], the attractor is high dimensional but highly structured and resembles a persistent transient: trajectories spend long periods of time in the vicinity of one equilibrium before making a rapid transition to a different equilibrium in a different part of phase space. This alternation of fast switches between long transients continues *ad infinitium* and does not depend on there being a global slow/fast decomposition of the dynamics – it is an emergent effect. Closely related structures are attractors with chaotic itinerancy [57], which consist of chaotic saddles with connections between them. As the Kupka–Smale Theorem implies that heteroclinic loops are, in some sense, exceptional, such networks need to rely on special structures (such as the governing equations being of Lotka–Volterra form) or symmetries for their robustness.

A more recent and closely related development that we highlight in this review is the idea of network attractors of *excitable connections* [4]. Networks of excitable connections provide a useful paradigm for discussing input-driven computations while avoiding the problems with robustness that heteroclinic networks present. In these models, the presence of noise or inputs above a given threshold can give rise to a transition between states. The noise can be interpreted as a combination of intrinsic noise within the system and the effect of other parts of the neural system that are not modelled in detail.

Excitable and heteroclinic network attractors

A *network attractor* of an input-free dynamical system consists of an attracting set X that can be decomposed into a number of invariant sets A_i and orbits (or trajectories) that connect these sets. These connections may or may not involve a threshold, or minimum perturbation which is required for trajectories to traverse the connection [4]; Figure 1 illustrates two forms of network attractor.[1]

A *heteroclinic network* consists of connecting orbits between invariant sets—for those connecting orbits the threshold is zero—with the consequence that the A_i are saddles rather than attractors (though note that for some Milnor chaotic attractors with riddled basins can have connections from them—see for example [35]). The existence and dynamics of heteroclinic networks in coupled cell systems are discussed for example in Refs. [8,23,60,14]; in particular a heteroclinic network between equilibria may or may not attract a neighbourhood of initial conditions, depending on the relative size of the contraction and expansion of the dynamics. Conditions for stability can become very complicated even for quite small networks; see for example [44,52,15,27,45].

As already mentioned, existence criteria for robust heteroclinic networks [39,60] will typically only be approximately present in realistic models. *Excitable networks*—those for which the thresholds for connections are non-zero—are less restrictive, but inputs are required to get any non-trivial dynamics beyond an initial transient. If we go beyond the realm of deterministic models to include stochastic inputs, *noisy network attractors* originating from heteroclinic or excitable networks cannot be easily distinguished from each other [5] and it becomes a modelling decision as to which type of network attractor to use. The presence of noise may lead to interesting behaviours such as memory of previous visits, even in the low noise limit [3,10]. It is these noisy network attractors that we argue are a plausible model for neural computations.

Winnerless competition and neural dynamics

Network attractors can be found in a variety of coupled cell systems inspired by neuroscience. Heteroclinic dynamics occur frequently in systems with oscillatory dynamics [9] or in the form of winnerless competition (WLC) dynamics for systems of Lotka–Volterra type [50,1,48]. Such network dynamics are interesting in that they can generate input-dependent sequences or even (via amplification of small-scale stochasticity) random sequence generation. The underlying attractor for WLC networks is a sequence of metastable states with heteroclinic orbits joining them. The reason for the success of WLC dynamics in capturing reproducibility under small noise conditions is precisely due to this structure: trajectories stay near the underlying heteroclinic network for an arbitrarily large time.

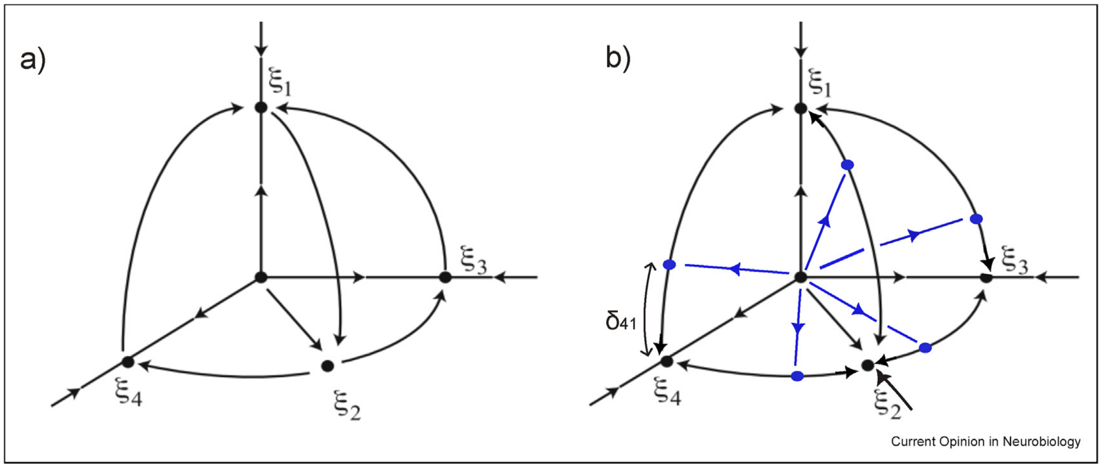
These and related models have found application in a range of neural dynamics. This includes switching between various aspects of brain function [46,51,47,52,48,32], and as models of behavioural states of *C. elegans* [41]. Further applications include models for intrinsic temporal behaviour of brain perception as in binocular rivalry [21].

Computing with network attractors

Computing with heteroclinic networks has gained traction in over the past years: from reproducible sequence generation under small noise [50,52] to modelling the interaction of different cognitive modalities [51]. Applications of this paradigm to understand computational

[1] More specifically we define a *connection with amplitude* δ to exist between states A_i and A_j, if a perturbation of size at most $\delta > 0$ from A_i gives a dynamical path to A_j for the input-free dynamics. The connection from A_i and A_j is said to have *threshold* $\delta_{ij} \geq 0$ if there is a connection for any amplitude $\delta > \delta_{ij}$. Heteroclinic connections have zero threshold.

Figure 1

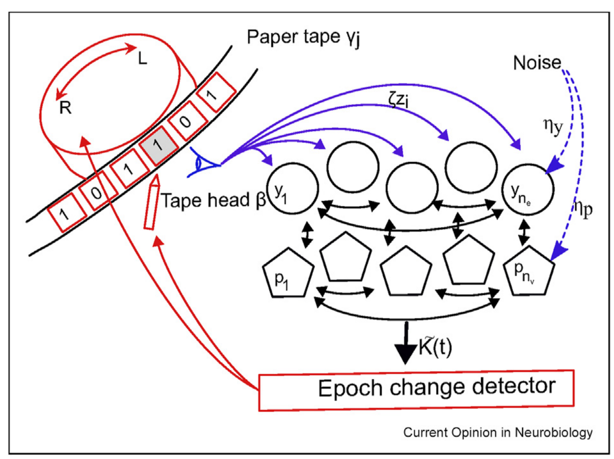


The dynamics of network attractors. **a**) Transitions between states for a Kirk-Silber heteroclinic network [36] in phase space. Each state ξ_k is a saddle equilibrium with an arrow indicating the direction of a heteroclinic (connecting) orbit. **b**) An excitable network with the same network topology as a) but between attracting equilibria. Saddles and their stable manifolds are indicated in blue in b). The quantity δ_{41} is the smallest perturbation required to have a dynamical path from ξ_4 to ξ_1. A notable difference between these two is that transitions in b) require nontrivial input (or noise) above a threshold while a) will show spontaneous transitions even in the absence of any input.

properties of the dynamics of neural models include 'heteroclinic computing' as described by Neves and others [54,42,56]. Heteroclinic networks can also be used to design systems with particular properties for application in robotics. Daltorio et al. use stable heteroclinic channels to generate rhythmic output of varying periods in response to sensory inputs to drive a peristaltic crawling robot [20]. Lyttle et al. use a neuromechanical model of the feeding apparatus of a marine mollusc [40] which exhibits a highly sensitive 'heteroclinic mode'. Egbert et al. use heteroclinic network as a controller for a robot trained to perform a categorical perception task [22]. An interesting phenomenon observed in the latter work was that such controllers can make discrete decisions about continually evolving environments. In all of these examples, the use of a heteroclinic network as a controller allowed for simpler interpretation, or design, of the controller, due to the close relation of the dynamics with a finite-state machine. Even though there is a lack of structural stability of attracting heteroclinic they can be useful in explaining more general dynamics in terms of a perturbed heteroclinic skeleton. The stable heteroclinic channels of [47] show that for small perturbations and low noise, trajectories can remain close to a perturbed heteroclinic network.

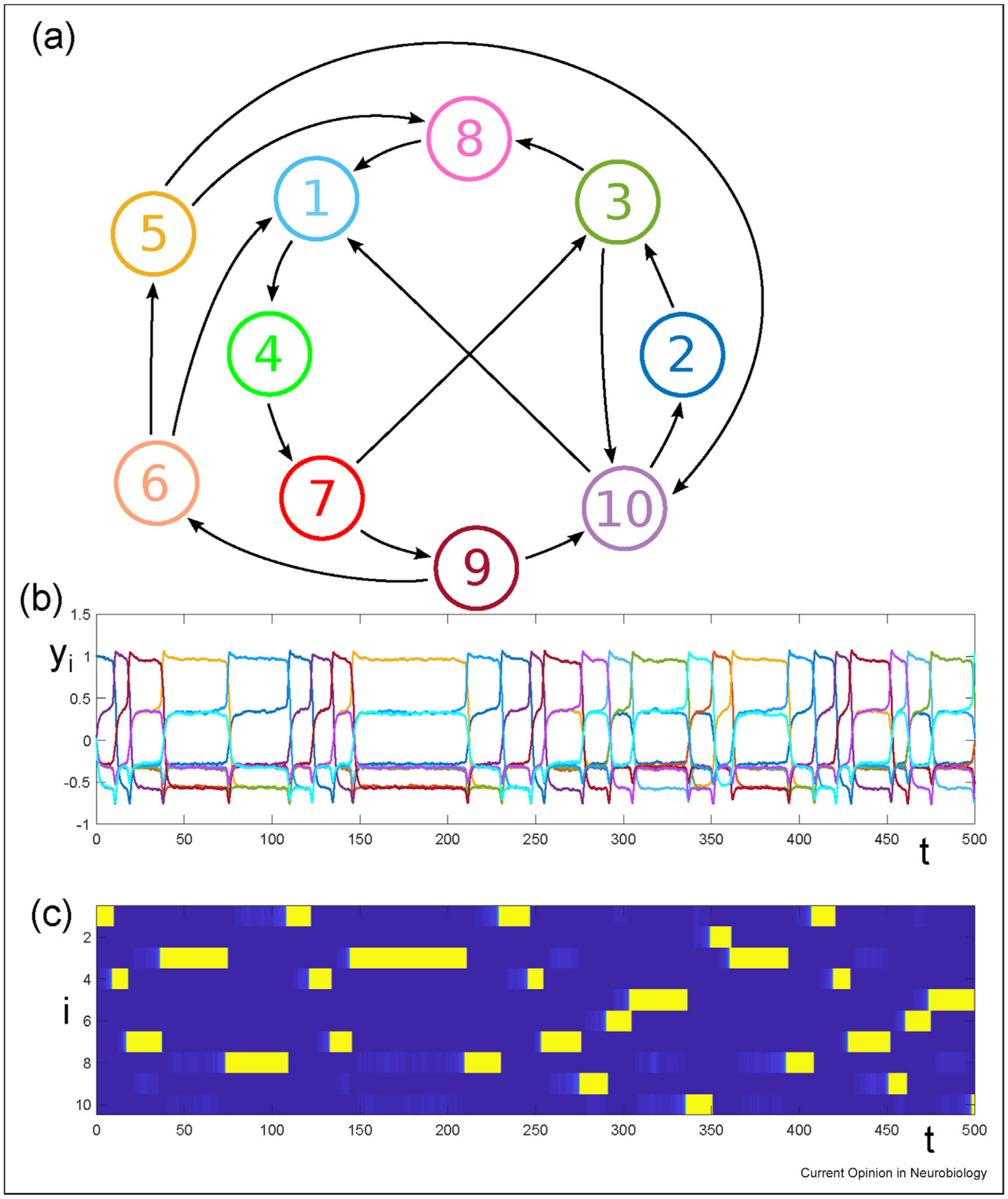
On the other hand, excitable networks are well-adapted for understanding input-driven computations, especially finite state computations. Indeed, in the absence of input, their dynamics is remarkably simple - progression to one of the attracting states. Excitable networks can be used to construct continuous time systems that realise network architectures of any desired design and input level. More specifically, we have shown that they can be used to construct *Turing machines* [6] with arbitrary sensitivity to inputs. In Figure 2, we show the scheme used in Ref. [6] for robustly realising a Turing machine within the dynamics of an excitable network. Moreover, as illustrated in

Figure 2



Realising a Turing machine using an excitable network attractor. Schematic diagram showing a robust realisation of a Turing machine using noisy transitions in a two-layer network with cells y_i, p_i that has an excitable network attractor [6]. The detector $\widetilde{K}(t)$ classifies system state according to a neighbourhood of an attractor. The input from tape is assumed to have amplitude ζ and there is noise of amplitude $\eta_{y,p}$ within the network. The computation requires no external clock and can be made arbitrarily sensitive, i.e. in the absence of noise it is possible to have successful computations for arbitrarily small ζ, but the rate of computation will be very slow for small ζ. In the presence of noise, various types of error can occur as discussed in Ref. [6] (Reproduced with permission from Ref. [6]).

Figure 3



A typical path around a noisy excitable network. Panel **a**) shows an example of a ten-state finite state graph realised as an excitable attractor for a CTRNN using the method in Ref. [7]. Panel **b**) shows a typical trajectory for this network realised as a ten-node system with coordinates $y_i(t)$ subjected to i.i.d. Wiener noise. Panel **c**) shows the same information as b) but as a raster plot; yellow regions show where the *i*th cell is above the threshold (Reproduced with permission from Ref. [7]).

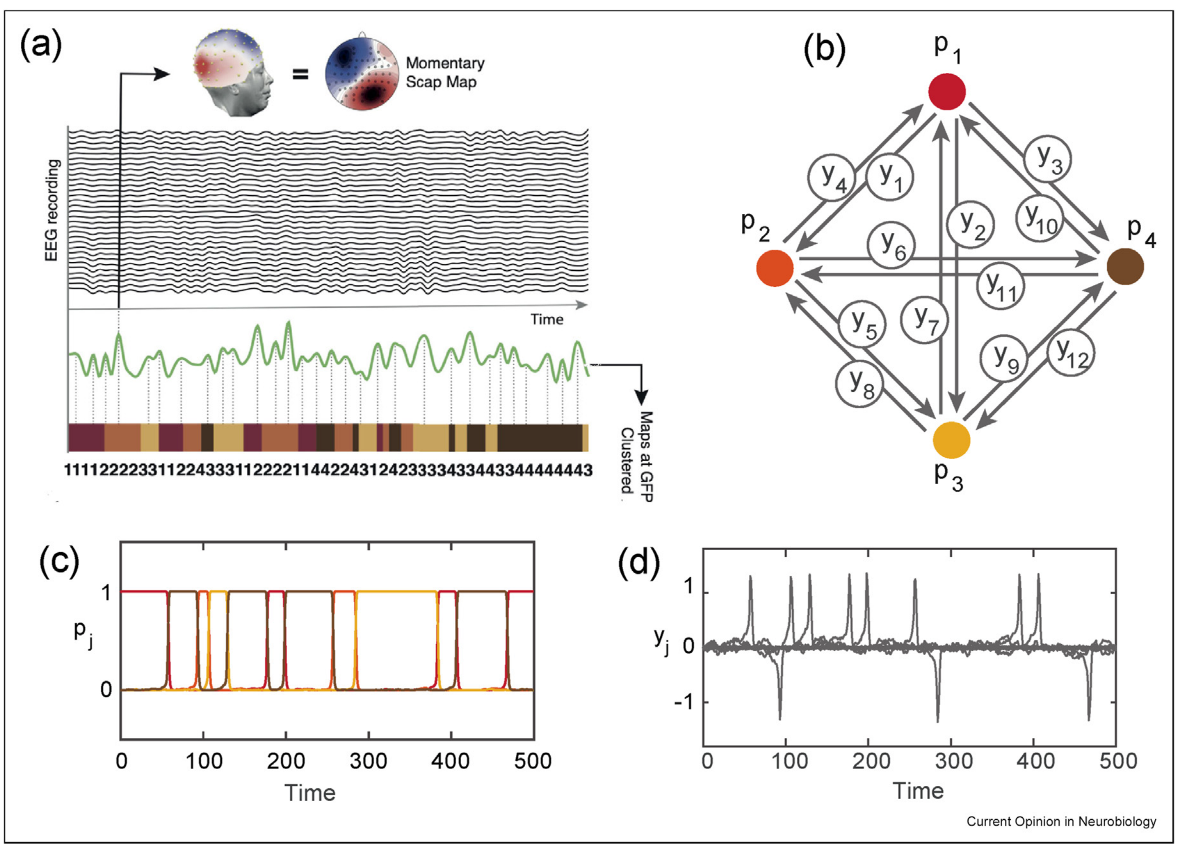
Figure 3, excitable networks with arbitrary topology and thresholds can be realised using standard continuous time and state-coupled neural rate models such as the CTRNN (or equivalently, a Wilson-Cowan model [61]) through a suitable choice of connection matrix [7].

A common problem faced by models highlighted in Ref. [1] is the trade-off between sensitivity (the ability to produce responses for inputs that may be of low amplitude) and robustness (the need for the system to function correctly in the presence of noise). Indeed, it is easy to come up with models of cognitive processes that have one but not the other. Excitable network attractors have dynamics that make them robust to subthreshold inputs/noise and sensitive to super-threshold signals. This is because every connection in an excitable network attractor has an associated excitability threshold: the minimum perturbation required to make a switch via that connection. Since the effect of noise is usually much smaller than those of inputs from the environment, the excitability threshold for a connection can be adaptively chosen, for example by evolving weights within the network, to be larger than the effect of noise and smaller than the input amplitude. This does not discount the possibility of noise-driven transition if the system runs for a sufficiently long time [25]. In turn, the dynamics of excitable networks are intermittent with trajectories spending long periods of time close to one state before the correct inputs induce a switch to another state. An application of this is the computational modelling of transitions between multichannel Electroencephalogram (EEG) microstates and their residence time. Microstates are short periods with coherent spatial patterning that have been implicated to be electrophysiological correlates of functional states in resting-state networks. A model involving a four-node noisy excitable network attractor (see Figure 4) has been used to capture transition probabilities between measured microstates [19]. Adding non-observed states can give improved probabilistic models that also account for heavy-tailed distributions of residence times between microstates. Due to their scale-free nature, such timings have been shown to be a crucial feature in modelling the temporal dynamics of microstates [17,62].

Outlook

The network attractors discussed in this review that can be analysed in detail have mostly simple temporal (equilibrium) dynamics at the invariant sets representing discrete states, as well as simple spatial structure (e.g., a single active cell in Ref. [7]). In practical applications to neural systems, the dynamics will be much more complex than this, both in terms of time dynamics and in terms of spatial patterning. There have been some attempts to extract such dynamics from data about neural activity (e.g., [32,19]) but general methods will be hard to establish, partly because the individual excitable states are likely to be spatiotemporal states that are much more complex than in the simple examples studied so far. There is clearly much more to be done before we can understand the contexts where network attractors will play a useful role in understanding such data.

Figure 4



Modelling transition between microstates in fMRI using excitable networks. Panel **a**) shows EEG data and extraction of four predominant microstates identified in Ref. [37]. Panel **b**) shows an excitable network model fitted to this microstate data [19]. This has 16 cells of two types; each cell is either a *p*-cell or a *y*-cell. The *p*-cells keep track of the closest equilibrium while the *y*-cells control transitions. For example, the *y*-cell y_4 is activated when there is a transition from p_2 to p_1. Panel **c**) shows a time series of the *p*-cells. Panel **d**) shows the time series of the *y*-cells. These become non-zero only during transitions between different microstates. (Reproduced with permission from Ref. [19]).

Although we have focused on natural neural dynamics in this review, excitable networks can also be a useful paradigm to understand malfunction of trained artificial neural networks. For example [18] shows that for a high dimensional Echo State Network trained for a particular trained task, an effective excitable network attractor can be reconstructed where errors in the response can be interpreted in terms of errors to correctly navigate the network in response to inputs.

In the longer term, a probabilistic understanding of network attractors is likely to be very helpful to give a quantitative picture of how they respond to inputs and their potential utility in understanding a variety of neural functions (e.g., the role of such dynamics in short-term memory) [33].

Declaration of competing interest

The authors have no conflicts of interest to declare.

Data availability

No data was used for the research described in the article.

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