

Sliding Global Attractors of Neural Learning and Memory

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Abstract: The highly variable nature of neural firing has been recognized by diverse empirical and analytic findings. Here, the underlying morphology of neural firing is shown to be governed by a bilinear map, prescribing eight types of neuronal global attractors and their points of local bifurcation. While synaptic learning gives rise to irregular firing, membrane memory is shown to guarantee that, under the same external activation, learning and retrieval end at the same global attractor. Forced and spontaneous changes in membrane conductance are shown to cause sliding of the global attractors, switching them from passive to active state and vice versa, and creating secondary firing modes. Selective activation of interacting neurons is shown to create a shunting effect, yielding combinatorial retrieval, concealment and revelation of stored global attractors. The utility of the global attractors is explained not only by their individual dynamic characteristics, but also by their high power of combinatorial expression.

1 INTRODUCTION

Empirical and analytic evidence show high dynamic variability of neuronal firing. Individual neurons of the same type are often capable of producing different firing modes, switching from one to another in a seemingly unpredictable manner. The transition from one dynamic mode to another has been called local bifurcation when caused by a change in parameter values, and global bifurcation when caused by the landscape of the underlying map under fixed parameter values (Blanchard et al., 2006). Variation in synaptic efficacy, widely associated with learning and memory (Dudai, 1989), has been shown to play a key role in the disorderly dynamics of neural firing (Baram, 2012). While almost all theoretical and experimental studies make the implicit assumption that synaptic efficacy is both necessary and sufficient to account for learning and memory, it has been suggested that learning and memory in neural networks result from an ongoing interplay between changes in synaptic efficacy and intrinsic membrane properties (Marder et al., 1996). It seems equally plausible that changes in membrane efficacy play a role in shaping the firing dynamics.

Employing widely accepted models of neuronal firing arising from the conductance paradigm (Hodgkin and Huxley, 1952), we show that the firing rate process is governed by a bilinear discrete

iteration map. The map is shown to have a singular value that defines the local bifurcation points between eight global attractor types, comprising the variable landscape of neural firing activity. The global attractor types are grouped by elementary firing modes into six classes, divided into two categories: chaotic attractor (mixed), square attractor (periodic), point attractor (constant) and attractor at infinity (saturated), associated with positive activation, form the active attractor category, while attractor at zero (silent), and bipolar attractor at zero and infinity (binary), associated with positive activation, form the passive attractor category. Changes in membrane conductance are shown to cause sliding of the global attractors, modifying their dynamic properties. In particular, sliding may transform active attractors into passive ones (concealment), and passive attractors into active ones (revelation), and vice versa. In the case of time-dependent conductance variation (Connor and Stevens, 1971), such transformation may in itself become a secondary dynamic mode. Membrane memory, manifested by invariance to changes in lateral feedback activity in the absence of external intervention, guarantees that neuronal retrieval will produce a stored global attractor. Selective activation of interacting neurons is shown to create a shunting effect, producing globally stable combinatorial patterns of stored, concealed and revealed neuronal global attractors.

2 GLOBAL ATTRACTORS OF NEURONAL FIRING

The firing dynamics of interacting neurons have been formulated as (Gerstner, 1995)

$$\tau_{v_i} \frac{d}{dt} v_i(t) = -v_i(t) + f_i \left(\omega_i^T \int_{-\infty}^t \kappa_i(t-\sigma) \mathbf{v}(\sigma) d\sigma - \beta_i(t) \right) \quad (1)$$

where $v_i(t)$ is the membrane current, or the firing rate, of the i 'th of n neurons in a neural network, τ_{v_i} is a time constant, f_i is the neuronal kernel, ω_i is the synaptic weights vector at the input to the i 'th neuron, $\kappa_i(t)$ is a function representing the membrane speed of response to the input current, $\mathbf{v}(t)$ is the vector of firing rates corresponding to the pre-neurons, and $\beta_i(t)$ is the equilibrium potential, or the conductance threshold, which may also encompass external activation and may generally take positive or negative values (Dayan and Abbott, 2001). Employing the exponential kernel $\kappa_i(t) = e^{-t/\tau_i}$, which incorporates the time constant τ_i of the membrane potential response to an input pulse, a discrete-time version of (1) is given by

$$v_i(k) = \frac{(\tau_{v_i} - 1)}{\tau_{v_i}} v_i(k-1) + \frac{1}{\tau_{v_i}} f_i \left(\omega_i^T \sum_{p=1}^{\infty} e^{-p/\tau_i} \mathbf{v}(k-p) - \beta_i \right) \quad (2)$$

The conductance-based rectification neuronal kernel f_i , first derived from empirical data (Granit et al., 1963, Connor and Stevens, 1971), then formulated mathematically (Carandini and Ferster, 2000), and widely assumed in firing-rate models (Dayan and Abbott, 2001), is

$$f_i(x) = f(x) = \begin{cases} x & \text{if } x \geq 0 \\ 0 & \text{if } x < 0 \end{cases} \quad (3)$$

As lateral feedback from other neurons can be expected to be slower than self-feedback, the ergodic nature of neural firing (Herveet al., 1990) implies that (2) can be written as

$$v_i(k) = \frac{(\tau_{v_i} - 1)}{\tau_{v_i}} v_i(k-1) + \frac{1}{\tau_{v_i}} f_i(\omega_{i,i} v_i(k-1) + \alpha_i - \beta_i) \quad (4)$$

where

$$\alpha_i = \sum_{j=1}^n \omega_{i,j} \sum_{p=2}^{\infty} e^{-p/\tau_i} v_j(k-p) = \bar{v} \frac{e^{-2/\tau_i}}{1 - e^{-1/\tau_i}} \sum_{j=1}^n \omega_{i,j} \quad (5)$$

where \bar{v} is the ensemble average of the neuronal firing rate processes.

The map (4) divides into two parts. The first, corresponding to the domain $\omega_{i,i} v_i(k-1) + \alpha_i - \beta_i \leq 0$, is

$$v_i(k) = f_1(v_i(k-1)) = \frac{\tau_{v_i} - 1}{\tau_{v_i}} v_i(k-1) \quad (6)$$

The second, corresponding to the domain $\omega_{i,i} v_i(k-1) + \alpha_i - \beta_i > 0$, is

$$v_i(k) = f_2(v_i(k-1)) = \frac{\tau_{v_i} - 1 + \omega_{i,i}}{\tau_{v_i}} v_i(k-1) + u_i \quad (7)$$

where

$$u_i = \frac{1}{\tau_{v_i}} (\alpha_i - \beta_i) \quad (8)$$

is the *total activation*. Clearly, the line $v_i(k) = f_1(v_i(k-1))$ has a positive slope smaller than 1, hence, it intersects the diagonal $v(k) = v(k-1)$ only at the origin. On the other hand, when the line $v_i(k) = f_2(v_i(k-1))$ intersects the diagonal, it will be at

$$p_i = \frac{u_i \tau_{v_i}}{1 - \omega_{i,i}} \quad (9)$$

The latter is, then, the only possible *fixed point* of the map beside the origin. The dynamic nature of the map is determined by its singular values. The singular value of $f_2(v_i(k-1))$ is its slope at p_i , that is

$$\lambda_i = \frac{\tau_{v_i} - 1 + \omega_{i,i}}{\tau_{v_i}} \quad (10)$$

An *attractor* (Abraham et al., 1997) is a subset A of the state space, which has a neighborhood $B(A)$, called a basin, such that any trajectory originating from $B(A)$ stays in it, and no proper subset of A has the same property. A *global attractor* is an attractor whose basin is the entire state space. The domain of $u_i \times \omega_{i,i}$ divides into eight subdomains, each defining a type of global attractor. Positive total activation ($u_i > 0$) defines the *active* global attractors:

(a) Chaotic attractor for $\omega_{i,i} < 1 - 2\tau_{v_i}$, yielding

$$\lambda_i < -1$$

(b) Square attractor at for $\omega_{i,i} = 1 - 2\tau_{v_i}$, yielding

$$\lambda_i = -1$$

- (c) Alternate point attractor for $1 - 2\tau_{v_i} < \omega_{i,i} \leq 1 - \tau_{v_i}$, yielding $-1 < \lambda_i \leq 0$
- (d) f_2 -dominated monotone point attractor for $1 - \tau_{v_i} < \omega_{i,i} \leq 1$, yielding $0 < \lambda_i \leq 1$
- (e) Attractor at infinity for $\omega_{i,i} > 1$, yielding $\lambda_i > 1$ while non-positive total activation ($u_i \leq 0$) defines the *passive* global attractors:
- (f) f_1 -dominated attractor at zero for $u_i \leq 0$ and $\omega_{i,i} \leq 0$
- (g) Bi-modal (piece-wise f_1 and f_2 - dominated) attractor at zero for $u_i < 0$ and $0 < \omega_{i,i} \leq 1$, yielding $(\tau_{v_i} - 1) / \tau_{v_i} < \lambda_i \leq 1$
- (h) Bi-polar attractor at zero and infinity for $u_i < 0$ and $\omega_{i,i} > 1$, yielding $\lambda_i > 1$

A diagram of the eight attractor types is posted at <http://www.cs.technion.ac.il/~baram/Attractors.pdf>

Case (a) represents a so-called *homoclinic orbit* (Ott, 1994) which, initiating at a neighborhood of \mathbf{p} , first diverges, then snaps back to \mathbf{p} , making the latter a *snap-back repeller* (Marotto, 1978, 2005). It has been shown for invertible smooth maps (Marotto, 1978, 2005) and extended to noninvertible piece-wise smooth maps (Gardini and Tramontana, 2011), that the existence of a snap-back repeller is a sufficient condition for chaotic behavior in the Li-Yorke sense (Li and Yorke, 1975).

Case (b) represents a period-2 oscillation. A trajectory initiating at any point in the state space will converge to such oscillation within the interior of a square, which is, then, an attractor (it might be noted that, in general, a free oscillator, such as an undamped pendulum, is not a cyclic attractor, as its limit orbits, depending on initial conditions, are not isolated).

Case (c) represents a point attractor at \mathbf{p} , resulting in periodic convergence (increasing $v(k)$ step followed by decreasing $v(k)$ step).

Case (d) also represents a point attractor at \mathbf{p} , but the mode of convergence, dominated by f_2 , is monotonic.

Case (e) represents an attractor at infinity, which, in reality, will be rectified at the maximal sustainable physical firing limit, defining saturation.

Case (f) represents the passive, silent versions of the active attractors (a-c).

Case (g) represents the passive, silent, bimodal version of the active attractor (d).

Case (h) represents a bipolar attractor at zero and infinity, which is the passive version of case (e). The final destination of a trajectory of case (h) at zero or infinity (or, rather, the saturation value) will be determined by the initial condition, with \mathbf{p} the point of separation between the two basins.

The attractors (a-h), each dominating the entire state space, are *global*. As the total activation u is represented by the point of contact of f_2 with the coordinate $v(k)$, a change in u will have a sliding effect, moving f_2 , and its point of intersection, \mathbf{p} , with the diagonal $v(k) = v(k-1)$, up or down in parallel to the coordinate $v(k)$. This will change the parameters of the global attractor, but, as long as u does not change in sign, not its dynamic nature. As u is changed from positive to non-positive value, the corresponding active attractor will turn into a passive attractor, and, in the case of attractor at zero, may be regarded as concealed in this state. Conversely, as u is changed from non-positive to positive value, the active state of the attractor is revealed as one of the active attractor types. Moreover, the sliding effect of time-dependence conductance (Connor and Stevens, 1971), such as post-inhibitory rebound (Perkel and Mulloney, 1974), can produce secondary firing modes, such as oscillatory bursting, by switching elementary firing modes, such as saturation, from passive to active state and vice versa.

Combining the point attractor types, (c,d), into one, and the attractor at zero types, (f,g), into one, the group of eight global attractor types may be rearranged into a group of six global attractor classes, associated with different dynamic modes: chaotic attractor (mixed), square attractor (oscillatory), point attractor (constant), attractor at zero (silent), attractor at infinity (saturated) and bipolar attractor at zero and infinity (binary). We call it *the elementary code of global attractors*.

Our analysis shows that the domain of the singular value λ_i is divided into subdomains corresponding to different global attractor types. As the analysis involves statistical averaging (manifested by α_i , representing the ensemble average of lateral activity), the boundaries between the λ_i - subdomains may not precisely match the empirical transition (or local bifurcation) points between the firing modes. Yet, these analytic

bifurcation points seem to be highly valuable. For instance, as our analysis implies the arousal of a snap-back repeler when $\lambda_i < -1$, the latter may be regarded as an analytic indicator of chaos. Such an indicator seems highly desirable, in view of the often reported inadequacy (Sprott, 2003) of empirical measure of chaos, such as the first Lyapunov exponent (Wright, 1984). In neighborhoods of the λ_i -bifurcation points one might expect to find combined, mixed and transient modes. It has been suggested that chaotic neural firing gives rise to multiplexed oscillatory modes (Baram, 2012).

3 COMBINATORIAL RETRIEVAL BY INTERACTING NEURONS

The learning process is characterized by variation of the synaptic weights. Mathematical manifestations of the Hebbian learning paradigm introduce products of firing rates into the dynamic equations involved, turning them into essentially polynomial maps, prone to noninvertibility and chaos (Baram, 2012). While such properties represent a high degree of irregularity, it has been shown that the behavior of the synaptic weights in certain manifestations of Hebbian learning (Oja, 1982; Bienenstock et al., 1982) is highly regular. In particular, it has been shown that, under bounding conditions on the inputs, the synaptic weights under the BCM rule converge to final values (Cooper et al., 2004). Moreover, it has been shown that, in the BCM framework, the neuronal fixed points are not altered by lateral connectivity if the neuronal kernel is invertible and differentiable (Castellani et al., 1999). These properties are shared by linear and sigmoidal kernels but not by the rectification kernel (4). Yet, the bilinear map associated with the rectification kernel implies that the fixed point p associated with f_2 is not altered by lateral connectivity, as long as the nature of the map is not changed (a change may eliminate p altogether). This property may be defined as *local invariance* of the global attractor to lateral activity. Employing the index ℓ to denote conductance and activation values during learning and the index r to denote conductance and activation values during retrieval, the equality

$$\beta_{i,r} = \beta_{i,\ell}$$

coupled with the local invariance of the global attractor to lateral activity, will guarantee that,

without external intervention, the retrieved global attractor will be the same as the stored one. As the equilibrium threshold, β_i , is widely assumed to be constant (Dayan and Abbott, 2001), the local invariance of the global attractor to lateral activity may be viewed as *membrane memory*.

The nature of the map, hence, the global attractor, can only change if the sign of u_i changes. It follows that changing the lateral activity, α_i , has the same effect on the nature of the map as changing the conductance equilibrium threshold, β_i . As noted before, the definition of β_i can be changed to include external activation. The nature of the map, or the global attractor, can be controlled, then, by external activation, or by some internal mechanism, enforcing $\beta_i < \alpha_i$ for a positive total activation, hence, an active attractor, or $\beta_i \geq \alpha_i$ for a negative total activation, hence, a passive attractor. In particular, the state $\beta_i = \alpha_i$ will enforce a strict attractor at zero (case f), hence, silence, which may be regarded as the ground state of the neuron.

External activation of the neuron at hand, or of laterally connected neurons, can, by the sliding effect, change the nature of the map, and, with it, the very existence of the fixed point p . Specifically, the transition of any of the active attractors (a-c) to the passive attractor (f) and of the active attractor (d) to the passive attractor (g) will eliminate the fixed point associated with the respective attractor of any of the types (a-d). The transition of the active attractor (e) to the passive attractor (h) will give rise to the fixed point p in (h). On the other hand, the transition from the passive attractor (f) to any of the active attractors (a-c) will give rise to the corresponding fixed point p , as will the transition from the passive attractor (g) to the active attractor (e), while the transition from the passive attractor (g) to the active attractor (e) will eliminate the fixed point p in (h). The result will be concealment of a stored active global attractor (if $u_{i,\ell} > 0$ and $u_{i,r} \leq 0$), or revelation of the active state of a stored passive global attractor (if $u_{i,\ell} \leq 0$ and $u_{i,r} > 0$).

Applying a network-wide activation pattern, by which some of the neurons receive positive external activation and the others non-positive external activation, will produce retrieval and concealment of stored active global attractors, and revelation of the

active state of stored passive global attractors. For instance, in learning, a neuron i may store a global attractor of one of the active types (a-c), which, due to the activation level, may slide and become a passive global attractor of type (f), concealing the nature of the active state of the stored attractor. On the other hand, in selective retrieval, inhibitory effects of the lateral feedback activity may be eliminated by negative activation of an interacting neuron j , causing an upward slide and revelation of the active state of the global attractor stored in neuron i . This shunting effect allows for the creation of a large variety of network-wide patterns from the stored active and passive neuronal patterns. A group of n neurons can retrieve, by choice of neuron activations, any permutation of neuronal stored pattern, and their complimentary active or passive states. Assuming that neural information is represented by firing mode, the expressive power of a group of n neurons employing the elementary code of global attractors alone is the retrieval capacity of 6^n globally stable patterns, which may be written as the set

$$M = A^n \quad (11)$$

where A is the set of firing modes associated with the global attractor types and $A^n = A^{n-1} \times A$, with \times the Cartesian product. In general, A includes not only the elementary firing modes but also the secondary modes comprising combination, mixture and multiplexity of elementary modes.

4 CONCLUSIONS

The neuronal global attractors can be directly related to empirically observed firing modes. For instance, seemingly random spiking can be represented by a chaotic attractor, tonic spiking by a point attractor, oscillatory spiking by a square attractor, and bursting by saturation, representing an attractor at infinity. The singularity parameter λ_i defining local bifurcation points between global attractors and their corresponding firing modes, constitutes a valuable tool for dynamic analysis of neural firing. For instance, the arousal of chaos does not appear to have been analytically identified with specific parameter values. The empirical manifestation of the first Lyapunov exponential (Wright, 1984) has been known to produce highly unreliable results, even when applied to data generated by simulating low dimensional models (Spratt, 2003). We have shown

that, for bilinear maps, and, specifically, the important class of such maps associated with neuronal firing, the singular value $\lambda_i = -1$ provides, in some statistical sense, an analytic characterization of chaotic arousal. We have seen that the neighborhoods of points of local bifurcation, represented by certain values of the singularity parameter λ_i , define regions of secondary firing modes, comprising combination, mixture and temporal multiplexing of elementary modes. Secondary modes, such as periodic bursting, may also arise from the sliding effect caused by time-dependent conductance (Connor and Stevens, 1971), such as post-inhibitory rebound (Perkel and Mulloney, 1974), switching elementary firing modes, such as saturation, from passive to active state and vice versa. While there seems to be a clear relationship between certain firing modes and neural functions (e.g., oscillation, or periodic bursting, seem related to heartbeat, walking and chewing) the utility of others is not as commonly recognized or understood. The chaotic trajectories of learning (Baram, 2012), wandering over a wide range in the state space, may serve the purpose of rapid search, or formation, of a global attractor of memory. A chaotic global attractor, mixing different firing rates in a single sequence, may provide temporal multiplexing for inter-neural communication purposes. The maximum-energy response of a neuron storing a bi-polar attractor, aroused by initial condition at a threshold determined by memory, may represent instinct. A global attractor at zero, representing silence, may serve the purpose not only of neural rest, but also a common initial condition for combinatorial learning and retrieval. The combinatorial emergence of active and passive global attractors may give rise not only to stored subpatterns, but also to previously un-aroused patterns, representing innovation.

REFERENCES

- Abraham, R. H., Gardini, L. and Mira, C., 1997. *Chaos in Discrete Dynamical Systems*. Springer-Verlag, Berlin.
- Baram, Y., 2012. Noninvertibility, Chaotic coding and chaotic multiplexity in synaptically modulated neural firing. *Neural Computation* 24(3): 676-699.
- Bienenstock, E. L., Cooper, L. N. and Munro, P. W., 1982. Theory for the development of neuron selectivity: orientation specificity and binocular interaction in visual cortex. *J. Neurosci.* 2, 32-48.
- Blanchard, P., Devaney, R. L. and Hall, G. R., 2006. *Differential Equations*. London: Thompson.

- Carandini, M. and Ferster, D., 2000. Orientation tuning of membrane potential and firing rate in cat primary visual cortex. *J. Neurosci.*, 20 (1), 470-484.
- Connor, J. A. and Stevens, C. F., 1971. Prediction of repetitive firing behaviour from voltage clamp data on an isolated neuron soma. *J. Physiol.*; 213(1), 31-53.
- Castellani, G. C., Intrator, N., Shouval, H., and Cooper, L. N., 1999. Solutions of a BCM learning rule in a network of lateral interacting non-linear neurons *Network* 10:111-121.
- Cooper, L. N., Intrator, N., Blais, B. S. and Shouval, H. Z., 2004. *Theory of Cortical Plasticity*. New Jersey: World Scientific.
- Dayan, P. and Abbott, L. F., 2001. *Theoretical Neuroscience*. MIT Press, Cambridge, MA.
- Dudai, Y., 1989. *Neurobiology of Memory*. New York, Oxford University Press.
- Gardini, L. and Tramontana, F., 2011. Snap-back repellers in non-smooth functions. *Regular and Chaotic Dynamics* 2-3: 237-245.
- Gerstner, W., 1995. Time structure of the activity in neural network models. *Phys.Rev. E* 51: 738-758.
- Granit, R., D. Kernell, D. and Shortess, G. K., 1963. Quantitative aspects of repetitive firing of mammalian motoneurons caused by injected currents. *J. Physiol.* 168, 911-931.
- Herve, T., Dolmazon, J. M. and Demongeot, J., 1990. Random field and neural information. *Proc. Natl. Acad. Sci. USA* 87: 806-810, Biophysics.
- Hodgkin, A., and Huxley, A., 1952. A quantitative description of membrane current and its application to conduction and excitation in nerve. *J. Physiol.* 117:500-544.
- Li, T-Y and Yorke, J. A., 1975. Period three implies chaos, *Am. Math. Month.*, 82 (10): 985-992.
- Marder, E., Abbott, L. F., Turrigiano, G., G. Liu, Z. and Golowasch, J., 1996. Memory from the dynamics of intrinsic membrane currents. *Proc. Nat. Acad. Sci. USA* 93: 13481-13486.
- Marotto, F. R., 1978. Snap-back repellers imply chaos in R^n . *J. Math. Anal. Appl.* 63(1): 199-223.
- Marotto, F. R., 2005. On redefining a snap-back repeller. *Chaos, Solitons & Fractals* 25 25-28.
- Oja, E., 1982. Simplified neuron model as a principal component analyzer. *J. Math. Biol.* 15 (3): 267-273.
- Ott, E., 1994 *Chaos in Dynamical Systems*. Cambridge University Press.
- Perkel, D. H. and Mulloney B., 1974. Motor pattern production in reciprocally inhibitory neurons exhibiting postinhibitory rebound. *Science*, 185, 181-182.
- Sprott, J. C., 2003. *Chaos and Time-Series Analysis*. New York, Oxford University Press.
- Wright, J., 1984. Method for calculating a Lyapunov exponent, *Phys. Rev. A*, 29(5), 2924-2927.