

MULTISTABILITY, STATISTICAL STABILITY  
AND THE BRAIN:  
A SET OF NOTES IN OUTLINE FORM  
FOR FUTURE RESEARCH  
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Michael C. Mackey & John G. Milton

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A. A Linear Chain of Neurons

1. Consider a linear chain of neurons, show that as one proceeds along the chain the firing frequency continually drops until it is no longer possible to sustain activity. Each neuron is assumed to have both an absolute and a relative refractory time.
2. The case when the input is an excitatory spike train (i.e. composed of only EPSP's) which is periodic is developed in John's book, Chapter 2 [39], and early computations of Mike in notebooks from the middle 1970's.
3. Lasota and Mackey notes calculate the output density of interspike intervals of  $f_O$  to an input spike train of EPSP's with an arbitrary interspike density  $f_I$ . We need to see if these results can be extended to show that the mean frequency of the output is less than the mean frequency of the input, or alternately if the mean output interspike interval is greater than the mean input interspike interval:

$$\int x f_O(x) dx > \int x f_I(x) dx. \quad (1)$$

4. To obtain an analogous result when both excitatory and inhibitory inputs are present we make the following simplification. Namely,

we assume that the main effect of the inhibitory synapses is to shunt the excitatory synaptic currents, and not to add hyperpolarization to the somatic membrane potential. This assumption is physiologically realistic as has been discussed by Abeles [1] and Kandel and Schwartz [20], and all it does is to decrease the magnitude of the maximal EPSP and consequently increase the difference between the input and output spike train frequencies.

## B. The Convergence Problem

1. To overcome the frequency dilemma of the previous section, we assume that there is a convergence of many presynaptic spike trains to a single postsynaptic cell. The frequency of the spike train obtained by superimposing all of the individual spike trains is higher than that of an individual presynaptic train.

If the presynaptic spike trains are each distributed with a given density, what is the density of the summated signal going to the postsynaptic cell? We know the answer to this, since the density of the summated signal is just the multiple convolution of the various input densities.

2. Geisler and Goldberg [13] developed a model of this type. They assumed that because a cortical neuron received so many inputs (both excitatory and inhibitory), the membrane potential could be represented as a random variable: an output (postsynaptic) spike occurs when the membrane potential exceeds the threshold. They suggested that under these conditions the statistical properties of the output spike train are determined exclusively by the dynamics of the threshold (e.g. the relative refractory dynamics).
3. Extend the Geisler and Goldberg [13] model for the generation of the density of the distribution of interspike intervals in single neurons.

Do this by utilizing a version of the patient survival paper of [23, 33] wherein an asymptotically stable map generates a chaotic time series (corresponding to the fluctuating input of the presynaptic inputs) and thus a stable density  $f_*(x)$ .

However, in this heuristic model, the dynamics of the interspike interval histogram will be controlled entirely by the dynamics of the “hole”, which really means that these density dynamics are the sole consequence of the threshold behaviour when faced with a train of spikes.

We will assume that after a spike is generated:

- (a) The hole first closes for a period of time equal to the absolute refractory time  $t_a$ , and then slowly opens to mimic the decreasing threshold, finally approaching a maximum of  $\theta_0$ ; and
- (b) The initial condition of the map is reset to an arbitrary value to destroy correlations between successive interspike intervals.
- (c) To mimic the effects of recurrent inhibition we could have the threshold go to zero initially for a period of time  $t_a$ , then rise to a maximum, and then decrease again.

### C. The Convergence–Divergence Problem

1. Consider (discuss, extend) the Abeles argument [1] related to the convergence and divergence effects.
2. Consider a situation in which  $N$  neurons each receive two types of inputs:
  - (a) an identical temporally patterned spike train; and
  - (b) a noisy input  $\xi(t)$  which is temporally uncorrelated between neurons so  $\langle \xi_j \xi_k \rangle = 0$  for all  $i, j = 1, \dots, N$  and  $i \neq j$ .

The effect of this noisy input is to convert each neuron into a weak signal detector, i.e. there is a finite probability (albeit small) that the neuron will fire in response to a single spike though normally (without noise) this is not possible.

It is straightforward to see that if the outputs of the  $N$  neurons are summed at a common point we will recover the initial temporal patterned spike train. This is the essence of a model recently proposed by Collins et al. [8] and extended by John Hunter.

### D. Distribution/Temporal Coding in the Nervous System

Here we summarize some of the results of the older and more recent papers that suggest a temporal and/or distribution coding within the nervous system. In particular, these results include those of Werner and Montcastle [49], and others [44, 50, 9, 46, 37, 48, 34, 11, 38, 35].

1. Temporal coding Recently the old idea that the neural code was simply a **rate code**, i.e. that neural stimuli are encoded as an average firing rate along neurons, has been embellished by extending it to the notion that the **actual timing or sequence**

**of action potentials, and therefore the sequence of interspike intervals, might indeed be the vehicle by which information is transmitted in the nervous system.**

- (a) In a recent study Middlebrooks et al. [38] examined the firing patterns of single neurons in the auditory cortex of cat in response to different spatial location of auditory stimuli. They discovered that these single neurons can respond to sound locations throughout 360 degrees, and even more interestingly that these individual units responded with patterns of action potentials that varied systematically with the location of the auditory stimulus. They speculated that, in contrast to a *place code*, an auditory stimulus at nearly any location activates a diffuse populations of neurons, and that each of the active neurons in this population signals, with its temporal firing pattern, the approximate location of the auditory stimulus and that the precise location is signaled by the concerted activity of many such neurons.
  - (b) A speculative, but informative, article by Ferster and Spruston [11] considers alternative candidates for the neural code—including a temporal coding process—and is well worth reading for its discussion of the relevant issues and pointing to some of the important literature.
2. Distributional (Ensemble) Coding [JGM—Where does the Optician and Richmond [40] reference go here?]
- (a) One observation leading to the supposition that there is widespread distributional neural patterning is that of Penfield [jgm—?ref] who showed that even though there are clear sensory and motor areas in the cortex, sufficiently strong stimulation of virtually any area of the cortex is capable of eliciting sensory and/or motor responses.
  - (b) To this we should add the old observations of Lashley [mcm—?ref] who showed that ablation of large areas of the cortex in the rat could take place without any eventual loss of the ability to solve maze problems.
  - (c) To our knowledge, one of the first published experimental studies suggesting that neural information might be encoded in a distributional, or density manner, is that of Werner and Montcastle [49].

In their study of the firing of thalamic neurons in monkeys in response to sensory stimuli they found clear evidence of a strict causal relationship between the mean interspike interval  $\bar{\Delta}t$  and the standard deviation  $\sigma$  of the instantaneous firing rate. Namely, they found that to a good approximation

$$\sigma = \frac{1}{2}\bar{\Delta}t, \quad (2)$$

which is **quite similar to a relationship first pointed out to me by John Tyson that holds for the statistics of the cell division process in a number of cell lines** and which should be followed up. Werner and Montcastle [49] speculated that this relationship might be indicative of the utilization of interspike interval density information to transmit information in the nervous system.

In addition, Werner and Montcastle [49] found that in both spontaneous firing and firing in response to a constant stimulus the resulting records of firing rate (impulses/second) showed a clear and statistically significant “periodicity” with period ranging from 0.09 to 1.4 hertz. One might wonder if this is experimental evidence for the statistical periodicity that we discuss in two sections below.

- (d) The next work to suggest the potential role of densities in transmitting information in the nervous system was that of Sanderson et al. [44] working in the retinal ganglion cells of cats. They presented data indicating that there was a clear change in the density of the distribution of the interspike interval histograms between light and dark, and speculated that it was in fact the density that was carrying the neural code in the visual system.
- (e) Wu et al. [50] studied two different behaviours (gill withdrawal and respiratory pumping) in *Aplysia* while recording from about 70 neurons. They discovered that the populations of neurons that were active during the two behaviours were highly overlapping, but that the pattern of activity across the populations was quite different during the two behaviours. These results were interpreted by them as indicating a distributed neuronal organization in which virtually the entire population of neurons participated in the two responses, but with totally different patterns (densities of activity).

- (f) As a more modern extension to the work of Penfield, Ungersleider has recently shown [48] that both learning and memory involve many of the same areas in which motor and sensory processing primarily takes place.
- (g) Deadwyler and Hampson [9] have recently given an interesting and clearly written exposition of the hypothesis that there is an association between sensory inputs, ensemble encoding of the sensory information, and ensemble processing leading to behaviour.

### E. Multistability and Why We Should be Interested In It

1. One need go not very far up in the nervous system before encountering recurrent loops, both inhibitory as well as excitatory. These loops form local neural circuits as well as long range connections involving, for example, descending cortical influences. As a consequence of these interactions, autonomous dynamics such as limit cycles may become important. The occurrence of an autonomous limit cycle would obscure input output relations.

2. We attach particular importance to the possible occurrence of multistability in networks of interacting neurons.

What is multistability? From a mathematical point of view, it refers to the co-existence of multiple attractors such that there is a dependence of the eventual behaviour of a dynamical or semi-dynamical system on the initial condition that the system is faced with.

We conjecture that different attractors may correspond to different memories or different responses. From the nervous systems point of view, the speed with which it could switch between different basins of attraction is clearly of importance. However, there are two (not necessarily mutually exclusive) ways of dealing with an acceleration of switching.

- (a) One is to ensure that the individual dynamics containing the coexisting attractors has a relatively rapid switching speed (large negative real part of an eigenvalue)
  - (b) The second will become apparent below when we discuss the concept of the behaviour of densities.
3. Note that multistability in this sense is not that much different from what is typically discussed in the current neural network literature.

- (a) The consensus in the neural network literature is that there is an intimate connection between associative memory and multistability, as summarized in Hertz et al. [15].
  - (b) The possibility has been raised by Canavier [7] that some forms of memory in the CNS, specifically active short term memory, might also be related to multistability.
  - (c) The one difference is that in neural networks, this multistability is dependent on a modification of the synaptic weights in response to usage (Hebbian synapses, or something akin to them.)
  - (d) The multistability found in neural networks in which Hebbian synapses are used to embed multiple memories suffer from the defect that when they are overloaded (i.e. presented with more memories than the maximum allowed by the network size and dynamics), their total performance is degraded in the sense that the recall of all memories becomes poorer as has been discussed in Abeles [1].
  - (e) In contrast, psychological experience seems to indicate that slight overloading may affect some memories but in fact leaves most intact.
  - (f) This synaptic modification is not necessary for the type of dynamic multistability that we have in mind, but it is certainly possible that it could be incorporated in which case we might have a new type of multistable behaviour emerging as a consequence.  
But note here that training implies a modification of dynamics!
4. From the perspective of neurobiology, multistability might be important if the CNS was such that it were multistable and thus different stimuli were capable of evoking different solutions from the harem of multistable solutions that the CNS was capable of generating.
  5. In the real CNS it is unclear which (if any) mechanisms could lead to multistability and what the nature of the locally stable attractors might be. Neurons are well known to be bistable, e.g. the squid giant axon as shown by Guttman et al. [14] and the  $\alpha$ -motoneuron as studied by Hounsgaard et al. [16], and may in fact be multistable [7]. Further, small neural circuits may be multistable in both their electronic realizations as shown in

the work of Foss et al. [12] and in the real biological situation studies by Kleinfeld et al. [21]. What happens in large neural populations?

6. Another strength is the following. In the multistability that occurs in systems of ordinary differential equations, a single suitably timed stimulus (initial condition) of the proper magnitude is capable of switching between eventual behaviors.

However, in the multistability displayed by differential delay equations (or functional equations for that matter), an entire history of the stimulus pattern for some finite interval of time is required to determine the eventual behavior. Thus in this case one has a way of eliciting different responses to a “temporal code” extending over a finite period of time.

#### F. What do We Know About Multistability?

1. From an experimental point of view in biological situations it is known that the squid giant axon is capable of generating bistable behaviour [14], as is the  $\alpha$ -motoneuron [16]. Furthermore, in the work of Martinez and Segundo [36] it is highly likely that multistable behaviour was *induced* via the addition of a recurrent inhibitory feedback to a crayfish stretch receptor, while in the work of Kleinfeld et al. [21] the existence of multistable behaviour in an *Aplysia* neuron inserted into **biologically constructed** recurrent inhibitory loop was demonstrated beyond a doubt.
2. Also, from an experimental perspective there are neural circuits that control motor outputs in which the same group of neurons and interneurons are capable of firing in a variety of different patterns, a characteristic of multistability, cf. Delcomyn [10], Kristan [22], Selverston [45], and Roberts and Roberts [43].
3. From a modeling perspective, the mathematical model of Canavier et al. [7] has shown the existence of seven coexisting solutions in a model for the R15 neuron of *Aplysia*. Of these patterns, have any been seen experimentally?
4. Many of our other examples of multistability derive from studies of first order differential delay equations with mixed feedback, some of which were motivated by studies of a model for the ubiquitous occurrence of recurrent inhibition in the nervous system. Thus from an analytic point of view we have the studies



of [5, 4, 32, 3, 30] and Foss et al. [12]. Note however that in the model of Foss et al. [12] for recurrent inhibition, the feedback is not of “mixed” type, but rather is negative feedback.

5. It has been shown by Foss et al. [12] that temporal pattern codes are produced by neural circuits which have the property of multistability. This observation is of particular interest given the current excitement surrounding temporal pattern coding in the nervous system.
6. These analytic studies have been extended to second order delay systems and it is clear that in these one can have multistable solution behaviour in the even simpler case of negative feedback as shown in the studies of an der Heiden et al. [2] for piecewise constant negative feedback (which may be applicable to the bistable behaviour found in the pupil light reflex), and Campbell et al. [6] for continuous negative feedback.
7. From a perspective of problems motivated by examples in physics we have only to turn to the work of Ikeda and Matsumoto [18] and Ida and Davis [17] that was motivated by experimental work on laser cavity experiments and which demonstrated the existence of multistable behaviour.
8. The property of multistability has also been demonstrated in high order discrete time semi-dynamical systems called coupled map lattices. Though this phenomenon has been observed in CML’s by many investigators [citeREFS] without realizing what it was, perhaps the clearest explicit demonstration of it is contained in the work of [26, 27], and Losson et al. [31] for deterministic systems, and [29] for stochastic systems.

### G. Densities and the Nervous System

1. The experimental studies described above in the section on temporal and distribution coding make it clear that there may be a likelihood, at least in some situations, that ensemble coding is of importance in the nervous system.
2. Because of the extensive convergence and divergence properties of the nervous system, as well as the large number of neurons involved, this is not especially surprising.
3. If indeed ensemble coding is of importance, then the only natural way to describe the ensemble activity is through the density of the distribution of the activity in the ensemble.

4. Typically one only thinks of density descriptions of systems as being of use in the calculation of static statistical properties. However, much is now known about the evolution of densities (statistical properties) under the action of deterministic dynamics [25], and a number of types of convergence behaviour of densities are now described.
5. One of the most attractive aspects of thinking that the nervous system might operate by computing with densities is that their speed of convergence is typically many orders of magnitude larger than one can expect from examining the statistical convergence along the trajectory of an individual unit even if the underlying dynamics are ergodic.
6. From our perspective, one of the most attractive types of convergence behaviors of densities with respect to the possible functioning of the nervous system is that of statistical periodicity which we consider extensively in the next two sections.

#### H. What is Statistical Periodicity, and Why Should we be Mindful of It?

1. Statistical periodicity is a periodicity property of **densities** that was first demonstrated to exist by Ionescu Tulcea and Marinescu [47] for discrete time systems (maps). The essence of statistical periodicity is that although a trajectory may appear to be “chaotic”, if one examines the evolution of densities under the action of a map then the densities actually exhibit a strictly periodic behaviour.
2. Statistical periodicity may be either an inherent property of a completely deterministic system, or it may be a property of a stochastic system induced by the injection of noise (additive or parametric) into a deterministic system. [The simplest, but trivial, example of the latter situation is the statistical periodicity induced by the addition of noise to a deterministic system with a limit cycle behaviour.]
3. One of the attractive aspects of statistical periodicity is that the nature of the limiting oscillations of the densities is **continuously dependent on the initial density** in spite of the fact that the period of the oscillation is fixed by the dynamics.
4. Thus if you were thinking of statistical periodicity as a dynamic mechanism for storing memory one could have a virtually contin-

uous relationship between dynamic responses and the stimulus. The ability to discriminate between the continuous array of responses would be only limited by our ability to discern “tiny” differences.

### I. What do we Know of Statistical Periodicity?

1. The mathematical foundation for the existence of statistical periodicity (also sometimes known as asymptotic periodicity) was laid by Ionescu Tulcea and Marinescu [47]. See also Lasota and Mackey [25] for a treatment of the characteristics of statistical periodicity.
2. A concrete one dimensional dynamical system demonstrating statistical periodicity is the “tent map” studied by [41] who extended the analytical work of Ito et al. [19] and Yoshida et al. [?].
3. The work on statistical periodicity of the single tent map was extended by [26] to the case of two coupled tent maps.
4. Work on high dimensional dynamical systems (coupled map lattices) displaying statistical periodicity can be found in a number of papers including [27] and Losson et al. [31], which considered coupled lattices of the tent map and the “quail map”.
5. The demonstration that statistical periodicity can be induced in a discrete time one dimensional dynamical system that has no continuous statistical behaviour (in the sense of the existence of densities) in the absence of noise is contained in the work of Lasota and Mackey [24] who examined the effect of additive noise in the “Keener map”. These studies were extended by Provatas and Mackey [42].
6. Further considerations of noise induced statistical periodicity are to be found in the coupled map papers of [29] who considered collections of interconnected stochastically perturbed maps.
7. It has been claimed that the phenomenon of statistical periodicity is impossible in continuous time dynamical or semi-dynamical systems. [The fact that this claim is false is easily seen by reference to the situation described above in which noise is added to a system with limit cycle behaviour.] However, the analytic demonstration of non-trivial statistical periodicity in continuous time systems has not yet been achieved.

8. The above observations notwithstanding, statistical periodicity has been demonstrated in discrete time representations of differential delay equations that capture the essence of recurrent inhibition, for example [28] showed that numerical solutions of a “tent map” differential delay equation display statistical periodicity, while evidence for this property was also found in a “stochastic Keener map” differential delay equation [28].
9. A natural extension of statistical periodicity is to think of **statistical chaos**—the situation in which there is a non-periodic evolution of densities.

MCM thinks that a necessary condition for the occurrence of this behavior would be that the Frobenius Perron operator should be nonlinear, i.e. depend on the previous density in a manner that destroys the additivity property.

A potential way to generate statistical chaos is to take a tent map in which the slope parameter  $a$  is dependent on the previous density, e.g.

$$a_{i+1} = 1 + \int_A f_i(x) dx \quad (3)$$

and  $A \subset [0, 1]$ .

## J. What is the Connection Between Multistability & Statistical Periodicity?

1. In the studies of high dimensional coupled map lattices of [27] and Losson et al. [31] we have the strongest connection between multistability and statistical periodicity.
  - (a) On the analytic side Losson and Mackey [27] and Losson et al. [31] have given sufficient analytical conditions for the existence of **statistical periodicity of densities** in large  $N \times N$  coupled map lattices, so they are in fact high dimensional discrete time dynamical systems of dimension  $= N^2$ .
  - (b) However, on the numerical side Losson and Mackey [27] and Losson et al. [31] have shown that starting from two random initial conditions in these  $N^2$  dimensional systems the eventual patterns of activity in the system corresponding to the two realizations were different both to the eye, and as evaluated by the less subjective index of the “collapsed density” which also showed clear behaviour indicative of statistical periodicity.

- i. Note that the collapsed density is **not** a representation of the density of the  $N^2$  dimensional dynamical system.
    - ii. Remember also that the statistically periodic behaviour of the collapsed density, taken as numerical evidence for multistability, was also shown to exist analytically.
  - (c) **Thus there is a clear correspondence in the coupled map lattices between the occurrence of multistability on the one hand, and statistical periodicity on the other.**
2. Exactly the same type of evidence linking multistability and statistical periodicity in the square lattices of Losson and Mackey [27] and Losson et al. [31] was found in the “one dimensional” lattice representations for differential delay equations presented in Losson and Mackey [28]. Thus we must conclude that it is highly likely that there is a strong connection between the occurrence of multistability in high dimensional dynamical systems, of which differential delay equations are but one example since they are effectively infinite dimensional, and the property of statistical stability.
  3. To nail this problem further, two numerical studies are proposed:
    - (a) Claude Lacoursiere will examine the tent map differential delay equation of [28] to identify parameter values at which multistability and/or statistical periodicity occur, and determine the degree of overlap of the parameter spaces for these two phenomena; while
    - (b) Jennifer Foss will carry out exactly the same programme for her positive feedback model [12] of recurrent inhibition.
    - (c) Both of the above programmes offer the definite advantage of being based on systems about which a good deal is known analytically, though we realize that the knowledge in each case is of a somewhat different nature.

#### K. Open Questions to Consider in the Future.

1. Can multistability exist in systems with distributions of delays?
2. What is the connection between the existence of statistical periodicity and the generation of patterns in coupled map lattices? Originally we hedged our bets in Losson et al. [31], but recently

JL told MCM that he was convinced that there was a strong connection. Check with him to find out why, etc.

3. Integrate and fire models (like the RED/WHITE/BLUE) model show cycling through activity patterns that have the same period but which change details depending on the initial condition given to the system. MCM thinks that this is evidence for the existence of statistical periodicity of **measures** which could be developed along the lines of Chapter 12 of Lasota and Mackey [25].
4. What is the connection between the development of a pattern and a concept? What does this question mean?
5. If a “neurologically motivated” coupled map lattice were constructed, would it have the behaviour of statistical periodicity?

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