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Information coding, processing and transport by means of phase-coupled neurons

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Abstract—In biological neural networks, the noise component is often of a size comparable to the - under these conditions not so well defined - signal strength. This and the as yet unexplained computational efficacy of biological systems is of particular interest to technical applications, since miniaturization drives hardware chips naturally towards conditions where noise and precision need to be complementarily used, to encode and process information. Our theoretical explanation of how this can be achieved is based on weakly coupled neurodynamical limit-cycles. In order to account for physiological conditions, we investigate the properties of locking in nontrivial network structures and draw conclusions on the optimal organization of neural networks, if information processing is by means of phase locking. We find that the network structure has a decisive role on the laws of information transport in such systems.

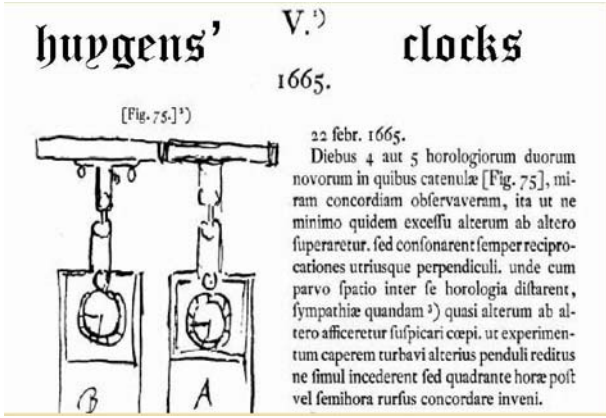
huygens' V.[1] clocks
1665.
[Fig. 75.][2]
22 febr. 1665.
Diebus 4 aut 5 horologiorum duorum novorum in quibus catenulæ [Fig. 75], miram concordiam obſervaveram, ita ut ne minimo quidem exceſſu alterum ab altero ſuperaretur. ſed conſonarent ſemper reciprocationes utriusque perpendiculi. unde cum parvo ſpatio inter ſe horologia diſtarent, ſympathiæ quandam [3]) quasi alterum ab altero afficeretur ſuſpicari cœpi. ut experimentum caperem turbavi alterius penduli reditus ne ſimul incederent ſed quadrante horæ poſt vel ſemihora rurſus concordare inveni.

Figure 1: Huygens' clocks, jointly suspended from a common construction.

1. Introduction

In 1657, Christiaan Huygens [1] revolutionized the measurement of time by creating the first working pendulum clock. In early 1665, he discovered ".. an odd kind of sympathy perceived by him in these watches [two pendulum clocks] suspended by the side of each other." The pendulum clocks swung with exactly the same frequency and 180 degrees out of phase; when the pendulums were disturbed, the antiphase state was restored within a half-hour and persisted indefinitely. Huygens deduced that the crucial interaction for this effect came from "imperceptible movements" of the common frame supporting the two clocks.

These observations are part of a set of properties that are generic for any weakly coupled limit-cycle systems: 1) Phase and frequency locking, 2) Farey-tree ordering of winding numbers, 3) devil's staircase structure of locked intervals [2]. These properties distinguish synchronization among limit cycles from synchronization among chaotic systems. In the latter case, the nonlinearity is usually maximally chosen, in order to generate chaotic individual systems. Coupling then leads to a synchronization hyperplane for the symmetric solution, which is, upon a further increase of the coupling, usually lost by means of a blow-out bifurcation [3]. In the coupling of the limit cycles, the systems that synchronize are generally not identical, which gives rise to higher-dimensional periodic solutions rather than to synchronized chaotic solutions. Here, an infinity of states of synchronization is primarily due to the individual frequencies of the limit cycles, and not so much to the nonlinearity. The nonlinearity resides in the coupling, and can be chosen arbitrarily small.

2. Chaotic neurons or not?

The question of whether neurons can be chaotic in themselves, or not, has not been answered so far. Selverston et al. [4] have found that somatogastric ganglion cells can behave chaotically. However, the questions of how realistic their experimental situation is and how significant these neurons are for cognition, appear difficult to assess. We have shown [5] that connected neurons in slice, when driven by constant currents, engage in locking. For this system, we have identified the Arnold tongues along which these lockings emerge, by using experimentally derived phase-return functions

$$f : I \to I : x_{i+1} = x_i + \Omega + g(K, x_i), \qquad (1)$$

where $x_i \in I = [0, 1]$ is the phase of the incoming perturbation with respect to the system perturbed, Ω is the ratio of the firing frequencies of the two involved neurons, K their interaction strength, and $g(x_i) = T(x_i)/T_0$ is the phase response function. This function indicates to what extent the interval T_0 between two adjacent firing events is modified

by a perturbation of strength K arriving at phase x_i [5]. For inhibitory pair-coupling, the phase-return function can become chaotic. This, however, only at very high interaction strengths on a small, though nonzero, part of the parameter set [5]. On one hand, this justifies the analytical modeling of pyramidal neurons by means of limit cycles, on the other hand it also yields insight into the ways these neurons could use to encode and process arriving information. One may, however, argue that these experiments poorly correspond to the realistic biological behavior, as the quasistatic conditions used in these experiments are difficult to find within the ever-varying currents characteristic for the in vivo brain.

To investigate the validity of these arguments, we have studied neuronal in vivo time series. We found regular and chaotic responses where of the samples, $\sim \frac{1}{3}$ was low-dimensional chaotic; $\sim \frac{1}{3}$ was high-dimensional with no real scaling properties, and $\sim \frac{1}{3}$ showed random spiking behavior many of them with long-tail distributions [6]. From our in vitro experience, we attribute this to network-induced effects. The first two groups we believe to be generated by chaotic modulations of the network input (potentially even of endogenous origins), whereas for the last group we believe local interactions with no dominating contributions to be responsible. We therefore investigated whether freqency and phase locking could emerge for biologically strongly connected detailed neuron models when driven by temporally strongly variable currents, and found this indeed to be the case [8]. In comparison to the corresponding slice experiments, the stabilization, however, appears to be delayed, as if a mechanism were built into the biology dedicated to a faster stabilization.

3. Physiological basis of phase-locking

The outcome of these experimental and numerical experiments indicates that locking could provide a valuable means for information coding, in the frequency as well as in the temporal coding sense. The question of whether the brain uses a frequency or a temporal code has been discussed fiercely, but is still not resolved. Our work shows that locking provides a mechanism that is working in both paradigms, in particular as quite generally phase-locking is accompanied by frequency-locking (see Fig. 2). The only necessary condition for locking to take place is a sufficient distinction between the modulations of the driving and the neuron's intrinsic firing frequencies, and a separation into weak and strong inputs. As a realization of this paradigm, many of the weak synapses could drive the neurons, whereas strong ones – or a few synchronized ones – would provide the locking. As the mechanism for establishing this, synaptic plasticity emerges.

Locking among biological neurons thus requires a degree of separateness between CLT-like noisy drivings, and strongly coordinated pulses among the locked neurons. Is such a situation likely to occur, taking into account the physiological facts? It has recently been observed that when a neuron is stimulated according to some regular pattern (as would emerge yet from very weakly locked neurons), this may trigger LTP and STP mechanisms, which may facilitate the synapses' efficacy by a factor of 1.5 [7]. I.e., locking is a self-enhancing process, up to the extent allowed by this factor. In the Arnold picture, this effect can be associated with an increase of K by an identical factor. Yet another observation in the field of physiology comes at the aid of the proposed mechanism. In hippocampus, two clearly distinguishable classes of synapses emerge, that differ in their release probability by a factor of about 6, which also should transfer into similar classes of efficacy. The percentage of efficient synapses is relatively small ($\sim$ 15 vs. 85%), which seems compatible with the situation we envisage. If we have about 100 active synapses of small efficacy from estimated $50 - 100$ neurons needed for the firing of the target neuron, already one strong synapse (or a small number of temporally synchronized strong synapses) could indeed be sufficient for leading to the above-outlined situation.

4. Nontrivial topologies of phase-locked networks

Bi-directional coupling: The described locking among neurons – in biophysically crude and detailed models – has been tested so far only for the most simplest topology, the mono-directional coupling between two neurons. For temporally interluding mono-directional coupling, we would have to deal with two phase-return functions

$$f^1 : x^1_{i+1} = x^1_i + \frac{1}{\Omega} - g^2(K^1, x^1_i),\ f^2 : x^2_{i+1} = x^2_i + \Omega - g^1(K^2, x^2_i).$$

For truly bi-directional coupling, the phase-return functions changes [9] into

$$f(x_i, s = 0) = \frac{1}{\Omega} g^1(\Omega(g^2(x_i) - x_i) - g^2(x_i) + x_i, \qquad (2)$$

where $s + 1$ counts how many times neuron 1 spikes before neuron 2 spikes. The above given map for $s = 0$ can be used to define more complicated interactions involving multiple interspike perturbations recursively: If $f(x_i, 0) > 1$ then $s = 1$, if $f(x_i, 1) > 1$, then $s = 2$, etc. Using this approach, we can prove that both neurons will display the same qualitative firing behavior (periodic, quasiperiodic, chaotic). They cannot display chaotic behavior if none of them is supercritical. For two excitatory neurons, chaos therefore cannot be generated. A unique stable solution emerges for two inhibitory or two excitatory bi-directionally coupled neurons. However, uniqueness will fail for excitatory/inhibitory coupling, if the excitatory neuron has a larger period than the inhibitory neuron [8].

Chains and rings of length three: Chains and rings of length three constitute the next-complicated case. Here, the motion is confined to a 3-torus that can be reduced

by means of a Poincaré section to a 2-torus. The 2-dimensional torus map could now, in principle, display chaos, even if it is invertible. This, however, happens only within the fully locked region on a very small set of systems. The nature of the points in the set is that of unstable periodic orbits, giving rise to structurally unstable, unobservable, chaotic motion. The number of elements to be synchronized offers the possibility of partial or complete phase locking. In the first alternative, only two of the three neurons are phase-locked. As in the case of two neurons, the phase-locked regions can be described by a generalized Fairy construction for three relatively prime frequencies $\{p_x, p_y, q\}$. The quasiperiodically forced circle map

$$x_{i+1} = x_i + \Omega_i + \frac{K}{2\pi}\sin(2\Pi x_i) \bmod 1, \qquad (3)$$

with Ω_i a quasiperiodic sequence, falls within this type of topologies, as it can be viewed as the case of a neuron perturbed by two other ones by means of equal perturbation strength. However, also more general types of interaction are described by the Fairy paradigm. When translated into geometrical language, the latter implies that on all commensurate lines of frequencies, there exists a partially phase-locked strip. At intersection points of the latter, completely phase-locked states emerge. Only if the two perturbing inputs of a single neuron do not communicate, their Lebesque measure will be zero. Because of the underlying common building principle, one can assume that the metric properties between the different topologies (directed, bi-directional, ring) can be continuously transformed one into another by means of variation of their connection strengths [9].

5. Computation by phase-locking

Locking among neurons can be understood as a computation by which, from two frequencies, the periodicity of the locking emerges as the result. This paradigm has important features that seem to make it attractive as a model of general biophysical computation. First, the way the result is encoded is Huffman-like. With the largest measures of the input spaces, the simplest result (period one, having the shortest respresentation) is associated. Moreover, this result also is the most stable with respect to perturbation by noise. Second, the result is invariant with respect to a common driving of the inputs. From an axiomatic formulation of the computation in neuronal networks, this would emerge as an obvious postulate. We note that this property in particular requires sufficiently linear input/frequency relationships of the computational elements. That this is indeed the case has been verified in detailed neuron models (see Fig. 2). Third, as a result essentially of the first property, the computation is self-refining. Given a longer time, or higher firing frequencies when sweeping over the input relationships, more details, i.e. higher periodicities indicating a refined computation, can be resolved (see Figs. 2, 3).

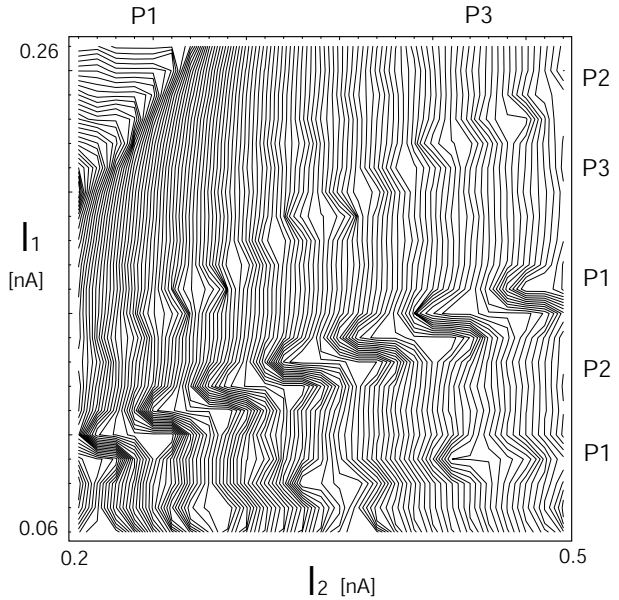

Figure 2: Frequency locking among detailed neuron models driven by inputs I_1, I_2, using the NEURON simulation environment [10]. Stripes of periodicities are labeled by their periodicity P, see [8].

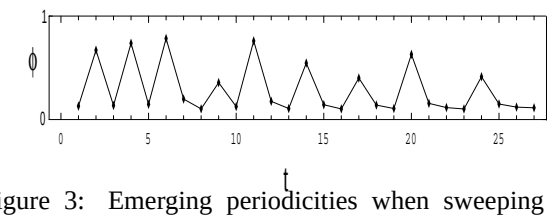

Figure 3: Emerging periodicities when sweeping over Ω (one frequency was held fixed, the other was varied). For faster sweeping, only the most fundamental frequencies would be detected, for higher frequencies (or slower sweeping), more details of the Fairy ordering would emerge [8].

6. Transport of information

Transport of information in phase coupled map lattices is in remarkable contrast to that found in chaotic maps, which is why we recollect the properties of the latter quickly. In map lattices of chaotic maps, the information transfer increases with the number of connections. In a nearest neighbor coupled map network, the speed of information transfer can be calculated by the spreading of the wave front initiated by perturbing the original system and comparing it with the unperturbed one [11]. It can be shown that the speed of the information transfer originates from two contributions, the instability of the individual lattice map and the Gaussian spreading contribution. Using the convective Lyapunov exponent μ, the critical velocity emerges as

$$v^* = (4D\mu)^{\frac{1}{2}}, \qquad (4)$$

where D is the diffusion coefficient that can be calculated from a Markov model of the perturbation, using a one-dimensional random walk. By performing the analysis for bi-power adjency topology, it is found that fractally coupled networks that have next-neighbor coupling in the vicinity and power-law decaying far connections, minimize the number of connections needed to attain a given velocity. They are superior to single power-law networks on the one hand and to next neighbor networks on the other hand, where the latter network emerges as the least efficient network type.

The above result already indicates that a constant propagation speed as defined above, cannot be obtained from phase-coupled map lattices. How then can information, expressed as the result of such computations, be transported through the network? First, we investigated directed phase-coupled chains. In the beginning, the neuron periods are chosen arbitrarily from the interval $[0.95, 1.05]$ and the perturbation strengths from $[0.4, 0.8]$. After an initial transient, all neurons fire regularly, with individual frequencies. Mimicking an arriving signal, the input period to the first neuron is then varied within $[1, 2]$. When using equal frequencies and a quasiperiodic golden-mean signal, we find that mono-directional chains and bi-directional rings display very different transport properties. Whereas in the first case the readability of a transmitted code falls off with the order of the neighbor according to a power law, in the bidirectional ring, the corresponding property obeys an exponential law.

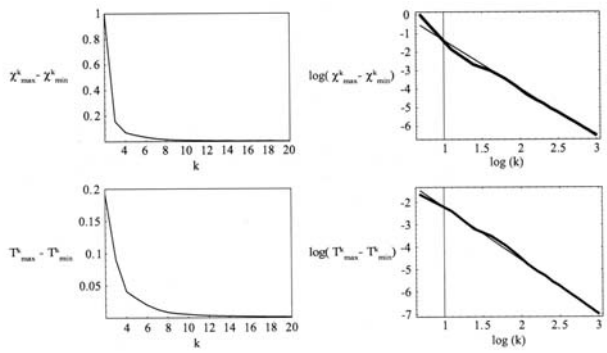

Figure 4: Decay of the information as a function of the neighbor distance k. The maximal phase difference $x^k_{max} - x^k_{min}$ (the maximal interspike interval difference $T^k_{max} - T^k_{min}$, respectively) is evaluated as a function of the neighborhood k. A power-law decay is found for linear directed chains [9].

7. Recurrent networks

This result can be interpreted from the point of view of computation. In biology, computation means the destruction of information. Writing down the inputs to the computation would in principle allow reversible computing. However, in the context of biology, where ressources are handled with care, we consider this to be a non-typical case. Rather, we should assume that in biological networks the information will wear out across the different computational units. The obtained results corroborate this point of view. A typical topological setting for biological neural networks are recurrent networks. In the simplest forms, these can be approximated by the bi-directional ring topology mentioned above. The fact that for this network an exponential decay is found, can be interpreted in the computational context as an indication of the superior computational potential of recurrent network topologies that is generally attributed to these systems.

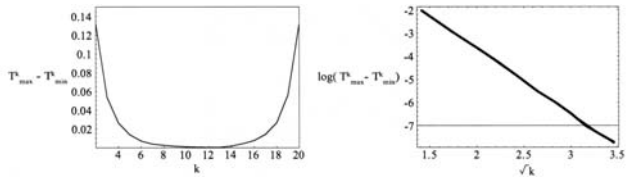

Figure 5: Decay of the information as a function of the neighbor distance k. The maximal phase difference $x^k_{max} - x^k_{min}$ (the maximal interspike interval difference $T^k_{max} - T^k_{min}$, respectively) is evaluated as a function of the neighborhood k. An exponential decay law is found for bi-directional rings [9].

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