Where noise and precision join forces: Coding of neural information via limit cycles

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Abstract—In biological neural networks, the noise component often is of the same order as the signal strength. This, and the (as yet unexplained) computational efficacy of biological systems, is of particular interest for technical exploitation, since miniaturization drives hardware chips naturally towards these conditions. We discuss a framework in which noise and precision are complementarily used to encode information. Our approach is based on weakly coupled neurodynamical limit-cycle solutions, which are investigated under natural conditions of transient temporal behavior. We have developed tools to show that locking is preserved under a large variety of such conditions, although in these cases the locked states are difficult to assess. We find that the range of conditions under which coding by locking is operational, is large enough for a realization in nature, hinting at a large potential also in technical applications. The described coding mechanism may be fundamental for achieving the highly efficient computations observed in biological systems.

1. On neuronal limit-cycle firing

Driving of neurons by means of constant currents leads to oscillatory behavior. However, different mechanisms may be behind this phenomenon, which leads to differing stability properties of the oscillations. This is of paramount interest in the context of neuronal firing, as they largely determine the responses to perturbations arriving at the neuron in the form of spikes. The most common type of neuronal oscillatory behavior is generated from a limit-cycle solution. Limit cycles are of interest because of their relation to noise. Noise is an ubiquitous phenomenon in biological neural networks. For a limit-cycle solution, a particular stability property must be satisfied. Whereas $n-1$ stability exponents must be contracting, the largest one is of marginal type, pointing into the direction of the flow. Limit cycles are a typical nonlinear phenomenon. Whereas for linear systems, the behavior is determined by the vicinity of the origin, limit cycles are spatially extended regions of stable behavior, with the origin being unstable. In dimension one or two, flow limit cycles are forbidden by the so-called Bendixon-Poincaré theorem [1].

How does limit-cycle firing of neurons emerge from subthreshold behavior? As the simplest alternative, neurons
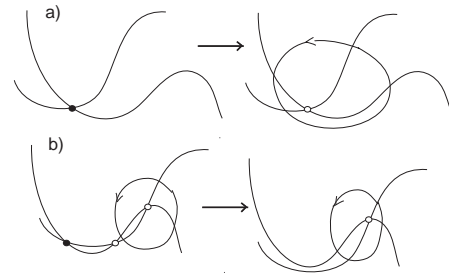

Figure 1: Scheme of the birth of limit cycles in 2-d, a) by a Hopf bifurcation, b) by a saddle-node bifurcation. Nullclines ($dx/dt = 0, dy/dt = 0$) are drawn. Open circles: unstable, filled circles: stable fixed points.

may undergo a Hopf bifurcation, which naturally leads to limit cycles. This is what happens for a Hodgkin-Huxley (H.-H.) [2] neuron. In this case, the oscillation starts at a nonzero onset frequency Ω (called hard onset, class II oscillations [3-4]). The intrinsic example for this phenomenon is the differential equation [5] $\dot{z} = (\mu + i\omega_{ch})z - |z|^2 z, \quad z(t) \in \mathbb{C}$, where ω_{ch} is the natural frequency of the oscillation and $\mu \in \mathbb{R}$ denotes the bifurcation parameter. In the presence of a forcing, an additional term $Fe^{i\omega t}$ appears on the rhs. The above equation is the generic system displaying a Hopf bifurcation: For $\mu < 0$, the solution $z(t) = 0$ is a stable fixed point, whereas for $\mu > 0$, the fixed-point solution becomes unstable and a stable limit cycle of the form $z(t) = \sqrt{\mu}e^{i\omega_{ch}t}$ appears. However, in most observed neuronal firing, firing starts at arbitrarily low frequency (soft onset, class I oscillations [3-4]), which implies that the oscillation is likely to be generated by a saddle-node bifurcation, an alternative mechanism generally leading to limit cycles.

2. Experimental proof of the limit-cycle property of pyramidal neurons

As the exact equations of biological neurons are unknown, any information reducing this lack of knowledge is highly welcome. Of particular interest is whether the firing is actually based on a limit-cycle solution, or whether this is not the case. In the following, we will provide evidence on different levels that biological neurons are indeed on limit-

cycle solutions, if the driving is not too wild so as to impose its own nature. As we are unaware of the existence of an explicit proof for the limit-cycle property of cortical neurons, we provide it here for pyramidal neurons [6]. This proof is by the experimental evidence that coupled biological neurons lock along Arnold tongues [7], a phenomenon unique to limit-cycle solutions. To this end, regular pulses were put on the axon of a neuron that was connected to a target pyramidal neuron. The latter was also driven by a current at, however, differing frequency. When sweeping over the product space of the frequencies, we observed the typical locking along Arnold tongues, see Fig. 2 [7]. The figure was obtained from experimental pulse experiments with pyramidal neurons from the rat somatosensory cortex. From these, a prototypical phase-response map was derived and used for the generation of the Arnold tongues. When the experimental neurons were swept across the tongues, they reliably fired according to the theoretical predictions, see Fig. 3. This proves that the pyramidal neurons are on limit-cycle solutions indeed.

The above insight into the nature of cortical neuronal firing is nontrivial, because a neuron, when on a limit-cycle solution, ideally combines noise and precise timing, in the following sense. The noise can be thought of as the driving source for the neuron, if it follows a central limit theorem (CLT) behavior closely enough. Superimposed on noise, the neuron emits and receives precisely timed firing events. Provided that one agrees that precise timing has a meaning for the cortex, the exact relationship between the spikes emitted can be understood as a coding scheme. Information can always be understood as a departure from background behavior, in a statistically significant way. This is achieved in the locking paradigm by setting off precise timing against noisy driving. For an illustration, assume for the moment temporally piecewise constant currents. By means of a second neuron (locked to the first), driven by an alternative current strength, the analogue information is converted into an essentially digital one, namely the periodicity of its firing:

$$Coding: \quad currents \ \{I_1, I_2\} \quad \rightarrow \quad periodicity \ p_2.$$

In this way, the amount of a current driving a neuron is coded with reference to the current driving the target neuron. As the outcome, the encoded information is of analog and the coded information of digital type. Although there is an infinity of periodic solutions in the Arnold tongues, the velocity of the sweep limits the detected periodicities to the most fundamental ones. Note that also the firing frequency follows this scheme. Being mostly thought of as analogue quality when seen as the input, it becomes a digital one, when seen as the output. In fact, the effective emergent firing rate is organized along a devil's staircase. The generated coarse graining is destroyed when many neurons from different areas impinge on one single neuron. Their input then generally approximates well an analogue driving current, as we will discuss in the next section.
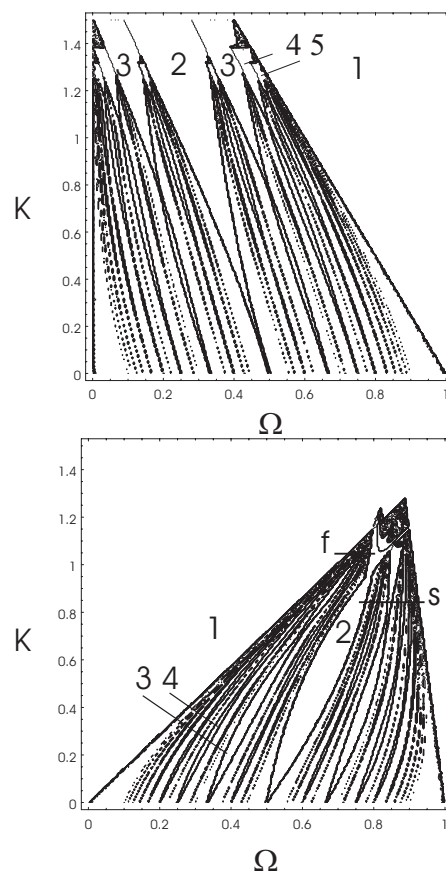

Figure 2: Arnold tongues of locked behavior (above: excitatory, below: inhibitory, one-sided interaction), as a function of the quotient Ω between the two intrinsic firing frequencies, and the strength of the coupling (i.e., the synapse) K. The numbers indicate the order of the generated periodicities, letter s the direction of the sweep of Fig. 3.

3. Supporting physiological evidence

The more separated the analog aspect is from the digital one, the better the composed scheme works. 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 [8-9]. 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. Properties of Arnold coding

As has been worked out earlier, the Arnold coding scheme has optimality properties that are reminiscent of the Huffman code. The largest coding area correspond to the simplest code of a period 1, the second largest to period 2, and so on. This not only applies to the coding area, but also to temporal aspects: When sweeping over the tongues (i.e., when the relationship between the two neurons changes), the code is self-refining in the following sense. With a fast sweep, only the lowest periodicities are probed (see Fig. 3). An increase of the firing rate, with a fixed velocity of the sweep, then is tantamount to a decrease of the effective velocity of the sweep, which now allows witnessing also of very high periodicities, that before were missed.
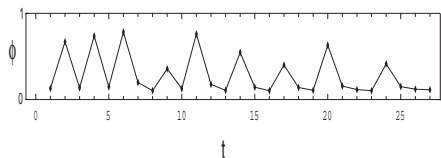

Figure 3: Sweep over inhibitory tongues with a biological neuron, across the cut s in Fig. 2. The phases ϕ indeed show repeated periodicities 2,3,4,5, as predicted by the Arnold tongue paradigm.

5. Limit-cycle and coding stability under modulated driving

These attractive features suggest that Arnold coding could play a prominent role for the efficiency of cortical information processing. Moreover, the above sweeping experiments suggest that the Arnold coding scheme is sufficiently robust to also be effective in the context of non-quasistatic situations. To investigate this important aspect in more detail, we performed numerical experiments. In a first set of experiments, we simulated H.-H. neurons that were reciprocally excitatory/inhibitory coupled via α-type synapses. For the neuron indexed by 1, this modifies the normally constant driving current to

$$I_1(t_1)(1 - sp(sp_2 - t_1)), \tag{1}$$

where $sp(t) = gp \cdot te^{-t/0.5} + 2$, $gp = 0.5$, and sp_2 is the time when neuron 2 emitted the last spike. For the first experiment, we chose constant currents $I_1(t) = 15.2$, $I_2(t) = 45.5855$ and observed, as can be expected from the Arnold tongue structure, periodicity 2. In order for locking to be a valuable coding scheme, we have to verify that the limit cycle is sufficiently stable with respect to varying driving currents, which is the situation encountered in nature. To this end, we drive the previously constant currents $I_i(t)$, $i = 1, 2$, by a function $d(t)$ common to both, which leads to the currents $\tilde{I}_i(t) := d(t)I_i(t)$. Examples of driving currents are shown in Fig. 4. If the driving is sufficiently variable, this is still equivalent to a CLT driving [6] and the locking is preserved, as it is when the driving is sufficiently slowly varying.

Arnold coding only fails in an intermediate range when the modulation substantially interferes with the neuron's own firing frequency. In this case, "broad" interspike interval distributions are generated. Because of the strong response and suppressed adaptation, this is the preferred experimental situation, although from the point of view of the working brain, it is probably as inadequate as it could be.
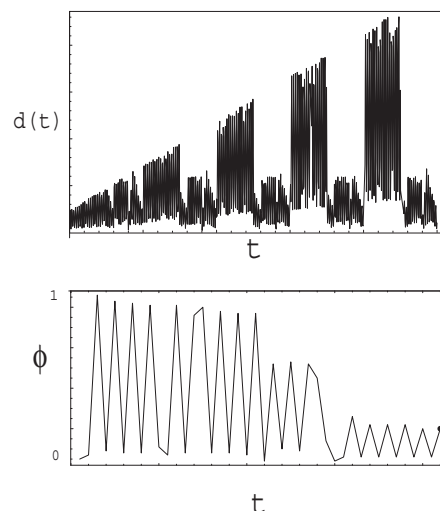

Figure 4: Even wildly varying driving $d(t)$ a) of currents generate locked interspike intervals b) if the driving is applied to both neurons, but scaled down for one of them by a factor determining Ω (in our case: $\Omega \sim 1/2$). The same behavior is obtained for slowly modulated driving currents. Only when the driving current's modulation is of the order of the neurons own preferred frequency, the locking breaks down. ϕ: phases at perturbations.

6. Is Hodgkin-Huxley good enough?

The H.-H. model is a rather simple neuron model that disregards, e.g., the spatial aspects of the biological neu-

rons. Therefore, the question is appropriate to what extent the obtained results can be considered relevant. Moreover, by its onset of oscillations via a Hopf bifurcation, the H.-H. model is unable to generate interspike interval distributions that come close to biological ones. From the biological point of view, the H.-H. model has one major advantage and one major shortcoming. The shortcoming is that its variance on the interspike interval length is strictly bounded by its onset frequency, due to its Hopf-type birth process. Together with the refractory period, this limits the variability of interspike intervals so much that it is impossible to model realistic distributions that often even show broad distributions of Lévy type. With the Morris-Lécar model, however, this shortcoming can be removed. This point seems to have been partially overlooked even in investigations that have this issue as the focus. The major advantage of the H.-H. model is at the same time that it starts at nonzero frequency. This yields a current-frequency (I/F) relationship that has a relatively constant slope. This property comes in support of a coding scheme that ideally would have the frequency relationship $\Omega = f_1/f_2$ be directly transcribed into the equivalent relationship between the driving currents I_1, I_2. The latter obviously is the case if they are based on a linear I/F relationship.

To investigate whether these issues play a part in nature, we repeated the previous experiments with the Morris-Lécar neuron model and with detailed neuron models using the environment NEURON [10]. The results confirm the validity of the coding scheme, by showing locking over huge linear areas of the $I_1 \times I_2$ parameter space. A curvature that could be introduced by the nonlinearity of the I/F-curve does not play a significant role. It is largest at the onset (which generally can be considered as abrupt-like) and in the saturation regime. In the latter, however, further effects need to be taken into account as well, the most relevant of which are counteracting this disturbance (e.g., improved synaptic efficacy, leading to an increased K). It is worthwhile noting that the Arnold tongues for the detailed neuron model match extremely well with the one obtained from biophysical measurements [6-7]. With these neuron models, it is even possible to generate broad distributions as observed in nature, by locked states. This is achieved by using a vastly-varying driving current at fixed ratio for the two neurons, visiting in particular, areas of low spiking frequencies. For an outside observer, without the knowledge of the driving, it is impossible to infer that the neurons are in the locked state.

We know that in the brain, frequency as well as spike-time coding is used. For the latter, however, only ungeneric models have been presented so far. The presented model provides a framework that is not only based on a generic phenomenon, it also combines the two coding aspects, frequency and precise timing. How from this the increased efficiency emerges that characterizes the brain will be the focus of another contribution.
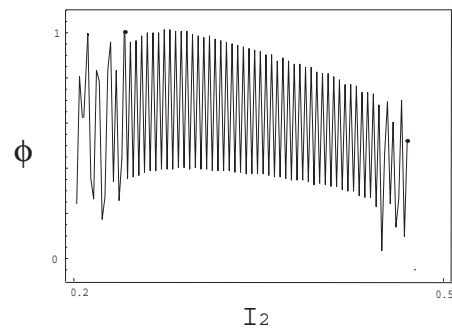

Figure 5: Emerging phases ϕ show that period-2 locked behavior persists over a huge range of driving currents I_1, I_2, if the ratio $I_1/I_2(\sim \Omega) \simeq 1/2$ is maintained (from detailed compartmental neuron modeling using NEURON).

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