

Oscillations can reconcile slowly changing stimuli with short neuronal integration and STDP timescales

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Abstract

Oscillatory brain activity has been widely reported experimentally, yet its functional roles, if any, are still under debate. In this review we argue two things: firstly, thanks to oscillations, even slowly changing stimuli can be encoded in precise relative spike times, decodable by downstream “coincidence detector” neurons in a feedforward manner. Secondly, the required connectivity to do so can spontaneously emerge with spike timing-dependent plasticity (STDP), in an unsupervised manner. The key here is that a common oscillatory drive enables neurons to remain under a fluctuation-driven regime. In this regime spike time jitter does not accumulate and can thus be lower than the intrinsic timescales of stimulus fluctuations, which leads to so-called “temporal encoding”. Furthermore, the oscillatory drive formats the spikes in discrete oversampling volleys, and the relative spike times between neurons indicate the eventual differences in their activation levels. The oversampling accelerates the STDP-based learning for downstream neurons. After learning, readout only takes one oscillatory cycle. Finally, we also discuss experimental evidence, and the question of how the theory is complementary to the so-called “communication through coherence” theory.

Keywords: *Network models, oscillations, spiking neurons, synaptic plasticity*

The problem: continuous signal transmission through spikessystems (Eeckman, Frank H., Ed.)

Consider a problem that neurons might be faced with: to transmit with as less loss as possible a continuous signal – their input currents – through the output spikes. Let us assume that to do so, they are able to adapt their thresholds.

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Rapidly fluctuating input

If the input signal varies rapidly, that is with timescales not much longer than the membrane time constant τ_m (~ 20 ms), one appealing option is to select a high threshold. This way input remains subthreshold most of the time, with occasional short suprathreshold peaks. Such a regime is called a “fluctuation-driven”, or “coincidence detector” regime (as opposed to respectively a “mean-driven”, or “integrator” regime). This option of a high threshold is illustrated in Figure 1(A): two neurons receive the same rapidly fluctuating input, plus some independent noise. Mean input remains subthreshold. In this regime, jitter does not accumulate across output spikes, the times of which are thus precise (Abeles 1982; König et al. 1996; Brette and Guigon 2003; Brette 2012). Hence these spikes reliably and rapidly signal the suprathreshold peaks. Another advantage of this regime is that initial conditions are quickly forgotten. The main disadvantage, however, is that, most of the time, the input current remains subthreshold and thus cannot be transmitted. Therefore this regime is most suitable for signals that are temporally sparse.

Another option, illustrated in Figure 1(B), is to select a low threshold, so that input remains suprathreshold most of the time. This constitutes a mean-driven (or integrator) regime. Jitter accumulates and so individual spike times make little sense. For example, two identical neurons that receive the same suprathreshold signal, plus an arbitrarily weak independent noise, may end up completely desynchronized (Brette and Guigon 2003), in agreement with experimentation (Mainen and Sejnowski 1995). Only spike counts over long time-windows that contain several spikes, say of ~ 100 ms or above, make sense, and allow the recovery of the (low pass filtered) input signal. In other words, only rate coding is possible, which is only suitable for slow processing. Note that we included this option for the sake of completeness; in the brain, however, neurons appear to operate mainly in the fluctuation-driven regime – not in the mean-driven regime (Abeles 1982; König et al. 1996; Rossant et al. 2011; Brette 2012).

Slowly fluctuating input: a common rapidly fluctuating drive can help

What if the input signal is constant, or varies much more slowly than τ_m (say with frequencies of at most ~ 1 Hz for $\tau_m \sim 20$ ms)? Then whatever the threshold, the suprathreshold periods will last, and this in turn leads to jitter accumulation. Furthermore, even the first spikes after threshold crossing tend to be highly jittered (see Figure 1C). It appears then that the only option is rate coding. Unless neurons receive, in addition to their (subthreshold) individual inputs, a common rapidly fluctuating drive. This way the total input current can be subthreshold most of the time, but with short suprathreshold peaks (see Figure 1D,E,F), leading to the fluctuation-driven regime. In such a scenario, spikes are confined to the suprathreshold peaks, and relative latencies between neurons reflect differences in the slow signal magnitudes (Thorpe 1990; Buzsáki and Chrobak 1995; Hopfield 1995; Mehta et al. 2002; Brody and Hopfield 2003; Buzsáki and Draguhn 2004; Lisman 2005; VanRullen, Guyonneau, and Thorpe 2005; Schaefer et al. 2006; Markowitz et al. 2008; Masquelier et al. 2009b). The (relative) input signal

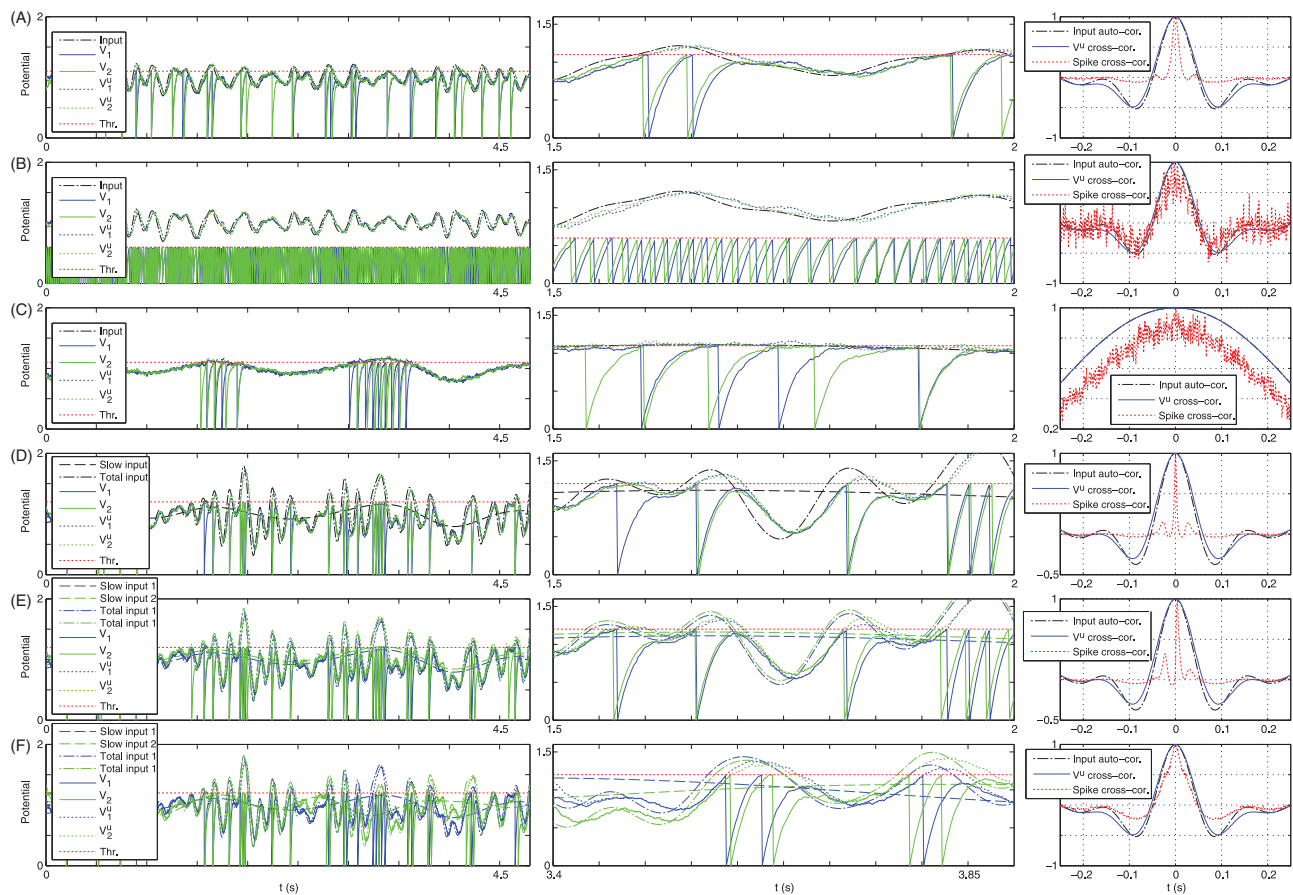


Figure 1. Current-to-spike transformation by leaky-integrate and fire (LIF) neurons (see Methods for details). Each line corresponds to a different scenario. Left column shows the time courses of input currents ("Input"), membrane potentials ("V") and unconstrained membrane potentials ("V^u")

Continued

that ignores the threshold. The horizontal dotted line is the threshold ("Thr."). Middle column zooms in on a subperiod for clarity. Right column shows auto- and cross-correlations of input and output signals (to focus on their timescales rather than on their magnitudes, we have normalized them: their maximum is always 1.0). (A) Fluctuation-driven regime with a rapidly fluctuating input. (A-Left) Two identical neurons receive the same input: a 2-8 Hz band-pass filtered white noise, plus some independent white noise. Mean input (1.0) is below threshold (1.1). (A-Middle) The two neurons tend to spike synchronously. (A-Right) Unsurprisingly, input auto-correlation has timescales corresponding to the 2-8 Hz band. V^u is nothing more than a running average of the input current, with exponentially decaying weights (with timescale $\tau_m = 20$ ms). Thus the cross-correlation between V^u and V^u has timescales that are only slightly longer than those of the input. Interestingly, spike time cross-correlations can have much shorter timescales, because spike time precision only depends on the noise level – not on the input timescales. In particular, when noise level goes to 0, precision converges to 0 ms rather than to the input timescales (Brette 2012). Here this precision is down to ~ 10 ms, whereas the timescales of the input signals are much longer (~ 125 -500 ms) which means, by definition, that there is "temporal encoding" (Theunissen and Miller 1995; Butts et al. 2007). (B) Mean-driven regime with the same rapidly fluctuating input, but the threshold is now 0.6. (B-Left and Middle) The input strength modulates the spike rates, but because of jitter accumulation, individual spike times are not reproducible. (B-Right) Input and V^u are the same as in (A), therefore their correlations are the same. Yet spike time cross-correlations now have much longer timescales, only reflecting the input's ones. (C) Slowly fluctuating input. The input is now a 0.25-1 Hz band-pass filtered white noise. (C-Left and Middle) Even with a high threshold (1.1), subthreshold peaks are long enough to suffer from jitter accumulation (note: output spike rate is already very low (~ 3 Hz), and most of the input signal is lost, therefore selecting an even higher threshold is not really an option here). Furthermore, since input slope when crossing threshold is typically low, even the first spikes are already highly jittered. (C-Right) Input auto-correlation and V^u cross-correlations now have much longer timescales (corresponding to the 0.25-1 Hz band). Spike time cross-correlation timescales just reflect the input's ones. (D) Slowly fluctuating input + rapidly fluctuating common drive. The neurons receive the same slowly (0.25-1 Hz) fluctuating input as in (C), plus an additional rapidly (2-8 Hz) fluctuating drive. (D-Left) The total input is subthreshold on average, but with short suprathreshold peaks, avoiding jitter accumulation (D-Middle) The two neurons tend to spike synchronously, as in (A). (D-Right) Again spike cross-correlation timescales are much shorter than input signal's: there is temporal encoding. (E) Two shifted slowly fluctuating inputs + rapidly fluctuating common drive. Here neurons 1 and 2's slowly fluctuating inputs differ by a constant (0.05 a.u.), while the rapidly fluctuating drive is the same for both neurons. (E-Left and Middle) Due to the shift, neuron 2 tends to fire shortly before neuron 1. (E-Right) As a result, the spike time cross-correlogram peaks at a non-zero lag (here + 4 ms). (F) Two slowly and independently fluctuating inputs + rapidly fluctuating common drive. (F-Left) Neurons still tend to fire together. (F-Middle) Taking a closer look, one can observe that the relative latencies tend to reflect the relative magnitudes of the slow signals: on the left part of the plot Slow input 1 > Slow input 2, and neuron 1 fires before neuron 2. On the right part it is the opposite. (F-Right) Since the input signal magnitude ratio varies, so do the spike time lags between neurons, leading to a broader peak than in (E).

magnitudes can thus be rapidly extracted from the relative latencies of the first spikes that follow the suprathreshold peaks, without having to count spikes on long time-windows, as in the above-mentioned mean-driven regime. The temporal resolution of the readout is given by the prominent frequencies of the common drive, which, by definition, are faster than the stimulus frequencies, thus leading to oversampling.

To summarize, a common fluctuating drive is a way to encode slowly changing stimuli (or even static) in discrete spike volleys with precise relative spike times (~ 10 – 20 ms or below). As we will see, this precision enables rapid feedforward decoding via spike timing-dependent plasticity (STDP) and coincidence detection. Importantly, periodicity of the fluctuating drive is not required to get precise relative spike times (Nikolić et al. 2012). In the remainder of the paper we use the term “oscillations” without implying periodicity – a common practice (Nikolić et al. 2012). Finally, although we have thus far been considering continuous individual input currents and common drives, these currents are, in fact, thought to be generated by (possibly numerous) incoming spikes, with each spike leading to a (possibly tiny) excitatory or inhibitory post-synaptic current.

Experimental evidence and the reference-time issue

Our hypothesis H in this paper is that, thanks to a hidden oscillatory drive, a static or slowly changing stimulus is encoded in discrete spike volleys with reproducible relative spike times. To test H experimentally one must simultaneously record multiple neurons to determine whether time-lags between neurons are reproducible and stimulus-dependent. This approach was taken by ref. (Schneider et al. 2006; Havenith et al. 2011), and this indeed showed evidence for H .

If only one neuron is recorded, then an intermediate step might be to use a prominent local field potential (LFP) oscillation as reference-time. If we assume that this oscillation corresponds to a common input for several neurons (even if in practice only one is recorded) – a debatable hypothesis given the controversies about the origin of LFP, see for e.g. ref. (Rasch et al. 2009; Zanos et al. 2011) – then reproducible and stimulus-dependent spike phases, a phenomenon referred to as “phase-of-firing coding” (PoFC), implies reproducible and stimulus-dependent time lags between these neurons. The converse, however, is false, so the approach might be missing some evidence for H (if the LFP turns out not to reflect a common input). It thus should be used with caution. That being said, evidence for PoFC has been accumulating. It was first observed in the rat’s hippocampus, where spike phases with respect to theta oscillations encoded the animal’s position (O’Keefe and Recce 1993; Mehta et al. 2002). More recently, it has been observed in the somatosensory (Siadatnejad et al. 2013), auditory (Kayser et al. 2009) and visual (Montemurro et al. 2008; Vinck et al. 2010; Tureson et al. 2012) modalities of mammals.

In some cases, oscillations come from a certain overt sensor sampling cycle, allowing the testing of whether with respect to this cycle spike phases are reproducible and stimulus-dependent. This appears to be so in the case of sniffing in the olfactory system (Cury and Uchida 2010; Shusterman et al. 2011), whisker movements in the rat’s somatosensory system (Panzeri and Diamond 2010),

or licking in the gustatory system (Gutierrez et al. 2010). In vision, it has been suggested that saccades or micro-saccades play a similar role (VanRullen et al. 2005; Masquelier 2012; Martinez-Conde et al. 2013). To our knowledge, however, any direct evidence for latency coding with respect to (micro) saccade landing times is lacking.

Finally, it should be noted that if the oscillatory drive is not phase-locked to the stimulus, then the spikes are not stimulus-locked either. So using the stimulus onset as a reference-time may fail to reveal evidence for H (Masquelier 2013).

A possible variant: binary coding

In some cases spikes lock to an LFP oscillation, yet the preferred phases do not vary with the stimulus (Jacobs et al. 2007; Ray et al. 2008), which rules out PoFC. However, it is possible that certain neurons remain silent during certain cycles, indicating weak individual input. In principle then, some information about the stimulus should be inferable just by looking at the set of neurons that fire at least one spike during a cycle (ignoring their phases). This is referred to as binary coding. To our knowledge, however, direct evidence for this in oscillatory regimes is inexistent, although the scheme is theoretically appealing (Shamir et al. 2009). It is worth mentioning that binary coding cannot be evidenced using “spike-centered” measures (e.g. spike-triggered average, spike-field coherence). It can only be evidenced using a LFP-triggered window (e.g. ± 10 ms of a peak), a stimulus-triggered window in case of stimulus-locked oscillations, or, when simultaneously recording multiple neurons, a population-triggered window (e.g. around a population activity peak as in ref. (Panzeri and Diamond 2010)).

STDP-based decoding

If we now admit that H is true, how could the information in the relative spike times be extracted by downstream neurons? That is, how could those downstream neurons selectively respond to certain stimuli, or to certain features of stimuli? And how could they learn to do so? It turns out that all that is needed is STDP.

Whenever the slowly changing stimulation corresponds to a particular spatial pattern (“the target”), the oscillations generate similar spatiotemporal spike volleys (Masquelier et al. 2009b). So when the target appears frequently and/or stays for a long time, the corresponding spike volley is repeated many times (oversampling), allowing the downstream neurons equipped with STDP to become selective to such a repeating spike volley, thanks to feedforward coincidence detection, in an unsupervised manner (Masquelier et al. 2008; Masquelier et al. 2009a; Gilson et al. 2011). Importantly, a teaching signal is not necessary, although such a signal, if available, could certainly facilitate the STDP-based learning (Legenstein et al. 2005; Legenstein and Maass 2006; Franosch et al. 2013), and so could a simple reward signal (Izhikevich 2007; Legenstein et al. 2008; Pawlak et al. 2010; Cassenaer and Laurent 2012).

To summarize, the oscillations could be a way to “repeat” a stimulus several times, even if it only appears once, thereby accelerating its STDP-based memory encoding. Consistent with this idea is a growing body of experimentalevidence

in animals and humans that demonstrates that successful long-term memorization correlates with increased oscillatory activity across a broad range of frequencies (from theta to gamma), and in both the sensory and associative areas (Jensen et al. 2007; Klimesch et al. 2008; Tallon-Baudry 2009; Benchenane et al. 2011). Interestingly, and also in line with our proposal, beyond the mere oscillation power, what appears to be a prerequisite for successful memory formation is that single units must be phase-locked to the oscillation (Rutishauser et al. 2010).

Finally, it is worth mentioning that STDP-based decoding is only a possibility. To discriminate the oscillation-generated spike volleys, other biologically plausible learning mechanisms could be used, especially when a teaching signal is available (Gütig and Sompolinsky 2006; Ponulak and Kasiński 2010; Florian 2012; Yu and Ferster 2013). Yet, to our opinion, these mechanisms are not as well established as STDP. Furthermore, the fact that STDP-based decoding can work without supervision is appealing. Lastly, STDP has another desirable effect in oscillatory regimes: it stabilizes the firing phases (Cassenaer and Laurent 2007), thereby enabling robust PoFC.

Communication through coherence

Thus far, we have only considered one “pool” of neurons that all receive a common oscillatory drive. Let us now consider two pools, A and B, each oscillating at the same frequency. A projects on B, but A’s output spikes significantly influence B neurons if, and only if, they arrive during a critical period of excitability. Thus, by shifting the phase between the pools, one can virtually activate or deactivate the communication link between the pools. In other words, rhythmic synchronization allows the flexible routing of information between neuron pools. This is known as the “communication through coherence” (CTC) hypothesis (Fries 2005). It is still somewhat speculative today, but data at least consistent with the proposal has been accumulating (Womelsdorf et al. 2007; Colgin et al. 2009; Bosman et al. 2012; Koralek et al. 2013).

CTC and our hypothesis H are complementary: CTC suggests a way to temporally activate a directed communication link between two pools $A \rightarrow B$. Once this is achieved, H explains how information could be transmitted in the relative spike times. Additionally, B neurons could extract this information thanks to STDP, which would shape the $A \rightarrow B$ synapses accordingly. Let us now imagine that the $A \rightarrow B$ link is temporally deactivated. A fundamental issue is the extent to which the $A \rightarrow B$ synapses would be altered by STDP during the deactivation period, possibly leading to catastrophic forgetting. More research is needed to address this issue.

Methods

Below are the details of the numerical simulations of Figure 1. We have used Leaky Integrate-and-Fire (LIF) neurons, of which the membrane potential V obeys the following Langevin equation:

$$\tau_m \frac{dV}{dt} = -V + I(t) + \sigma \sqrt{2\tau_m} \xi$$

Table 1. Numerical parameters.

Common	
Mean input $\overline{I(t)}$	1.0 (arbitrary units)
σ	0.02 (a. u.)
τ_m	20ms
Bandpass filter	Butterworth (order: 10)
Scenario A	
Input frequencies	2–8Hz
Standard deviation of $I(t)$	0.1 (a. u.)
Threshold	1.1 (a. u.)
Scenario B	
Input frequencies	2–8hz
Standard deviation of $I(t)$	0.1 (a. u.)
Threshold	0.6 (a. u.)
Scenario C	
Input frequencies	0.25–1Hz
Standard deviation of $I(t)$	0.1 (a. u.)
Threshold	1.1 (a. u.)
Scenario D, E, F	
Slow input frequencies	0.25–1Hz
Slow input standard deviation	0.1 (a. u.)
Fast drive frequencies	2–8Hz
Fast drive standard deviation	0.3 (a. u.)
Threshold	1.2 (a. u.)

Where τ_m is the membrane time constant, $I(t)$ the input, $\xi(t)$ a Gaussian white noise (with $\langle \xi(t) \rangle = 0$ and $\langle \xi(t)\xi(s) \rangle = \delta(t-s)$), and σ the resulting standard deviation of the membrane potential. Whenever V reaches the threshold, it is instantly reset to 0, and the integration starts over (for simplicity's sake we have ignored the refractory period).

All the numerical parameters are gathered in Table 1.

Conclusion

In many cases the world around us evolves in timescales in the order of a second or more. It follows that to optimally average-out noise, the brain should accumulate evidence over such long timescales before coming to a decision. This is possible by using a neural network with strong recurrent connectivity, and slow NMDA currents (see (Masquelier et al. 2011) and references therein). In this article, we have suggested that in a number of cases an alternative strategy is used. Oscillations cut the input into discrete oversampling “snapshots”, the duration of which is compatible with feedforward neuronal integration and readout. This scheme, although being more sensitive to noise, has two main advantages: the first one is higher reactivity (classic speed-accuracy tradeoff); and the second one is that, due to the oversampling, the same stimulus tends to get “repeated” many times over, thereby facilitating its STDP-based long-term memory encoding.

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