I Got Rhythm: The Significance of Synchronized Neural Spiking

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ABSTRACT

When a population of neurons fire (spike) synchronously (within a millisecond), the information in the resulting pulse travels as fast as any information can in the brain. The information that can be carried in such a pulse is restricted to the identity of the neurons whose firing contributed to the pulse and the time of the pulse. Nonetheless, because of the reverberant characteristics of neuro-glial circuits, temporal information can be encoded spatially and transmitted in a pulse.

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What is the question to which the answer is: Synchronous firing of neurons in the brain? Wolf Singer (1999) phrases the question a little differently, noting that "The evidence for an internal coordination of spike timing raises the question of whether it serves a function in cortical processing or whether it is merely an epiphenomenon." The answer is: Both.

It serves a function and it is an epiphenomenon, which is to say that its significance is to be found at a different level of analysis. The function it serves is to enable patterns of information to move through the brain at maximum velocity, but it is no more than an epiphenomenon of the leaky-integrate-and-fire nature of neurons.

Consider: when a population of neurons fire synchronously, their outputs arrive synchronously as inputs to the set of target neurons to which that population connects. From the standpoint of an individual target neuron, pre-synaptic inputs have maximum effect (and thus, most rapid effect) when they arrive simultaneously. Accordingly (at least in the general case, because the target neurons could be in a refractory state under certain circumstances), if the synchronously arriving inputs are sufficient by themselves to trigger a significant (however defined) population of the target neurons, those target neurons will fire synchronously and the process repeats with respect to the next target neurons. Abeles (1982) called this a "synfire chain."

What is important to note here, is that there is no faster way for information to propagate through neuro-glial circuits in the brain than via this cascading action of an incoming synchronous "wave" of spikes incident upon a target population triggering an outgoing synchronous wave of spikes and the entire process repeating itself some number of times. As long as each group of synchronized depolarizations is sufficient in and of itself to trigger another such group in its target neurons, the information carried by the synchronized neurons will propagate as swiftly as possible, picking up and being transformed by information currently in the neurons and glia it propagates through.

Suppose there are pre-existing excitatory post-synaptic potentials in some neurons in the target population of a pulse. The arrival of the pulse may cause some of those "primed" neurons to fire immediately even though the pulse would not be in and of itself capable of triggering them. The primed neurons recruited by the pulse become a full-fledged part of the resulting pulse that propagates to its next target(s). In effect, a pulse can "read out" information from its target population. In like manner, pre-existing inhibitory post-synaptic potentials in the target population, by suppressing the firing of neurons that would otherwise be triggered by the excitatory spikes in a pulse, can also modify the information carried by the pulse when it passes through.

The fact that synchronized firing takes place within a population of neurons and glia does not, of course, mean that the same neurons are involved every time a synchronization phenomenon occurs. What the phenomenon assures is that whatever subset of neurons are caused (by whatever circumstances) to fire synchronously, the information carried by the distribution of those neurons (that is, which particular neurons fired synchronously) becomes privileged in the sense that it has the potential to propagate more rapidly than unsynchronized co-temporal information.

A pulse arriving at a target population may be unable (for whatever reason) to trigger an outgoing pulse. If it cannot, its information load has been delivered and will persist for some time in the form of excitatory or inhibitory post-synaptic potentials in its target population. The information in the pulse is thus available to shape or contribute to a subsequently arriving or occurring pulse.

A pulse may be excitatory or inhibitory (or both, for that matter). The key characteristic is just that the pulse gets there fastest. But, note that an inhibitory pulse does not have the ability to propagate beyond its target neurons (except indirectly as discussed below). By implication, the fastest way to turn something off—to stop the music, as it were—is with a sequence of excitatory pulses culminating in an inhibitory pulse.

If the target neurons of an inhibitory pulse are themselves inhibitory, the result of the arrival of the pulse would be synchronous disinhibition (really a misleading term because it suggests an effect as rapid as either excitation or inhibition, which I don't think it is—correct me if I'm wrong), better: synchronous cessation of inhibitory spikes. If there was no signal being inhibited at the next stage, the pulse stops here. If there *was* something being inhibited, then that something can now start having whatever effect it has, but it doesn't necessarily start as a synchronized pulse.

Let's formalize the terminology. Consider a population of brain neurons *B* and a subset of that population *b*, where *b* contains a "significant" number of the neurons in *B*. A pulse *p* is created when every neuron in *b* depolarizes (spikes) exactly once at time *t*. As a practical matter this should be taken to mean that every neuron in *b* spikes within an operationally definable (probably sub-millisecond) time interval centered on the time *t*. The requirement for "significance" is an attempt to establish at least a subjective distinction between an event in which two or three neurons in *B* just happen to spike simultaneously and an event in which a large number (however judged) of neurons in *B* spike simultaneously.

A minimum requirement for "significance" might be that the activity from a pulse must propagate with minimum delay through the target population(s) of neurons. That is, to be considered a pulse, incoming synchronous activity (however triggered) must give rise immediately to outgoing synchronous activity.

Note that the information carried by the pulse is just the composition of *b*, that is, which neurons of *B* were triggered simultaneously (and, implicitly, *when* the triggering took place, although I don't think that is significant in and of itself, because it is always the same, i.e., one spike propagation interval ago. Any significance *when* acquires is purely contextual, that is the effect of a pulse is shaped by whatever else is going on at its target *at the time the pulse arrives*. I realize this is tendentious, but it deserves consideration.).

Summarizing thus far: pulses are the fastest way information can propagate in the brain, and the *only* information they can carry is the identity of the neurons that spiked in the pulse.

This does not, however, imply that temporal information is not or cannot be transmitted in a pulse. Maass, et al. (2003) have shown that a realistically modeled recurrent spiking neural network containing a pitifully small number of neurons (compared to the real world) can maintain unstructured (by design) information for at least (order of) three seconds. So, a pulse originating in a population of neurons could communicate (order of) three seconds of (processed) information all at once. Note that what would be transmitted in the pulse is a spatial pattern, part of which encodes a temporal stimulus history. With time represented spatially, diachronic stimuli can be processed synchronically. This capability is, of course, really handy for, *inter alia*, things like phoneme/spoken word recognition and object from motion extraction, etc.

And what's going on in those three seconds or so? Presumably (after Hopfield (1986) and many others) the activation pattern is moving toward an attractor state (established by some "learning" process akin to Hebb's (1949)) where the "computational energy" of the (local) neuro-glial circuitry will be locally minimized. Perhaps an additional characteristic of the circuitry is this: As an activation state evolves towards an attractor state, the closer it gets, the more likely it becomes that activity associated with the attractor state will become synchronized. How might that happen?

In the discussion so far, we've looked at what happens once a pulse is triggered (there's no magic in the word "triggered," it's just shorthand for whatever happens, the result of which is a pulse). We've noted that the arrival of a pulse p_{in} at *B* may create a continuation pulse p_{out} from *b*. But besides resulting from the arrival of a preexisting pulse: How else does a synchronized pulse start?

Obviously, there is no general answer: a pulse could begin in response to synchronized onset of an external stimulus or because random activity in some group of neurons and glia just happened to create one. Still, because of the fast-track privileges a pulse enjoys, it does not seem unreasonable to think that evolution would have found a way to take advantage of it and to set things up so that initial pulses are produced other than just randomly. Having mentioned glia, it occurs to me to propose that their ability to fine-tune activity at multiple nearby synapses (Fields & Stevens-Graham, 2002), in effect nudging the timing and/or strength of post-synaptic activity a little bit one way or the other, plays a role in the triggering or suppression of pulses.

Singer (1999) and others have noted the existence of oscillatory neural circuits and these also could serve to help collect ongoing activity into a pulse once the activity gets "close" to forming a pulse. The idea is that if a neuron were just a bit shy of depolarizing, the arrival of a "timing" spike might be enough to trigger a depolarization and if timing spikes were themselves synchronized and relatively widely distributed and the number of neurons in the "almost" state was large enough, a significant pulse could be started in synchrony with the timing spike.

Actually, any broadly distributed spike would do the trick, but depending on a spike from a single neuron is fraught with danger—what if it gets hit by a cosmic ray and dies? So, neuro-glial assemblies that send out timing pulses seem like a much better bet.

In computer systems the technique of checking at regular intervals to see if anything is ready to be processed—polling—is a well-known technique for dealing with data that arrive over time but need to be processed as a unit. Moreover, read-out pulses from neuro-glial assemblies targeting differing (possibly overlapping) sub-populations can in effect "read out" different pieces of information from a larger population, thus providing a kind of feature extraction. Properly timed, such multiple read-out pulses could accomplish time-division multiplexing as envisioned by Singer (1999).

Because the information transmitted in a pulse is (by definition) processed all together by the target neurons of the pulse, one may think of the information in each pulse as being "bound together" in the pulse. However, each time an incoming pulse gives rise to an outgoing pulse, the information in the pulse changes. I am firmly convinced that the brain does not just relay information at synapses. Rather, each population of neurons in a synaptic chain transforms its inputs in some significant way into its outputs. If no transformation is required, there is a direct connection without intervening synapses.

Information processing in the neuro-glial circuits of the brain is characterized by the continual transformation of stimulus information into response information. Recurrent connections and synaptic modifications over a wide range of time scales ensure that the transformation takes into consideration the history of the organism over the same range of time scales. In this context, the creation and propagation of synchronous pulses takes place at the smallest time scale and thus provides the fastest path from stimulus to response. As such, it is key to the just-in-time processing that the brain must always provide.

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