The timing game

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In two publications presented as a contest, Hopfield and Brody propose a mechanism for detecting groups of neurons receiving similar levels of sensory input.

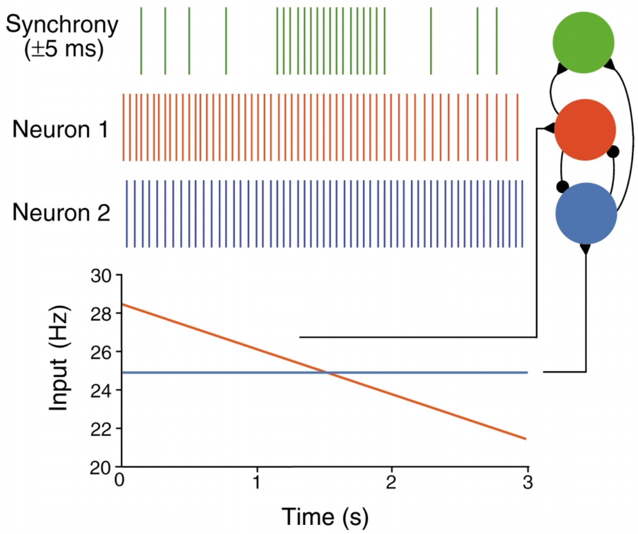
Over the past few months, the neuroscience community has been experiencing, or perhaps has been the subject of, a novel experiment in the presentation of scientific results. I refer, of course, to 'The Contest' proposed by John Hopfield and Carlos Brody. For those unaware of this event, Hopfield and Brody built a model network with interesting properties[1], but rather than discuss their work in a conventional manner, they described its 'anatomy,' 'physiology' and 'behavior,' more or less as if it were a real organism. The information provided included a basic circuit diagram, characteristics of individual model neurons, and responses of the system to various inputs. Hopfield and Brody then challenged the community to figure out how the model worked based on these data. A web site was set up, on which contestants could experiment with the model[2], and prizes were offered. Hopfield and Brody revealed the details of their model only recently[3]. I will discuss the contest and its winners[4] in due course, but first the science.

The output neurons in Hopfield's and Brody's model respond selectively to input representing the word 'one', even if it is spoken at different speeds and by different speakers. But at the heart of the model is a solution to a much simpler problem. How can the nervous system determine if a group of neurons is firing at the same rate? Hopfield and Brody's answer is, try to synchronize them. Neurons that are firing at the same rate can be synchronized simply by shifting their spike trains relative to one another. Even weak excitatory or inhibitory synaptic inputs can generate such temporal shifts and induce synchrony. On the other hand, getting neurons with different firing rates to fire together repetitively requires adding and dropping spikes; it cannot be achieved solely by shifting spike sequences. As a result, asking whether appropriately coupled neurons are firing synchronously is a sensitive way to determine if they are firing at the same rate.

The basic operating principle of the Hopfield–Brody model can be illustrated in a simple two-neuron circuit (Fig. 1). In this example, one neuron (blue) receives constant input current that would cause it to fire at 25 Hz in the absence of coupling. The other (red) receives a ramping input current that would cause its firing rate, if it too were uncoupled, to vary from around 28 Hz to about 22 Hz over the course of the run. The actual responses, indicated by the red and blue spike sequences, have slightly different firing rates than this, due to the presence of inhibitory synapses between the red and blue neurons. More importantly, the synaptic connections tend to make these two neurons fire synchronously, but only if their inputs are nearly equal. The green spikes show the response of a hypothetical downstream neuron (green) that only generates an action potential if the red and blue neurons fire within five milliseconds of each other. Aside from some chance coincidences, a period of synchrony is indicated by a burst of action potentials from the green coincidence-detecting neuron. This bursting only occurs if the red and blue neurons are receiving nearly identical inputs, inputs that would make them fire within about 1 Hz of each other if they were uncoupled. Thus, in this simple circuit, a coincidence-detecting neuron is able to determine very precisely whether the two interconnected neurons that drive it are receiving the same input.

The idea of using synchrony and coincidence detection to determine whether groups of neurons are receiving comparable inputs is likely to have a

Fig. 1. A simple model for detecting equal inputs through synchrony. Two integrate-and-fire neurons (red and blue) inhibit each other through synapses (filled circles) that generate postsynaptic conductances that peak 15 ms after a presynaptic action potential and then decay to zero with a time constant of 15 ms. (Similar models and their synchronization properties are discussed in ref. 5.) The blue neuron receives a constant input and the red neuron a ramping input (bottom). Input currents are reported in terms of the firing rates they would produce if the neurons were uncoupled. The output of the two-neuron circuit is read out by a hypothetical coincidence detector (green) that generates an action potential whenever its two inputs (red and blue spikes) fire within 5 ms of each other. The result is a burst of activity from the coincidence detector (green spikes) when the inputs to the two interconnected neurons are close to being equal.



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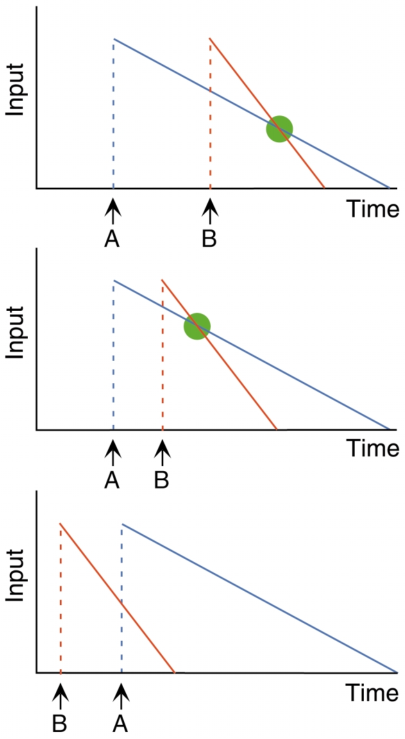

Fig. 2. Inputs for sequence detection. The inputs used in a Hopfield–Brody type model to detect the stimulus sequence AB over a range of interstimulus time intervals are illustrated. When stimulus A occurs, the input to the blue neuron (**Fig. 1**) jumps to a fixed level and then decays to zero. When B occurs, the input to the red neuron jumps to the same level but decays more rapidly. A coincidence detector, such as the green neuron (**Fig. 1**), will burst when the two inputs cross (green dots), which occurs whether A and B are separated by a long (top) or short (middle) interval, but not for the sequence BA (bottom).

number of potential uses. A simplified description of what Hopfield and Brody did with this idea is provided by Fig. 2. Suppose we wanted a neural circuit to signal whether stimulus A was followed, within a variable but limited time, by stimulus B. In the spirit of their more complex model, Hopfield and Brody would arrange, using additional circuitry, for the red and blue neurons in Fig. 1 to receive the input depicted by the red and blue lines in Fig. 2. When stimulus A is presented, the input to the blue neuron (the blue line) jumps to a fixed value and then decays slowly to zero. When stimulus B appears, the input to the red neuron (red line) jumps up similarly but decays more quickly. The crossing of the two input levels (green dot) signals that the sequence AB has occurred, independent, over a fairly broad range, of the precise time interval between A and B. The crossing never occurs for the sequence BA. Using the idea discussed in the previous paragraph, the crossing point for the two input levels can be identified by a downstream coincidence detector, which thereby serves as an interval- invariant (over a finite range) detector of the sequence AB.

Hopfield and Brody applied the idea of detecting crossing firing rates to auditory word recognition by constructing inputs with the characteristics of those in Fig. 2, but that were also selective to sound frequency. In this way, the events labeled A and B (Fig. 2) were generalized to onsets and offsets (through corresponding 'off' cells that responded to sound terminations) of sounds in various frequency ranges. The firing rate crossings, identified by coincidence-detecting output neurons, then indicated the presence of specific temporal features within a large number of different frequency bands of the sound being identified.

And what of the contest? A *New York Times* article made it widely known, and the contest web site received hits from over 20,000 different IP addresses, resulting in more than 5000 downloads of the original paper announcing the contest. Around 1500 experiments were run on the site. In the end, twelve people submitted entries discussing how they thought the model worked. (There were six additional entries to a second part of the contest asking entrants to build their own system.)

And the winner is…David MacKay and members of his group at Cambridge University, who submitted an impressive example of clear thinking and logical deduction. In setting up the contest, Hopfield and Brody stated that they wished to provide the neuroscience community with an exercise in deductive reasoning that had an obtainable and verifiable solution, something that is frustratingly lacking in work on actual biological systems. The entry of MacKay and collaborators shows that the solution was obtainable (actually with $n = 2$; Benjamin Rahn, a graduate student at the California Institute of Technology also came up with the solution), and is an exceptionally clear example of the type of reasoning Hopfield and Brody wanted to foster. Hopfield and Brody also set up the contest so that people could think about the model and the issues it raises on their own, even if unsuccessfully, before having the solution presented to them. In this sense, the real winners of the contest may not have been the people who won the prizes.

Reactions to the contest format through which Hopfield and Brody presented their work have been mixed. On one side, the contest was stimulating, challenging and fun. From my experience, it certainly made for a number of lively conversations. On the other hand, holding back knowledge somehow seems contrary to the spirit of free scientific discourse. The contest was proposed as an educational device, and it illustrates the difficulties inherent in mixing educational and research styles of presentation. Ironically, many commonly used educational techniques, such as withholding information for the purpose of challenging or testing students, clash with the standards of equality and openness that we strive for in scientific research.

As with any work in theoretical neuroscience, the ultimate judgment is whether the proposed mechanism is actually used in a biological system. It may prove challenging to make the synchronization and coincidence-detection mechanisms work in as noisy an environment as a cortical circuit, although Hopfield and Brody report positive evidence along these lines[1,3]. Independent of the contest, the proposed mechanism for detecting groups of neurons receiving similar levels of sensory input is a valuable addition to our knowledge of the computational capacity and strategies that neural circuits could and might use.

1. Hopfield, J. J. & Brody, C. D. *Proc. Natl. Acad. Sci. USA* 97, 13919–13924 (2000).
2. http://shadrach.cns.nyu.edu/~carlos/Organism/
3. Hopfield, J. J. & Brody, C. D. *Proc. Natl. Acad. Sci. USA* (in press).
4. http://shadrach.cns.nyu.edu/~carlos/Organism/Docs/winners.html
5. van Vreeswijk, C., Abbott, L. F. & Ermentrout, G. B. *J. Comp. Neurosci.* 1, 313–321 (1994).