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Exploring Another Metaphor

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[JIS, JCH] The development of scientific understanding must often navigate through tangles of seeming contradictions. A standard example is that of the nature of light. Is light a particle or a wave? In certain situations, light acts clearly as a particle, while in other situations it acts clearly as a wave. By now, physicists have dispensed with being disturbed by the situation, and have proceeded to alternate between the particle and wave descriptions when appropriate, with ease. It is a well-established fact that light is, in some sense, both a particle and a wave, and that this is not a paradox.

As arguments over the role of the cerebellum continue, the resolution will probably not lie in the victory of one group over another, but in the development of novel approaches to view the problem. The key is that "approaches" is plural. Complex systems have been characterized by need to use several different approaches in order to arrive at a complete understanding (Segel 1995). The central nervous system is certainly complex, and only the use of many different viewpoints will guide our path to understanding the functional role of the many components.

To eventually fit the pieces of the cerebellar picture together, the distinction must be made between *facts* and *metaphors*. Scientists are proficient in metaphors, without necessarily realizing it. However, metaphors are most useful when the scientist realizes that a description *is* a metaphor. While factual words may include "change", "pause", "correlate" (used with caution), "spike", etc., words used for metaphors include "teach", "learn", "unexpected", "pattern generator", "calculate", and "control". Does an underwater balloon "calculate" the water depth with its volume? Does an individual walking down the street "control" the air next to the body? For the nervous system, many words are used as *metaphors* to aid the human scientist in forming a conceptual picture.

Care must be taken when using computational metaphors as in the article by **Houk, et al.** The use of artificial neural networks continues to provide a great deal of insight due to the malleability of learning algorithms, but it is this advantage that can be misleading in applications to biological systems. Since artificial networks are able to simulate most nonlinear dynamical systems, simulations provide an un-disprovable hypothesis. The behavior of the network may not be dependent upon its architecture, but may be simulating a system that was unimagined by its designers.

Another metaphor suggested by the cerebellar data is resonance. Taking seriously the subthreshold oscillation that is well supported by the olivary cells' internal physiology leads to a metaphor of many oscillators, oscillating at physiological resonance, with a phase reset by stimulation. This cellular resonance approach yields, on an ensemble scale, both rhythmic and "unexpected event" behaviors (McCollum 1995).

On an ensemble level, we have also developed a method to classify the rhythmic behavior of dynamic biological networks (Roberts 1995) that can be used to probe questions concerning the climbing fiber system of the cerebellum. Given the known synaptic connections and cellular properties of the anatomical modules described in **Simpson et al.** (Fig. A), one may delineate all possible rhythmic patterns for a single module or several modules coupled together. Although individual modules can readily oscillate independently, this behavior is suppressed when modules are linked together by gap junction in the olive, or convergence in the cerebellar nuclei.

The results of this investigation are displayed in the figure (B and C). The rhythms generated by the cellular and synaptic properties of the circuit form clusters in the space of all possible rhythms. The members of each cluster are superimposed where the nuclear cell sets the beginning of each phase (details of this method are given in Roberts 1995). Suitable time courses are assigned to each mechanism and the overall time of the cycle is normalized. The depth of each cell's activity is represented by how dark that sector of the phase is colored as the scale to the right of each phase diagram in the figure shows. Darker shading during any part of the cycle indicates that more reinforcing mechanisms are available to drive a particular cell's activity. Thus, one may interpret the shading as an indicator of the probability of cellular activity during each point of the cycle.

In Fig. B, there is only one cluster of 32 rhythms generated by the circuit with the added assumption that the olivary cells are oscillating. Without such oscillations, no rhythms are generated. These results suggest that the circuitry of the climbing fiber system can maintain rhythms if the neurons of the inferior olive are oscillating. The source of olivary oscillations is not addressed, but the rhythms favor synchrony of complex spike activity along parasagittal strips.

Simpson et al. report that there is no correlation between rhythmicity of complex spike activity and synchronous firing, so we repeated the analysis without the gap junction between the olivary cells and show the results in Fig. C. In this case there are 24 rhythms that fall into 8 clusters. Clearly, strict adherence to synchrony is broken as only one cluster of 8 rhythms shows the two Purkinje cell firing complex spikes together. It should be emphasized that since a network of five cells can have 362,880 possible rhythms, rhythmic behavior of the cerebellar modules is quite weak. This may explain why the phenomenon has been so elusive to experimental probes.

Since rhythmic behavior and synchrony appear to be inherent in the anatomical modules, it is difficult to draw conclusions about their functional significance. The behavior may simply reflect a property of the local circuitry rather than serve a global organizational function. Until a greater consensus about the function of the climbing fiber system is achieved, there is little that can be said for certain about this aspect of the system. Such a consensus can come about by recognizing the complementary aspects of different approaches and metaphors, rather than focusing on their conflicts.

References

[1] McCollum G. (1995) Climbing fiber ensemble activity indicated by receptive fields (submitted for publication).

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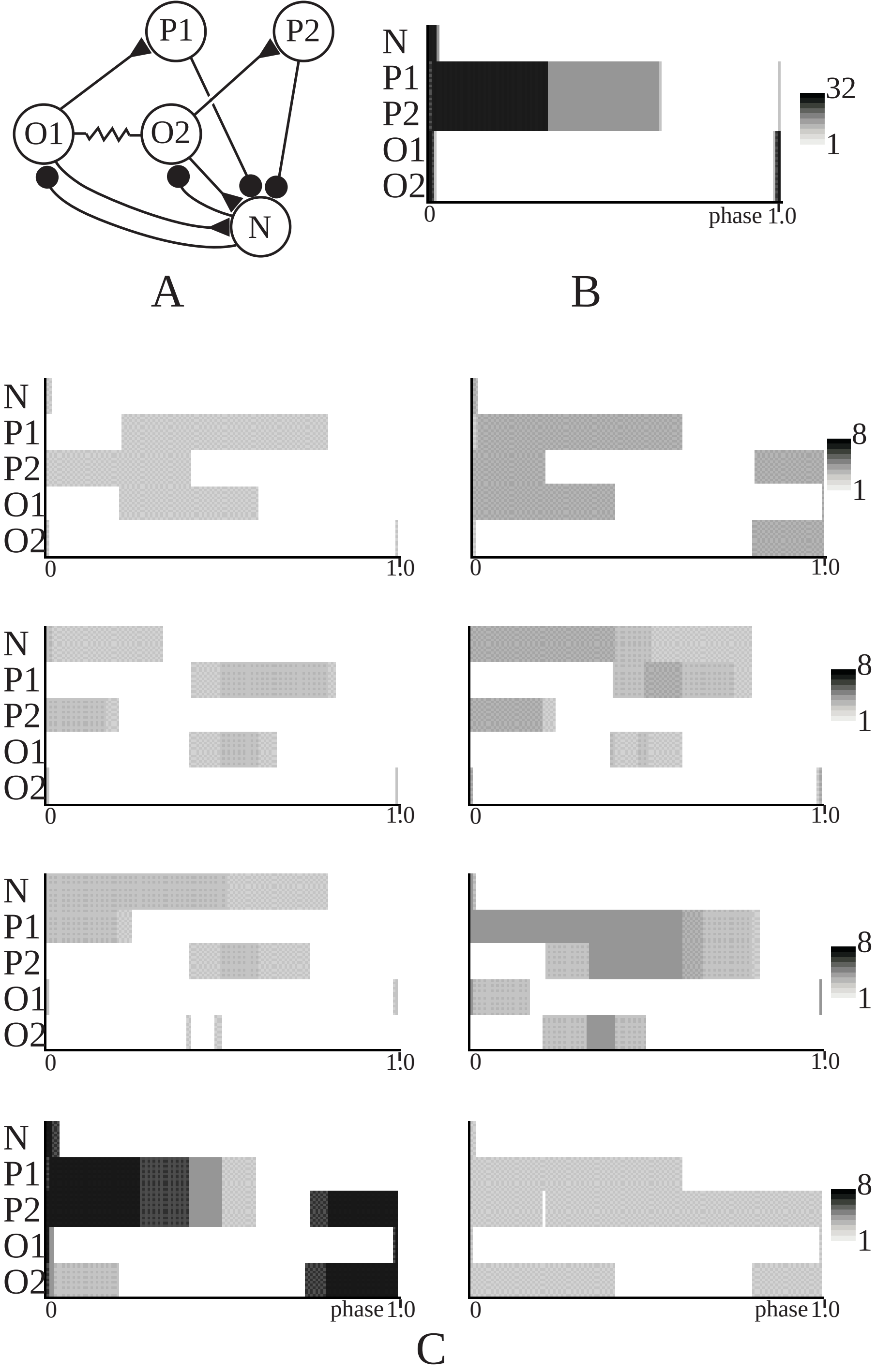
[3] Segel L.A. (1995) Grappling with complexity. *Complexity* **1** 18-25.

Figure caption:

Phases of neuronal activity in cerebellar anatomical modules. (A) Circuit diagram of two anatomical modules. Abbreviations: O1 and O2 are two olivary cells, P1 and P2 are two Purkinje cells, and N is a cell in the cerebellar nuclei. Synapses: Filled circles are inhibitory synapses, triangles are excitatory synapses, and the zig-zag (resistor) is a gap junction. (B) Phase diagram for superposition of rhythms in the cluster generated by circuit in A where the olivary cells are oscillating. (C) Phase diagram for superposition of rhythms in the 8 clusters generated by the circuit without the gap junction between the two olivary cells. See text for details.



P1
P2
O1
O2
N
A
N
P1
P2
O1
O2
0
phase 1.0
32
1
B
N
P1
P2
O1
O2
0
1.0
8
1
phase 1.0
C