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Neuromimes: Self-Exciting Alternate Firing Pattern Models

Perkel and Mulloney (1) described an elegant model for production of alternating bursts of impulses in a neuronal network. Models of circuits producing alternate single impulses go back to McDougall (2), who proposed separate continuous inputs to two neurons which mutually inhibit each other. Later, Reiss (3) reintroduced McDougall's ideas and modified his model to a reciprocally inhibiting pair of neurons driven by a common, constant frequency source. Using electronic neuron models similar to Harmon's (4) with a few modifications, we designed and tested three circuits exhibiting alternate firing patterns (5). Our purpose was (i) to arrive at a simple scheme that will simulate alternate firing and (ii), as suggested by Perkel and Mulloney (1), to create a self-exciting circuit. Our circuits represented one, two, and three neurons, and all but the oneneuron model can be triggered by a single pulse, whereupon the systems become selfperpetuating.

Figure 1a shows the output pattern of a self-exciting, three-neuron network. A single pulse input (Fig. 1a, top trace) to any one of the three neurons will trigger the system. Essentially the same network in the non-self-exciting mode was proposed

Fig. 1. Neuron schemes and alternate output patterns; solid circles depict inhibitory inputs, solid triangles excitatory inputs. Calibration bar, 300 msec. (a) Three-neuron model is triggered by single pulse (top trace) to any of the neurons 1, 2, or 3. Activity of neuron 1 is shown in second trace from top. Alternate firing of neurons 2 and 3 is shown in the bottom two traces. (b) Two-neuron model showing alternate firing (top two traces). Bottom two traces show inhibitory synaptic inputs to neurons 1 (bottom trace) and 2 (second trace from bottom). (c) Singleneuron scheme with branching axon. Top trace shows d-c analog of the cell body's firing frequency; second trace shows the exponential firing of the soma. Triangles 1 and 2 are frequency band-pass filters. The alternating outputs of the axon branches are shown in the bottom two traces

by Wilson (6) to explain motor neuron function in flight, and was later modeled by Harmon (7). The output of neurons 2 and 3 in Fig. 1a can be varied to give alternating bursts of various durations and pulse numbers by adjustment of synaptic input rise and decay times.

This network can be simplified for a two-neuron model (Fig. 1b). The two neurons are linked by mutual excitation and inhibition inputs. Adjustment of the characteristics of each pair of synapses impinging on one neuron produces an alternating burst output, as shown in the two upper traces of Fig. 1b. The inhibitory synaptic inputs to neurons 1 and 2 are shown in the lower two traces of Fig. 1b. To get an alternating output, the inhibitory input of neu-



ron 1 must be in phase with the excitatory input of neuron 2, while the two inputs to any one neuron must have a phase shift between them. Duration of bursts and degree of overlap of the output of the two neurons will depend on the phase shift between the inputs to each neuron. This model is very similar to the one proposed by Perkel and Mulloney (1). However, whereas their model is based on the postinhibitory rebound phenomenon, ours incorporates a biphasic (inhibitory-excitatory) synaptic input.

The scheme in Fig. 1c depicts a hypothetical neuron with two branches. Each branch is shown with a band-pass filter-a low-pass filter on the left and a high-pass filter on the right. Thus, the soma of a neuron which generates a sinusoidal frequency pattern (8) will show alternating bursts of spikes as an output of its two branches. The branch with the low-pass filter will pass the initial part of the sinusoidal burst cycle and then will reach its cutoff point, while the branch with the high-pass filter will pass the remaining high-frequency part of the cycle. The driving frequency can be varied to produce bursts of various durations, while the degree of burst overlap or delay between alternate bursts may be adjusted by the filter bandwidth Qfactor. Although this single-neuron model is hypothetical, different outputs from branches of one neuron have been described (9). This one-neuron scheme may be incorporated into the previous models to generate a self-exciting system, in agreement with Perkel and Mulloney's (1) proposal for systems without tonic driving inputs.

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We are pleased that Dagan et al. have found an earlier reference (1) than Reiss (2), whom we cited (3), on the production of alternating single impulses in a network of model neurons. The general properties of reciprocally inhibitory neuronal networks are discussed by Sherrington (4), who in turn cites a number of 19th-century examples of similar alternating behaviors, both experimental and theoretical.

We are also pleased that they have corroborated our statement [note 9 in (3)] that the precise mechanisms are not important for producing alternating burst patterns, but that the patterns "follow essentially from the phenomenon of burst production following cessation of synaptic inhibition." The biphasic inhibitory-excitatory synap-

Thermochemical Hydrogen Generation: Heat Requirements and Costs

The costs and energy requirements of the processes for thermochemical hydrogen generation presented by Wentorf and Hanneman (1) are so grossly underestimated that it is highly questionable whether these thermochemical processes can compete with other hydrogen generation techniques. To demonstrate this I will discuss process B presented in (1), although the comments apply equally well to the other two processes discussed by Wentorf and Hanneman and to very similar cy-

tic input of Dagan et al. is seen to be sufficient to produce a stable alternation of bursts. We have emphasized postinhibitory rebound (PIR) rather than such postulated components as high- and low-pass filters because PIR is a widespread phenomenon in many nervous systems and is a likely candidate for the mechanism underlying the production of such motor patterns.

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cles proposed in (2) and (3). The chemical reactions and the thermodynamic data used in (1) are given in Table 1, together with the estimated heat requirements.

A simple thermodynamic argument shows that, if the heat requirements and thermal efficiencies were really as reported by Wentorf and Hanneman, we could build a perpetuum mobile of the second type. Assume that we have three heat sources, at temperatures $T_{I} = 100^{\circ}$ C, $T_{II} = 350^{\circ}$ C, and $T_{\text{III}} = 600^{\circ}\text{C}$. We could now build a

| Table 1. Thermodynamic data and heat requirements from (1) | Table 1. | Thermody | ynamic data | and heat | requirements | from | (1 |). |
|--|----------|----------|-------------|----------|--------------|------|----|----|
|--|----------|----------|-------------|----------|--------------|------|----|----|

| Sten | Reaction | Reaction tempera- | Energies (kcal) for reactions as written | | Heat |
|------------|--|----------------------|--|--------------------|--------------------|
| 200p | | (°C) | ΔH° | ΔG° | requirements |
| B 1 | $2Cu(c) + 2HCl(aq) \rightarrow 2CuCl(c) + H_{a}(g)$ | 100° | -8 | 2 | |
| B2 | $4CuCl(c) \rightarrow 2CuCl_{2}(c) + 2Cu(c)$ | 30° to 100° | 30 | 38 | 30 kcal at 100°C |
| B 3 | $2CuCl_{2}(c) \rightarrow$ $2CuCl(c) + Cl_{2}(g)$ | 500° to 600° | 30 | 0 | 30 kcal at 600°C |
| B 4 | Cl ₂ (g) + Mg(OH) ₂ (aq) → MgCl ₂ (aq) + H ₂ O(<i>t</i>) + $\frac{1}{2}O_{2}(q)$ | 80° | -38 | -46 | |
| B 5 | $MgCl_{2}(c) + 2H_{2}O(g) \rightarrow Mg(OH)_{2}(c) + 2HCl(g)$ | 350° | 4 | 8 | 26.5 kcal at 350°C |
| Irrever | sible losses | | | | 15 kcal |
| Total h | neat input | | | | 101.5 kcal |
| | | | | | |

*The heat required for the production of 1 mole of H_2

power plant by using process B to split water, drawing heat Q from these reservoirs, and then reacting the hydrogen with oxygen in an ideal fuel cell, neglecting all irreversible losses. For each mole of H₂ produced we will get 57 kcal of electricity, using 30 kcal from source I, 26.5 kcal from source II, and 30 kcal from source III.

On the other hand, an ideal Carnot engine would generate only 37.4 kcal of electricity:

$$\Delta G = \Sigma Q_{input} (1 - T_{ambient}/T_{input}) = 30(1 - 300^{\circ}/373^{\circ}) + 26.5(1 - 300^{\circ}/623^{\circ}) + 30(1 - 300^{\circ}/873^{\circ}) = 37.4 \text{ kcal}$$

(where ΔG is the Gibbs free energy charge, and T_{ambient} and T_{input} are given in degrees Kelvin). Thus process B violates the second law of thermodynamics. What the authors neglect is the vast energies of separation [see (4)], which are even larger than appear from the above, as it is also necessary to generate the free energy lost in step B4. Otherwise, we could improve on the above perpetuum mobile by using step B4 to generate electricity in a fuel cell.

We have estimated the minimum separation work to be 37 kcal for process B and 45 kcal for process A. The separation processes generating this free energy are all carried out at low temperatures. In current practice, their real efficiencies ($\Delta G/Q$) are below 5 percent. The authors also underestimate the large irreversible heat loss incurred in heating the process streams to reaction temperature. The overall thermal efficiency for any of the three processes should be closer to 5 percent than to the 50 percent given.

Thermal efficiencies by themselves mean very little as no process can improve on the theoretical efficiency of electrolysis. It is the cost of obtaining it that counts. To put the cost in proper perspective, an ideal mass balance to produce 106 British thermal units (1 Btu = 0.95 kj = 0.25 kcal) of hydrogen fuel or 16 pounds (1 pound = 454 g) of H_2 is given below (the units are those used in American industry).

To produce 106 Btu worth, or 16 pounds of H_2 , we would have to hydrolyze about 0.4 ton (1 ton = 908 kg) of $MgCl_2$ at high temperature with steam; manufacture 1 ton of concentrated hydrochloric acid (30 percent); dissolve 0.5 ton of copper in hydrochloric acid; disproportionate about 1.6 tons of CuCl in aqueous dispersion into $CuCl_2$ and Cu, with all the associated steps; crystallize 1.4 tons of CuCl₂. 2H₂O in a multiple evaporator crystallizer; dry 1.4 tons of CuCl₂·2H₂O and drive off the water of crystallization; and melt, decompose, solidify, and cool 1.15 tons of CuCl₂—not to mention all the filtering,