Hebbian Reverberation in Small Idealized Networks

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Before Hodgkin and Huxley's experimental measurements and theoretical explanations of action potentials had reached textbooks (for example, Wenger, Jones, & Jones, 1956), the all-or-none phenomenon of action potentials was simply accepted as an experimental fact. Action potentials arose after sufficient stimulation, and the neurons of a network could contribute to each other's stimulation after axonal conduction delays and synaptic delays, to the extent permitted by absolute and relative refractory periods.

If powerful computers had been available at that time, the oscillatory behavior of simple hypothetical networks with multiple feedback loops might have been studied with computer simulations. Nonlinear dynamics had not yet taken shape as a separate mathematical discipline, but nonlinear mechanics was available in engineering and physical science. To aid in understanding the oscillations, they might have been regarded as approaching exactly cyclic oscillations similar to classical limit cycles. Such cyclic oscillations are here called cyclic modes. Apart from their representations in computers, cyclic modes are only abstract entities, but they may serve as explanations of observed or calculated oscillations. In particular, cyclic modes may elucidate the mathematical character of the reverberations hypothesized by Hebb (1949, 1972).

Does the concept of cyclic modes survive in the more complex realm of Hodgkin-Huxley theory? It is evident from a plot of a typical sequence of Hodgkin-Huxley action potentials in a multiloop network that the heights of the "all-or-none" spikes are not quite uniform, and this arises from slightly different circumstances in the development of the individual action potentials. Further, the spikes are not instantaneous, and therefore do not occur at precisely fixed times which would be referenced in checking for cyclicity. To pursue these questions further, they will be considered in the context of the GENESIS tutorial CPG (Bower & Beeman, 1998).

Adaptation of the CPG Tutorial

The CPG tutorial is presented as a simulation environment for studying the mathematical basis for central pattern generators (CPGs). CPGs generate oscillatory patterns of muscle activity for such functions as locomotion, breathing, chewing and scratching. But the CPG tutorial is written in a general form which permits wider application. In particular, the duration of stimulation can be shorter than the length of the run, so that sustained reverberatory activities can be studied. The biological existence of such oscillations is still in question, more than fifty years after Hebb's conjecture concerning cell assemblies (Seung, 2000). There are also conceptual difficulties. One is that it is not clear what would finally turn off reverberations. But reverberatory activity appears potentially so explanatory that it should not be neglected. Cyclic modes are clearly relevant to reverberatory activity. They are the nonlinear attractors which reverberations approach in the limit. (An intoduction to nonlinear dynamics is available in Kaplan & Glass, 1995.)

Some minor modifications have been introduced in CPG to tailor it to study of reverberations. In preparation, the contents of the CPG directory have been copied to a new directory, and CPG.g has been renamed CPG_Rev.g. In initialize.g, the default run time (STEP) has been changed from 200 to 300 msec, to span more firings of a neuron. The corresponding xmax has been changed in two places in graphs.g. In CPG_Rev.g, the two setclock statements have been changed, one to change the time step dt from 0.1 to 0.0001, and the other to change the output interval from 1 to 0.001 msec.

To check for cyclicity, firing times must be calculated precisely. As in the GENESIS spikegen object, the spike time is defined as the time when V_m first becomes positive. These times are determined by first saving all V_m to disk, and then selecting the first positive V_m with a postprocessor, named postpro.g. For saving V_m to disk, I introduced lines of the following form in initialize.g:

```
create asc_file /VmL1
setfield /VmL1 flush 1 leave_open 1
useclock /VmL1 1
addmsg /L1/soma /VmL1 SAVE Vm
```

These lines are for cell L1. They were placed in initialize.g following the line which begins `create xdialog stepsize....` Similar lines were added for cells R1, L2, and R2. The end product of postprocessing is a file which gives the firing order of the four cells. It is named FireOrd2.

The First Experiment: A Simple Loop

For the first simulation experiment, all inhibitory weights in defaults.g have been reduced to zero. This results in the disappearance of the inhibitory connections in the viewform window. All excitatory weights have been set to zero except the one from L1 to R2. This leaves a network without a loop, so the excitatory weight from R2 to L1 has been changed from zero to 100, giving a simplest possible loop. In inputs.g, CPG originally sets the same default injection for all cells, namely 0.00015 for current and 200 for duration. These have now been set to zero. The desired injection will be set interactively.

Now begin the first experiment. Give the command:

```
genesis CPG_Rev
```

After the windows appear, click on "L1 Hidden" in the Inputs window, and in the /L1/Inputs window which appears change "input to /L1/soma" to 0.0004 for current and 10 for duration. In the Graphs window, make L1 visible. Click RESET and STEP in the CPG window. The resulting execution time on my 700MHz laptop is about $11 minutes$, and L1 and R2 each fire 9 times. The size of the saved VmL1 and VmR2 files is about 5.2MB. After quitting CPG, give the command:

```
genesis postpro
```

The execution time for postpro.g is about $3\,minutes$. The resulting firing record in the file FireOrd2 is:

Table 1

Spike Time	Cell		Difference	Rounded Difference
7.0133	L1	fires	7.0133	7.013
23.9931	R2	fires	16.9798	16.980
40.9992	L1	fires	17.0061	17.006
57.9977	R2	fires	16.9985	16.998
74.9961	L1	fires	16.9984	16.998
91.9945	R2	fires	16.9984	16.998
108.9929	L1	fires	16.9984	16.998
125.9913	R2	fires	16.9984	16.998
142.9897	L1	fires	16.9984	16.998
159.9881	R2	fires	16.9984	16.998
176.9865	L1	fires	16.9984	16.998
193.9849	R2	fires	16.9984	16.998
210.9833	L1	fires	16.9984	16.998
227.9817	R2	fires	16.9984	16.998
244.9801	L1	fires	16.9984	16.998
261.9785	R2	fires	16.9984	16.998
278.9769	L1	fires	16.9984	16.998
295.9753	R2	fires	16.9984	16.998

The listed spike times are the result of a linear interpolation based on the values of V_m just before and after the zero crossing. If they differ by 1 in the 4th decimal place from the spike times found by spikegen, they are more accurate values for the time of zero crossing. In this example, the 4-decimal place differences settle on a fixed value. If this is not true in later examples, a fixed value in the rounded 3-decimal place differences may be accepted as a weaker indication of stability. See the Appendix for further discussion of attainable accuracy.

The value of the uniform difference in Table 1 should be compared with the chosen value for axonal conduction delays. This is found in defaults.g, which lists 15 $msec$ for all delays. One such delay accounts for only 15 $msec$ of the differences. The remaining 1.998 $msec$ must arise in the synapse, dendrite and axon hillock. The delays in the synapses and dendrites will vary somewhat depending on the circumstances of their initiation, but their variations may be relatively small. It is expected that the relative refractory period will introduce substantial variations in the delay at the axon hillock.

Influence of the Refractory Periods

In the absolute refractory period, no stimulation, however strong, is enough to generate an action potential. In the relative refractory period, stronger than normal stimulation is required. That is to say, a higher (less negative) V_m is required to open the sodium channels. A plot of required V_m versus the time since the last spike declines very rapidly just after the absolute refractory period. Imagine that the plot of V_m, including the effect of recent stimulation at the synapse(s), is at a relatively low level. Then when the two curves cross, the cell will fire.

The refractory periods are intrinsic features of the Hodgkin-Huxley neuron. In the spikegen object, there is a field for "abs_refract". This is an artificial feature whose purpose is really to reject positive values of V_m other than the first, while searching for the time at which the action potential crosses $V_m = 0$. Its default value is 10 $msec$. This is too long for the present purpose. Judging from the results of Exercise 7 for the *Squid* tutorial, on page 49 of *BoG* (Bower & Beeman, 1998), the intrinsic absolute refractory period will be about 7 or 8 *msec*. The widths of action potentials at $V_m = 0$ in the present first experiment were only about 1.15 *msec*. Therefore it should be satisfactory to set abs_refract in spikegen in cell.g to 3 *msec*.

It is expected that as the axonal conduction delays are reduced moderately, the spacings between spikes will be reduced by approximately the same amount. But this relation will cease when the conduction delay is reduced sufficiently to enter the relative refractory period. Test these expectations by first changing the conduction delay in defaults.g from 15 to 10. Then L1 fires 13 times, and R2 fires 12 times,and the record is as follows:

Table 2

Spike Time	Cell		Difference	Rounded Difference
7.0133	L1	fires	7.0133	7.013
18.9689	R2	fires	11.9556	11.956
30.9144	L1	fires	11.9455	11.945
42.9823	R2	fires	12.0665	12.065
91.2444	R2	fires	12.0652	12.065
103.3097	L1	fires	12.0653	12.065
115.3750	R2	fires	12.0653	12.065
127.4403	L1	fires	12.0653	12.065
139.5056	R2	fires	12.0653	12.065
151.5709	L1	fires	12.0653	12.065
163.6362	R2	fires	12.0653	12.065
175.7015	L1	fires	12.0653	12.065
187.7668	R2	fires	12.0653	12.065
199.8321	L1	fires	12.0653	12.065
211.8974	R2	fires	12.0653	12.065
223.9627	L1	fires	12.0653	12.065
236.0280	R2	fires	12.0653	12.065
248.0933	L1	fires	12.0653	12.065
260.1586	R2	fires	12.0653	12.065
272.2239	L1	fires	12.0653	12.065
284.2892	R2	fires	12.0653	12.065
296.3545	L1	fires	12.0653	12.065

From Table 1, assuming that the delays in the synapses, dendrites and axon hillocks are constant, the expected difference in Table 2 would be

$$16.998 - (15 - 10) = 11.998,$$

which approximates 12.065.

In Exercise 7 for the *Squid* tutorial, the relative refractory period is found to extend to about 16 or 17 *msec* from the last spike. From the discussion following Table 1, if there were no refractory period the combined delay in the synapse, dendrite, and axon hillock would be about 1.998. Choosing 3 *msec* for the axonal conduction delay, a signal would travel around the loop in

$$2 * (3 + 1.998) = 9.996\, msec.$$

This invades the relative refractory period, and therfore is not permitted. Firing will be postponed until the V_m required by the refractory period drops to the existing V_m. Test this by changing the conduction delays in defaults.g to 3. Then L1 fires 27 times, R2 fires 26 times, and the first few spikes are as follows:

Table 3

Spike Time	Cell		Difference	Rounded Difference
7.0133	L1	fires	7.0133	7.013
12.1186	R2	fires	5.1053	5.105
17.7397	L1	fires	5.6211	5.621
23.3660	R2	fires	5.6263	5.626
28.9598	L1	fires	5.5938	5.594
34.5265	R2	fires	5.5667	5.567
40.1005	L1	fires	5.5740	5.574
45.6699	R2	fires	5.5694	5.569
51.2400	L1	fires	5.5701	5.570
56.8096	R2	fires	5.5695	5.570
62.3792	L1	fires	5.5697	5.570
67.9488	R2	fires	5.5696	5.570
73.5185	L1	fires	5.5696	5.570
79.0881	R2	fires	5.5696	5.570

Beyond this the differences are constant to 300 *msec*. Without refractory periods, the expected difference in Table 3 would be

$$16.998 - (15 - 3) = 4.998,$$

which is substantially less than 5.570.

For network dynamics, it is important to note the different roles of axonal conduction delay and relative refractory period in determining firing order. The delay due to relative refractory period can vary continuously as the system seeks stability, but the delay due to a particular axon is either there or not there.

One Loop or Many?: A Misunderstanding

Networks of 3 or 4 neurons will now be considered. With a multiple cell network, notation is needed for ordered specification of connections. The array of synaptic strengths for the first example of a 3-cell network is as follows:

	L1	R1	L2	R2
L1	0	100	0	100
R1	30	0	0	0
L2	0	0	0	0
R2	30	0	0	0

To provide for symbolic reference, L1, R1, L2, and R2 will be replaced with 1, 2, 3, and 4, and the synaptic strength array will in general be represented by:

$$S = \begin{vmatrix} s_{11} & s_{12} & s_{13} & s_{14} \\ s_{21} & s_{22} & s_{23} & s_{24} \\ s_{31} & s_{32} & s_{33} & s_{34} \\ s_{41} & s_{42} & s_{43} & s_{44} \end{vmatrix},$$

where s_{ij} is the synaptic strength from cell i to cell j. Comparing the above 3-cell network with the earlier 2-cell networks, the value of s_{14} has been retained as 100, while s_{41} has been reduced to 30. With only these two nonzero strengths, oscillation in the 2-cell network stops after 2 spikes for each cell. With the addition of $s_{12} = 100$ and $s_{21} = 30$ as indicated in the array above, the resulting 3-cell, 2-loop network has sufficient feedback to keep L1 going. Choosing 3 for the delay in each axon, L1, R1, and R2 each fire 25 times, and the firing order starts as follows:

Table 4

Spike Time	Cell		Difference	Rounded Difference
7.0133	L1	fires	7.0133	7.013
12.1186	R1	fires	5.1053	5.105
12.1186	R2	fires	0.0000	0.000
18.4646	L1	fires	6.3460	6.346
23.9592	R1	fires	5.4946	5.495
23.9592	R2	fires	0.0000	0.000
30.3302	L1	fires	6.3710	6.371
35.7826	R1	fires	5.4524	5.452
35.7826	R2	fires	0.0000	0.000
42.1343	L1	fires	6.3517	6.352
47.5887	R1	fires	5.4544	5.454
47.5887	R2	fires	0.0000	0.000
53.9374	L1	fires	6.3487	6.349
59.3920	R1	fires	5.4545	5.455
59.3920	R2	fires	0.0000	0.000
65.7403	L1	fires	6.3484	6.348
71.1949	R1	fires	5.4546	5.455
71.1949	R2	fires	0.0000	0.000
77.5432	L1	fires	6.3483	6.348
82.9977	R1	fires	5.4545	5.455
82.9977	R2	fires	0.0000	0.000
89.3460	L1	fires	6.3483	6.348
94.8005	R1	fires	5.4545	5.455
94.8005	R2	fires	0.0000	0.000
101.1488	L1	fires	6.3483	6.348
106.6033	R1	fires	5.4545	5.454
106.6033	R2	fires	0.0000	0.000
112.9516	L1	fires	6.3483	6.348
118.4061	R1	fires	5.4545	5.454
118.4061	R2	fires	0.0000	0.000
124.7544	L1	fires	6.3483	6.348

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Spike Time	Cell		Difference	Rounded Difference
130.2089	R1	fires	5.4545	5.454
130.2089	R2	fires	0.0000	0.000
136.5572	L1	fires	6.3483	6.348
142.0117	R1	fires	5.4545	5.454
142.0117	R2	fires	0.0000	0.000
148.3600	L1	fires	6.3483	6.348
153.8145	R1	fires	5.4545	5.454
153.8145	R2	fires	0.0000	0.000

Beyond this the cycle (6.348, 5.454, 0.000) continues to at least 300 *msec*, except for a deviation of 1 in the 3rd decimal place at 248.2369 *msec*.

It is clear that if the nonzero s_{12} and s_{21} were replaced with nonzero s_{13} and s_{31}, L2 would fire instead of R1. L1 would fire as usual. This might be interpreted as the beginning of "redundancy": two of the possible three loops are sufficient to sustain firing of the main cell L1. Of course all three loops acting together can also sustain L1, as calculated in the following example, in which $s_{13} = 100$ and $s_{31} = 30$ have been added to the previous example. L1 fires 27 times, the other 3 cells each fire 26 times, and the record is:

Table 5

Spike Time	Cell		Difference	Rounded Difference
7.0133	L1	fires	7.0133	7.013
12.1186	L2	fires	5.1053	5.105
12.1186	R1	fires	0.0000	0.000
12.1186	R2	fires	0.0000	0.000
17.8691	L1	fires	5.7505	5.751
23.4684	L2	fires	5.5993	5.599
23.4684	R1	fires	0.0000	0.000
23.4684	R2	fires	0.0000	0.000
29.1957	L1	fires	5.7273	5.727
34.7400	L2	fires	5.5443	5.544
34.7400	R1	fires	0.0000	0.000
34.7400	R2	fires	0.0000	0.000
40.4465	L1	fires	5.7065	5.707
45.9935	L2	fires	5.5470	5.547
45.9935	R1	fires	0.0000	0.000
45.9935	R2	fires	0.0000	0.000
51.6962	L1	fires	5.7027	5.703
57.2433	L2	fires	5.5471	5.547
57.2433	R1	fires	0.0000	0.000
57.2433	R2	fires	0.0000	0.000
62.9455	L1	fires	5.7022	5.702
68.4927	L2	fires	5.5472	5.547
68.4927	R1	fires	0.0000	0.000
68.4927	R2	fires	0.0000	0.000

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Spike Time	Cell		Difference	Rounded Difference
74.1949	L1	fires	5.7021	5.702
79.7420	L2	fires	5.5472	5.547
79.7420	R1	fires	0.0000	0.000
79.7420	R2	fires	0.0000	0.000
85.4441	L1	fires	5.7021	5.702
90.9913	L2	fires	5.5472	5.547
90.9913	R1	fires	0.0000	0.000
90.9913	R2	fires	0.0000	0.000
96.6934	L1	fires	5.7021	5.702
102.2406	L2	fires	5.5472	5.547
102.2406	R1	fires	0.0000	0.000
102.2406	R2	fires	0.0000	0.000

The rounded differences with 3 decimal places continue in the cycle (5.702, 5.547, 0.000, 0.000) beginning at 62.9455 *msec*. The differences to 4 decimal places continue in a fixed cycle beginning at 74.1949.

The above example can be described as having 3 loops, as is evident from the viewform window and the S-array. Counting loops becomes less meaningful with more connections. In the following example $s_{24} = 30$ and $s_{43} = 30$ have been added. Again L1 fires 27 times and the other 3 cells fire 26 times, and the record is:

Table 6

Spike Time	Cell		Difference	Rounded Difference
7.0133	L1	fires	7.0133	7.013
12.1186	L2	fires	5.1053	5.105
12.1186	R1	fires	0.0000	0.000
12.1186	R2	fires	0.0000	0.000
17.8691	L1	fires	5.7505	5.751
23.3726	L2	fires	5.5035	5.504
23.3726	R2	fires	0.0000	0.000
23.4684	R1	fires	0.0958	0.096
29.1465	L1	fires	5.6780	5.678
34.5787	R2	fires	5.4322	5.432
34.5855	L2	fires	0.0068	0.007
34.6992	R1	fires	0.1137	0.114
40.3421	L1	fires	5.6429	5.643
45.7718	R2	fires	5.4297	5.430
45.7813	L2	fires	0.0094	0.009
45.8998	R1	fires	0.1186	0.119
51.5351	L1	fires	5.6352	5.635
56.9638	R2	fires	5.4288	5.429
56.9742	L2	fires	0.0103	0.010
57.0935	R1	fires	0.1193	0.119
62.7275	L1	fires	5.6340	5.634

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Spike Time	Cell		Difference	Rounded Difference
68.1560	R2	fires	5.4286	5.429
68.1666	L2	fires	0.0106	0.011
68.2860	R1	fires	0.1194	0.119
73.9198	L1	fires	5.6338	5.634
79.3484	R2	fires	5.4286	5.429
79.3590	L2	fires	0.0106	0.011
79.4784	R1	fires	0.1194	0.119
85.1122	L1	fires	5.6338	5.634
90.5407	R2	fires	5.4285	5.428
90.5513	L2	fires	0.0107	0.011
90.6707	R1	fires	0.1194	0.119
96.3045	L1	fires	5.6338	5.634
101.7330	R2	fires	5.4285	5.428
101.7436	L2	fires	0.0107	0.011
101.8630	R1	fires	0.1194	0.119
107.4968	L1	fires	5.6338	5.634
112.9253	R2	fires	5.4285	5.428
112.9359	L2	fires	0.0107	0.011
113.0553	R1	fires	0.1194	0.119
118.6891	L1	fires	5.6337	5.634
124.1176	R2	fires	5.4285	5.428
124.1282	L2	fires	0.0107	0.011
124.2476	R1	fires	0.1194	0.119
129.8814	L1	fires	5.6338	5.634
135.3099	R2	fires	5.4285	5.428
135.3205	L2	fires	0.0107	0.011
135.4399	R1	fires	0.1194	0.119
141.0737	L1	fires	5.6337	5.634
146.5022	R2	fires	5.4285	5.428
146.5128	L2	fires	0.0107	0.011
146.6322	R1	fires	0.1194	0.119
152.2660	L1	fires	5.6337	5.634
157.6945	R2	fires	5.4285	5.428
157.7051	L2	fires	0.0107	0.011
157.8245	R1	fires	0.1194	0.119
163.4583	L1	fires	5.6337	5.634
168.8868	R2	fires	5.4285	5.428
168.8974	L2	fires	0.0107	0.011
169.0168	R1	fires	0.1194	0.119
174.6506	L1	fires	5.6337	5.634
180.0791	R2	fires	5.4285	5.428
180.0897	L2	fires	0.0107	0.011
180.2091	R1	fires	0.1194	0.119
185.8429	L1	fires	5.6338	5.634
191.2714	R2	fires	5.4285	5.428

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Spike Time	Cell		Difference	Rounded Difference
191.2820	L2	fires	0.0107	0.011
191.4014	R1	fires	0.1194	0.119
197.0352	L1	fires	5.6337	5.634
202.4637	R2	fires	5.4285	5.428
202.4743	L2	fires	0.0107	0.011
202.5937	R1	fires	0.1194	0.119
208.2275	L1	fires	5.6337	5.634
213.6560	R2	fires	5.4285	5.428
213.6666	L2	fires	0.0107	0.011
213.7860	R1	fires	0.1194	0.119
219.4198	L1	fires	5.6337	5.634
224.8483	R2	fires	5.4285	5.428
224.8589	L2	fires	0.0107	0.011
224.9783	R1	fires	0.1194	0.119
230.6121	L1	fires	5.6337	5.634
236.0406	R2	fires	5.4285	5.428
236.0512	L2	fires	0.0107	0.011
236.1706	R1	fires	0.1194	0.119
241.8044	L1	fires	5.6338	5.634
247.2329	R2	fires	5.4285	5.428
247.2435	L2	fires	0.0107	0.011
247.3629	R1	fires	0.1194	0.119
252.9967	L1	fires	5.6337	5.634
258.4252	R2	fires	5.4285	5.428
258.4358	L2	fires	0.0107	0.011
258.5552	R1	fires	0.1194	0.119
264.1890	L1	fires	5.6337	5.634
269.6175	R2	fires	5.4285	5.428
269.6281	L2	fires	0.0107	0.011
269.7475	R1	fires	0.1194	0.119
275.3813	L1	fires	5.6337	5.634
280.8098	R2	fires	5.4285	5.428
280.8204	L2	fires	0.0107	0.011
280.9398	R1	fires	0.1194	0.119
286.5736	L1	fires	5.6338	5.634
292.0021	R2	fires	5.4285	5.428
292.0127	L2	fires	0.0107	0.011
292.1321	R1	fires	0.1194	0.119
297.7659	L1	fires	5.6338	5.634

The difference between the firing times of R1 and L1 is still varying by 1 in the 4th decimal place near the end of the record. This must be a computational artifact; the particular times at which differences occur can be changed by changing dt. The differences rounded to 3 decimal places show periodicity beyond 85.1122 msec.

The simple point to be made in this section is that the firing order in a cycle does not represent a sequence of links in a single loop. The objection has been made that reverberation is implausible because the neurons of a central nervous system are not typically so strongly connected that one alone could fire another, as would be required in a single loop. But the examples in this section are not single loops, and firing of L1 requires summed excitation from 2 other neurons to be sustained. With systems of more neurons the requirement could be many more than 2 neurons. Also, L1 might be purely a sensory neuron, perhaps one of several, and not the representative of the assembly pattern. The essential pattern could exist in the absence of some components.

Inhibition

It would be desirable to offer an idealized model of the type of behavior exhibited by the mouse when it perceives the cat, and then freezes, and finally scurries back to its hole. Unfortunately four neurons apparently are not sufficient for all that. But test the action of an inhibitory connection as a simple switch for turning off a behavior pattern. Let the pattern be in cells L1, L2, and R2, and be mediated by the the following synaptic strength array:

$$S = \begin{vmatrix} 0 & 0 & 30 & 100 \\ 0 & 0 & -600 & 0 \\ 100 & 0 & 0 & 30 \\ 0 & 0 & 30 & 0 \end{vmatrix}$$

The negative s_{23} indicates an inhibitory connection from R1 to L2. Continue to use 3 *msec* for the delay in axons. As in previous examples, the stimulus for the next example will be a current pulse of 0.0004 *microamp* in cell L1, with duration 10 *msec*. Then L1, L2, and R2 each fire 22 times, and the firing record is as follows:

Table 7

Spike Time	Cell		Difference	Rounded Difference
7.0133	L1	fires	7.0133	7.013
12.1186	R2	fires	5.1053	5.105
13.4924	L2	fires	1.3738	1.374
18.9160	L1	fires	5.4236	5.424
24.2007	R2	fires	5.2847	5.285
27.0111	L2	fires	2.8103	2.810
32.3148	L1	fires	5.3037	5.304
37.4373	R2	fires	5.1225	5.123
40.3829	L2	fires	2.9456	2.946
45.6848	L1	fires	5.3019	5.302
50.8038	R2	fires	5.1190	5.119
53.7798	L2	fires	2.9760	2.976
59.0795	L1	fires	5.2997	5.300
64.1960	R2	fires	5.1165	5.117
67.1813	L2	fires	2.9853	2.985
72.4806	L1	fires	5.2993	5.299
77.5964	R2	fires	5.1157	5.116
80.5841	L2	fires	2.9877	2.988
85.8832	L1	fires	5.2991	5.299

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Spike Time	Cell		Difference	Rounded Difference
90.9988	R2	fires	5.1155	5.116
93.9871	L2	fires	2.9884	2.988
99.2863	L1	fires	5.2991	5.299
104.4018	R2	fires	5.1155	5.116
107.3903	L2	fires	2.9885	2.989
112.6895	L1	fires	5.2992	5.299
117.8049	R2	fires	5.1154	5.115
120.7935	L2	fires	2.9886	2.989
126.0927	L1	fires	5.2992	5.299
131.2081	R2	fires	5.1154	5.115
134.1967	L2	fires	2.9886	2.989

The record to 3 decimal places becomes cyclic at 107.3903 *msec* and continues with the cycle to at least 300 *msec*.

If the stimulus at L1 is augmented with a similar stimulus at the inhibitory neuron R1, cells L1, R1, and R2 each fire once as follows:

Table 8

Spike Time	Cell		Difference	Rounded Difference
7.0133	L1	fires	7.0133	7.013
7.0133	R1	fires	0.0000	0.000
12.1186	R2	fires	5.1053	5.105

Firings cease beyond 12.1186 *msec*. Before using the large value -600 for s_{23}, -100 and -300 were tried in this example. They were not sufficient to stop the firings.

If the stimulus at the inhibitory neuron is delayed until 50 *msec*, L1 fires 5 times, R1 once, L2 4 times, and R2 5 times, as follows:

Table 9

Spike Time	Cell		Difference	Rounded Difference
7.0133	L1	fires	7.0133	7.013
12.1186	R2	fires	5.1053	5.105
13.4924	L2	fires	1.3738	1.374
18.9160	L1	fires	5.4236	5.424
24.2007	R2	fires	5.2847	5.285
27.0111	L2	fires	2.8103	2.810
32.3148	L1	fires	5.3037	5.304
37.4373	R2	fires	5.1225	5.123
40.3829	L2	fires	2.9456	2.946
45.6848	L1	fires	5.3019	5.302
50.8038	R2	fires	5.1190	5.119
51.2469	R1	fires	0.4431	0.443
53.7798	L2	fires	2.5329	2.533
59.0795	L1	fires	5.2997	5.300
64.1960	R2	fires	5.1165	5.117

Firings cease beyond 64.1960 *msec* in Table 9.

It has not been shown that an inhibitory connection can be part of a cyclic mode. For such a case, change the above example by diminishing s_{23} to -100, and add the connection $s_{42} = 60$. Stimulate L1 as before. Then L1 and R2 each fire 21 times, R1 and L2 each fire 20 times, and the firing record is as follows:

Table 10

Spike Time	Cell		Difference	Rounded Difference
7.0133	L1	fires	7.0133	7.013
12.1186	R2	fires	5.1053	5.105
13.4924	L2	fires	1.3738	1.374
17.5070	R1	fires	4.0146	4.015
18.9160	L1	fires	1.4090	1.409
24.2007	R2	fires	5.2847	5.285
30.0113	L2	fires	5.8106	5.811
30.2967	R1	fires	0.2853	0.285
35.1899	L1	fires	4.8932	4.893
38.1444	R2	fires	2.9545	2.955
43.9192	L2	fires	5.7748	5.775
44.0232	R1	fires	0.1041	0.104
49.1859	L1	fires	5.1626	5.163
52.4932	R2	fires	3.3073	3.307
58.3085	R1	fires	5.8153	5.815
58.4430	L2	fires	0.1345	0.134
63.6848	L1	fires	5.2418	5.242
66.8414	R2	fires	3.1565	3.157
72.6518	R1	fires	5.8105	5.810
72.8189	L2	fires	0.1670	0.167
78.0658	L1	fires	5.2470	5.247
81.2337	R2	fires	3.1679	3.168
87.0395	R1	fires	5.8058	5.806
87.2126	L2	fires	0.1731	0.173
92.4590	L1	fires	5.2464	5.246
95.6265	R2	fires	3.1675	3.168
101.4320	R1	fires	5.8055	5.805
101.6035	L2	fires	0.1716	0.172
106.8501	L1	fires	5.2465	5.247
110.0185	R2	fires	3.1684	3.168
115.8240	R1	fires	5.8055	5.806
115.9945	L2	fires	0.1704	0.170
121.2410	L1	fires	5.2465	5.247
124.4099	R2	fires	3.1689	3.169
130.2154	R1	fires	5.8055	5.806
130.3854	L2	fires	0.1700	0.170
135.6319	L1	fires	5.2465	5.246
138.8009	R2	fires	3.1690	3.169
144.6065	R1	fires	5.8056	5.806
144.7764	L2	fires	0.1698	0.170

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Spike Time	Cell		Difference	Rounded Difference
150.0229	L1	fires	5.2465	5.246
153.1919	R2	fires	3.1690	3.169
158.9975	R1	fires	5.8056	5.806
159.1674	L2	fires	0.1698	0.170
164.4139	L1	fires	5.2465	5.246
167.5829	R2	fires	3.1690	3.169
173.3885	R1	fires	5.8056	5.806
173.5584	L2	fires	0.1698	0.170
178.8049	L1	fires	5.2465	5.246
181.9739	R2	fires	3.1690	3.169
187.7794	R1	fires	5.8056	5.806
187.9493	L2	fires	0.1698	0.170
193.1958	L1	fires	5.2465	5.247
196.3649	R2	fires	3.1691	3.169
202.1704	R1	fires	5.8056	5.806
202.3403	L2	fires	0.1698	0.170
207.5868	L1	fires	5.2465	5.246
210.7558	R2	fires	3.1690	3.169
216.5614	R1	fires	5.8056	5.806
216.7313	L2	fires	0.1698	0.170
221.9778	L1	fires	5.2465	5.246
225.1468	R2	fires	3.1690	3.169
230.9524	R1	fires	5.8056	5.806
231.1223	L2	fires	0.1698	0.170
236.3688	L1	fires	5.2465	5.247
239.5378	R2	fires	3.1690	3.169
245.3433	R1	fires	5.8055	5.806
245.5132	L2	fires	0.1698	0.170
250.7597	L1	fires	5.2465	5.246
253.9288	R2	fires	3.1691	3.169
259.7343	R1	fires	5.8056	5.806
259.9042	L2	fires	0.1698	0.170
265.1507	L1	fires	5.2465	5.246
268.3197	R2	fires	3.1691	3.169
274.1253	R1	fires	5.8056	5.806
274.2952	L2	fires	0.1698	0.170
279.5417	L1	fires	5.2465	5.246
282.7107	R2	fires	3.1690	3.169
288.5163	R1	fires	5.8056	5.806
288.6862	L2	fires	0.1698	0.170
293.9327	L1	fires	5.2465	5.246
297.1017	R2	fires	3.1690	3.169

The rounded differences in this record settle into a cycle of 4 firings beginning at 115.8240 *msec*, except for occasional variations of 1 in the 3rd decimal place for the firing of L1. These firings of L1 to 4 decimal places all end in 5, so rounding must depend on variations further out than the 4th decimal place.

Concluding Remarks

The records for the examples considered have all either settled into cyclic modes to 3 decimal places within about 100 *msec*, or have terminated. There has been no indication of chaotic attractors.

Hebbian reverberations need not be exactly cyclic to do their jobs. They are essentially combinations of neurons which are all oscillating simultaneously. Presumably the effectiveness of an oscillating neuron in behavior is determined by the frequency and duration of the oscillation.

No consideration has been given to the formation of cell assemblies in learning and memory. That could be explored with more neurons. Would 6 be sufficient for a beginning?

APPENDIX

Attainable Accuracy

The logically most straightforward way of obtaining precise spike times (defined as zero crossings) from the existing CPG_Rev program would be to use the value 0.0001 *msec* for both dt and the output interval. Unfortunately this would result in the production of four very long files, each of about 52MB. Increasing the output interval to 0.001 reduces a file to about 5.2MB.

Precision and a qualified accuracy can be regained through linear interpolation based on the values of V_m just before and after the zero crossing. If the interpolated values differ by 1 in the 4th decimal place from the spike time found by spikegen, they are most likely more accurate values for the time of zero crossing (assuming that V_m versus time is a nearly straight line as it crosses zero). But, accurate or not, it is the values from spikegen that determine subsequent firings. Thus discrepancies of 1 in the 4th decimal place are to be expected.

The use of interpolation suggests that the size of files could be reduced further without loss of accuracy, by means of a further increase in the output interval.

If the long execution time for CPG_Rev becomes a problem, dt might be increased to 0.001. With interpolation, this might still give satisfactory values for the differences. But a test indicated that the value of spike time near the end of the record would differ by about 0.04 from the values obtained when dt is 0.0001 or 0.00005.

References

Bower, James M. and Beeman, David (1998). *The Book of GENESIS*, second edn., Springer-Verlag, N.Y.

Hebb, D. O. (1949). *The Organization of Behavior*, Wiley, N.Y. Hebb proposed that reverberations occur in cell assemblies, with cells stimulating one another in the assembly, in a cyclical pattern. His Figure 10 is apparently intended as an abstract representation of the activity in a cell assembly, or perhaps in several assemblies chained together. It is indefinite and confusing. A simpler and more specific example is given in Hebb (1972).

Hebb, D. O. (1972). *Textbook of Psychology*, third edn., Saunders, Philadelphia. Chapter 4 contains an easy introduction to Hebb's theory of cell assemblies. Figure 33 is a simple example of connectivities.

Kaplan, Daniel and Glass, Leon (1995). *Understanding Nonlinear Dynamics*, Springer-Verlag, N.Y.

Seung, H. Sebastian (2000). Half a century of Hebb. *Nature Neuroscience*, Volume 3 Supplement November 2000: page 1166. Seung asks whether the delay activity that has been observed in nervous systems is truly reverberatory activity. He suggests studying the simplest possible examples, and notes that settling the mechanistic question will still be technically demanding. Wouldn't it help to get a head start on the type of computational simulation involved?

Wenger, M. A., Jones, F. N. and Jones, M. H. (1956). *Physiological Psychology*, Henry Holt, N.Y.