

CHAPTER 10 CASE STUDY: NEURAL INTEGRATORS

ABSTRACT. This chapter provides some applications of the present study on threshold transformations and dynamical systems of neural networks. In particular, neural integrators, which keep track of the position of eye movement, are described in our framework.

10.1 INTRODUCTION

In dynamical systems of neural networks, as in any other dynamical systems, there are two kinds of stability, one structural another orbital. In discrete-time and finite-state models, the structural stability is ensured, if the generating function is expressed by a self-dual Boolean form. In the previous chapters, almost all results are expressed in Boolean functions, so that there is no problem about the structural stability.

These chapters is primarily concerned with the orbital stability. The orbital stability is expressed in terms of attractors. First, the enhanced Arimoto theorem (Theorem 5.5.2 of Chapter 5.5) asserts that there exists a first order system on \mathbf{Q}^n having a unique cycle of any length $k \leq 2^n$. This is an existence theorem for attractors. Starting at any initial state, the state will eventually be on the unique cycle. However, I thought this dynamical system was too strong. Often it is more desirable that the eventual states depend on initial states. Still, it is essential that the eventual states are orbitally stable. Therefore, the remaining chapters have been all devoted to existence of attractors that their basins for attraction are proper subsets of the whole state-space. Particularly, Chapter 6 and 7 are concerned with autonomous systems with spatial summation only, which are called first-order. Chapter 8 is concerned with autonomous systems with spatial summation and temporal summation over two time points, which are called second-order. Chapter 9 is concerned with non-autonomous first-order systems, which receive an input sequence from their outside. These chapters clearly defined what attractors are and proved the existence of such attractors having particular cycle structures.

Now, at more concrete level, "Does there exist a mechanism that sets and resets an initial state in real nervous systems? If it does, then how?" If a system is not evolving, that is, if the efficacies of its synaptic connections are not plastic but fixed, then only the input to the system from its outside can alter the initial state. But how?

Concerning this question, I encountered models of saccadic eye movements. It seems that a huge quantity of documents on such models have been published, but Van Gisbergen, Robinson, and Gielen (1981) have been a basic source. Their models like most others have, as their main components, neural integrators, which keep eye position, and burst neurons, which send pulses to the neural integrators.

To my above question, it seems Seung et al (2000) seems most relevant. A common denominator of their research and mine is attractors in neural networks. They characterize a neural integrator as a dynamical system having multiple attractors.

Further, as the integrator receives pulses from burst neurons, new attractors of different firing rates are activated. The integrator is a special case of a general memory model in which a piece of data is retrieved by input. Therefore, my above general question had a clear answer. That is, input from burst neurons is responsible for resetting initial states of a dynamical system.

However, the model of Seung et al (2000) is continuous as currently conventional dynamical systems of neural networks that are based on physiological studies. The continuous models may be better than discrete model in incorporating physiological data. However, the original models cannot deal with population dynamics. Therefore, for example, the state space must be drastically simplified to the space of firing rates or its equivalent. In general, what are stable or attractive in a neural network are not the firing rates but a synchronic and diachronic specific firing patterns. For example, the firing rates of the temporal firing patterns 10101010.. and 110011001100.. are both $1/2$, but one may be an attractor and the other may be not. For the firing patterns of a pair of neurons

$$\begin{array}{ll} 1010101010101010..... & 1010101010101010.... \\ 0101010101010101..... & 1010101010101010....., \end{array}$$

one may be an attractor and the other may be not. The simplified continuous models cannot distinguish these patterns.

In contrast, our discrete dynamical systems based on the classical McCulloch and Pitts model do distinguish these firing patterns. In the same discrete framework, my project here is first to construct an autonomous NN(neural network) having multiple attractors of tonic firing patterns with different firing rates. Then the second part of the project is to construct a non-autonomous NN having two input connections, one excitatory and another inhibitory by determining appropriate efficacies for the connections. The third part is to determine a necessary burst pattern that resets the initial state in a push-pull manner when the pulses of the pattern are input to the excitatory and inhibitory connections. That means a stable state changes from one tonic attractor to another tonic attractor. In summary, the project is to construct a discrete model of neural integrators. Generation of such a burst pattern will be also addressed in section 10.7.

10.2 AUTONOMOUS NN HAVING MULTIPLE TONIC ATTRACTORS

Let $\mathbf{Q} = \{0, 1\}$ be the minimal Boolean algebra with the binary operation \cdot and \vee and the unary operation \neg . For any positive integer n , \mathbf{Q}^n is a Boolean algebra and also a metric space defined by the Hamming distance. Let $x(t)$ be the state of a neuron at time t , where $t = 1, 2, 3, \dots$, and $x(t) \in \mathbf{Q}$. The sequence x is called a *tonic* sequence of firing rate $0 \leq i/m \leq 1$, where m is a positive integer and m and i are relatively prime, if x is a periodic sequence of period m , the number of 1s in $x(1), \dots, x(m)$ is i , and 1s are the most uniformly distributed. The last sentence is not rigorous, but practically will be clear. For example, 1011010110..... is tonic with firing rate $3/5$.

$$1010100101001010100101001010100101001010010100...$$

is tonic, but

$$10101010010010101010010010101010010010100100...$$

is not tonic, although their firing rates are both $5/12$. For a sequence x in \mathbf{Q}^n , if every component sequence of x is a tonic sequence of firing rate i/m , then x is called a tonic sequence of firing rate i/m .

A large number m is necessary, if virtually continuous firing rates are required. However, if an eye position is determined by an $(m+1)$ -adic number corresponding to a set of firing rates of several integrators, then m in each integrator can be small.

For the first step for constructing a schematic neural integrator, it suffices to construct an autonomous network such that for each firing rate of 0 , $1/4$, $1/2$ and $3/4$ there exists an attractor consisting of one or more tonic sequences of the firing rate. These tonic sequences are

```
00000000000000000000...
10001000100010001000...
10101010101010101010...
11101110111011101110...
11111111111111111111...
```

Here, a sequence obtained by shifting another is also tonic. These tonic sequences may be expressed by just their first 4 terms, namely, 0000, 1101, 1011, 0101 and the like to be distinguished from each other. We call them also *tonic*.

A simple method will be to construct a 4th-order NN of dimension 3. In this case, 3 neurons are involved. Starting from the initial states

$$\begin{aligned} x(1)x(2)x(3)x(4), \\ y(1)y(2)y(3)y(4), \\ z(1)z(2)z(3)z(4), \end{aligned} \tag{10.2.1}$$

the subsequent states are successively determined by a threshold function $H : \mathbf{Q}^{12} \rightarrow \mathbf{Q}^3$ and

$$\begin{aligned} (x(i), y(i), z(i)) = & H(x(i-4), y(i-4), z(i-4), \\ & x(i-3), y(i-3), z(i-3), \\ & x(i-2), y(i-2), z(i-2), \\ & x(i-1), y(i-1), z(i-1)). \end{aligned}$$

This fourth-order NN is equivalent to a first-order NN of dimension 12. For this conversion we rename the above matrix of variables $x(1), y(1), z(1), \dots, x(4), y(4), z(4)$ to the 12-dimensional vector by the correspondence,

$$\begin{array}{l} 1, 4, 7, 10 \\ 2, 5, 8, 11 \\ 3, 6, 9, 12. \end{array}$$

The converted first-order NN is generated by the transformation F of \mathbf{Q}^{12} defined by

$$\begin{aligned} F : (v_1, \dots, v_{12}) & \mapsto (w_1, \dots, w_{12}), \\ w_i &= v_{i+3} \text{ for } i = 1, \dots, 9, \\ (w_{10}, w_{11}, w_{12}) &= H(v_1, v_2, \dots, v_{12}). \end{aligned} \tag{10.2.2}$$

In general, F is defined by its component function $F_i = p_i F, i = 1, \dots, 12$, but in the present case, only $F_{10}(= H_{10})$, $F_{11}(= H_{11})$, and $F_{12}(= H_{12})$ are yet to be determined.

Let ρ denote the cyclic permutation $(1, 2, \dots, 12)$. Starting at (10.2.1), H creates a tonic sequence such that

$$x(i+4) = x(i), y(i+4) = y(i), \text{ and } z(i+4) = z(i)$$

for every i , if and only if

$$Fv = \rho^{-3}v$$

for every $v = \rho^{-3j}u$ for every j , where

$$u = (u_1, u_2, \dots, u_{12}) = (x(1), y(1), \dots, z(4)).$$

For example,

$$\begin{aligned} x &= 1110111011101110\dots \\ y &= 0111011101110111\dots \\ z &= 1101110111011101\dots, \end{aligned}$$

if and only if

$$101.111.110.011 \mapsto 111.110.011.101 \mapsto 110.011.101.111 \mapsto 011.101.111.110 \mapsto \dots$$

by F , where $.$ is inserted every 3 components of a point in \mathbf{Q}^{12} .

Let's call v in \mathbf{Q}^{12} tonic, if (v_1, v_4, v_7, v_{10}) , (v_2, v_5, v_8, v_{11}) , and (v_3, v_6, v_9, v_{12}) are all tonic with the same firing rate. Let's determine an F that satisfies a stronger condition

$$Fv = \rho^{-3}v' \tag{10.2.3}$$

for any v in the 1-neighborhood of any tonic v' in \mathbf{Q}^{12} . In (10.2.3), a sufficient condition for attractiveness of any tonic sequence is combined with the necessary and sufficient condition that any tonic sequence is a limit orbit.

We assume F is self-dual. Then, F_i is in turn defined by $f_i = p_i \cdot \neg F_i$, its $[\]$ -representation. Then, to determine f_i means to determine the set of points v such that $v_i = 1$ and $(Fv)_i = 0$.

To determine f_{10} , we assume $v_{10} = 1$ and obtain some necessary conditions for $F_{10}v = 0$, v being in the 1-neighborhood of a tonic point, and (10.2.3) being satisfied.

First, suppose $((Fv)_1, (Fv)_4, (Fv)_7, (Fv)_{10}) = (1, 1, 1, 0)$. Then v must be in the 1-neighborhood of a tonic point of firing rate $3/4$. Therefore, if $v_1 = 0$, then $(v_2, v_3, v_5, v_6, v_8, v_9, v_{11}, v_{12})$ must contain at least one 0. If $v_1 = 1$, then $(v_2, v_3, v_5, v_6, v_8, v_9, v_{11}, v_{12})$ must contain at least two 0s.

Second, suppose $((Fv)_1, (Fv)_4, (Fv)_7, (Fv)_{10}) = (1, 0, 1, 0)$. Then v must be in the 1-neighborhood of a tonic point of firing rate $1/2$. Therefore, if $v_1 = 0$, then $(v_2, v_3, v_5, v_6, v_8, v_9, v_{11}, v_{12})$ must contain at least three 0s. If $v_1 = 1$, then $(v_2, v_3, v_5, v_6, v_8, v_9, v_{11}, v_{12})$ must contain at least four 0s.

Third, suppose $((Fv)_1, (Fv)_4, (Fv)_7, (Fv)_{10}) = (0, 0, 1, 0)$, which implies v is in the 1-neighborhood of a tonic point of firing rate $1/4$. Therefore, if $v_1 = 0$, then $(v_2, v_3, v_5, v_6, v_8, v_9, v_{11}, v_{12})$ must contain at least five 0s. If $v_1 = 1$, then $(v_2, v_3, v_5, v_6, v_8, v_9, v_{11}, v_{12})$ contains at least six 0s.

The case where $((Fv)_1, (Fv)_4, (Fv)_7, (Fv)_{10}) = (0, 1, 1, 0)$ is out of our consideration, since $(0, 1, 1, 0)$ is not part of a tonic point of firing rate $i/4$ (It can be part of a tonic sequence of firing rate $2/3$).

Combining the above conditions, we obtain the following necessary conditions. If $(v_1, v_4, v_7) = (0, 1, 1)$, then $F_{10}v = 0$ implies that $(v_2, v_3, v_5, v_6, v_8, v_9, v_{11}, v_{12})$ contains at least one 0s. If $(v_1, v_4, v_7) = (1, 1, 1)$, then $F_{10}v = 0$ implies that

$(v_2, v_3, v_5, v_6, v_8, v_9, v_{11}, v_{12})$ contains at least two 0s. If $(v_1, v_4, v_7) = (0, 1, 0)$, then $F_{10}v = 0$ implies that $(v_2, v_3, v_5, v_6, v_8, v_9, v_{11}, v_{12})$ contains at least three 0s. In any other cases, $F_{10}v = 0$ implies that $(v_2, v_3, v_5, v_6, v_8, v_9, v_{11}, v_{12})$ contains at least four 0s.

A function F_{10} that satisfies the above conditions is, for example,

$$f_{10} = p_{10} \cdot (\neg p_1 \cdot p_4 \cdot p_7 \cdot S_1 \vee p_4 \cdot p_7 \cdot S_2 \vee \neg p_1 \cdot S_3 \vee S_4), \quad (10.2.4)$$

where S_i is the disjunction of all conjunctions of i functions selected from

$$\{\neg p_2, \neg p_3, \neg p_5, \neg p_6, \neg p_8, \neg p_9, \neg p_{11}, \neg p_{12}\}.$$

We construct F as a symmetric transformation in the sense $F\tau = \tau F$ for permutations $\tau = (1, 2)(4, 5)(7, 8)(10, 11)$, $(1, 3)(4, 6)(7, 9)(10, 12)$, and $(2, 3)(5, 6)(8, 9)(11, 12)$. Therefore, f_{11} and f_{12} are immediately obtained from f_{10} .

Unfortunately, f_{10} is not a threshold function, so that the function H must be realized by a composition of several neural circuits. However, from the above construction, it will be easily proved that each of all 36 tonic cycles is an attractor. Computer simulation also shows that there is no other cycle. Therefore, leaving another construction for later time, I will use the autonomous NN generated by F for the next stage in the to construct an integrator.

10.3 NON-AUTONOMOUS NNs HAVING BURST INPUT

We assume that pulses input from a burst neuron resets initial states, but what happens when it finished its job and becomes silent? The synaptic connection for the burst neuron always exists. This situation is totally different from the case where no input exists. If the connection is excitatory, then a prolonged input of the resting potential produces inhibitory effects and takes the new state back to the original attractor and even further activates another attractor in the opposite direction. Therefore, there must exist some other input that neutralizes the inverse effects during the time when the burst neuron is silent. Fortunately, in a neural integrator for saccadic eye movements, there exist two kinds of synaptic connections in each integrator neuron for burst input, one inhibitory and the other excitatory. When burst neurons connected two these synapses are both silent, the effects of resting potentials of both neurons cancel each other out. This situation is the same as the case where no input exists, that is, an autonomous network. In short, eye position is kept steady not only by attractiveness of a tonic firing and but also by pairs of excitatory and inhibitory connections for burst neurons.

Now let the vector sequences input from burst neurons to the inhibitory synapses of three neurons be b , and the vector sequence input from burst neurons to the inhibitory synapses of three neurons be c . Both b and c are indexed as

$$\begin{array}{l} 1, 4, 7, 10, 13, 16, \dots \\ 2, 5, 8, 11, 14, 17, \dots \\ 3, 6, 9, 12, 15, 18, \dots, \end{array}$$

so that b_1 is the state input to the first neuron at time 1, b_8 is the state input to the second neuron at time 3, etc.

To accept burst input from these sequences, we add \mathbf{Q}^{24} . The weights of the synaptic efficacies of the input connections relative to the efficacies between the integrator neurons depend on the dimension and burst input and need some feedback

from the next stage. In the present case, I make the relative weights equal to each other.

Then, by modifying the transformation F defined by (10.2.2) and (10.2.4), we obtain the function $G : \mathbf{Q}^{36} \rightarrow \mathbf{Q}^{12}$ defined by

$$G : (v_1, \dots, v_{36}) \mapsto (w_1, \dots, w_{12}), w_i = v_{i+3} \text{ for } i = 1, \dots, 9.$$

w_i for $i = 10, 11, 12$ are determined by g_i , where $g_i = p_i \cdot \neg(p_i G)$, defined by

$$g_{10} = p_{10} \cdot (\neg p_1 \cdot p_4 \cdot p_7 \cdot S_5 \vee p_4 \cdot p_7 \cdot S_6 \vee \neg p_1 \cdot S_7 \vee S_8), \quad (10.3.1)$$

where S_i is the disjunction of all conjunctions of i functions selected from

$$\{\neg p_2, \neg p_3, \neg p_5, \neg p_6, \neg p_8, \neg p_9, \neg p_{11}, \neg p_{12}, p_{13}, p_{16}, p_{19}, p_{22}, \neg p_{25}, \neg p_{28}, \neg p_{31}, \neg p_{34}\}.$$

G is symmetric in the sense $G\tau = \tau G$ for permutations

$$\tau = (1, 2)(4, 5)(7, 8)(10, 11)(13, 14)(16, 17)(19, 20)(22, 23)(25, 26)(28, 29)(31, 32)(34, 35)$$

and

$$\tau = (1, 3)(4, 6)(7, 9)(10, 12)(13, 15)(16, 18)(19, 21)(22, 24)(25, 27)(28, 30)(31, 33)(34, 36).$$

Therefore, g_{11} and g_{12} are immediately obtained from g_{10} . G is also self-dual, so that $\neg p_i \cdot F_i = \bar{g}_i$.

The non-autonomous dynamical system $\varphi : \mathbf{Q}^{12} \times \mathbf{Z}_+ \rightarrow \mathbf{Q}^{12}$ generated by G and the input sequence b and c is defined by

$$\begin{aligned} \varphi(v, 0) &= v, \\ \varphi(v, t) &= G(\varphi(v, t-1), b_{1+3(t-1)}, \dots, b_{12+3(t-1)}, c_{1+3(t-1)}, \dots, c_{12+3(t-1)}). \end{aligned}$$

10.4 DETERMINATION OF BURST PATTERNS

Determination of burst patterns was unexpectedly hard. I tried a lot of failed patterns before I hit the jackpot.

First I tried a single pulse being input to three neurons with the same timing. In this case, (10.3.1) was different in that more weight should be put on the burst input and the equation (10.3.1) should be more complex. For example, in one of several variants of (10.3.1), in order that the tonic firing patterns were changed by a pattern of inhibitory burst neurons, from 1111 to 1110, 1110 to 1010, 1010 to 1000, 1000 to 0000, the pattern 1110 was not only changed to 1010, but also further changed to 1000. Then, I tried some examples where one neuron receives a burst pulse after another neuron, so that, for example,

$$\begin{array}{ccc} 1111 & & 011101 \\ 1111 & \mapsto \dots \mapsto & 101110 \\ 1111 & & 110111. \end{array}$$

Also, I changed the burst pattern from just one pulse 000100000.. to 0001010000.. and the like. Things improved. Still, the best example I obtained failed in one case of timing between the burst pattern and one particular tonic sequence.

We must consider at least two factors. 1. A desired change in each tonic pattern must occur at specific time points of the pattern. For example, for the change from 1110 to 1010, the change must occur at the second time point. If this time point is missed, then another one period of 4 time points is required for the change. In

the present model temporal summation is over 4 time points. Therefore, there is only one chance, if the change is made by one pulse of burst input. On the other hand, from the pattern 1111 to the pattern 1110, there are 4 chances in one period. For one kind of change there is too few chances and for another kind of change too many chances.

Attractiveness of these tonic patterns during the time when both inhibitory and excitatory neurons are silent is made by cooperation by the three neurons. This cooperative nature is alive during the transient period of change from one pattern to another by burst input. Therefore, a change in one neuron influences another neuron. In particular, if two neurons are changed from one pattern to another pattern, the third neuron will be changed without any pulse of the burst neuron input thereto.

My first trials where a single pulse is simultaneously input to the three neurons have no problem for the above factor 2, but were severely affected by the above factor 1. My attempts to diversify the phases of patterns and increasing the number of burst pulses relieved the factor 1 but brought some effects of the factor 2. Therefore, a neuron receives burst pulses later than another should receive fewer burst pulses.

After several trials in this way, I finally got an example where one burst pattern can change each tonic pattern to another tonic pattern one step lower, when starting from

```
111111111...
111111111...
111111111...
```

The burst pattern is:

```
101010000000...
000010100000...
000000000000...
```

Here, the first line is the burst input to neuron 1, the second is the burst input to neuron 2, and the third is the burst input to neuron 3. The dynamical system is self-dual, so that starting from

```
000000000
000000000
000000000,
```

with excitatory burst input of the same pulse pattern, the firing of the three neuron reaches

```
111111111...111111111...111111111...
```

through 4 changes, each change occurring whenever the pulse pattern is input.

I have not checked all cases where excitatory burst input is followed by inhibitory burst input and vice versa. But it seems the push-pull property is also satisfied.

10.5 CIRCULAR THRESHOLD CONSTRUCTIONS

Now we address the pending problem that the function H in the transformation F in Section 10.2 is not a threshold function. It seems impossible to modify the function f_i to a threshold function such that the modified F has tonic attractors of firing rates $i/4, i = 0, 1, 2, 3, 4$. Therefore, we try to construct a totally new network.

First, let us consider only the following types of tonic sequences of four neurons.

```
00000... 100010... 01010... 011101... 11111...
00000... 010001... 10101... 101110... 11111...
00000... 001000... 01010... 110111... 11111...
00000... 000100... 10101... 111010... 11111...
```

Then, we can distinguish these tonic sequences of firing rates $i/4$ from each other in any of their synchronic cross sections.

For example, the first and third cross sections are respectively

```
0 1 0 0 1
0 0 1 1 1
0 0 0 1 1
0 0 1 1 1
```

and

```
0 0 0 1 1
0 0 1 1 1
0 1 0 0 1
0 0 1 1 1
```

That is, these tonic sequences can be distinguished by their cross sections, which are elements in \mathbf{Q}^4 . We call the firing rate in each cross section a synchronic firing rate in contrast to a diachronic firing rate, which is the normal definition of firing rate. In the present case, each synchronic firing rate of a tonic sequence is equal to its diachronic firing rate. However the minimum distance between the cross sections of two different sequences is 1. Therefore, in order to separate the cross sections at least by distance 3 and make each tonic sequence an attractor in a dynamical system, we consider the state space of \mathbf{Q}^{12} . The tonic sequences now become

```
00000... 100010... 01010... 011101... 11111...
00000... 010001... 10101... 101110... 11111...
00000... 001000... 01010... 110111... 11111...
00000... 000100... 10101... 111011... 11111...
00000... 100010... 01010... 011101... 11111...
00000... 010001... 10101... 101110... 11111...
00000... 001000... 01010... 110111... 11111...
00000... 000100... 10101... 111011... 11111...
00000... 100010... 01010... 011101... 11111...
00000... 010001... 10101... 101110... 11111...
00000... 001000... 01010... 110111... 11111...
00000... 000100... 10101... 111011... 11111...
```

The first and the last sequences are constant-term sequences in \mathbf{Q}^{12} . The second and fourth are cyclic sequences of period 4, and the third is the cyclic sequence of period 2. Also the component sequence is the right shift of the immediately above component sequence.

We now try to construct a first-order NN of dimension 12, in which the above 5 tonic cyclic sequences are attractors. After several attempts, I obtained the following self-dual circular threshold transformation F of \mathbf{Q}^{12} defined by $F = \langle f_1 \rangle$,

$$f_1 = p_1 \cdot S_2\{\neg p_4, \neg p_8, \neg p_{12}\}. \quad (10.5.1)$$

This threshold translation is described in Example 7.2.5 of Chapter 7 for general dimension. In fact, according to Chapter 7.2, this NN has only 6 cycles and all of them are strong attractors. Five of them correspond to those illustrated above, and the other correspond to the non-tonic cyclic sequence of period 4,

```

11001100...
01100110...
00110011...
10011001...
11001100...
01100110...
00110011...
10011001...
11001100...
01100110...
00110011...
10011001...

```

The next problem is how to resolve this unwelcome non-tonic attractor. However, it seems again impossible to modify the circular threshold transformation to another having only the five tonic attractors. For non-threshold constructions, see Section 10.8. we use this autonomous NN to construct a neural integrator. An advantage is that we can easily generalize the dimension of this transformation. However, there will be more and more non-tonic attractors as the dimension becomes higher.

A non-autonomous network having burst input for an integrator can now be defined by the mapping $G: \mathbf{Q}^{36} \rightarrow \mathbf{Q}^{12}$, $G = \langle g_1 \rangle$,

$$g_1 = p_1 \cdot (S_2\{\neg p_4, \neg p_8, \neg p_{12}\} \cdot S_1\{p_{13}, \neg p_{25}\} \vee S_2\{p_{13}, \neg p_{25}\}), \quad (10.5.2)$$

where the indices 13 to 24 respectively represent the inhibitory burst input to neuron 1 to 12, and the indices 25 to 36 respectively represent the excitatory burst input to neuron 1 to 12. See Chapter 9.3 for the notation $\langle g_1 \rangle$ (Modify the definition for one input 13 to 24 into two inputs 13 to 24 and 25 to 36).

10.6 FUNCTIONS OF BURST GENERATORS

The functions of a generator of burst sequences to be input to a neural integrator defined by (10.5.2) should be very sophisticated and complex. First, the generator supplies pulses so that non-tonic attractors should be avoided. Moreover, the generator supplies pulses with exact timing. For example, in order to reduce a firing rate from 3/4 to 1/2, at a time when the state (cross section) is

$$111011101110, \quad (10.6.1)$$

and the excitatory burst generator is silent, the inhibitory burst generator supplies a pulse to at least two of neurons 3, 7, 11. If pulses are input to neurons 3, 7, and 11, then the next state is

$$0101001010111.$$

By the attractiveness, the next state will be a tonic cross section of firing rate 1/2, if no more pulses are supplied. Therefore, a tonic sequence of firing rate 1/2 is obtained. However, if the inhibitory burst generator supplies pulses to neurons 1 and 5 at the state (10.6.1), then there is no change in the firing rate in the next

cross section, just a circular shift. If the inhibitory burst pulses are supplied to neurons 2 and 6, then the next cross section is

001100110111.

By the attractiveness, the next state will be a non-tonic cross section of firing rate $1/2$. Therefore, a non-tonic sequence will succeed, when both burst generators are silent. According to Van Gisbergen, Robinson, and Gielen (1981), the heart of the local feedback hypothesis is that the output E' of the integrator is relayed back to burst generators. The burst generators also receive a command signal E_d from higher centers. "Burst cell is driven by a signal proportional to motor error, which is the difference between where the eye is (E') and where it should be (E_d)" (p. 419).

For our integrator network defined by (10.5.2), the matter is not only of firing rate but also of precise timing. Therefore, designing a neural circuit of the burst generators and the local feedback system is another combinatorial problem to be studied in the next stage.

10.7 GENERATOR-INTEGRATOR FEEDBACK SYSTEM

Now, we try to construct a burst generator and a local feedback system for the burst generator and integrator. Van Gisbergen, Robinson, and Gielen (1981) contains a proposed model, which is not a neural circuit in a strict sense but rather a conceptual block diagram for the feedback system. The proposed model simulates experimental data in terms of firing rate. But what is a neural circuit that receives two signals and outputs a signal having the firing rate of the difference between the firing rates of two input signals. To construct such a circuit will require resolving the same kind of difficulties as the generator-integrator feedback system does, such as timing between two signals and limitations of threshold functions. To describe the generator-integrator feedback system in terms of the "difference" of two signals is as tautological as to say that an integrator gives a signal whose firing rate is the sum of the firing rates of two signals. In our following model, it is the burst generator itself that produces a kind of difference as burst signals.

Here our purpose is not to simulate a real nervous system for saccadic eye movements. Instead, we are concerned with an idealized abstract system in contrast to statistical analysis and parameter physics that simulate experimental data, where firing rate represents a crude abstraction of reality. Therefore, we try to construct neural circuits of a feedback system, as a basis for a concrete system, in terms of pulse signals and Boolean functions in place of firing rates. Still, this approach deals with intrinsic properties of neural circuits, such as timing and threshold functions. We do not take into account the time required for transmission of signals between the burst generator and the integrator, but slight modification will easily incorporate the delays.

When we describe a system in terms of 0-1 pulse signals and not in terms of firing rate, we can define the difference of two signals, that is, two sequences x and y in \mathbf{Q}^n by a pair of h and c defined by,

$$\begin{aligned} h(t+1) &= x(t) \cdot \neg y(t), \\ c(t+1) &= y(t) \cdot \neg x(t). \end{aligned} \tag{10.7.1}$$

For example, consider the following three sequences in \mathbf{Q}^4 . Note that the firing rate of the first is $3/4$. The second and the third sequences differ only in their phases, and their firing rate is $1/4$.

```

101110111011  100010001000  010001000100
110111011101  010001000100  001000100010
111011101110  001000100010  000100010001
011101110111  000100010001  100010001000
    
```

For the first two sequences, h and c are respectively

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001100110011  000000000000
100110011001  000000000000
110011001100  000000000000
011001100110  000000000000
    
```

Therefore, h is a sequence having a firing rate $1/2$ that is the difference of the firing rates of the first and the second. However, for the first and the third sequences, h and c are respectively

```

101110111011  010001000100
110111011101  001000100010
111011101110  000100010001
011101110111  100010001000
    
```

Here, the firing rate of h is $3/4$ and the firing rate of c is $1/4$. Therefore, we have not obtained a sequence of firing rate $1/2$. Therefore, we have faced another timing problem to produce a signal having the difference firing rate of two signals. In order to avoid a complex timing problem, it is better not to seek such a signal but to use the pair (h, c) for the difference of two signals.

Now assume that the above sequence x is an integrator signal and y is a command signal. Further assume that h is the inhibitory burst signal, and c is the excitatory burst signal. Then we can construct the following feedback system.

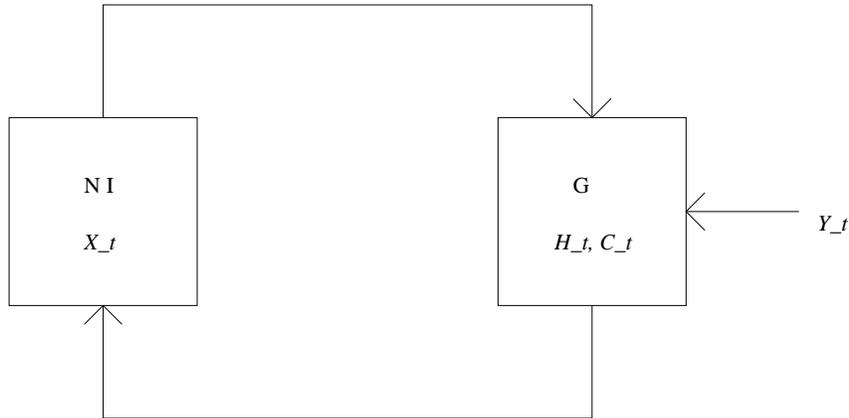


FIGURE 1.

where, besides (10.7.1),

$$\begin{aligned}
 x_{t+1} &= G(x(t), h(t), c(t)), & G &= \langle g_1 \rangle, \\
 g_1 &= p_1 \cdot (\neg p_4 \cdot (p_5 \vee p_9) \vee p_5 \cdot \neg p_9).
 \end{aligned}
 \tag{10.7.2}$$

(10.7.2) is a simplified function of (10.5.2) obtained by removing attractiveness. If we consider the state space \mathbf{Q}^{12} in place of \mathbf{Q}^4 , we can use (10.5.2) as it is. Two problems should be addressed now. First, for an integrator to change the firing rate $3/4$ of x to $1/4$, it must receive $h(t)$ and $c(t)$ that may, depending on the timing between x and the command signal as described above, be simultaneously active at some time t from the burst generator. This does not pose any serious mathematical problems. It also agrees with reality, since Van Gisbergen, Robinson, and Gielen (1981, p.418) says, "... during any saccade, ... burst neurons on both sides of the brain stem often are active simultaneously."

The second problem was already discussed in the last section. The function G is very sensitive to the timing between the inputs x and (h, c) . In fact, the above feedback system defined by (10.7.1) and (10.7.2) does not work. There are two time lags between the measuring of the difference and the realization of changing the synchronic firing rate of x . At the same time period, if all components of h and c are all 0, then the cross section of x will round-shifted by 2. Therefore, (10.7.1) should be modified to

$$\begin{aligned} h(t+1) &= \rho^2(x(t) \cdot \neg y(t)), \\ c(t+1) &= \rho^2(y(t) \cdot \neg x(t)), \end{aligned} \quad (10.7.3)$$

where ρ is the cyclic permutation (1,2,3,4). Clearly h and c are threshold functions. Computer simulation expects that this feedback system will work. For example, for the first and third sequences in the beginning of this section respectively as $x(t)$ and $y(t)$, we obtain

```

                                10000100
                                11100010
x(t) :                          11010001
                                01001000

                                01000100
                                00100010
y(t) :                          00010001
                                10001000

                                01100000
                                00100000
h(t) :                          01000000
                                01100000

                                00000000
                                01000000
c(t) :                          00100000
                                00000000

```

Next, we prove a theorem that validates the generator-integrator feedback system constructed in above. The state spaces are now \mathbf{Q}^m , and ρ is the cyclic permutation (1, 2, ..., m). Let y be a tonic sequence in \mathbf{Q}^m . If $y(t+1) = \rho y(t)$ for every t , we call x a *circular tonic sequence*.

G is a circular function: $\mathbf{Q}^{3m} \rightarrow \mathbf{Q}^m$, that is, $\rho G(u, v, w) = G(\rho u, \rho v, \rho w)$ for $u, v, w \in \mathbf{Q}^m$, defined by $g_1 = p_1 \cdot \neg(p_1 G)$, that is, $G = \langle g_1 \rangle$,

$$g_1 = p_1 \cdot (\neg p_m \cdot (p_{m+1} \vee \neg p_{2m+1}) \vee p_{m+1} \cdot \neg p_{2m+1}). \quad (10.7.4)$$

The command signal $y(t)$ is a given circular tonic sequence in \mathbf{Q}^m , and the integrator signal $x(t)$ is a sequence in \mathbf{Q}^m defined by

$$x_{t+1} = G(x(t), h(t), c(t)). \quad (10.7.5)$$

The burst signals $h(t)$ and $c(t)$ are sequences in \mathbf{Q}^m defined by

$$\begin{aligned} h(t+1) &= \rho^2(x(t) \cdot \neg y(t)), \\ c(t+1) &= \rho^2(y(t) \cdot \neg x(t)) \end{aligned} \quad (10.7.6)$$

In the following, $M = \{1, \dots, m\}$ is regarded as the residue class ring with m as the zero element. For example, $1 - 2 = m - 1$. Further, $o = (00, \dots, 0) \in \mathbf{Q}^m$.

Theorem 10.7.1 Let $h(0) = c(0) = o$. Then, $x(2) = y(2)$, and $x(3) = y(3)$.

Proof. Let $h(1)_k = 1$ and $c(1)_k = 0$. Clearly $x(2)_k = 0$. On the other hand, we have $x(0)_{k-2} = 1$ and $y(0)_{k-2} = 0$, since $h(1)_k = 1$. Therefore, $y(2)_k = y(0)_{k-2} = 0$. Therefore, $x(2)_k = y(2)_k$. By self-duality, if $h(1)_k = 0$ and $c(1)_k = 1$, then $x(2)_k = y(2)_k$.

Next, let $h(1)_k = c(1)_k = 0$. If $x(1)_k = 1$ and $x(1)_{k-1} = 0$ then $x(2)_k = 0$. If $x(1)_k = 1$ and $x(1)_{k-1} = 1$, then $x(2)_k = 1$. Therefore, by self-duality, $x(2)_k = x(1)_{k-1}$. On the other hand, $x(0)_{k-2} = y_{k-2}$, since $h(1)_k = c(1)_k = 0$. Therefore, $x(1)_{k-1} = x(0)_{k-2}$, since $h(0) = c(0) = o$. Therefore, $x(2)_k = x(0)_{k-2}$. Clearly $y(2)_k = y(0)_{k-2}$. Therefore, $x(2)_k = y(2)_k$. Therefore, $x(2) = y(2)$.

Further, $x(1) = \rho x(0)$ and $y(1) = \rho y(0)$. Therefore,

$$\begin{aligned} h(2) &= \rho^2(x(1) \cdot \neg y(1)) = \rho^3(x(0) \cdot \neg y(0)) = \rho h(1). \\ c(2) &= \rho^2(y(1) \cdot \neg x(1)) = \rho^3(y(0) \cdot \neg x(0)) = \rho c(1). \end{aligned}$$

Let $h(2)_k = 1$. Then $h(1)_{k-1} = 1$, so that $x(2)_{k-1} = 0$. Therefore, if $x(2)_k = 1$, then $x(3)_k = 0 = x(2)_{k-1}$. If $x(2)_k = 0$, then $x(3)_k = 0 = x(2)_{k-1}$. If $c(2)_k = 1$, then $x(3)_k = 1 = x(2)_{k-1}$ by self-duality. Next, let $h(2)_k = c(2)_k = 0$. Then clearly $x(3)_k = x(2)_{k-1}$. Therefore, $x(3) = \rho x(2) = \rho y(2) = y(3)$. \square

The above Theorem 10.7.1 shows that if $h(0) = c(0) = o$, then, $x(2) = y(2)$ and $x(3) = y(3)$, so that $h(3) = c(3) = o$, so that $x(4) = y(4), \dots$. Therefore, if $h(0) = c(0) = o$, then $x(t) = y(t)$ for every $t \geq 2$, and $h(t) = c(t) = o$ for every $t \geq 3$. Therefore, if y changes to another circular tonic sequence at some time $t' \geq 3$, then $x(t) = y(t)$ for every $t \geq t' + 2$, since $h(t') = c(t') = o$. It is well known that omni-pause neurons make burst generators silent. The input from the omni pause neurons to the burst generator is one feature that is absent from the present generator-integrator feedback model.