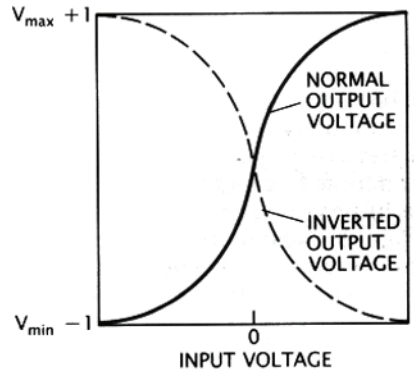
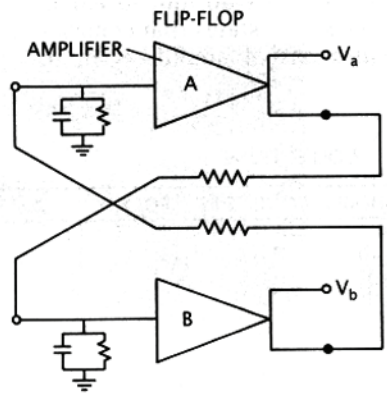
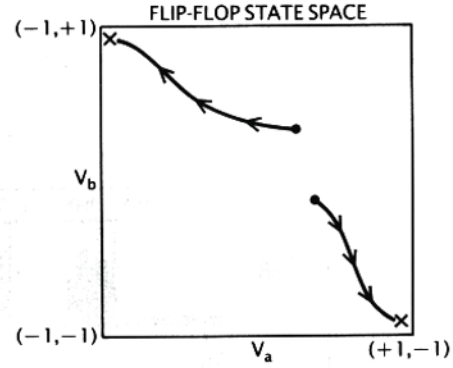
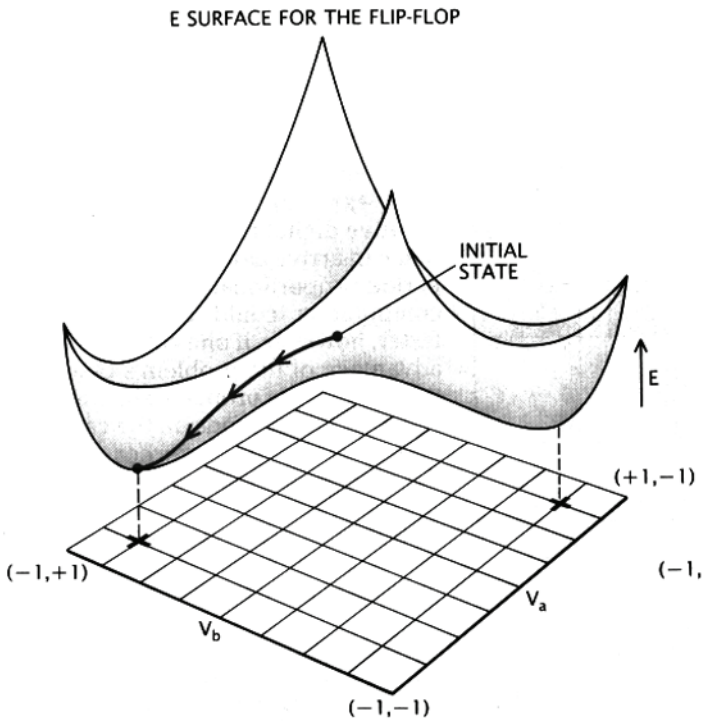
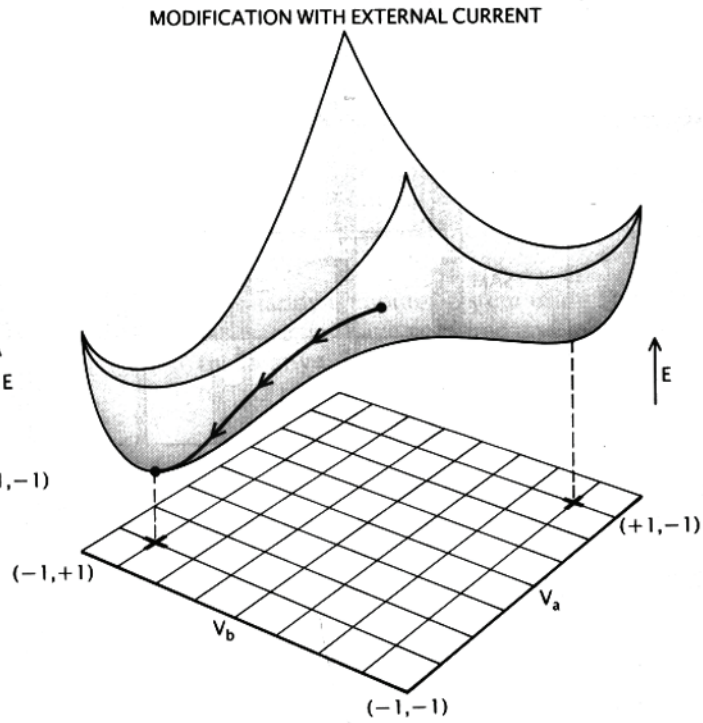
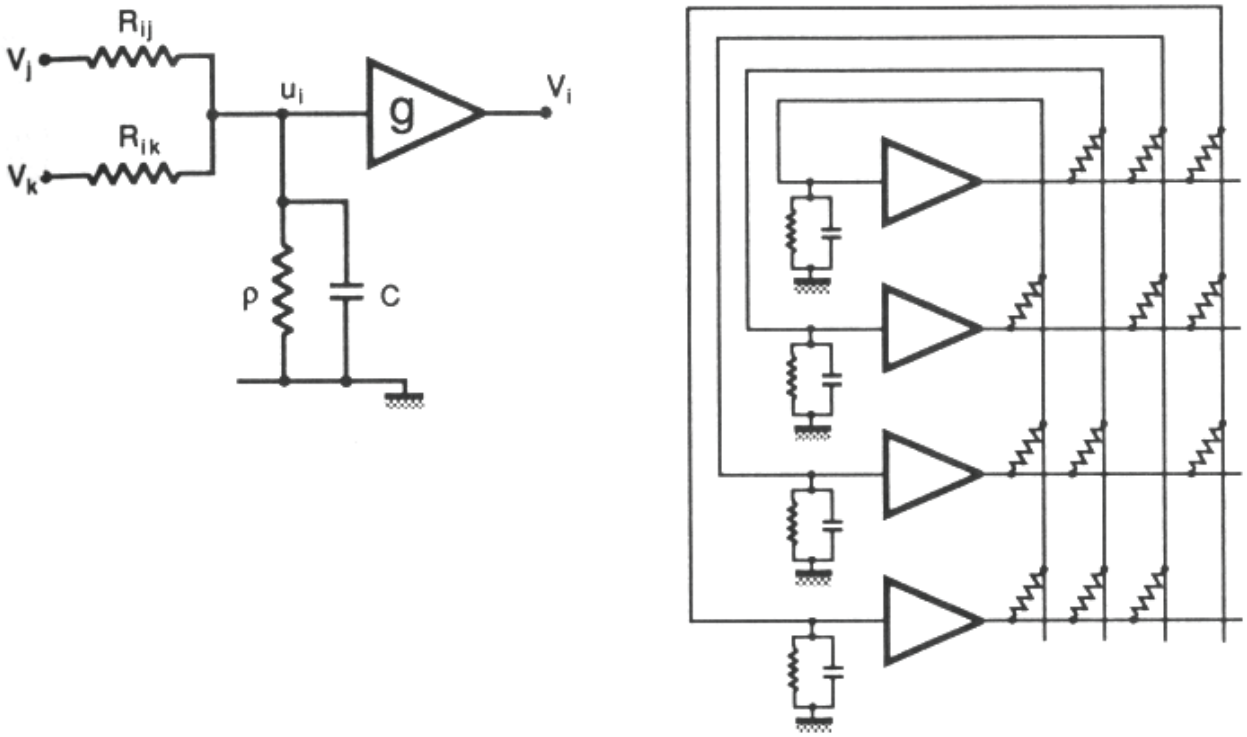

V_{max} +1
NORMAL OUTPUT VOLTAGE
INVERTED OUTPUT VOLTAGE
V_{min} −1
0
INPUT VOLTAGE


FLIP-FLOP
AMPLIFIER
A
B
V_a
V_b


FLIP-FLOP STATE SPACE
(−1,+1)
(−1,−1)
(+1,−1)
V_a
V_b


E SURFACE FOR THE FLIP-FLOP
INITIAL STATE
E
(+1,−1)
(−1,+1)
(−1,−1)
V_a
V_b


MODIFICATION WITH EXTERNAL CURRENT
E
(+1,−1)
(−1,+1)
(−1,−1)
V_a
V_b



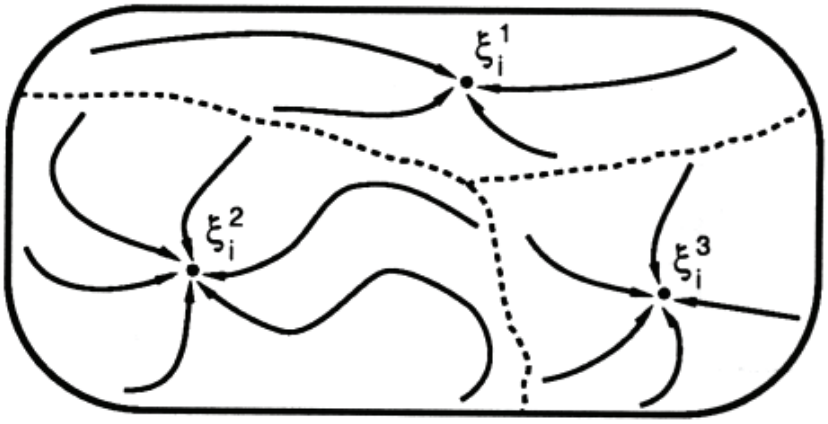


FIGURE 2.2 Schematic configuration space of a model with three attractors.

Herz_Fig.2.2

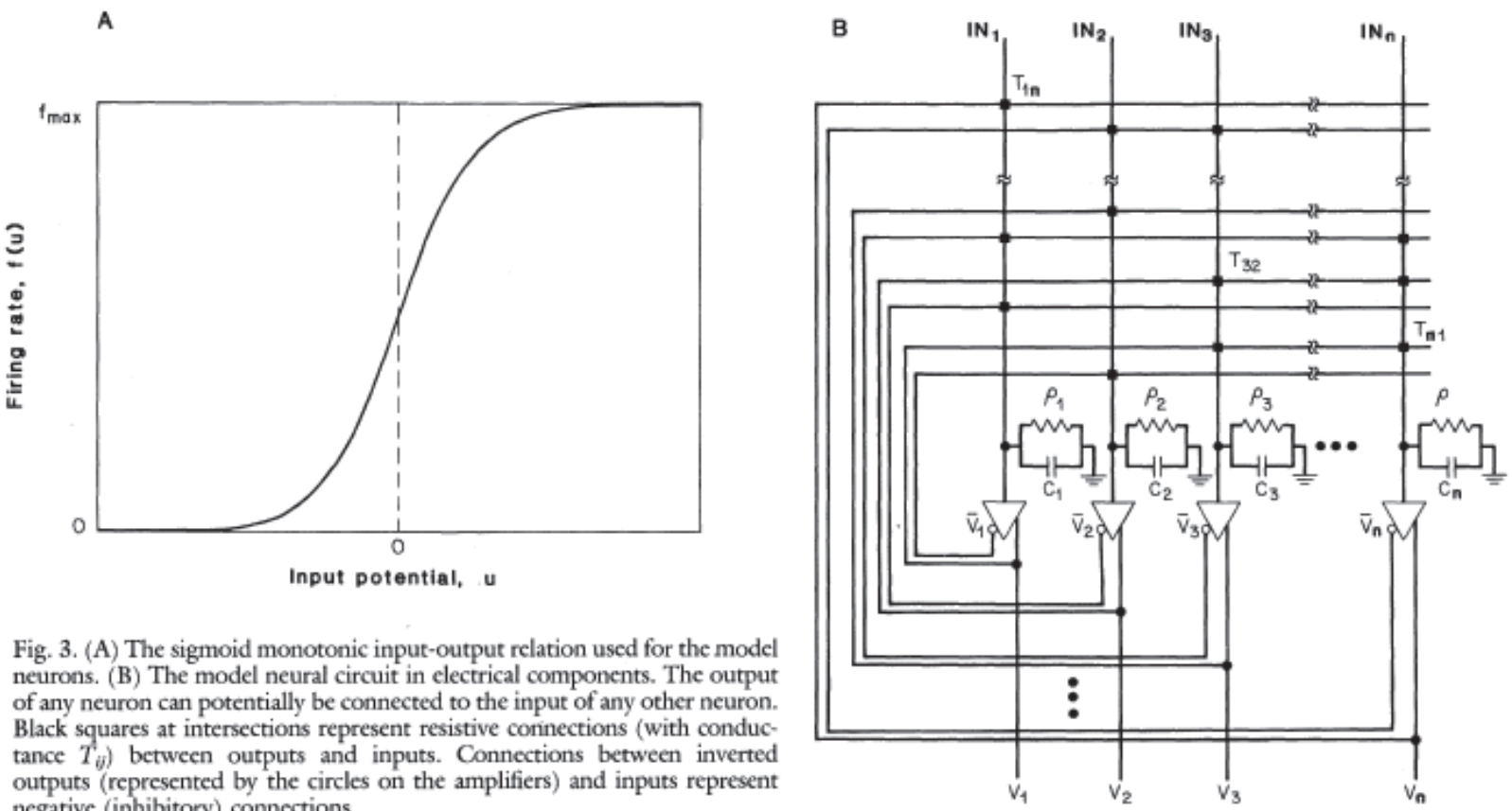


Fig. 3. (A) The sigmoid monotonic input-output relation used for the model neurons. (B) The model neural circuit in electrical components. The output of any neuron can potentially be connected to the input of any other neuron. Black squares at intersections represent resistive connections (with conductance T_{ij}) between outputs and inputs. Connections between inverted outputs (represented by the circles on the amplifiers) and inputs represent negative (inhibitory) connections.

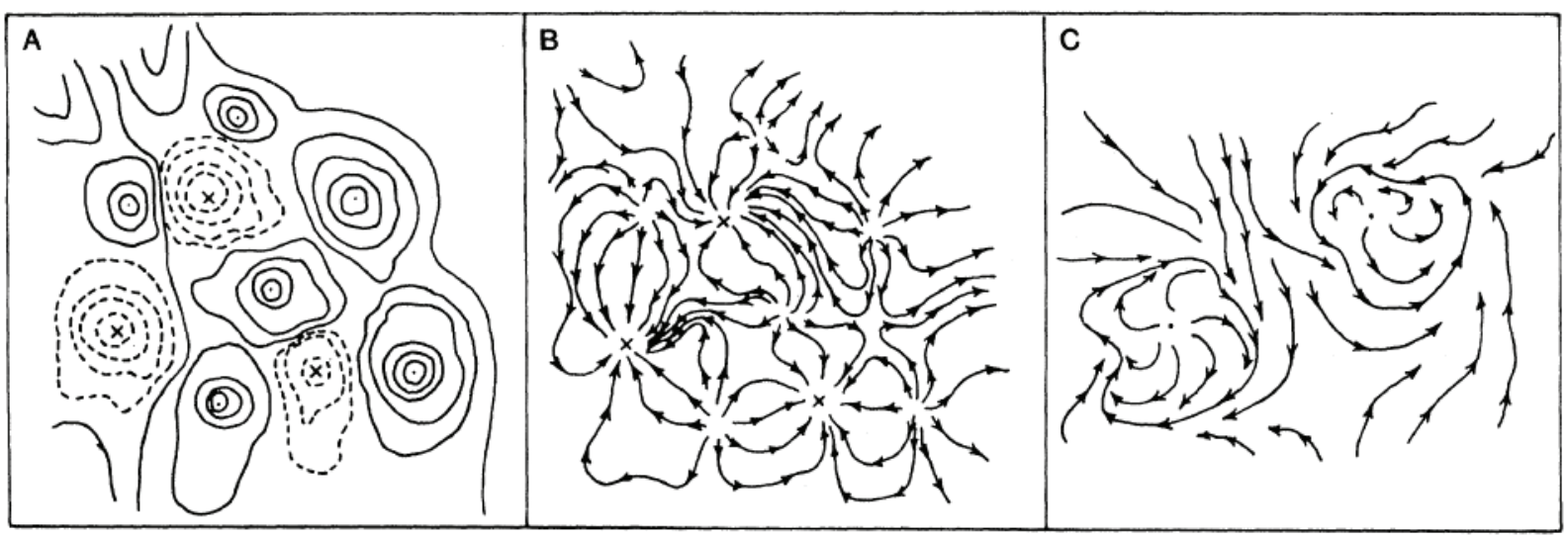


Fig. 4. (A) Energy-terrain contour map for the flow map shown in (B). (B) Typical flow map of neural dynamics for the circuit of Fig. 3 for symmetric connections ($T_{ij} = T_{ji}$). (C) More complicated dynamics that can occur for unrestricted (T_{ij}). Limit cycles are possible.

Box 1. Persistent activity as neural correlate of working memory

Cortical 'memory neurons' that show persistent activity are typically recorded during a delayed response task, in which a monkey is required to retain the information of a sensory cue across a delay period between the stimulus and behavioral response. Memory cells were first found, and seem to be especially abundant, in the prefrontal cortex (PFC)[a–e]. The crucial role of the PFC in working memory is also supported by lesion[f,g] and brain imaging studies[h]. However, neural persistent activity is a widespread phenonemon in association cortices, including the posterior parietal cortex[i–k], and the inferotemporal cortex[l,m]. According to the type of sensory stimulus that is encoded for storage, one can distinguish three kinds of working memory.

Discrete working memory

Figure Ia shows a delayed match-to-sample experiment, in which the behavioral response depends on the memory of one of the two items (the stimulus color, red or green). An inferotemporal neuron displays elevated activity through the entire delay period (16 s), which is selective to the color red. Such tasks engage a working memory circuit in which the stored information is a categorical feature of the stimulus or an object (a face, color or word). Arguably, the items form a discrete collection, and a given neuron or neural assembly is selective to one or a few items.

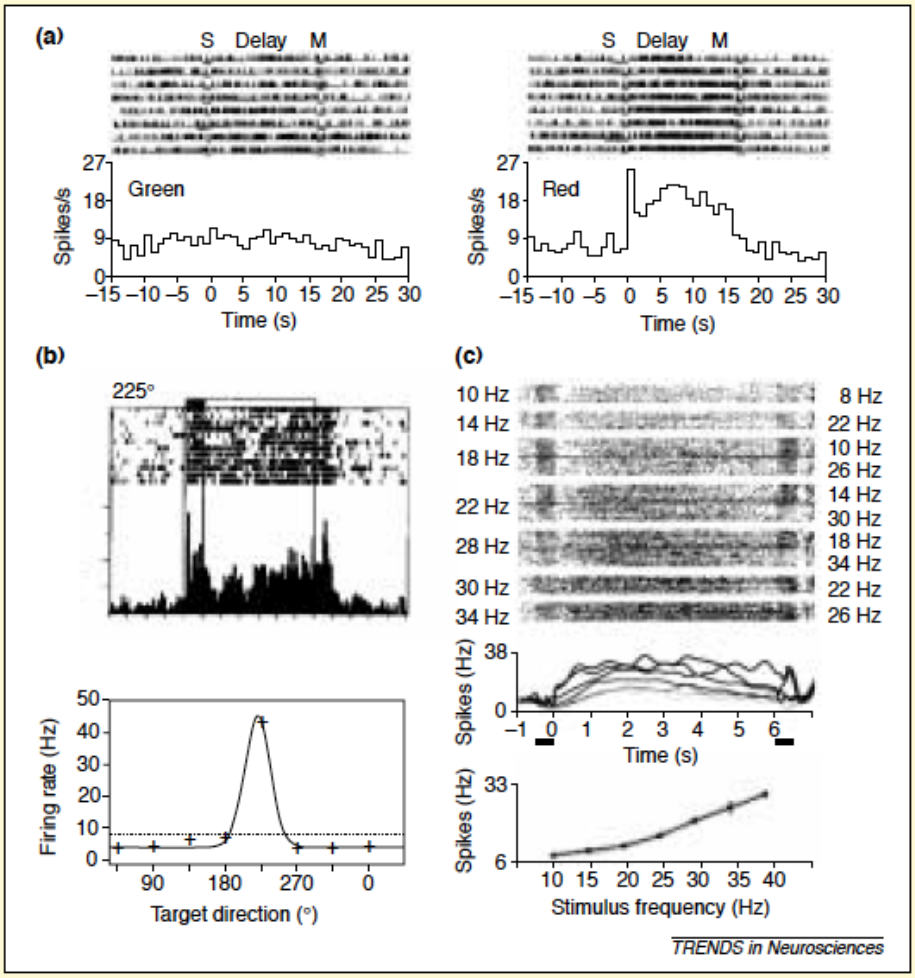
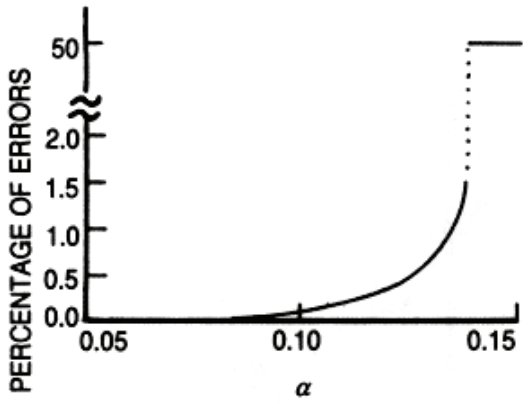


Fig. I. Three types of working memory encoding. (a) Discrete working memory. In a delayed match (M)-to-sample (S) experiment, an inferotemporal neuron shows sustained high activity for the color red (but not green) of a visual cue, during a delay period of 16 s. Redrawn, with permission, from Fuster and Jervey[l]. (b) Spatial working memory. In a delayed saccade experiment, a prefrontal neuron shows persistent activity that is tuned to a preferred location of a visual cue. Upper panel: rasters and cumulative spike histogram for a preferred cue; lower panel: spatial tuning curve of delay period activity. Redrawn, with permission, from Funahashi *et al.*[c] (c) Parametric working memory. In a delayed somatosensory discrimination task, a neuron in the inferior convexity shows persistent activity with a firing rate proportional to the cue frequency. Upper panel: rasters. Cue stimulus frequency indicated on the left, comparison stimulus frequency indicated on the right. Middle panel: trial-averaged firing rates as a function of time. Lower panel: mean firing rates, averaged across the entire delay period, as a function of the cue frequency. Redrawn, with permission, from Romo *et al.*[o]

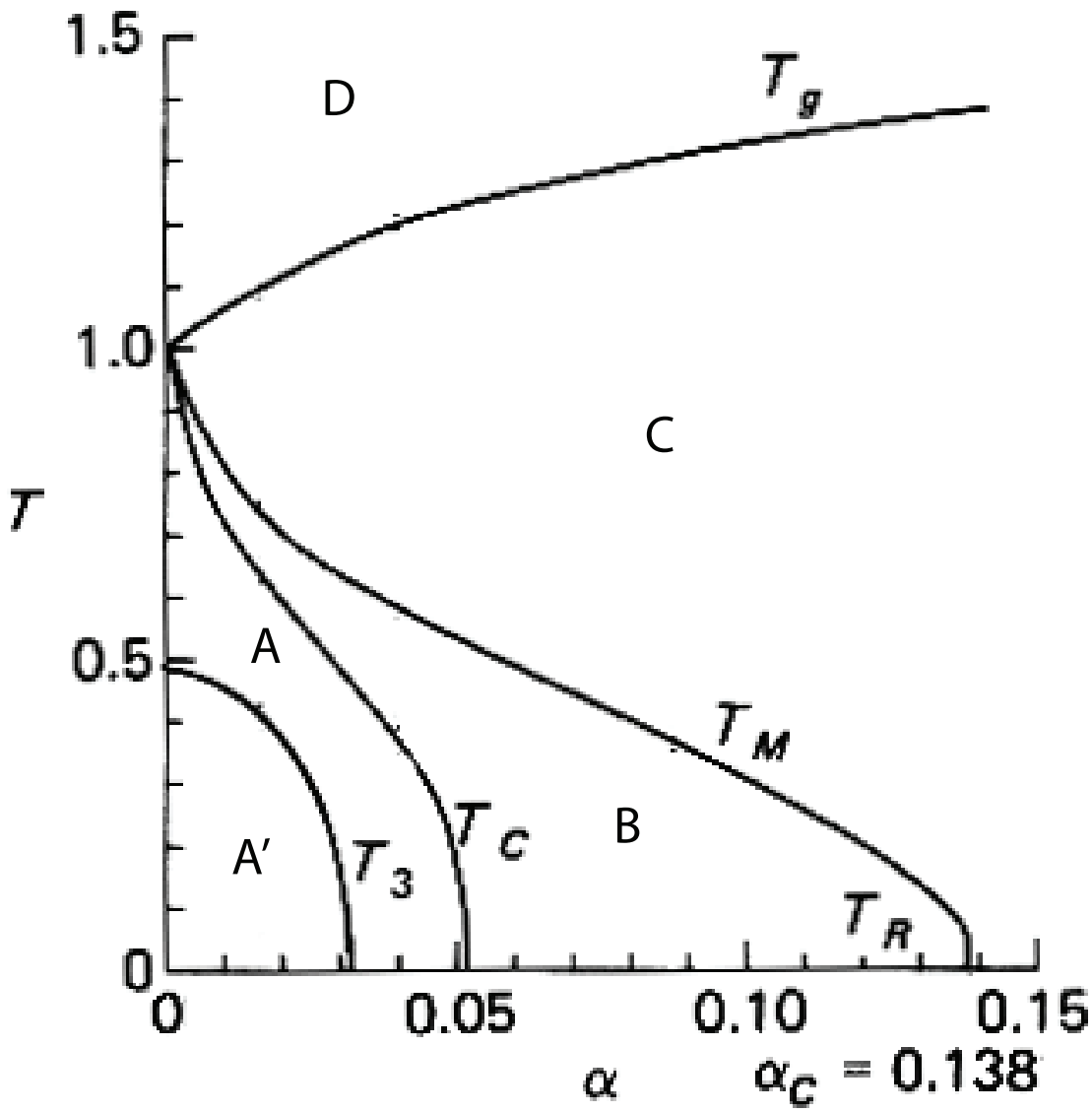
Spatial working memory

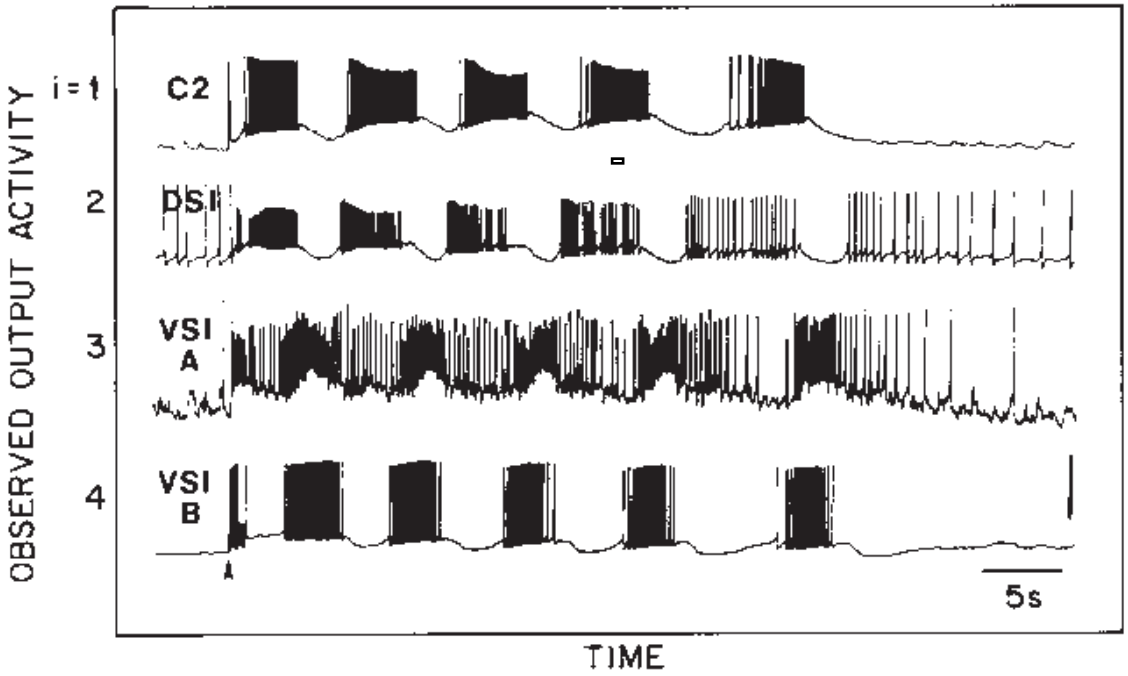
Figure Ib illustrates a delayed oculomotor experiment, in which a saccadic eye movement is guided by the memory of a spatial stimulus. In this case, the stored information is spatial location, which is an analog quantity. Neurons in the dorsolateral PFC display persistent delay activity that is spatially selective. The 'memory field' of a cell is characterized by a smooth tuning curve, peaked at a preferred spatial cue, which is different from cell to cell. The memory of a given spatial location is stored by the neural population in the form of a spatially localized persistent firing pattern, or a 'bump attractor'. Bump states are common to



Errors per neuron increase discontinuously as $T \rightarrow 0$ in the Hopfield model, signaling a complete loss of memory, when the parameter $\alpha = p/N$ exceeds the critical value 0.14. Here p is the number of random memories stored in a Hopfield network of N neurons.

Sompolinsky(1988)_Fig.2




OBSERVED OUTPUT ACTIVITY
i = 1
C2
2
DSI
3
VSI
A
4
VSI
B
5s
TIME

The observed output sequences will be approximated by an oscillation between a state V^+ and its antiphase $V^- \equiv (1 - V^+)$, where

$$V^+ = \begin{pmatrix} \text{activity of} & C2 \\ & DSI \\ & VSI - A \\ & VSI - B \end{pmatrix} = \begin{pmatrix} +1 \\ +1 \\ 0 \\ 0 \end{pmatrix} \quad \text{and}$$

$$V^- = \begin{pmatrix} 0 \\ 0 \\ +1 \\ +1 \end{pmatrix}$$

These states are used as the stable embedded states in our model.

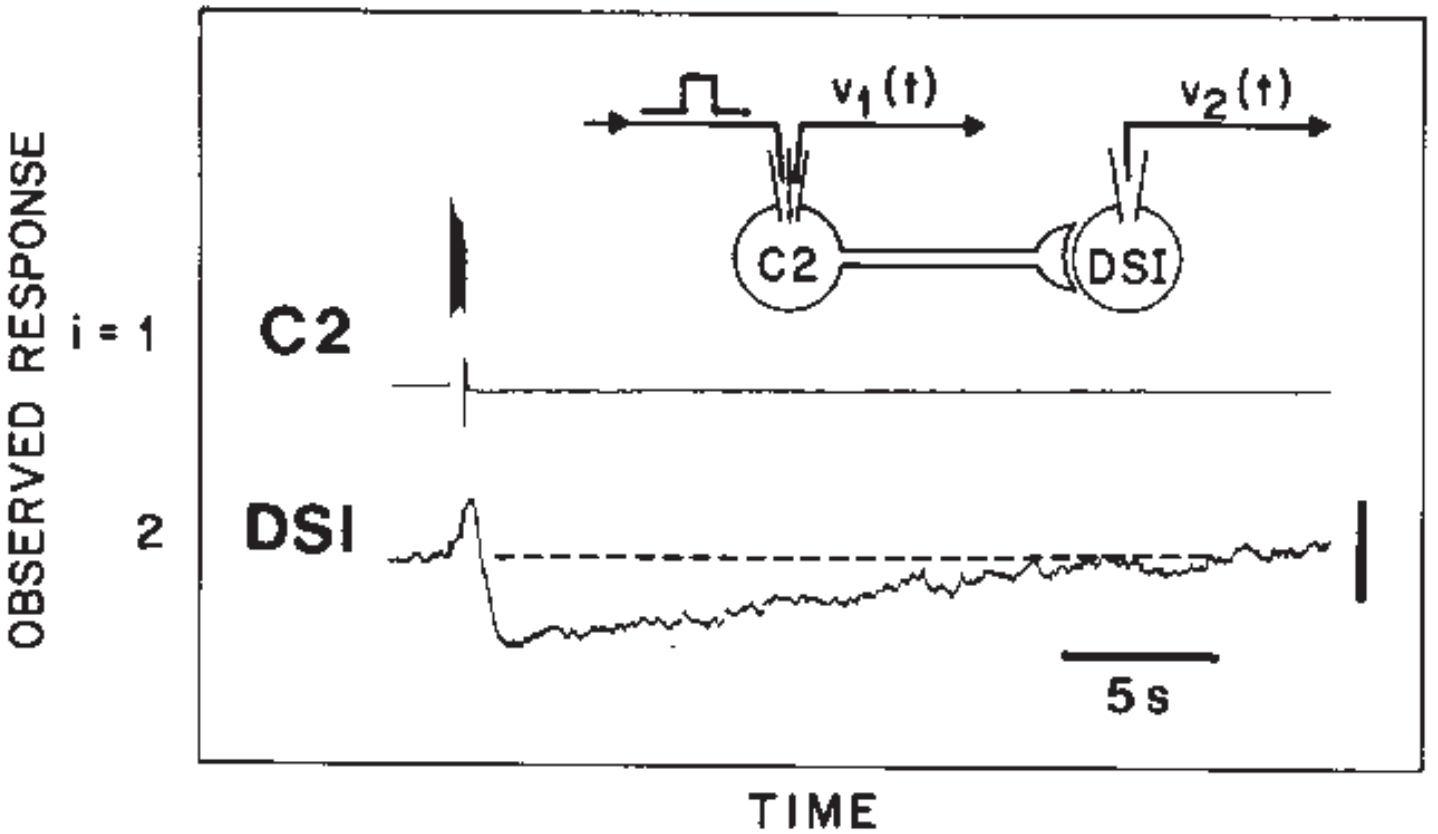


Figure 7.8
An example of the synaptic interaction between two neurons in the CPG in *Tritonia*. Shown is the presynaptic activity measured in the C2 neuron, $v_1(t)$, and the postsynaptic response measured in a DSI neuron, $v_2(t)$, as the result of a short pulse of current injected into C2. The measurement was performed under conditions that insured that only monosynaptic connections contributed to the observation. The observed response applies to two out of the three DSI neurons (DSI_B and DSI_C); the other DSI neuron (DSI_A) exhibits only a slow response. The area under the initial, positive-going response corresponds roughly to T_{21}^S; that under the slowly decaying response corresponds to T_{21}^L. The time dependence of the slow decay corresponds to the time dependence of the slow synaptic response function, $w(t)$. Vertical bar: 40 mV for C2 and 2 mV for DSI. Adapted from Getting (1981).

Fast Synaptic Components, T^S_{ij}		Slow Synaptic Components, T^L_{ij}
Theory	$\frac{J_0}{4}\begin{pmatrix} 0 & +1 & -1 & -1 \\ +1 & 0 & -1 & -1 \\ -1 & -1 & 0 & +1 \\ -1 & -1 & +1 & 0 \end{pmatrix}$	$\lambda\frac{J_0}{4}\begin{array}{c} j = \begin{matrix} 1 & 2 & 3 & 4 \end{matrix} \\ \begin{pmatrix} 0 & -1 & +1 & +1 \\ -1 & 0 & +1 & +1 \\ +1 & +1 & 0 & -1 \\ +1 & +1 & -1 & 0 \end{pmatrix} \end{array} \begin{matrix} \\ i = 1 \\ 2 \\ 3 \\ 4 \end{matrix}$
Observed[a]	$\frac{J_0}{4}\begin{pmatrix} 0 & +1 & \bullet & -1 \\ +1 & 0 & -1 & -1 \\ -1 & -1 & 0 & +1 \\ \bullet & -1 & \bullet & 0 \end{pmatrix}$	$\lambda\frac{J_0}{4}\begin{array}{c} \begin{matrix} C & D & VA & VB \end{matrix} \\ \begin{pmatrix} 0 & \bullet & \bullet & \bullet \\ -1 & 0 & \bullet & \bullet \\ +1 & +1 & -0 & \bullet \\ +1 & \bullet & \bullet & -0 \end{pmatrix} \end{array} \begin{matrix} pre/post \\ C \\ D \\ VA \\ VB \end{matrix}$

(a) Abstracted from the data of Getting (1981, 1983b); see text for details. Dots (•) indicate synaptic connections that are not present in *Tritonia*; their value is taken to be zero for purposes of calculation [*e.g.*, Eqs. (3.3) to (3.5)].

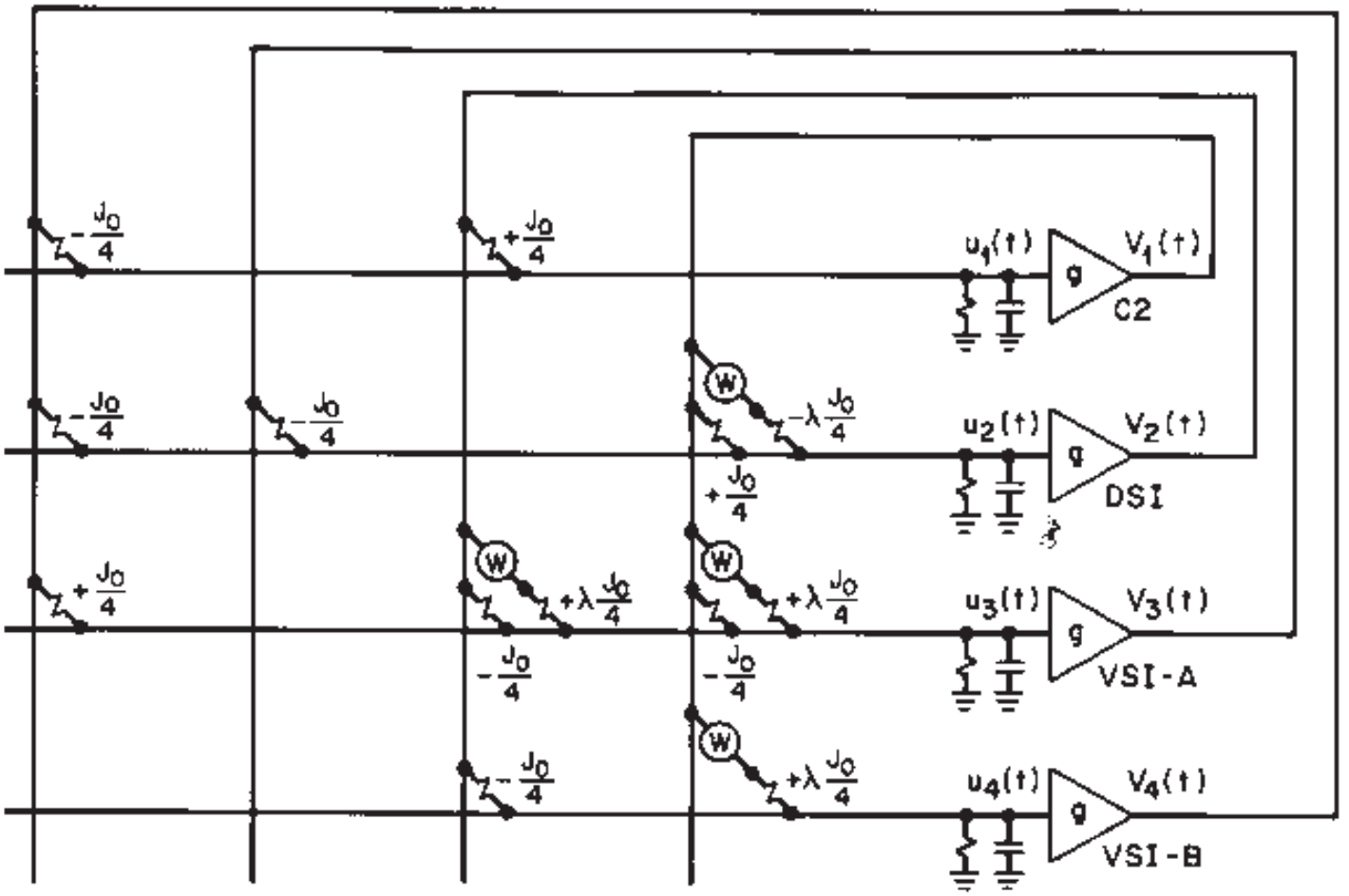
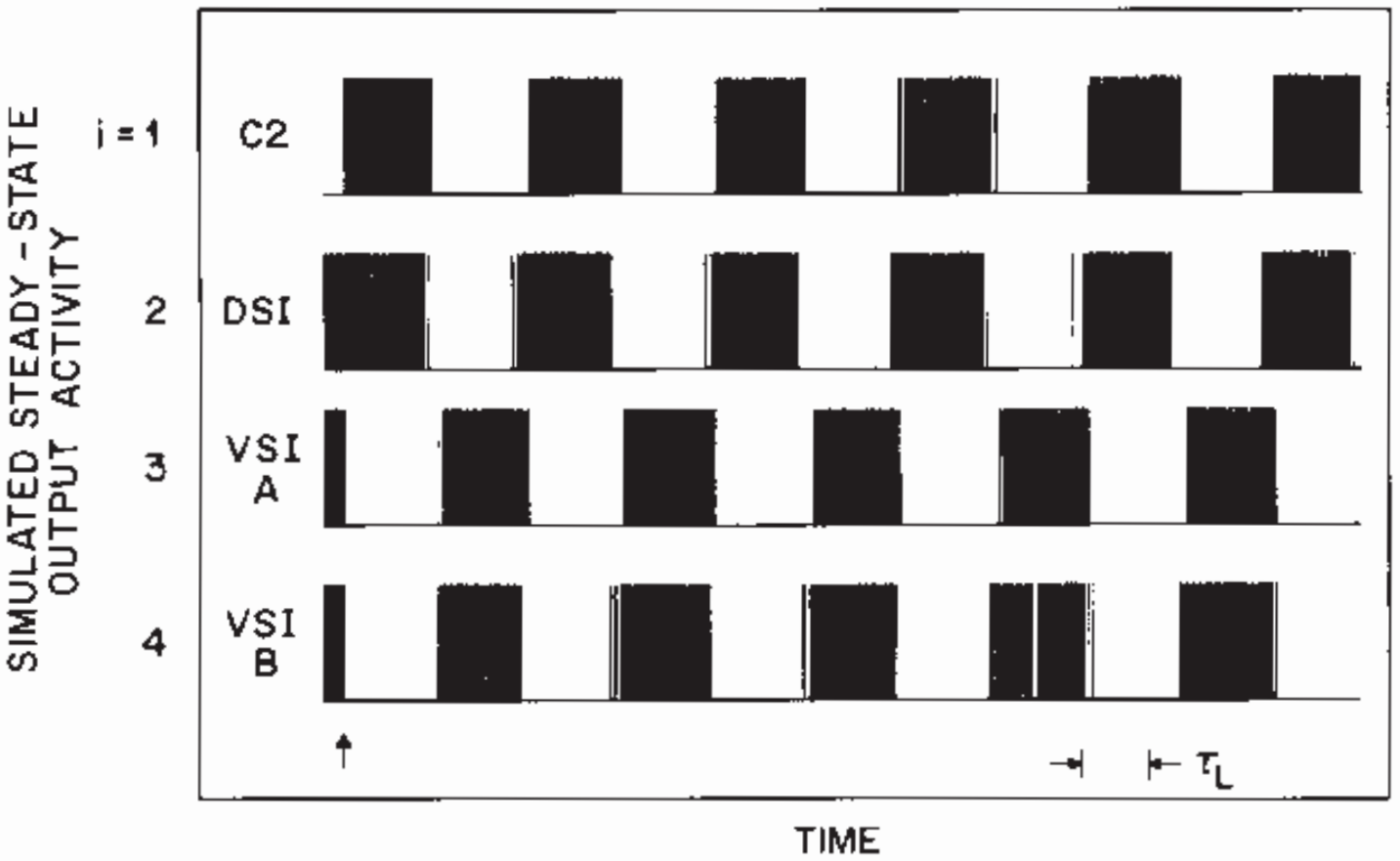


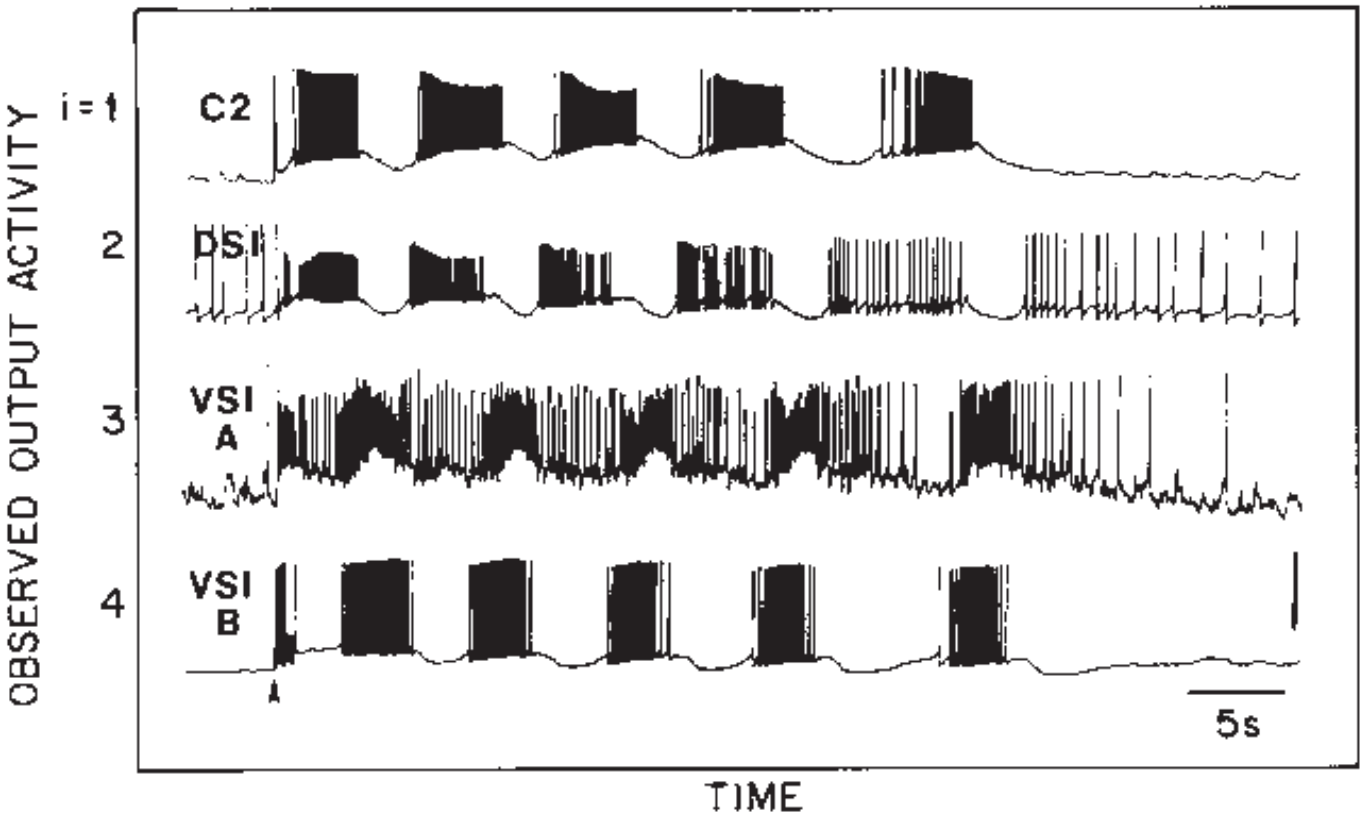
Figure 7.9
Schematic representation of the equivalent circuit for the analog network model describing the CPG in *Tritonia*; symbols as in fig. 7.3. The synaptic strengths contained in this circuit correspond to the observed connections T^S_{ij} and T^L_{ij} (table 7.1).

$$
\begin{aligned}
V_i(t+\tau_S) &= stp\left[\frac{1}{2}\sum_{j=1}^{4} T_{ij}^{S}\left(2V_j^{+}-1\right)+T_{ij}^{L}\left(2V_j^{-}-1\right)\right] \\
&= stp\left[\frac{J_0}{8}\begin{pmatrix} 0 & +1 & 0 & -1 \\ +1 & 0 & -1 & -1 \\ -1 & -1 & 0 & +1 \\ 0 & -1 & 0 & 0 \end{pmatrix}\begin{pmatrix} +1 \\ +1 \\ -1 \\ -1 \end{pmatrix}\right. \\
&\qquad \left. +\lambda\frac{J_0}{8}\begin{pmatrix} 0 & 0 & 0 & 0 \\ -1 & 0 & 0 & 0 \\ +1 & +1 & 0 & 0 \\ +1 & 0 & 0 & 0 \end{pmatrix}\begin{pmatrix} -1 \\ -1 \\ +1 \\ +1 \end{pmatrix}\right] \\
&= stp\left[\frac{J_0}{8}\begin{pmatrix} 2 \\ 3+\lambda \\ -3-2\lambda \\ -1-\lambda \end{pmatrix}\right] = \begin{pmatrix} +1 \\ +1 \\ 0 \\ 0 \end{pmatrix} \qquad \text{for} \qquad \lambda > 0 \\
&= V_i^{+}
\end{aligned}
$$

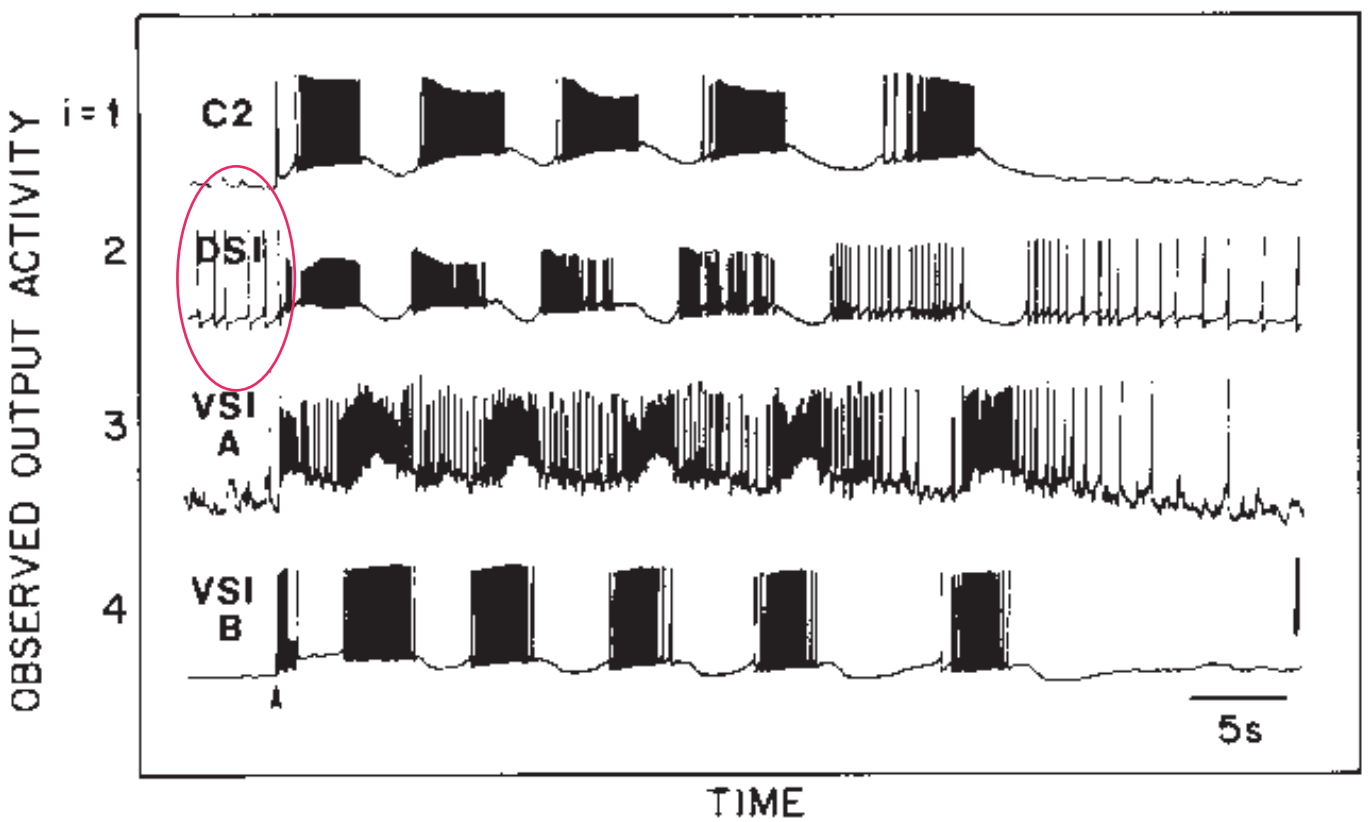
$$
\begin{aligned}
V_i(t+\tau_L+\tau_S) &= stp\left[\frac{1}{2}\sum_{j=1}^{4} T_{ij}^{S}\left(2V_j^{+}-1\right)+T_{ij}^{L}\left(2V_j^{+}-1\right)\right] \\
&= stp\left[\frac{J_0}{8}\begin{pmatrix} 2 \\ 3-\lambda \\ -3+2\lambda \\ -1+\lambda \end{pmatrix}\right] = \begin{pmatrix} +1 \\ 0 \\ +1 \\ +1 \end{pmatrix} \quad \text{for} \quad \lambda > 3
\end{aligned}
$$

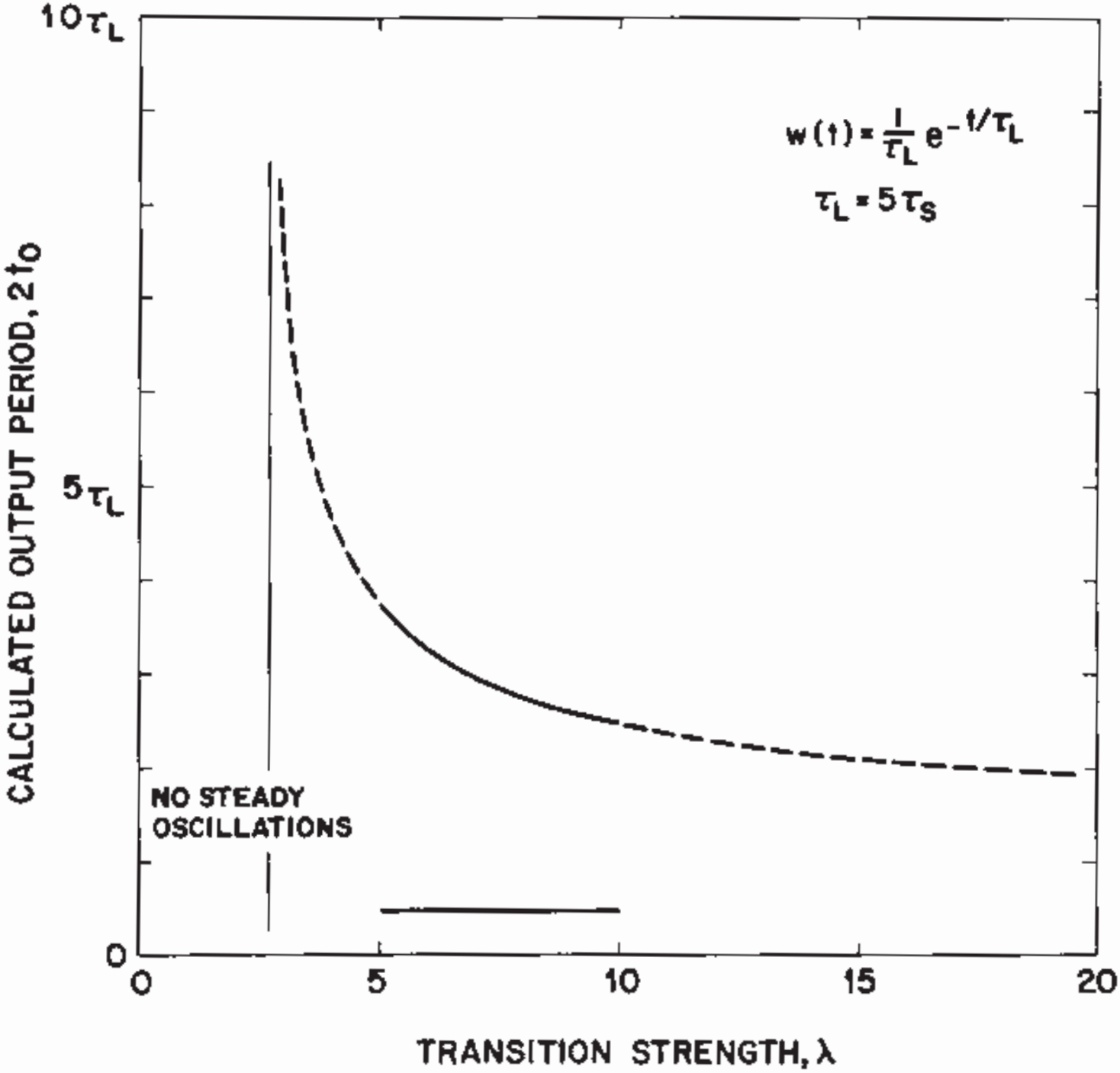
$$
\begin{aligned}
V_i(t+\tau_L+2\tau_S) &= stp\left[\frac{1}{2}\sum_{j=1}^{4} T_{ij}^{S}\left(2V_j(t+\tau_L+\tau_S)-1\right)\right. \\
&\qquad \left. +T_{ij}^{L}\left(2V_j^{+}-1\right)\right] \\
&= stp\left[\frac{J_0}{8}\begin{pmatrix} -2 \\ -1-\lambda \\ 1+2\lambda \\ 1+\lambda \end{pmatrix}\right] = \begin{pmatrix} 0 \\ 0 \\ +1 \\ +1 \end{pmatrix} \\
&= V_i^{-}
\end{aligned}
$$


SIMULATED STEADY-STATE OUTPUT ACTIVITY
i = 1
C2
2
DSI
3
VSI A
4
VSI B
τ_L
TIME


OBSERVED OUTPUT ACTIVITY
i = 1
C2
2
DSI
3
VSI A
4
VSI B
5s
TIME

$$\theta_i \simeq I_{stim_i} + \frac{1}{2}\sum_{j=1}^{4}\left(T_{ij}^{S} + T_{ij}^{L}\right) = I_{stim_i} + \frac{J_0}{8}\begin{pmatrix} 0 \\ -1-\lambda \\ -1+2\lambda \\ -1+\lambda \end{pmatrix}$$




10τL
5τL
0
CALCULATED OUTPUT PERIOD, 2t0
w(t) = 1/τL e^-t/τL
τL = 5τS
NO STEADY
OSCILLATIONS
0
5
10
15
20
TRANSITION STRENGTH, λ