Dynamics of Pattern Formation in Lateral-Inhibition Type Neural Fields*

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Abstract. The dynamics of pattern formation is studied for lateral-inhibiton type homogeneous neural fields with general connections. Neural fields consisting of single layer are first treated, and it is proved that there are five types of pattern dynamics. The type of the dynamics of a field depends not only on the mutual connections within the field but on the level of homogeneous stimulus given to the field. An example of the dynamics is as follows: A fixed size of localized excitation, once evoked by stimulation, can be retained in the field persistently even after the stimulation vanishes. It moves until it finds the position of the maximum of the input stimulus. Fields consisting of an excitatory and an inhibitory layer are next analyzed. In addition to stationary localized excitation, fields have such pattern dynamics as production of oscillatory waves, travelling waves, active and dual active transients, etc.

1. Introduction

Cortical neural tissues can be regarded mathematically as neural fields which form and propagate interacting patterns of excitation. The dynamics of such patterns in neural field must play an essential role in cortical information processing. The present paper uses mathematical analysis to study the mechanism of formation and interaction of patterns in homogeneous fields. The neural model provides a good example of non-homogeneous pattern formation in a homogeneous field. This problem has recently attracted much attention in relation to morphogenesis, and has been studied extensively using the reaction-diffusion model [e.g., Turing, 1952; Levin, 1974; see also Grossberg, 1976].

There have so far been many neural field studies (see, e.g., Wiener and Rosenblueth, 1946; Beurle, 1956; Griffith, 1963, 1965; Farley and Clark, 1961; Coleman, 1971; Ahn and Freeman, 1973; Ellias and Grossberg, 1975; Stanley, 1976). Wilson and Cowan (1973) proposed a plausible field equation and showed by computer-simulated experiments that their equation has three interesting types of pattern dynamics. Reverberation and propagation of excitation patterns was studied in discrete homogeneous nerve nets (Amari, 1975). Recently, Boylls (1975) proposed an interesting field model of the cerebellum.

Most of the above neural fields are closely related to randomly connected nets. A small portion of a nerve field usually includes so many randomly connected neurons that a statistical manipulation yielding a continuous field equation is possible. The dynamics of randomly connected nerve nets has been studied in detail (e.g., Amari, 1971, 1972, 1974). Part of the mathematical difficulty involved in deriving such a macroscopic equation has been solved recently (Amari et al., 1977).

The field equation of the present paper is also derived by statistical considerations. We study first one-dimensional homogeneous fields of lateral-inhibition type consisting of one layer to describe the formation of patterns of excitation, their interaction, and their response to input stimuli. We prove that the equation has five types of pattern dynamics, and gives a complete taxonomy of such fields.

The first is a monostable field, in which all the excitation eventually dies out. The second is also a monostable field, in which the entire field becomes excited. These two have rather trivial dynamics. The third is an explosion-type bistable field, in which excitation spreads without limit if the initial stimulation
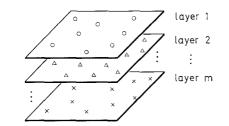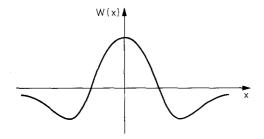
Fig. 1. Neural field

Fig. 2. Weighting function $w(x)$ of a lateral-inhibition type neural field

is given in a wide enough range, but dies out if the initial stimulation is given in a narrow range. The fourth is also a bistable field, in which initial excitation causes either a localized excitation of a definite length or its extinction. The localized excitation moves until it finds the position of the maximum of the input stimuli. The fifth type of field maintains a spatially periodic excitation pattern. The type of dynamics changes with the average stimulation level to the field.

It is in general difficult to prove the stability of pattern dynamics (see, e.g., Maginu, 1975). Oguztöreli (1975) recently proved the stability of the solution of a neural field. He, however, treated a monostable case, and excluded the multi-stable dynamics, which may play an essential role in neural information processing. We will give a rigorous proof of stability for our five types of dynamics.

It has been shown that neural oscillation occurs in a system consisting of excitatory and inhibitory neuron pools (Amari, 1971, 1972a; Wilson and Cowan, 1972). In order to study dynamic pattern formation related to neural oscillation, we need a field consisting of at least two layers. In this paper, I will demonstrate the simple mechanism of neural oscillation and active transients, which occur in a field consisting of excitatory and inhibitory layers. It will also be shown that traveling waves exist in such a field.

A competition and cooperation principle has been proposed as one of the common mechanisms in nerve nets (Arbib, 1976). Montalvo (1975) showed that a number of neural models (Kilmer et al., 1969; Didday, 1970; Dev, 1975) all make use of this principle. In future research, we intend to use the present field theory to

provide a basis for a neural competition-cooperation mechanism. However, it will be left to a later paper to explicitly analyze the models treated by Montalvo (see Amari and Arbib, in press).

2. The Neural Field Equation

Let us consider a neural field consisting of m types of neurons. We can arrange the neurons in m layers, each layer including one type of neuron (Fig. 1). The neurons may be connected in a random manner. By regarding small portions of each layer as homogeneous random subnets, we can treat the entire field as a net composed of these homogeneous subnets. We have already studied in detail the equations of a net composed of randomly connected subnets (Amari, 1971, 1974). We need only a limiting process to obtain the equation of a continuous field. For this purpose, it is convenient to start with random nets of analog neurons (Amari, 1972a).

Let $u_i(x, t)$ be the average membrane potential of the neurons located at position $x = (x_1, x_2)$ at time t on the ith layer. Then, we can assume that the average activity, i.e. the pulse emission rate, of the neurons at x at t is written as

$$Z_i(x, t) = f_i[u_i(x, t)],$$

where f_i is a non-linear function. Function f_i is called the output function, and is monotonically non-decreasing, saturating to a constant for large u_i. The function f_i can be derived by statistical considerations.

Let $w_{ij}(x, y)$ be the average intensity of connection from neurons in the jth layer at place y to neurons of the ith layer at place x. When we need to take pulse conduction time and synaptic delay into account, we must use a function $w_{ij}(x, y; t)$. This function represents the degree of stimulation of neurons at x in the ith layer by the pulses emitted from neurons at place y of the jth layer t time units before.

The intensity of the stimulus arriving at place x at time t of the ith layer can be decomposed into

$$\bar{s}_i + s_i(x, t),$$

where $\bar{s}_i$ denotes the average stimulation level at the ith layer and $s_i(x, t)$ denotes the deviation from the average $\bar{s}_i$. Let $-r_i$ be the resting potential. If there is no deviational input, the potential u_i will converge to

$$h_i = \bar{s}_i - r_i$$

with time constant τ_i, where τ_i is the time constant for dynamics of the ith type of neuron. The level h_i is usually negative, depending on the average stimulation $\bar{s}_i$. The value of h_i can thus be controlled from outside the field.

We can now write the field equation:

$$\tau_i \frac{\partial u_i(x,t)}{\partial t} = -u_i + \sum_{j=1}^{m} \int w_{ij}(x,x';t-t') Z_j(x',t') dx' dt' + h_i + s_i(x,t),$$

(1)

$$Z_i(x',t') = f_i[u_i(x',t')].$$

(2)

When $w_{ij}(x, y; t)$ depends on $x - y$ only, the field is homogeneous. If the effect of the time lag can be neglected, we can simplify the equation by using $w_{ij}(x, y)$ instead of $w_{ij}(x, y; t)$ and dropping the integration of time t'.

3. Single-Layer Field Equation of Lateral Inhibition Type

In the present paper, we study the mechanism of formation of a localized excitation pattern in homogeneous fields. To this end, we first consider simple fields which are 1. one-dimensional, 2. homogeneous, 3. have negligible time lag, and 4. consist of only one layer, including both excitatory and inhibitory neurons.

We further consider a special case in which the non-linear output function is the step-function:

$$f(u) = \begin{cases} 0, & u \leq 0 \\ 1, & u > 1. \end{cases}$$

This means that a neuron fires at its maximum rate when the potential exceeds a threshold, and does not fire otherwise. The origin of the potential is chosen such that the threshold is zero. The step-function is chosen only for mathematical convenience. The results of the present paper are valid even when the step-function is replaced by a moderate monotonically increasing function with saturation. In that case, the mechanism of pattern formation is qualitatively the same, because our system is structurally stable.

Since the field consists of only one layer, we can write the field equation in terms of only one $u(x,t)$

$$\tau \frac{\partial u(x,t)}{\partial t} = -u + \int w(x-y) f[u(y)] dy + h + s(x,t), \quad (3)$$

where we put

$$w(x-y) = w(x,y)$$

by virtue of the homogeneity. This is the basic equation of our simplified fields.

We treat fields of lateral inhibition type:

1. Excitatory connections dominate for proximate neurons,

2. Inhibitory connections dominate at greater distances.

This means that the weighting function $w(x)$ has a shape shown in Figure 2, i.e. $w(x)$ is positive in some neighborhood of the origin and negative or equal to 0 outside that neighborhood. For simplicity's sake, we assume symmetry of $w(x)$, so $w(x) = w(-x)$. There are no other restrictions on $w(x)$.

4. Equilibrium Solutions in the Absence of Input

We study equilibrium solutions of (3) in the absence of inhomogeneous input

$$s(x,t) = 0.$$

Since $\partial u/\partial t = 0$ at equilibrium, equilibrium solutions satisfy

$$u(x) = \int_{-\infty}^{\infty} w(x-y) f[u(y)] dy + h.$$

(4)

Given a distribution $u(x)$ of potential, neurons at place x are excited when

$$u(x) > 0.$$

Let

$$R[u] = \{x | u(x) > 0\}$$

be the excited region of the field for potential distribution $u(x)$. Then (4) can be rewritten as

$$u(x) = \int_{R[u]} w(x-y) dy + h.$$

(5)

An equilibrium $u(x)$, if any, satisfying $R[u] = \phi$, i.e. $u(x) \leq 0$ for all x so that no region is excited, is called a ϕ-solution. An equilibrium, if any, for which $R[u] = (-\infty, \infty)$, i.e. the whole region is excited, is called an ∞-solution.

Now, we define a localized excitation. By a localized excitation we mean a pattern $u(x)$ whose excited region is a finite interval. In other words, a pattern $u(x)$ for which

$$R[u] = (a_1, a_2)$$

is a localized excitation from place a_1 to place a_2 of length $a_2 - a_1 (a_1 < a_2)$.

Since the field is homogeneous, if $u(x)$ is an equilibrium solution, then $u(x-a)$ is also a solution. We call a localized excitation solution $u(x)$ of length a an a-solution, and assume without loss of generality that it satisfies

$$R[u] = (0, a).$$

The structure of the field is specified by the connection function $w(x)$. Let

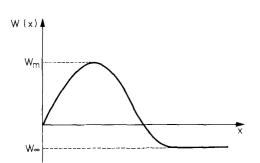$$W(x) = \int_{0}^{x} w(y) dy$$

(6)

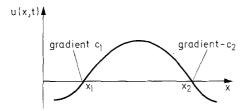Fig. 3. Integral $W(x)$ of weighting function $w(x)$

Fig. 4. A localized excitation

be the integral of $w(x)$. Then we can see from the definition that $W(0)=0$ and

$$W(x) = -W(-x).$$

Moreover, by inspecting Figure 3, we see that $W(x)$ has one peak, as is shown in Figure 3. There are two important quantities

$$W_m = \max_{x>0} W(x),$$

$$W_\infty = \lim_{x \to \infty} W(x)$$

by which properties of the field are specified.

The following theorem gives the conditions for the existence of equilibrium ϕ-, ∞-, and a-solutions.

Theorem 1. *In the absence of input:*

1. *There exists a ϕ-solution if and only if*

$$h < 0.$$

2. *There exists an ∞-solution if and only if*
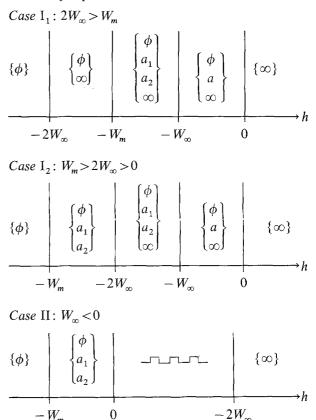
$$2W_\infty > -h.$$

3. *There exists an a-solution (a local excitation of length a) if and only if $h<0$ and $a>0$ satisfies*

$$W(a) + h = 0. \tag{7}$$

The proof is not difficult, but is given in the appendix. Let us classify the field into

Case I_1: $W_\infty > 0$; $2W_\infty > W_m$
Case I_2: $W_\infty > 0$; $2W_\infty < W_m$
Case II: $W_\infty < 0$.

We can then obtain the taxonomy of equilibrium solutions for varying stimulus level h.

Theorem 2. *The following diagrams show the sets of equilibrium solutions for various values of h in the absence of input.*

Case I_1: $2W_\infty > W_m$

Case I_2: $W_m > 2W_\infty > 0$

Case II: $W_\infty < 0$

where ϕ, ∞ and a denote, respectively, the existence of ϕ-, ∞-, and a-solutions. ⊓⊔⊓⊔ denotes the existence of multi-peak solutions but no localized solutions.

The proof of Theorem 2 is also given in the appendix. This theorem gives a complete list of equilibrium solutions in the absence of input[1]. The set of equilibrium solutions changes with the stimulus level h. Consider, for example, a field of Case II, $W_\infty < 0$, to see how the dynamics of the field changes with h. When h is smaller than $-W_m$, there exist no equilibrium solutions but a ϕ-solution, so that all excitation eventually dies out. When h increases to satisfy $-W_m < h < 0$, there exist two localized excitations, a_1- and a_2-solutions, besides a ϕ-solution. In this case, the field can be quiescent, and it can also retain a localized excitation. When h satisfies $0 < h < -2W_\infty$, neither localized excitation, infinitely wide excitation nor quiescent solutions can exist. The field displays a spatially periodic pattern of exitation.

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[1]   A number of localized solutions can coexist, if they are separated so far that no interaction occurs. See Section 7

For a strong stimulus level, $h > -2W_\infty$, an ∞-solution is the only equilibrium, and the whole field becomes excited.

5. Stability

We need to study the stability of solutions, in order fully to determine the dynamical properties of the field. The following analysis looks at the behavior of a single peak of a solution $u(x, t)$ which is not necessarily an equilibrium, so that it may be changing with t. Let the excited region at time t be

$$R[u(x, t)] = (x_1(t), x_2(t))$$

and let

$$c_1 = \frac{\partial u(x_1, t)}{\partial x}, \quad -c_2 = \frac{\partial u(x_2, t)}{\partial x}$$

be the gradients of $u(x, t)$ at the boundaries x_1 and x_2 of the excited region. After a short time dt, $u(x, t)$ changes to $u(x, t+dt)$, and accordingly, the excited region changes to

$$R[u(x, t+dt)] = (x_1(t+dt), x_2(t+dt))$$

(Fig. 4). Now we consider the motion of the excited region. The boundaries of the excited region satisfy

$$u(x_i, t) = 0 \qquad \text{at time } t$$
$$u(x_i + dx_i, t+dt) = 0 \qquad \text{at time } t+dt,$$

where $x_i(t+dt) = x_i + dx_i$ $(i = 1, 2)$. A Taylor expansion of the latter equation yields

$$\frac{\partial u(x_i, t)}{\partial x} dx_i + \frac{\partial u(x_i, t)}{\partial t} dt = 0, \quad i = 1, 2$$

for infinitesimally small dx_i and dt. Since $u(x_i, t) = 0$ at time t, we have from (3)

$$\tau \frac{\partial u(x_i, t)}{\partial t} = \int_{x_1(t)}^{x_2(t)} w(x - y)\, dy + h = W(x_2 - x_1) + h.$$

We thus have

$$\frac{dx_1}{dt} = -\frac{\partial u}{\partial t} \bigg/ \frac{\partial u}{\partial x} = -\frac{1}{\tau c_1}[W(x_2 - x_1) + h]. \tag{8}$$

Similarly, we have

$$\frac{dx_2}{dt} = \frac{1}{\tau c_2}[W(x_2 - x_1) + h]. \tag{9}$$

These show the velocities of the boundaries of the excited region. Let

$$a(t) = x_2(t) - x_1(t)$$

be the length of the excited region at time t. Then, by

subtracting (9) from (8), we have

$$\frac{da}{dt} = \frac{1}{\tau}\left(\frac{1}{c_1} + \frac{1}{c_2}\right)[W(a) + h]. \tag{10}$$

This is the dynamical equation describing the change of length of the excited region. We have thus reduced the complex field equation to a simple equation for the length of the excited region.

The equilibrium length of (10) is given by

$$W(a) + h = 0,$$

in agreement with Theorem 1. Moreover, an equilibrium a is stable if

$$\frac{dW(a)}{da} < 0$$

and unstable if

$$\frac{dW(a)}{da} > 0.$$

We can, therefore, easily check the stability of local excitation from the graph of $W(x)$ (Fig. 3). For example, when there are two solutions a_1 and a_2 $(a_1 < a_2)$, the a_1-solution is always unstable and the a_2-solution is stable. However, the condition

$$W_\infty + h > 0 \tag{11}$$

is necessary in order that a finite excited region grows to an ∞-solution. If this condition is not satisfied, an ∞-solution cannot be reached without stimulating infinitely wide regions. Therefore, we neglect ∞-solutions in the case when condition (11) fails. By deleting ∞-solutions from the entries of $h < -W_\infty$ in Cases I_1 and I_2, the dynamics of Cases I_1 and I_2 are simplified and coincide. We have the following stability theorem.

Theorem 3. *The stabilities of equilibrium solutions are shown in the following, where $a_2 > a_1$ and ˘ denotes unstable solutions.*
Case I. $W_\infty > 0$
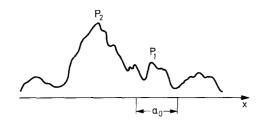

Case II. $W_\infty < 0$

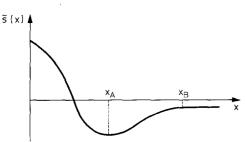**Fig. 5.** A weak inhomogeneous stimulation $s(x)$

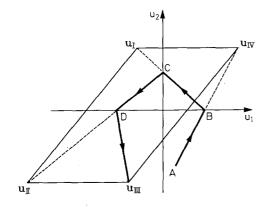**Fig. 6.** Stimulation $\tilde{s}(x)$ given by a localized excitation

Fig. 7. A solution of (15)

From the theorem, we can see that there are three types of dynamics besides the two trivial cases where a ϕ- or ∞-solution is the only equilibrium. They are

A: $\{\phi, \breve{a}, \infty\}$,

B: $\{\phi, \breve{a}_1, a_2\}$,

C: $\{\_\Pi\_\Pi\_\Pi\_\}$.

Type A dynamics is an explosion type: initial excitation whose length is less than a dies out, whereas that of length greater than a grows to infinity. Type B dynamics is bistable: initial excitation of length less than a_1 dies out, while excitation of length greater than a_1 converges to a localized excitation of length a_2. Type C dynamics shows a spatially periodic pattern. Again, the type of dynamics changes with the average stimulus level h.

6. Response to Stationary Input Stimulus Patterns

We have so far disregarded the inhomogeneous input term $s(x, t)$. Let us consider the effect of a stationary nonhomogeneous input stimulus $s(x)$. When $s(x)$ is very

strong compared with mutual excitation and inhibition, it will dominate the solution. We therefore consider the effect of an input $\varepsilon s(x)$, where ε is a small number.

Starting with a localized stable equilibrium excitation $u_0(x)$, we want to obtain a solution of the form

$$u(x, t) = u_0(x) + \varepsilon u(x, t),$$

where terms of order ε^2 are neglected. Let a_0 be the length of the excited region of $u_0(x)$. Then a_0 satisfies $W(a_0) + h = 0$. Let $x_1(t)$ and $x_2(t)$ be the boundaries of the excited region. Then, we can obtain the velocities of the moving boundaries as before, with $h + \varepsilon s(x)$ replacing h in (8) and (9) so that the equations now take the form

$$\frac{dx_1}{dt} = -\frac{1}{\tau c_1}[W(x_2 - x_1) + h + \varepsilon s(x_1)],$$

$$\frac{dx_2}{dt} = \frac{1}{\tau c_2}[W(x_2 - x_1) + h + \varepsilon s(x_2)].$$

The length of the excited region is written as

$$a(t) = x_2(t) - x_1(t) = a_0 + \varepsilon a_1(t) + \dots.$$

We can also expand the gradients c_i as

$$c_1 = \frac{\partial u(x_1, t)}{\partial x} = c + \varepsilon c_1'$$

$$c_2 = \frac{\partial u(x_2, t)}{\partial x} = -c - \varepsilon c_2',$$

where c is the gradient of the waveform $u_0(x)$ at the boundary. Since the field is symmetrical, $u_0(x)$ has also a symmetric shape and the gradients of both the boundaries coincide except the sign. By neglecting the higher order terms in ε, we obtain

$$\frac{1}{2}\frac{d(x_1 + x_2)}{dt} = \frac{\varepsilon}{2\tau c}[s(x_2) - s(x_1)], \tag{12}$$

while the increase $\varepsilon a_1(t)$ of the length of the excited region satisfies

$$\frac{da_1}{dt} = \frac{1}{\tau c}[2w(a_0)a_1 + s(x_1) + s(x_2)]. \tag{13}$$

The first equation describes the motion of the center of the excited region, and the second describes the change in the length of the excited region.

The excited region moves right if $s(x_2) > s(x_1)$, and to the left if $s(x_1) > s(x_2)$. Therefore, the excited region moves in the direction of increasing stimulus, searching for the maximum of $s(x)$. It stops at a peak around which $s(x)$'s are balanced. At the same time, the length of the excited region changes slightly. According to the equilibrium solution of (13), it becomes

$$a(t) = a_0 - \frac{\varepsilon[s(x_1) + s(x_2)]}{2w(a_0)}.$$

The dynamics (13) is stable, since $w(a_0) < 0$.

This is only a local search but may not be trapped by the nearest peak. The excited region is not trapped at a

small peak of width less than a_0, because there is no balancing of $s(x_1)$ and $s(x_2)$ around this peak, where $x_2 - x_1$ is nearly equal to a_0. In Figure 5, it is not trapped at P_1 but stops at P_2. It moves until it finds a maximum of $s(x)$, which spreads more than a_0.

7. Interaction of Excitation Patterns

When the excitation pattern has two positive regions (let us say "two excitations" for short), they interact with each other. Assume that an excitation exists on the region $(-a, 0)$. Activity in this region excites or inhibits other neurons. The total stimulation given to the neurons located at a point $x > 0$ is

$$\tilde{s}(x) = \int_{-a}^{0} w(x-y)\,dy = \int_{x}^{x+a} w(y)\,dy.$$

Hence, the effect produced by an excitation concentrated on $(-a, 0)$ is equivalent to an external input $\tilde{s}(x)$.

The function $\tilde{s}(x)$ usually has a shape of the kind shown in Figure 6. It decreases monotonically to point x_A; and then increases until $x = x_B$. After then, it keeps a constant value (this value may be 0). The exact shape, of course, depends on $w(x)$ and a.

When there is a second excitation around x, the neurons at that point receive stimulus $\tilde{s}(x)$ from the first excitation located on $(-a, 0)$. In this case, the second excitation moves searching for the maximum of $\tilde{s}(x)$. The effect of the second one on the first one is similar. Therefore, when they are located at a distance shorter than x_A, they attract each other, combining into one localized excitation. When two excitations are located at a distance between x_A and x_B, they repel each other, moving in opposite directions. When they are located at a distance greater than x_B, no motion is induced and they coexist independently. (An excitation pattern, however, may cause a change in the stimulus level h.) This explains the interaction of excitation patterns.

8. Formation of Dynamic Patterns

A field consisting of two layers can have the mechanism of forming dynamic patterns such as oscillatory patterns and travelling wave patterns. We consider fields consisting of excitatory and inhibitory layers, in which the inhibitory neurons inhibit only the excitatory neurons. Moreover, the excitatory neurons have very narrow fan-out connections to the inhibitory neurons so that the excitatory neurons at place x excite the inhibitory neurons at place x only. We then have the following field equation:

$$\tau \frac{\partial u_1(x,t)}{\partial t} = -u_1(x) + \int w_1(x-x')f[u_1(x',t)]dx'$$
$$\qquad - \int w_2(x-x')f[u_2(x',t)]dx' + h_1 + s_1$$
$$\tau \frac{\partial u_2(x,t)}{\partial t} = -u_2(x) + w_3 f[u_1(x,t)] + h_2 + s_2. \qquad (14)$$

8.1 Oscillation

We first look for spatially homogeneous solutions. A homogeneous solution

$$u_i(x, t) = u_i(t)$$

which does not depend on position x must satisfy the simplified equation

$$\tau \dot{u}_1 = -u_1 + w_1 f(u_1) - w_2 f(u_2) + h_1$$
$$\tau \dot{u}_2 = -u_2 + w_3 f(u_1) + h_2 \qquad (15)$$

which is obtained from (14) by integrating it over x, where

$$w_i = \int_{-\infty}^{\infty} w_i(x)dx, \qquad i = 1, 2$$

and we put $s_i = 0$.

This may be regarded as the equation of a lumped system consisting of excitatory and inhibitory neuron pools.

Since f is the step function taking on values 1 and 0, the terms $f(u_i)$ are constants on each quadrant of the u_1-u_2 plane. Let us adopt the vector notation,

$$\boldsymbol{u} = (u_1, u_2)$$
$$\boldsymbol{h} = (h_1, h_2)$$
$$\boldsymbol{c}_1 = (w_1, w_3)$$
$$\boldsymbol{c}_2 = (-w_2, 0)$$

Then, in the first quadrant where $u_1 > 0$, $u_2 > 0$, (15) reduces to

$$\tau \dot{\boldsymbol{u}} = -\boldsymbol{u} + \boldsymbol{u}_I, \qquad (16)$$

where

$$\boldsymbol{u}_I = \boldsymbol{h} + \boldsymbol{c}_1 + \boldsymbol{c}_2.$$

Therefore, $\boldsymbol{u}$ changes linearly in the direction toward $\boldsymbol{u}_I$. Similarly, in the second quadrant where $u_1 < 0$, $u_2 > 0$, $\boldsymbol{u}$ changes linearly toward

$$\boldsymbol{u}_{II} = \boldsymbol{h} + \boldsymbol{c}_2.$$

In the third quadrant where $u_1 < 0$, $u_2 < 0$, and in the fourth quadrant where $u_1 > 0$, $u_2 < 0$, $\boldsymbol{u}$ changes, respectively, toward

$$\boldsymbol{u}_{III} = \boldsymbol{h}$$
$$\boldsymbol{u}_{IV} = \boldsymbol{h} + \boldsymbol{c}_1.$$

Generally, $\boldsymbol{u}$ changes linearly toward $\boldsymbol{u}_J$ ($J = I, II, III, IV$) on the Jth quadrant.

The four points $\boldsymbol{u}_I$, $\boldsymbol{u}_{II}$, $\boldsymbol{u}_{III}$, and $\boldsymbol{u}_{IV}$ form a parallelepiped. It shifts in parallel as $\boldsymbol{h}$ changes. The solution of (15) can be obtained graphically. We show one example in Figure 7. When $\boldsymbol{u}$ starts initially at A in
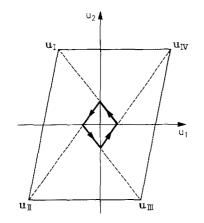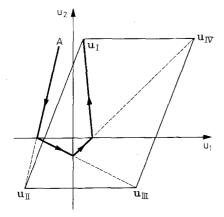
Fig. 8. An oscillatory solution

Fig. 9. Dual active transient

the IVth quadrant, it moves toward u_{IV}. However, it enters into the Ist quadrant at Point B, so that it changes the direction toward u_I. At Points C and D it changes the direction, and at last converges to the point u_{III} which lies in this case in the IIIrd quadrant.

In general, if u_J lies in the Jth quadrant, it is a stable equilibrium. The system is monostable or bistable depending on the number of the stable equilibria. In the case of Figure 8, there are no stable equilibria, because no u_J's are in the Jth quadrant.

We can prove that there exists in this case a stable oscillation, whose orbit is shown in Figure 8. At whatever initial state $u(t)$ starts, it becomes oscillatory. The period of the oscillation changes with the average stimulation level h. The oscillation occurs only in the systems with $w_1 < w_2$, i.e. the system in which the inhibitory connection is stronger than the self-excitatory connection. This fact is shown in the following theorem. (The proof is given in Appendix.)

Theorem 4. *In the case $w_1 \geq w_2$, the system shows either monostable or bistable behavior depending on h. In the case $w_1 < w_2$, the system shows any of monostable, bistable or oscillatory behavior, depending on h.*

We can also point out some interesting transient phenomena. In the case of Figure 7, the system is monostable, u_{III} being the only stable equilibrium. In this system, when u_1 is stimulated to become positive, then u enters in the IVth quadrant (A). In this case, going towards u_{IV}, u_1 becomes bigger and u_2 also becomes positive (B). Then, u_1 decreases while u_2 still is growing (C). They turn to decreasing (D) and at last, both u_1 and u_2 become negative converging to u_{III}. However, if the initial stimulation is small ($u_1 < 0$), u never enters the IVth quadrant and u monotonically converges to u_{III}. This is the phenomenon called the active transient (Wilson and Cowan, 1973).

We also have the dual of the above phenomenon. In the case shown in Figure 9, the system is monostable, the excited state u_I being the only stable state. When u is shifted to point A by some inhibitory stimulus, u_1 decreases further, and u_2 decreases, too. Both u_1 and later u_2, then, start to increase, returning to u_I. This may be called the dual active transient, and may have some relation with the cerebellum model of Boylls (1975).

In the case where inhibitory neurons have connections within themselves, a similar analysis is possible. The results are again similar. We need a three-neuron-pools model in order to obtain the soft oscillation, i.e. the case where there exists a stable oscillation around a stable equilibrium. Such a system usually lies in the equilibrium state. But, once strong stimulation arrives, the system begins to oscillate and keeps the oscillation even after the stimulation is removed. This kind of oscillation has been used in the model of the kindling effect (Lieblich and Amari, 1977).

8.2 Travelling Waves

We have studied the homogeneous solutions of the field equation. When a part of a field is stimulated uniformly, a homogeneous solution will be observed in that part of the field if the part is sufficiently wide. The active transient and oscillatory waves are aroused in the field in this manner. In any case, the aroused excitation will propagate over the field, in some cases gradually fading out but in other cases growing to a stationary travelling wave of a fixed shape. We look for the condition for the existence of a stationary travelling wave.

When the field equation has a stationary travelling wave solution, we can put

$$u_1(x, t) = g_1(x - vt)$$
$$u_2(x, t) = g_2(x - vt), \tag{17}$$

where v is the velocity of the wave, and g_1 and g_2 are the wave forms in the excitatory and inhibitory layers. We introduce the new variable

$$y = x - vt.$$

Then, y and t together form a moving reference frame of the field.

For the stationary travelling wave solution (17), we have

$$\frac{\partial u_1}{\partial t} = -vg_1'(y)$$

$$\frac{\partial u_2}{\partial t} = -vg_2'(y),$$

where

$$g'(y) = \frac{dg(y)}{dy}.$$

Therefore, the equation reduces to

$$-\tau vg_1'(y) = -g_1(y) + \int w_1(y-y')f[g_1(y')]dy'$$
$$-\int w_2(y-y')f[g_2(y')]dy' + h_1, \qquad (18)$$

$$-\tau vg_2'(y) = -g_2(y) + w_3 f[g_1(y)] + h_2. \qquad (19)$$

Let a be the length of the excited region of the travelling wave of the first layer, and assume

$$R[g_1] = (0, a).$$

Let the excited region of the second layer be

$$R[g_2] = (y_1, y_2).$$

Since

$$f[g_1(y)] = \begin{cases} 1, & 0 < y < a \\ 0, & \text{otherwise}, \end{cases}$$

we can solve (19) explicitly under the boundary condition

$$g_2(\pm\infty) = h_2,$$

i.e. the field is in the quiescent state at the infinities ($h_2 < 0$). The solution is given by

$$g_2(y) = \begin{cases} h_2, & y > a \\ w_3(1 - \exp\{(y-a)/v\tau\}) + h_2, & 0 < y < a \\ w_3\{1 - \exp(-a/v\tau)\}\exp(y/v\tau) + h_2, & y < 0. \end{cases}$$

Therefore, y_1 and y_2 can be solved from $g_2(y_i) = 0$ as

$$y_1 = v\tau \log \frac{h_2}{w_3\left\{\exp\left(-\frac{a}{\tau}\right) - 1\right\}}$$

$$y_2 = a + v\tau \log\left(1 + \frac{h_2}{w_3}\right)$$

which depend on the unknown parameters a and v.

Let

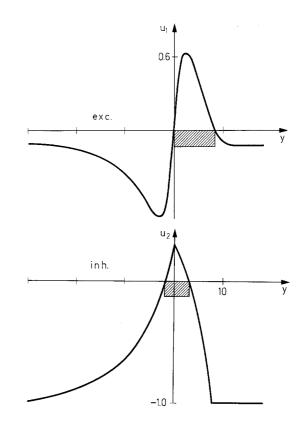$$K(y) = \int_0^a w_1(y-y')dy' - \int_{y_1}^{y_2} w_2(y-y')dy'.$$

Fig. 10. Waveform of travelling wave solution

Then, (18) can be explicitly solved under the boundary condition

$$g_1(\pm\infty) = h_1, \qquad (h_1 < 0)$$

as

$$g_1(y) = \frac{1}{v\tau}\int_y^\infty \exp\left\{\frac{y-y'}{v\tau}\right\}K(y')dy' + h_1.$$

This solution must satisfy the original assumption $R[g_1] = (0, a)$. We therefore require

$$g_1(0) = g_1(a) = 0$$

or

$$\int_0^\infty \exp\left\{\frac{y}{v\tau}\right\}K(y)dy + v\tau h_1 = 0$$

$$\int_0^\infty \exp\left\{-\frac{y}{v\tau}\right\}K(y+a)dy + v\tau h_1 = 0.$$

We can determine the unknown a and v from the above equations. If the equations have a positive solution (a, v), there surely exists a stationary travelling wave in the original field equation, with length a and velocity v.
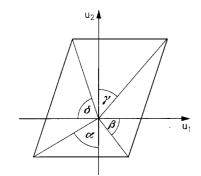
Fig. 11. Stability of oscillation

We show an example of the numerical calculation, where we put

$$w_i(x) = \frac{A_i}{\sqrt{2\pi\sigma_i}} \exp\left\{-\frac{x^2}{2\sigma_i^2}\right\}, \quad i = 1, 2$$

$$A_1 = 2.0 \quad A_2 = 4.0 \quad \sigma_1 = 1.0 \quad \sigma_2 = 1.5$$

$$w_3 = 2.0 \quad h_1 = -0.1 \quad h_2 = -1.0 \quad \tau = 1.$$

There exists a stationary travelling wave in this field. The length a and the velocity v are given by

$$a = 7.6, \quad v = 7.3$$

respectively. The waveforms are shown in Figure 10.

9. Concluding Remarks

We have shown three interesting types of dynamics which occur in single-layer homogeneous neural fields with lateral inhibitory connections. Though we have used a very simple model, it seems to have sufficient generality as far as the mechanism of formation of localized excitation patterns is concerned.

We have also shown the mechanism of formation of dynamic patterns such as oscillatory and travelling waves, which occur in double-layer homogeneous neural fields. Our method consists of reducing the field dynamics to the dynamics of the boundaries of excited regions.

There have been proposed many interesting models related to neural fields (e.g. Boylls, 1975; Didday, 1970; Dev, 1974). We propose to give a theoretical foundation to them. In future research, we shall explore the explanation of Didday's model by Type B dynamics; and Dev's model by a two-dimensional field in which the dynamics in the disparity dimension is of Type C and that in the spatial dimension is of Type A. This needs more detailed consideration.

We thus intend our field theory to give a theoretical basis to the study of competition and cooperation in brain theory (Arbib, 1976; Montalvo, 1975). Another basis will come from the theory of self-organizing nerve nets (Amari, 1972b). It seems important to unify statistical neurodynamics, field theory and self-organization theory.

Appendix

1. Proof of Theorem 1

1) If there is a ϕ-solution u, (5) yields $u(x) = h$. $R[u] = \phi$ requires $h < 0$. On the contrary, if $h < 0$, $u(x) = h$ is surely a solution of (5).

2) If there is an ∞-solution u, it satisfies $u(x) = \int_{-\infty}^{\infty} w(x-y)dy - h$
$= 2W_\infty - h$. $R[u] = (-\infty, \infty)$, however requires $2W_\infty > h$. On the contrary, if $2W_\infty > h$, $u(x) = 2W_\infty - h$ gives an ∞-solution.

3) If there is an a-solution u with $R[u] = (0, a)$, it satisfies

$$u(x) = \int_0^a w(x-y)dy + h = W(x) - W(x-a) + h. \tag{14}$$

This solution obviously should satisfy

$$u(0) = u(a) = 0, \tag{15}$$

which implies $W(a) = h$. On the contrary, when $W(a) = h$ holds, $u(x)$ given by (14) satisfies (15). Moreover, we can prove that $u(x) = W(x) - W(x-a) + h$ is positive on the interval $(0, a)$ and negative elsewhere, provided $h < 0$. This shows that (14) is the required equilibrium solution.

2. Proof of Theorem 2.

From the shape (Fig. 3) of $W(x)$, we can easily obtain the following lemma.

Lemma 1. *In case $W_\infty \geq 0$, $W(a) + h = 0$ has exactly two positive solutions a_1 and a_2, if $-W_\infty > h > -W_m$; it has one and only one positive solution if $-W_\infty < h < 0$; and no solutions for other h. In case $W_\infty < 0$, $W(a) + h = 0$ has exactly two positive solutions a_1 and a_2 if $0 > h > -W_m$.*

By combining this lemma with Theorem 1, the taxonomy of Theorem 2 is obtained. In the case of $-2W_\infty > h > 0$, there are no ϕ- and ∞-solutions, and no solitary a-solutions. We can instead find $a > 0$, $b > 0$ satisfying

$$\sum_{n=-\infty}^{\infty} [W(nb+a) - W(nb)] + h = 0.$$

This yields a periodic solution $u(x)$ of period b, $u(x) = u(x+b)$, consisting of localized excitations of length a. The numbers a and b are not unique. If the field is of finite length, boundary conditions will determine a and b. When the field is a ring form, we also have a finite number of pairs (a, b) each of which gives a periodic solution.

3. Proof of Theorem 4

The parallelepiped composed of u_I, u_{II}, u_{III}, and u_{IV} shifts in parallel as h changes. By choosing an appropriate h, it is always possible to let the system be monostable and bistable.

In the case of $w_1 < w_2$, it is always possible by choosing an appropriate h [e.g., $h = -(c_1 + c_2)/2$] to let the system have no equilibria. The system has an oscillatory solution in this case. It is, however, impossible in the case of $w_1 > w_2$ that the system has no equilibria, even if h is chosen adequately.

Since origin $u = 0$ is a singular point of the system, in order to prove the existence of a stable oscillation in the case of $w_1 < w_2$, we need to prove that u, starting at a sufficiently close to the origin, grows

to a large oscillation. We can prove that this occurs when the relation

$$\tan \alpha \tan \beta \tan \gamma \tan \delta > 1$$

is satisfied in Figure 11. The relation always holds for a parallelepiped of this shape.

References

Amari,S.:Characteristics of randomly connected threshold element networks and network systems. Proc. IEEE **59**, 35—47 (1971)

Amari,S.: Characteristics of random nets of analog neuron-like elements. IEEE Trans. on Syst. Man and Cybernetics SMC-**2**, 643—657 (1972a)

Amari,S.: Learning patterns and pattern sequences by self-organizing nets of threshold elements. IEEE Trans. Computers C **21**, 1197—1206 (1972b)

Amari,S.: A method of statistical neurodynamics. Kybernetik **14**, 201—215 (1974)

Amari,S.: Homogeneous nets of neuron-like elements. Biol. Cybernetics **17**, 211—220 (1975)

Amari,S., Yoshida,K., Kanatan,K.: Mathematical foundations of statistical neurodynamics. Siam J. Appl. Math. **33** (1977)

Amari,S., Arbib,M.A.: Competition and cooperation in neural nets. In: Systems neuroscience, Metzler,J. (ed.). New York: Academic Press 1977

Arbib,M.: Segmentations, schemas and cooperative computation. In: Studies in biomathematics. Levin,S., ed. Rhode Island Math. Assoc. of America 1976

Beurle,R.L.: Properties of a mass of cells capable of regenerating pulses. Trans. Roy. Soc. London B **240**, 55—94 (1956)

Boylls,C.C.: A theory of cerebellar function with applications to locomotion, I. The physiological role of climbing fiber inputs in anterior lobe operation. COINS Technical Rep. 75C-6 Univ. Mass. at Amhevst (1975)

Coleman,B.P.: Mathematical theory of lateral sensory inhibition. Arch. Rat. Mach. Analys. **43**, 79—100 (1971)

Dev,P.: Perception of depth surfaces in random-dot stereograms: a neural model. Int. J. Man-Mach. Stud. **7**, 511—528 (1975)

Didday,R.L.: The simulation and modelling of distributed information processes in the frog visual system. Tech. Rep. No. 6112-1, Stanford University Center for Systems Research (1970)

Ellias,S.A., Grossberg,S.: Pattern formation, contrast control and oscillations in the short-term memory of shunting on-center off-surround networks. Biol. Cybernetics **20**, 69—98 (1975)

Farley,B.G., Clark,W.A.: Activity in networks of neuron-like elements. Proc. 4th London Symp. on Inf. Theory. Cherry,C., ed. London: Butterworths 1961

Grossberg,S.: On the development of feature detectors in the visual cortex with application to learning and reaction-diffusion systems. Biol. Cybernetics **21**, 145—158 (1976)

Griffith,J.S.: A field theory of neural nets. I. Bull. Math. Biophys. **25**, 111—120 (1963)

Griffith,J.S.: A field theory of neural nets. II. Bull. Math. Biophys. **27**, 187—195 (1965)

Kilmer,W.K., McCulloch,W.S., Blum,J.: A model of the vertebrate central command system. Int. J. Man-Mach. Stud. **1**, 279—309 (1969)

Levin,S.A., ed.: Some mathematical questions in biology. VI. Rhode Island AMS 1974

Lieblich,I., Amari,S.: A first approximation model for amygdaloid kindling phenomenon. In: Systems Neuroscience, Metzler,J. (ed.) New York: Academic Press 1977

Maginu,K.: Reaction-diffusion equation describing morphogenesis. Math. Biosci. **27**, 17–98 (1975)

Montalvo,F.S.: Consensus versus competition in neural network: a cooperative analysis of three models. Int. J. Man-Mach. Stud. **7**, 333—346 (1975)

Oguztöreli,M.N.: On the activities in a continuous neural network. Biol. Cybernetics **18**, 41—48 (1975)

Stanley,J.C.: Simulation studies of a temporal sequence memory model. Biol. Cybernetics **24**, 121–137 (1976)

Turing,A.: The chemical basis of morphogenesis. Phil. Trans. Roy. Soc. London B-**237**, 32—72 (1952)

Wiener,N., Rosenblueth,A.: The mathematical formulation of the problem of conduction of impulses in a network of connected excitable elements, specifically in cardiac muscle. Arch. Inst. Cardiol. (Mexico) **16**, 204—265 (1946)

Wilson,H.R., Cowan,J.D.: Excitatory and inhibitory interactions in local populations of model neurons. Biophysical J. **12**, 1—24 (1972)

Wilson,H.R., Cowan,J.D.: A mathematical theory of the functional dynamics of cortical and thalamic nervous tissue. Kybernetik **13**, 55—80 (1973)

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