Synchronization of neural activity is a promising mechanism of memory information processing in networks of columns

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Abstract. Synchronization of the oscillatory discharge of cortical neurons could be a part of the mechanism that is involved in cortical information processing. On the assumption that the basic functional unit is the column composed of local excitatory and inhibitory cells and generating oscillatory neural activity, a network model that attains associative memory function is proposed. The synchronization of oscillation in the model is studied analytically using a sublattice analysis. In particular, the retrieval of a single memory pattern can be studied in the system, which can be derived from the original network model of interacting columns and is formally equivalent to a system of an isolated column. The network model simulated numerically shows a remarkable performance in which retrieval is achieved simultaneously for more than one memory pattern. The manifestations of this simultaneous retrieval in the network dynamics are successive transitions of the network state from a synchronized oscillation for a memory pattern to that for another memory pattern.

The column is considered to be the ubiquitous cortical organization of the mammalian cortex. It was found (Hevner and Wong-Riley 1992) that the human entorhinal cortex, which is strongly interconnected with the hippocampus and hence is thought to be involved in the memory consolidation process, possesses columnar organization. This suggests that the column is a basic functional unit of cortical memory-processing. In the present paper, I study how the synchronization of oscillation manifests itself in an associative-memory network of columns, paying particular attention to intercolumnar synaptic connections.

In so doing, I modify the Wilson-Cowan equation, which attempts to describe the activity of a single column, so that it may accommodate recent experimental results on the electrophysiological properties of cortical neurons. Then, using the modified Wilson-Cowan equation, I propose the associative-memory network of columns, which stores a finite or an extensive number of memory patterns. A simple form of the intercolumnar synaptic connections is assumed for analytically studying the synchronized oscillations generated by the model. I consider the following four types of intercolumnar wiring architecture: synaptic connections are sent from excitatory cells in a column to excitatory ones in other columns (E-E coupling), from excitatory cells to inhibitory ones (I-E coupling), from inhibitory cells to excitatory ones (E-I coupling), and from inhibitory cells to inhibitory ones (I-I coupling).

For the relative weights of intercolumnar connections, I assume the Hebb learning rule embedding random memory patterns. Then, using a sublattice analysis for a finite number of memory patterns, I show the existence of a memory-pattern-dependent synchronization if the isolated column exhibits oscillatory activity. This mode of oscillation (the out-of-phase solution) represents the retrieval of a single memory pattern in a rather general class of network models of columns, including the present one. Since the out-of-phase solution is described by a system which is equivalent to a certain system of a single column in the sublattice analysis, most of its dynamical properties other than its stability can be analytically studied. I show that only the I-E coupling

1 Introduction

In the modern strategy for understanding brain functions, one views the brain as a dynamic system of neurons and explores its information-coding mechanism generated by the activity of ensembles of neurons. In this strategy, it can be assumed that any memory trace is stored as an attractor of cooperative neural dynamics. Among attractors that can be used for modelling the cortical memory function, oscillatory neural activity has received greater attention after experiments on the mammalian visual cortex (Eckhorn et al. 1988; Gray et al. 1989). The authors claimed that cortical neurons responding to the stimuli from an object should exhibit a synchronized oscillatory activity, i.e., that the emergence of coherent oscillations indicates the visual perception. This assertion proposed by experimental observation seems to be realistic since the oscillatory activity arises easily from the interplay between excitatory and inhibitory cells (Wilson and Cowan 1972) within a local columnar organization.
allows such a solution in an almost unrestricted range of overall coupling strength. Other types of wiring architecture admit the out-of-phase solution only for rather small values of the coupling strengths. It is also shown that the system exhibits a pattern-independent synchronized oscillation (the in-phase solution) which is irrelevant to memory information processing.

I conducted numerical simulations to examine the analytical results obtained by the sublattice analysis and to study more complicated modes of synchronization other than the two solutions mentioned above. A remarkable feature revealed by the simulations is the existence of cases where the out-of-phase solution for a particular memory pattern does not exhibit stability but rather a gradual transition to a similar solution for another memory pattern. Therefore, the present network of columns can show a wandering around multiple memory patterns, spending a certain duration of time at each pattern. This wandering can be interpreted as a binding of multiple memory traces by the oscillatory behavior of the network of columns. Simulations were also conducted for a similar network model based on the ordinary Wilson-Cowan equation to examine whether these features of networks of columns depend on such physiological details as are incorporated into the present model.

2 Model

2.1 The modified Wilson-Cowan equation

Recent experiments showed that at least two kinds of neocortical neurons, i.e., the regular-spiking cells and the fast-spiking ones, are distinguished by their electrophysiological properties (McCormick et al. 1985; Prince and Huguenard 1988). The fast-spiking cells fire at much higher frequencies than the regular-spiking cells. The input-output relation of the regular-spiking cells is nonlinear and exhibits frequency adaptation, while that of the fast-spiking cells is almost linear and exhibits no frequency adaptation. Anatomical studies identified the regular-spiking cells as pyramidal cells, with exceptional cases where a minority of pyramidal cells exhibits burst firing, and the fast-spiking cells as stellate cells, which are probably y-aminobutyric acid (GABA)ergic. The pyramidal cells are known to be excitatory, while the GABAergic stellate cells are inhibitory (Kandel et al. 1991). Therefore, the basic assumption in this study is that neocortical columns are composed of the regular-spiking excitatory cells and the fast-spiking inhibitory cells. In the present paper, I only take into account regular-spiking cells as excitatory cells to make the model simpler.

Wilson and Cowan (1972) proposed a pair of equations which attempt to describe the excitatory and inhibitory neural activities of the local population of cells. A somewhat general expression of the Wilson-Cowan equation is

$$\frac{du_i}{dt} = -u_i + g_u(u_i, v_i, h_i^r)$$ \hspace{1cm} (1)

$$\frac{dv_i}{dt} = -v_i + g_v(u_i, v_i, h_i^r), \quad i = 1, \ldots, N$$ \hspace{1cm} (2)

where the units $u_i$ and $v_i$ represent the activities averaged for the excitatory and inhibitory cells in the $i$th subgroup (the column), respectively. The external inputs for the $i$th column are denoted by $h_i^r$ and $h_i^f$. Not much attention has been paid to the relative time scale $\tau$ in the dynamics of excitatory and inhibitory cells. As mentioned previously, the firing time-scale of inhibitory cells is shorter than that of excitatory ones, and therefore $\tau$ is assumed to be less than unity.

I adopt the following functions for the present model to describe the neural activity of the column:

$$g_u(u_i, v_i, h_i^r) = f_\beta(u_i - b_v - \theta_u + h_i^r),$$ \hspace{1cm} (3)

$$g_v(u_i, v_i, h_i^r) = au_i - 3(V_v^2 - \frac{3}{2})v_i + 3V_v^2v_i^2 - v_i^3 - \theta_v + h_i^r,$$ \hspace{1cm} (4)

$$f_\beta(x) = \frac{1}{2}(1 + \tanh(\beta x))$$ \hspace{1cm} (5)

The positive constants $a, b, V_v$ and $V_v^2$ stand for the weights of the intercolumnar synaptic connections, and $\theta_u$ and $\theta_v$ for excitatory and inhibitory thresholds, respectively. The input-output relation of the inhibitory cell was assumed to be a linear function rather than a sigmoidal one in order to represent the no frequency adaptation nature of inhibitory cells. To obtain relaxation oscillations with amplitudes of sufficient size, I assume the presence of nonlinear terms in $v_i$ in the intracolumnar synaptic transmission among inhibitory cells. Note that the unit $v_i$ produces an excitatory action on itself as well as an inhibitory one, depending on its temporal values. Physiologically, this can occur if the intracolumnar neural circuit involves inhibitory interneurons which provide disinhibition for inhibitory cells to produce virtual excitatory effects. Therefore, the above intracolumnar synaptic connections should be regarded as effective ones representing the overall effects of synaptic transmission between the cells $u_i$ and $v_i$.

It can be shown that the system described above can exhibit relaxation oscillations over a certain range of parameter values. To show this, I assume $h_i^r = h_i^f = 0$ and $\beta \to \infty$ for the time being. The latter assumption implies that the output function (5) turns into the step function. Define a line $l_u$ in the $(u_i, v_i)$-plane by $u_i - b_v - \theta_u = 0$ (Fig. 1). In the lower half of the plane divided by the line, (1) becomes $du_i/dt = -u_i + 1$, and $u_i$ approaches unity, while in the upper half of the plane, (1) becomes $du_i/dt = -u_i$ and $u_i$ approaches zero. Suppose that the line $l_u$ and the cubic nullcline $v_i = 0$ are given as those shown in Fig. 1. If $V_v > V_v^c$, the nullcline has two critical points (marked by the filled circles) with $v_i = \frac{V_v^2}{2} \pm \sqrt{V_v^2 - V_v^2}$. A periodic orbit consists of two (upper and lower) slow regions in the neighborhood of the nullcline and two fast regions connecting the slow ones. In the upper slow region, temporal state $(u_i(t), v_i(t))$ moves leftward ($u_i \to 0$) in the neighborhood of the nullcline to the upper critical point, at which the trajectory jumps downward to the lower slow region. Then it moves rightward ($u_i \to 1$) until it again jumps at the lower critical point.
For the sake of simplicity in analytical argument, I consider the case where \( l_u \) and the cubic nullcline pass the point \((1/2, 1/2)\) for \( h^* = h_u = 0 \) and that the nullcline has a point symmetry with respect to this point. Therefore, the point becomes the center of the area enclosed by the periodic orbit. The parameter values are set so that the periodic orbit can be confined in the unit square having corners \((0, 0), (0, 1), (1, 1), \) and \((1, 0)\).

The fixed point \((1/2, 1/2)\) determined by \( \frac{du}{dt} = \frac{dv}{dt} = 0 \) must be unstable to produce steady oscillations. The linear stability analysis yields the following conditions to make the fixed point unstable:

\[
1 - \beta + 3\gamma < 0, 
\]

\[
ab\beta + 3\gamma(1 - \beta) > 0
\]

where \( \gamma = \frac{\nu_u^2 - \nu_u}{4} + 1/4. \)

2.2 Intercolumnar synaptic connections

Now an associative-memory network model is built by explicitly giving intercolumnar synaptic connections to the above-mentioned system of \( N \) identical columns. Since the periodic orbit for the isolated column is assumed to be point-symmetric with respect to \((1/2, 1/2)\), it is convenient for the analysis of synchronized oscillations to preserve this symmetry even after the model includes the connection terms. Then the general connection terms respecting such a symmetry are

\[
h^*_l = C_{EE} \sum_{j \neq l} J_{lj}(2u_j - 1) + C_{EI} \sum_{j \neq l} J_{lj}(2v_j - 1),
\]

\[
h^*_l = C_{IE} \sum_{j \neq l} J_{lj}(2u_j - 1) + C_{II} \sum_{j \neq l} J_{lj}(2v_j - 1)
\]

In the present paper, I assume that the intercolumnar synaptic weights \( J_{lj} \) in (8) and (9) are given by a local learning rule of the Hebb type with \( p \) random memory patterns \( \{ \xi_i \} \): where \( \xi_i = \pm 1 \) with \( i = 1 \ldots N, u = 1 \ldots p \):

\[
J_{lj} = \frac{1}{N} \sum_{i=1}^{p} \xi_i \xi_j \tag{10}
\]

One may consider it slightly artificial to take terms like \( 2u_j - 1 \) and \( 2v_j - 1 \) in defining (8) and (9). However, it should not significantly spoil the reality of the model since the constant terms only give rise to the additional thresholds that obey distributions with vanishing means.

Note that the influences of individual cells at the intercolumnar synapses are either exclusively excitatory or exclusively inhibitory for \( J_{lj} \) given by (10). Physiologically, this can occur, as was mentioned for the intercolumnar connections, with inhibitory interneurons which provide suitable inhibition and disinhibition in the intercolumnar horizontal pathways.

3 The modes of synchronization

Let us study the types of synchronized oscillations which can occur in the network system described by (1), (2) and (10). In the following general argument, the coefficients in (8) and (9) can be, in principle, simultaneously nonvanishing. However, to avoid unnecessary complication, I omit the terms proportional to \( C_{EE}, C_{EI}, \) and \( C_{II} \) in (8) and (9) without loss of generality. Furthermore, I abbreviate the right-hand sides of (1) and (2) as \( G_u(u, v, h^*_l) \equiv u_l - g_u(u_v, v, h^*_l) \) and \( G_v(u, v, h^*_l) \equiv v_l - g_v(u_v, v, h^*_l) \), respectively. Consider the case of the finite number of memory patterns with an infinitely large \( N \). Therefore, the loading rate \( \alpha \equiv p/N \) vanishes. In this case, we can use sublattice analysis (van Hemmen 1982, Fukai and Shino 1990) to study the network dynamics. Let us begin with the case of \( p = 1 \) and then deal with the case for \( p > 1 \).

3.1 The case for \( p = 1 \)

The individual columns can be classified into either of two sublattices according to the corresponding bits of memory pattern \( \{ \xi_i \} \). Sublattice \( \Omega(\xi = +1) \) is the subgroup of columns which are found with \( \xi_i = 1 \), and \( \Omega(\xi = -1) \) the subgroup with \( \xi_i = -1 \). Within the limit \( N \to \infty \) each sublattice contains infinitely many columns. We are interested in the case in which the columns belonging to the same sublattice exhibit a coherent activity. I represent this activity in \( \Omega(\xi = +1)/\Omega(\xi = -1) \) by \( u_+ \) and \( v_+ \) \((u_-, v_-) \) and \( v_- \). Then the inputs to the columns are expressed as

\[
h^*_l = \pm C_{EE}[\tau_+ (2u_+ - 1) - \tau_- (2u_- - 1)]
\]

(11)

for \( N \to \infty \) if the \( i \)th column belongs to \( \Omega(\xi = \pm 1) \). The constants \( 0 \leq \tau_\pm \leq 1 \) stand for the ratios of sizes of sublattices to the total number of columns \( N \).

\( r_\pm = \lim_{N \to \infty} |\Omega(\xi = \pm 1)|/N \). If we assume \( r_+ = r_- = 1/2 \), we can further simplify the expressions as \( h^*_l = \pm C_{EE}(r_+ u_+ - r_- u_-) \). We obtain the following two sets of equations for \( (u_+, v_+) \) and \( (u_-, v_-) \):
It is easily seen from (11) that (12) admits a solution of the form
\[
    u_+(t) = u_-(t), \quad v_+(t) = v_-(t)
\]  
(13)
which represents a pattern-independent synchronization. As \( h_+ = 0 \) for the above solution (with \( r_+ = r_- = 1/2 \)), the system described by (12) reduces to two decoupled systems, each of which describes the activity of the isolated column. This implies that such a pattern-independent synchronization can always occur in principle as long as the single column exhibits oscillatory activity. The oscillation in this mode has no relation to the memory pattern and thus indicates unsuccessful memory retrieval. Hereafter, we shall call this oscillation the in-phase solution.

A more interesting solution can be obtained by putting
\[
    u_+(t) = 1 - u_-(t), \quad v_+(t) = 1 - v_-(t)
\]  
(14)
In this case, the external inputs to the sublattices become \( h_+ = C_{EE}(2u_+ - 1) \). Therefore, the two sets of equations for the sublattices become identical to each other. This implies that periodic solutions in one sublattice automatically describe those in the other. Moreover, there is a 'phase difference of \( \pi \) between the 'phases' of oscillations in the two sublattices. By saying 'a phase difference of \( \pi \)', I mean that the temporal states of two sublattices synchronously move on the opposite regions of the periodic orbit respecting the symmetry relation (14): the point \((1/2, 1/2)\) is at any moment the exact midpoint of the line connecting the two points \((u_+, v_+)\) and \((u_-, v_-)\). Therefore, the point \((1/2, 1/2)\) becomes the center of the area enclosed by the periodic orbit in this mode of coherent oscillation. Since this oscillation mode describes a pattern-dependent synchronization, it corresponds to memory retrieval in the present network model. This oscillation should occur when the coefficient \( C_{EE} \) is sufficiently small and the intercolumnar connections can be regarded as perturbations to the isolated column. I call this oscillation the out-of-phase solution.

3.2 The case of \( p > 1 \)

As in the case for \( p = 1 \), the individual columns can be classified into one of \( 2^p \) sublattices \( \Omega(\xi) \) where \( \xi = (\xi_1, \xi_2, \ldots, \xi_p) \) represents a vertex of the \( p \)-dimensional hypercube \( H^p \) of \( p \) coordinates. For instance, when \( p = 2 \), if \( (\xi_1, \xi_2) = (1, -1) \) for given \( i \), the \( i \)th column belongs to \( \Omega(1, -1) \). Each sublattice contains infinitely many columns as long as \( p \) is finite (and \( N = \infty \)). Time evolution equations for the coherent activities \( u(t; \xi) \) and \( v(t; \xi) \) in the sublattice \( \Omega(\xi) \) are written as

\[
    \frac{du(t; \xi)}{dt} = G_u(u(t; \xi), v(t; \xi), h(t; \xi)), \quad \frac{dv(t; \xi)}{dt} = G_v(u(t; \xi), v(t; \xi), h(t; \xi)),
\]  
(15)
in terms of the inputs to sublattices
\[
    h(t; \xi) = \sum_{\xi' \in H} \xi' \cdot r(\xi')(2u(t; \xi') - 1)
\]  
(16)
with \( r(\xi') = \lim_{N \to \infty} |\Omega(\xi')|/N \).

Let \( \{ \xi_i^1 \} \) be a reference pattern for retrieval. I define a \((p - 1)\)-dimensional vector \( \zeta = (\zeta_2, \ldots, \zeta_p) \) by eliminating the first component from \( \xi \). We are interested in the oscillation mode which exhibits synchronization \( \zeta \)-independently among the activities in the sublattices labeled by the same \( \xi^1 \)-value. I describe this mode of oscillation by putting
\[
    u(t; \xi^1) = u_\pm(t), \quad v(t; \xi^1) = \pm 1, \zeta = v_\pm(t)
\]  
(17)
With the above variables, the external inputs can be written as
\[
    h(t; \xi^1, \zeta)/C_{EE} = \xi^1 \sum_{\xi' \in H^{p-1}} [r(\xi')(2u(t; \xi') - 1)] - r(\xi')(2u(t; \xi') - 1) + \sum_{\mu > 1} \xi^\mu \sum_{\xi' \in H^{p-1}} [r(\xi')(2u(t; \xi') - 1) - r(\xi')(2u(t; \xi') - 1)]
\]  
(18)
where \( r(\xi) = r(\xi^1) = \pm 1, \zeta \). In the following analysis, I assume that all the sublattices contain the same number of columns: \( N = 1/2p \). Then the second term in (18) vanishes due to \( \sum_{\xi' \in \Omega} \xi^\mu = 0 \). We are left with the \( \zeta \)-independent external currents given by
\[
    h(t; \xi^1) = C_{EE} \xi^1 (u_+(t) - u_-(t))
\]  
(19)
Now we can see that the time evolution equations in each sublattice are independent of \( p \) for the mode given by (17) and are identical to (12). Therefore, the argument for \( p > 1 \) immediately follows that for \( p = 1 \); the pattern-dependent coherent oscillation (the out-of-phase solution) described by \( u_+(t) = 1 - u_-(t) \) and \( v_+(t) = 1 - v_-(t) \) should appear for a certain range of the coupling strength \( C_{EE} \); the pattern-independent coherent oscillation (the in-phase solution) described by \( u_+(t) = u_-(t) \) and \( v_+(t) = v_-(t) \) exists provided that the single column possesses a periodic solution.

For \( p = 2 \), the evolution equations are found to be accidentally decoupled for two subgroups of sublattices, \( S_1 = \{ \Omega(1, 1), \Omega(-1, -1) \} \) and \( S_2 = \{ \Omega(-1, 1), \Omega(1, 1) \} \). An immediate consequence of this fact is that the synchronized oscillation in \( S_1 \) occurs with an arbitrary phase relative to that in \( S_2 \) in any mode of oscillation. However, the 'relative phase' between the coherent oscillations in two sublattices belonging to either \( S_1 \) or \( S_2 \) is not 

\[
    \frac{du}{dt} = G_u(u, v, C_{EE}(2u - 1) + C_{EE}(2v - 1)),
\]

\[
    \tau \frac{dv}{dt} = G_v(u, v, C_{EE}(2u - 1) + C_{EE}(2v - 1))
\]  
(20)
which describes the synchronized oscillation obtained as the out-of-phase solution of the network of columns. In (20), the terms proportional to $C_{EE}$, $C_{EE}$ and $C_{II}$ were explicitly shown. This equation implies the following important result: as far as the out-of-phase solution representing the retrieval of a single memory pattern is concerned, the time evolution is governed by the equation for the single column with the coefficients of linear terms and the thresholds being shifted as

$$1 \rightarrow 1 + 2C_{EE}, \quad \text{(the coefficient of } u_i)$$

$$b \rightarrow b - 2C_{EI},$$

$$a \rightarrow a + 2C_{IE},$$

$$V_a^2 \rightarrow V_a^2 - \frac{2}{3} C_{II},$$

$$\theta_a \rightarrow \theta_a + C_{EE} + C_{EI},$$

$$\theta_a \rightarrow \theta_a + C_{EE} + C_{EI}$$

(21)

In other words, we can define an equivalent single-column system in studying the synchronization given by the out-of-phase solution in the network of an extensive number of columns. It is easily seen from the argument for deriving (20) that this equivalence of the out-of-phase solution to the single-column problem is ensured for a rather wide class of networks of columns provided that the intercolumnar connections are given by (8), (9), and (10).

4 Synchronization in the four types of intercolumnar connections

4.1 The conditions for intercolumnar coupling strength

In the preceding section, we have seen that the present network model can exhibit pattern-dependent synchronized oscillations. Here I investigate the ranges of coupling coefficients $C_{EE}$, $C_{EI}$, $C_{IE}$, and $C_{II}$ which allow the presence of the out-of-phase solutions by solving the equivalent single-column system (20) numerically.

I want to comment briefly on the stability of the out-of-phase solution. The stability of a periodic solution (with period $T$) to (20) can be studied in terms of a nonvanishing Floquet multiplier, say, $\lambda_1$: if the condition

$$\lambda_1 = \frac{1}{T} \int_0^T \left( \frac{\partial G_u}{\partial u} + \frac{\partial G_v}{\partial v} \right) dt < 0$$

(22)

is obeyed, the periodic solution is stable. (The other multiplier is zero for the periodic solution.) The condition (22), however, in general, neither ensures the stability of the out-of-phase solution of the 2^p-sublattice system (15) nor the corresponding orbit in the original network model with $N$ columns described by (1) and (2). Numerical simulations indicate that a stable periodic solution of the equivalent single-column system describes a stable periodic orbit in the 2^p-sublattice system except in certain cases of negative coupling coefficients. The solution, however, can correspond to only a quasi-stable, or even unstable, orbit in the original network model. Nevertheless, studying the properties of the out-of-phase solution is useful for achieving an insight into synchronized oscillations appearing in the original network model. In particular, it reveals the ranges of the coupling coefficients for ensuring synchronized oscillations from the appearance of fixed points.

In order to examine the behavior of this network model under simple and meaningful conditions, I restrict the intercolumnar wiring architecture to the four cases in which only one of the coefficients among $C_{EE}$, $C_{EI}$, $C_{IE}$, and $C_{II}$ is nonvanishing. It is known, as the so-called oscillator death (Ermentrout and Kopell 1990), that a system of oscillators may acquire a stable fixed point that corresponds to the cessation of oscillation when the coupling among the oscillators is strong. It is therefore expected that this network system will cease to exhibit oscillations and will develop a new stable fixed point when one of the coupling coefficients is large. This proves to be true except in the case of $C_{EE} \neq 0$.

The following fact is worth noting: the out-of-phase solution of the form (14) is obtained as a periodic or quasi-periodic orbit of the ordinary differential equation (20), but it cannot be a chaotic orbit since the equation is two-dimensional.

The parameter values used in the numerical simulations are $\beta=3$, $A=0.08$, $B=1.2$, $\theta_i=-0.1$, $\theta=-0.01375$, $V_a=0.5$, and $V_a=0.45$. As mentioned previously, $\tau$ is taken to be less than unity: $\tau = 0.4$. With these values of parameters, the single column described by (1) and (2) exhibits the relaxation oscillation whose waveform is presented in Fig. 2a. We see from the corresponding phase portrait in Fig. 2b that the area enclosed by the periodic orbit has its center at the point (1/2, 1/2). I first show the results obtained numerically for each case and then examine the simulation results using the sublattice analysis.

4.1.1 The case for $C_{EE} \neq 0$, $C_{EI} = C_{IE} = C_{II} = 0$. The solution of the equivalent single-column system (20) yields a periodic oscillation as long as the coupling is weak. The out-of-phase solution is also a stable solution of the 2^p-dimensional sublattice system (15) $p$-independently when $C_{EE}$ is positive. The range of the coupling coefficient to ensure the presence of this solution was found to be $0 < C_{EE} \leq 0.65$. Beyond the upper bound, the sublattice system gives stable fixed points. When $C_{EE}$ is negative, the out-of-phase solution is unstable as a solution of the sublattice system, although the equivalent single-column system still has a periodic solution. Therefore, the in-phase solution and the fixed points are the only stable solutions for $C_{EE} < 0$. For $C_{EE} \leq -0.74$, even the in-phase solution ceases to exist.

4.1.2 The case for $C_{EI} \neq 0$, $C_{EE} = C_{IE} = C_{II} = 0$. The out-of-phase solution exists for the range of the coefficient $-0.61 < C_{EI} \leq 0.52$. The solution of our model exhibits a stable solution for $C_{EI} < 0$. However, the sublattice system gives fixed points below the lower bound, the oscillatory solution of the 2^p-dimensional sublattice system ceases to satisfy the relation (14), although it still describes some kind of
pattern-dependent synchronization. At $C_{EE} \approx -2.9$, only the in-phase solution appears as a stable periodic solution of the sublattice system. For $-2.9 \leq C_{EE} \leq -0.61$, the behavior of the network depends on the number of embedded patterns. For instance, at $C_{EE} = -2.6$, the sublattice system for $p = 1$ exhibits a complex periodic orbit (Fig. 3a), while that for $p = 3$ exhibits a chaotic orbit (Fig. 3b) with the Lyapunov exponent $\approx 0.11$. To see the extent to which these orbits deviate from the out-of-phase solution, I present the quantity $u_+(t) + u_-(t)$ in Fig. 4a and b for the periodic and chaotic orbits, respectively. The fact that the quantity oscillates around unity periodically or chaotically allows us to interpret these orbits as retrieval solutions of the model.

4.1.3 The case for $C_{EE} \neq 0, C_{EE} = C_{IE} = C_{II} = 0$. The out-of-phase solution is obtained for any positive value of the coefficient: its existence was examined up to $C_{EE} \approx 10^3$. When $-0.018 \leq C_{EE} < 0$, only the in-phase solution appears as a stable periodic solution of the sublattice system. For $C_{EE} \leq -0.018$, only fixed points appear, while the in-phase solution disappears.

4.1.4 The case for $C_{II} \neq 0, C_{EE} = C_{IE} = C_{II} = 0$. The out-of-phase solution appears for $0 < C_{II} \leq 0.038$.

Beyond the upper bound, the equivalent single-column system as well as the 2D-dimensional sublattice system give fixed points. For $C_{II} < 0$, only the in-phase solution and the fixed points can be stable solutions.

4.2 Analysis using the equivalent single-column system

The above-mentioned behavior of this neural network model with nonvanishing positive coupling coefficients can be qualitatively understood using sublattice analysis since investigating the out-of-phase solution is equivalent to solving the dynamics of the single column with modified weights of intracolumnar connections and thresholds, as explicitly given in (20) and (21). I consider the cases where the coefficients are positive since otherwise the out-of-phase solution is an unstable solution of the sublattice system (15), as was shown by the simulations.

First it is noted that the modifications of weights and thresholds given in (21) ensure that the newly obtained line $l_c$ and cubic nullclcline pass the point $(1/2, 1/2)$. Then as
Fig. 4a,b. The quantities \(u_+(t) + u_-(t)\) for the orbits shown in Fig. 3. The deviation of this quantity from unity parallels that of the orbit from the pattern-dependent synchronized oscillation described by (14). The figures indicate that these orbits can still be regarded as memory retrieval a in a complex but periodic manner and b in a chaotic manner.

far as the out-of-phase solution is concerned, including a positive \(C_{EE}\) or \(C_{EH}\) in the network can be regarded as making the slope of \(L_u\) greater in the corresponding equivalent single-column system, which can result in generating fixed points at the intersection points of the cubic nullcline and two lines \(u = 0, 1\) (Fig. 5a). Similarly, including a positive \(C_{II}\) can be interpreted as making the critical points of the nullcline further apart and therefore can generate pairs of a stable and an unstable fixed point (Fig. 5b). While increasing the values of three coefficients \((C_{EE}, C_{EH}\) or \(C_{II}\)) results in generating fixed points, increasing the value of \(C_{III}\) does not affect the presence of oscillation since it merely gives the compression of the cubic nullcline along the \(u\)-axis in the equivalent single-column system (Fig. 5c).

I would like to comment on the possibility of using such fixed points as obtained in the present analysis for the purpose of associative memory information processing. It was in fact shown that memory retrieval can be attained by the equilibrium fixed points of a similar network model of columns (Fukai 1994). However, using synchronized oscillations in the information processing has an advantage which is not seen with the use of fixed points. I shall discuss this in the next section.

I note that the results obtained in this section qualitatively hold for a wider class of the network of columns.
including the one described by the conventional Wilson-Cowan equation:

$$\frac{du_i}{dt} = -u_i + f_p(u_i - bv_i - \theta_i + h_i),$$  \hspace{1cm} \text{(23)}$$

$$\frac{dv_i}{dt} = -v_i + f_p(au_i - cv_i - \theta_i + h_i) \quad i = 1, \ldots, N \hspace{1cm} \text{(24)}$$

If there are no coupling terms $h_{c,E,F,R}$, the dynamic behavior of a single column is determined by the locations of two lines: $u - bv - \theta_i = 0$, $au - cv - \theta_i = 0$ relative to four points \([0,0], (1,0), (0,1), (1,1)\). To obtain a steady oscillation, \((0,1)\) and \((1,1)\) \([0,0] \text{ and } (1,0)\) must be above (below) $t_i$, while \((0,1)\) and \((0,1)\) \([0,0] \text{ and } (1,1)\) must be above (below) $t_i$, see, for example, von der Malsburg and Buhmann 1992 for further details. The effects of the intercolumnar connections in (23) and (24) are again represented by the modifications of the intracolumnar weights and thresholds in the equivalent single-column system: the fourth equation in (21) should now be replaced by $c \rightarrow c - 2C_{G}$, Accordingly, one can define new lines $l_i$ and $l_{i'}$ to see that the effects of the intercolumnar connections on synchronized oscillations are qualitatively the same as those discussed for the present network model.

4.3 Simultaneous retrieval of more than one memory pattern

Besides the in-phase and out-of-phase solutions, there exist for $p > 1$ other modes of oscillation which exhibit synchronization among the sublattices other than that described by (14). In fact, the synchronization occurs in more complicated fashions, and therefore these modes are only numerically studied in this section.

To measure the coherence of oscillations in numerical simulations, I define the coherence order-parameter $g^p(t)$ as

$$g^p(t) = \left| \sum_{x \in \omega} \xi^p r(x) \exp(i\phi_x(t; \xi)) \right| \hspace{1cm} \text{(25)}$$

The phase variable $\phi_x(t; \xi)$ is given by the angle between two vectors $x = (u(t; \xi) - 1/2, v(t; \xi) - 1/2)$ and $y = (1,1)$:

$$\cos \phi_x(t; \xi) = \frac{u(t; \xi) + v(t; \xi) - 1}{\sqrt{(u(t; \xi) - 1/2)^2 + (v(t; \xi) - 1/2)^2}} \hspace{1cm} \text{(26)}$$

If, for instance, the network exhibits the out-of-phase solution for the $\mu$th memory pattern, $g^p(t)$ takes its value at unity and other $g^p(t)$'s ($v \neq \mu$) vanish. In other modes of synchronization, however, more than one $g^p(t)$ can alternately give nonvanishing values close to unity.

Typical examples of such oscillation modes obtained for the $2^p$-dimensional sublattice system (15) with $p = 3$ are given in Fig. 6a and b for $C_{G_{E}} = -0.5$ and $C_{G_{B}} = -2.1$, respectively. In Fig. 6a, $|g^p| \approx 1$ is satisfied alternately by two retrieved patterns, while in Fig. 6b, it is realized for each of the three memory patterns at certain moments.

In biological neural networks, these modes of oscillation represent the network states in which cortical neurons exhibit synchronized oscillations continuing to exchange temporally retrieved memory patterns. I propose to interpret this kind of synchronization as the simultaneous retrieval of more than one memory pattern by the network of columns. For instance, the network succeeded in simultaneously retrieving two memory patterns in Fig. 6a and three memory patterns in Fig. 6b. The simultaneous retrieval of memory patterns is considered to be a virtue of the present model, which attains the associative memory function by means of the synchronization of oscillatory neural activities. This interesting phenomenon was also observed for the other intercolumnar connections.
4.4 Simulations of the original network model

Since the sublattice analysis discussed in the preceding section assumes the stability of coherent oscillations in each sublattice a priori, numerical simulations for the original system of mutually connected columns are required to examine the assumption.

Figure 7 shows a periodic orbit obtained for a column in the original network system described by (1) and (2) with the same parameter values as those used in Fig. 3a. Both orbits prove to be almost identical. The orbit was numerically examined to be a stable solution of the original network system. A chaotic orbit (not shown) similar to that in Fig. 3b was also obtained for the original network system with the corresponding parameter values.

It was, however, found that the synchronized oscillations obtained in the sublattice analysis do not always correspond to stable solutions of the original network system. For instance, the orbit shown in Fig. 6a representing a simultaneous retrieval of two memory patterns for \( p = 3 \) was found to be unstable and appears only as a part of a more complex oscillation: one of the coherent oscillations occurring in the antiphases is gradually desynchronized and finally exchanged for a synchronized oscillation with the third memory pattern. Thus, the network exhibits the retrieval of two memory patterns which are different from the initial pair. The network repeats this behavior, and all the pairs of memory patterns are retrieved in turn (one cycle is completed in a period \( T \approx 700 \)). An oscillation similar to that shown in Fig. 6b was in fact observed in the original network system. In the following, I show some interesting examples of memory retrieval in the original network system.

An order parameter \( g'(t) \) is defined as the counterpart of (25):

\[
g'(t) = \frac{1}{N} \sum_{i=1}^{N} \xi_i \exp(i \phi_i(t))
\]  

(27)

where the phase variables are given by angles between vectors \( u(t) = \frac{1}{2}, v(t) = \frac{1}{2} \) and \( (1, 1) \). I also introduce another order parameter \( r'(t) = (1/N) \left( \sum_{i=1}^{N} \xi_i \exp(i \phi_i(t)) \right) + \sum_{i=1}^{N} \xi_i \exp(i \phi_i(t)) \). Here, \( Q_{n+Q_{m-}} \) is a set of columns loaded with \( \xi_i = -1 \). Unlike \( g'(t) \), \( r'(t) \) measures the occurrence of synchronization without paying particular attention to a relative phase of \( \frac{\pi}{n} \) between the coherent oscillations in \( Q_{n+} \) and \( Q_{m-} \). However, I show only \( g'(t) \) since the two measures were found to exhibit almost the same behavior in memory retrieval except for initial transients. This implies that the relative phase is given approximately by \( \pi \) whenever the synchronization occurs in memory retrieval.

Figure 8 presents the behavior of the network model with \( N = 300 \), \( p = 3 \), and \( C_{EF} = 5 \) in memory retrieval. The time evolution is shown for all three \( g'(t) \)'s and \( n(t) \)'s. The initial state for the simulation is taken to be the out-of-phase solution for \( \{ \xi_i \} \); \( g_1(0) = 1 \). The out-of-phase solution, however, is not stable, and the network state enters into another mode of oscillation in which synchronization is alternately achieved for two other memory patterns. Thus, the retrieval of \( \{ \xi_i \} \) is followed by the simultaneous retrieval of \( \{ \xi_i \} \) and \( \{ \xi_i \} \). It is worth noting that \( g_n(t) \) shows a very rapid oscillation together with the oscillation of its envelope with a longer periodicity. This implies that the degree of synchronization for a specific memory pattern frequently changes at short time scales during retrieval. Paying particular attention to this rapid oscillation, one may interpret the memory retrieval shown shown in Fig. 8 in a more complicated way than that mentioned above. Namely, the retrieval occurs for \( \{ \xi_i \} \) until \( t \approx 10 \), is then attained for the pair \((\{ \xi_i \}, \{ \xi_i \})\) during \( 10 \leq t \leq 15 \), and is finally repeated in the pattern of \( \{ \xi_i \} \) and \( \{ \xi_i \} \) and \( \{ \xi_i \} \). Other examples are given in Fig. 9 for the networks with \( N = 300 \), \( p = 5 \), and (a) \( C_{EF} = 0.6 \), (b) \( C_{EF} = 0.68 \), and (c) \( C_{EF} = 0.66 \), respectively. These values of the coupling strength are close to the critical one that ensures the presence of the out-of-phase solution. The order parameters for the five memory patterns are shown together in the same figure. In Fig. 9a, the out-of-phase solution is seen to be quasi-stable. In Fig. 9b, the out-of-phase solutions are unstable for some memory patterns, and the network state shows alternate transitions from one solution to the other in a rhythmic manner. Nonrhythmic successive transitions between the out-of-phase solutions for two memory patterns are seen in Fig. 9c.

Although the case for \( C_{EF} = 0 \) was not extensively studied in the numerical simulations since the small values of \( C_{EF} \) in the present model are not suitable for generating a rapid synchronization, the network seems to show a qualitatively similar behavior to that discussed above for the other three cases.

4.5 Simulations of the Wilson–Cowan network model

It is worth examining whether the transitions among synchronized oscillations for memory patterns occur for the network model described by (23) and (24) to achieve some insight into the generality of the phenomenon. To this end, I conducted numerical simulations for the
network model based on the Wilson-Cowan equation, assuming the four types of intercolumnar connections.

Figure 10 shows an example of the retrieval behavior exhibited by the network with a nonvanishing $C_4$ and five embedded patterns. (The values of parameters used in the simulation are given in the figure caption.) The $g^a(t)$'s are shown only for the three memory patterns for which they give values close to unity. It is now obvious that transitions can occur for this network.

I observed the occurrence of transitions for other types of intercolumnar connections. These results suggest that the simultaneous retrieval of more than one memory pattern can be rather a general phenomenon in a wide class of networks of columns acting as oscillators.

5 Discussion

The sublattice analysis has revealed that the out-of-phase solution describes a pattern-dependent synchronized oscillation which implies memory retrieval in networks of columns. This solution represents a stored memory as a specific pattern of synchronization exhibiting mutual phase differences of zero or $\pi$ among the oscillatory activities of columns. This implies that phase differences between coherent oscillations in clusters of columns (neural oscillators) can give valuable piece of information on stored memory contents. A remarkable feature of the out-of-phase solution is that it is described by the equations for an isolated column with the modified thresholds and weights for the intracolumnar connections, and
therefore some properties of synchronized oscillations in systems of mutually connected columns can be studied as a problem for a single column.

Furthermore, the sublattice analysis and the numerical simulations have shown that the present network of columns as well as the one described by the Wilson-Cowan equation can achieve simultaneous recognition of more than one memory pattern using successive transition from a synchronized oscillation for one memory pattern to that for another memory pattern. An unexplored mechanism which desynchronizes the coherent oscillations in each sublattice seems to be responsible for generating these transitions. The simultaneous perception, or linking, of multiple memory traces in oscillatory neural activity was first discussed as a possible solution to the binding problem in visual information processing (Eckhorn et al. 1988; Gray et al. 1989; Shuster and Wagner 1990; von der Malsburg and Buhmann 1992). The present study has demonstrated that using synchronized oscillations makes such information processing possible even in the associative memory.

Although the existence of the out-of-phase solution does not depend on a particular type of intercolumnar connection as long as memory patterns are embedded by a learning rule (10) of the Hebb type or, in other words, the details of the intercolumnar wiring architecture are not very essential for the occurrence of synchronization, some important aspects of memory retrieval were found to depend on which type is used in the network model. The intercolumnar connections of the type \( C_{II} \neq 0 \) allow synchronization to occur with complicated or chaotic orbits in memory retrieval. This enables the network to show a variety of behavior in memory retrieval. On the other hand, connections of the type \( C_{II} = 0 \) allow the presence of synchronized oscillations even for very large values of the overall coupling strength, which implies that the synchronized oscillations should be rather robust against perturbations or noises expected in the nervous systems. The features obtained for \( C_{II} \neq 0 \) and \( C_{II} = 0 \) are considered to provide potential flexibility for the present network in learning and retrieving memories.

Within the analytical and numerical studies conducted for a finite number of memory patterns, both network models described by the modified and ordinary Wilson-Cowan equations exhibited qualitatively similar behavior in memory retrieval with an exceptional case for \( C_{II} = 0 \), where the latter model shows chaotic behavior such as that shown in Fig. 6b only in the initial transients. The physiological details given by the differences in the time scales and response properties between excitatory and inhibitory cells are therefore suggested to be unimportant, at least for the associative memory function of the network of columns. However, the performance of the networks has still to be examined for an extensive number of memory patterns, for which the present analysis based on sublattices cannot be applied.

A possible answer to why there should be two different time scales in the cortical dynamics may be found in the recent report by Sommers and Kopell (1993), who investigated the dependencies of the synchronization performance on the intrinsic dynamic properties.
of oscillators. According to their results, a rapid and robust synchronization is obtained if the oscillators exhibit a certain class of relaxation waveform rather than a sinusoidal one. Such a relaxation waveform appears if the oscillation is generated by the interplay between slow and fast dynamic variables.

Some questions are now open for further research. For a network loaded with a relatively large number of memory patterns, the major cause of unsuccessful memory retrieval should be the breakdown of coherence in oscillatory activities. How large is the upper bound for $\alpha$ (the critical storage capacity) that ensures the occurrence of pattern-dependent synchronization? As extensively studied in this paper, networks of columns can in general generate the transitions between the synchronized oscillations. What is the mechanism that generates the transitions? Furthermore, how can the brain control the order and duration of the visit to a particular memory pattern in the transitions?

In summary, I have shown that embedding memory information into the weights for horizontal connections, which are not necessarily those between excitatory pyramidal cells as was suggested for the mammalian visual cortex (Gilbert 1992), can provide a promising mechanism for memory information processing by synchronization among activities of columns. In particular, the possibility has been pointed out that the network of columns develops an excellent ability for temporal information processing using a variety of synchronized oscillations and the transitions between them.

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