SYNCHRONIZED OSCILLATIONS FOR BINDING SPATIALLY DISTRIBUTED FEATURE CODES INTO COHERENT SPATIAL PATTERNS

Stephen Grossberg† and David Somers‡
Center for Adaptive Systems
and
Department of Cognitive and Neural Systems
Boston University
111 Cummington Street
Boston, MA 02215

Abstract

Neural network models are described for binding out-of-phase activations of spatially distributed cells into synchronized oscillations within a single processing cycle. These results suggest how the brain may overcome the temporal "jitter" inherent in multi-level processing of spatially distributed data. Coherent synchronous patterns of spatially distributed features are formed to represent and learn about external objects and events. Temporal jitter thus does not typically cause scenic parts to be combined into the wrong visual objects. During preattentive vision, such patterns may represent emergent boundary segmentations, including illusory contours. During attentive visual object recognition, such patterns may occur during an attentive resonant state that triggers new learning. Different properties of preattentive and attentive oscillations are predicted, and compared with neurophysiological data concerning rapid synchronization of cell activations in visual cortex.

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1. Introduction: The Role of Synchrony in Spatial Pattern Coding

This chapter discusses neural network models that are capable of rapidly synchronizing the activities of spatially distributed cells within a single processing cycle. The chapter also reviews electrophysiological data describing rapid synchronization of spatially distributed cell activations in the visual cortex, and suggests a theoretical explanation for the functional role of such synchronization *in vivo.*

A key idea in this theoretical analysis concerns the hypothesis that the functional units of short term memory (STM) and long term memory (LTM) in the brain are *spatial patterns.* This hypothesis was originally derived from a mathematical analysis of the interactive dynamics of STM and LTM during associative learning by a neural network (Grossberg, 1968, 1969, 1971, 1982b). For definiteness, denote the input to the i^{th} cell (or cell population) v_i by I_i. It was proved, under rather general conditions, that neural networks tend to learn the *spatial pattern* of relative input weights

$$\theta_i = \frac{I_i}{\sum_{k=1}^{n} I_k}. \tag{1}$$

The values θ_i measure the *relative* importance of the features coded by the cells v_i in the input pattern $(I_1, I_2, ..., I_n)$. It was also proved that the total input strength

$$I = \sum_{k=1} I_k \tag{2}$$

is used as energy to drive the learning process. When the relative importance of features remains fixed during a given time interval, the weights θ_i remain approximately constant, even if the total input I varies wildly through time. This may be expected to occur, for example, during sustained inspection of a fixed visual image. Thus the network tends to learn about the "temporally coherent part" of an input pattern. It tends to *factorize* the temporally coherent information $(\theta_1, \theta_2, ..., \theta_n)$ from the fluctuating energy I that mobilizes the learning process.

The mathematical analyses which led to the conclusion that the functional units of short term memory and long term memory are spatial patterns also provided a definition that could support this conclusion; namely, spatial patterns are temporally synchronized, spatially distributed activations that preserve their relative ordering through time. These results led to a series of investigations, some of which are reviewed in Grossberg (1982a, 1982b, 1988) and in Section 3 below.

Given these results, a potentially serious problem for brain processing can be described using Figure 1 as a guide. Figure 1 considers the processing of a visual image whose various parts are registered approximately synchronously at the eyes. Subsequent events at multiple processing stages may, however, destroy this synchrony. For example, spatially inhomogeneous noise may enable some cells to fire faster than others. Prior processing of previous images may also inhomogeneously habituate some neural pathways more than others, thereby slowing the processing rate in some pathways more than others. In all, even if an external source of spatially distributed information is synchronous, it may be represented with phase leads and lags at subsequent neural processing stages. If these various parts of the processed image are not ultimately recombined into synchronized spatial patterns, then they cannot be correctly learned and recognized by the brain as part of the same event.

Put another way, if the temporal "jitter" in the neural processing of distributed inputs is not corrected, then parts of different images that occur at different times could be scrambled together, leading to a maladaptive reorganization of scenic parts into the "wrong" visual objects. Although such scrambling can be made to occur *in vivo* using sufficient experimental

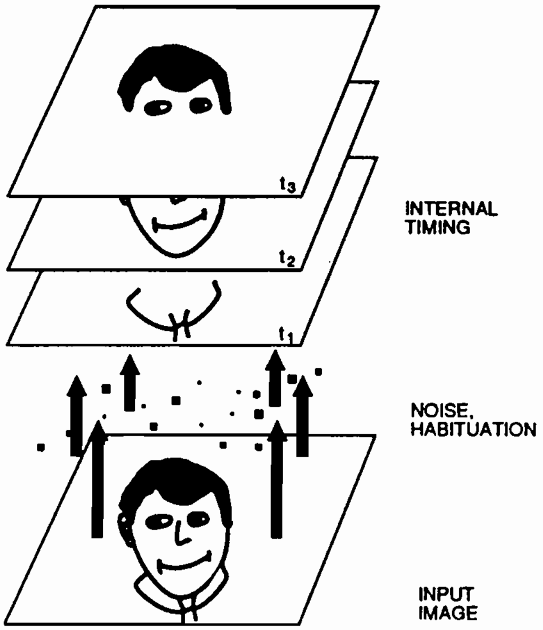


Figure 1. Multilevel processing of an image in noise may lead to phase leads and lags in the processing of different image regions. These temporally out-of-phase activations may be rapidly recombined into coherent spatial patterns by synchronized oscillations.

ingenuity, as in the case of "illusory conjunctions" (Treisman and Gelade, 1980), it would be all too frequent, with devastating results, in the absence of compensatory neural mechanisms. Synchronous binding of features into coherent spatial pattern codes has also been described as part of the process whereby complex acoustic signals are grouped into unitary auditory events (Bregman, 1990).

We suggest one such compensatory mechanism that reorganizes temporally out-of-phase spatial data into a synchronous spatial pattern, just so long as the phase lags and leads of these data lie within a critical time interval. In order to be effective during real-time perception, during which a series of rapidly changing images must be correctly processed, the synchronizer must be able to act quickly, within one or two processing cycles. This property holds in our model, as well as in the data.

2. Synchrony in Visual Cortical Cells

Using simultaneous, multielectrode, extracellular recordings, two labs (Eckhorn, Bauer, Jordan, Brosch, Kruse, Munk, and Reitbock, 1988; Gray and Singer, 1989; Gray, Konig, Engel, and Singer, 1989) have reported stimulus-evoked synchronized oscillations of 40–60 Hz in the primary visual cortex (Areas 17 and 18) of the cat. Coherence or synchrony of firing activity was found between cells within a cortical column (Eckhorn *et al.*, 1988; Gray and Singer, 1989), in neighboring hypercolumns (Eckhorn *et al.*, 1988; Gray *et al.*, 1989), in distant hypercolumns (Gray *et al.*, 1989), and lying in two different cortical areas (Eckhorn *et al*, 1988). Stimulus position, orientation, movement direction, and velocity were among the stimulus properties that yielded stimulus-evoked resonances. Synchronized oscillatory responses were frequently found at distant cortical positions when at least one of the primary coding properties was similar.

Using a single long moving bar as a stimulus, Gray *et al.* (1989) recorded simultaneously from cells which were separated by large cortical distances. They found that for cortical separations great enough that the receptive fields of the cells did not overlap (> 2 mm), coherent oscillations occurred only between cells with similar orientation preferences. Even at these large separations, the cross-correlations of the firing patterns of the cells indicated a tight synchrony, on average having a 0 ms phase lag. Nearly all phase-locked cells showed activity peaks within 3 ms of each other. Thus assuming a 25 ms period of oscillation, phase differences were typically less than 12% of the period.

Gray *et al.* repeated this procedure using two short disconnected bars as the stimuli. Using large interbar distances, only one bar would pass through the receptive field of one cell, and the second bar would pass through the receptive field of a second cell. When the two bars were moved colinearly in the same direction at the same speed, these two distant cells frequently synchronized their oscillations even though there was a gap between the stimuli. When the bars were moved in opposite directions, no synchrony resulted.

These stimulus-evoked resonances have been interpreted as reflecting the global properties of the stimulus, properties which might be expected to cohere in a single object. For instance, in the two bar stimulus paradigm, colinear but disconnected bars moving in the same direction at the same speed may be perceptually interpreted as a single continuous contour that is occluded in the middle, whereas two bars moving in opposite directions (without rotation) are likely to be perceptually interpreted as different contours. Segregation across occluding regions is a common problem that the visual system must solve regularly. In nature, occlusion may arise due to internal sources such as retinal veins in front of the photoreceptors or external sources such as a tree branch between the observer and the object of interest.

Before the present work was carried out, attempts to explain these oscillatory phenomena have typically been restricted to formal equations for the phase relations among abstractly defined oscillators (Atiya and Baldi, 1989; Baldi and Meir, 1990; Kammen, Holmes, and Koch, 1989). Herein we explain how suitably designed neural networks can give rise to such oscillations as an emergent property of their real-time dynamics. Moreover, we use neural networks which have previously been derived to explain and predict behavioral and neural data, other than the oscillatory phenomena themselves.

3. Different Predictions About Preattentive Visual Coding and Attentive Recognition Learning

Based upon the analyses of spatial pattern coding such as those reviewed in Section 1, Grossberg (1976b, 1978c) predicted that cortical codes would be expressed by resonant standing waves in which cooperatively linked cells oscillate in phase with one another. The mathematical analysis of such synchronous oscillations was begun in Ellias and Grossberg, (1975). It was also noted that these standing waves could be replaced by approach to an equilibrium point, or attractor, if no "slow" variables, such as inhibitory interneurons or chemical modulators, exist in the network. Both standing waves and equilibria can, in principle, support a feature-based cortical code. The standing waves were called "order-preserving limit cycles" to emphasize that the ordering, or relative importance, of feature detector activations should persist during each coding cycle, even if their absolute activations vary through time as the oscillation unfolds.

Mathematical analyses of both the standing wave and equilibrium point models were initiated in the 1970's. Studies of equilibrium point models led to a series of mathematical theorems, including a general theory for globally analysing equilibria and oscillations in competitive neural networks (Grossberg, 1978a, 1978b, 1980), and the Cohen-Grossberg model and theorem for content addressable memory (Cohen and Grossberg, 1983; Grossberg, 1982a). The Cohen-Grossberg model was designed to include the additive model, subsequently studied by Hopfield (1984), as well as the shunting model that describes interactions between cells that obey a membrane equation; see Grossberg (1988) for an historical overview. The present article continues the analysis of standing waves that was initiated in Ellias and Grossberg (1975).

The standing wave prediction was made in the context of a theory, called Adaptive Resonance Theory, or ART, which analyses the role of reciprocal top-down and bottom-up cortico-cortical and thalamo-cortical adaptive filters in the development of cortical feature detectors, recognition learning, attentional processing, and memory search (Grossberg, 1976a, 1976b, 1978c, 1982b). Within ART, a resonant standing wave can occur when bottom-up and top-down signals fuse into an attentional focus. Such an attentional focus can support new learning as it gives rise to a conscious perceptual experience. The predicted linkage between standing waves, attention, and conscious experience has recently begun to attract the interest of a large number of investigators.

Mathematical investigations of complete ART architectures have heretofore tended to analyse equilibrium point models (Figure 2), wherein slow variables that could sustain oscillations are eliminated for simplicity (Carpenter and Grossberg, 1987a, 1987b, 1990; Carpenter, Grossberg, and Reynolds, 1991; Carpenter, Grossberg, Markuzon, Reynolds, and Rosen, 1991). The present results illustrate how the ART standing waves predicted in Grossberg (1976b, 1978c) can be generated by the type of bottom-up and top-down feedback interactions among adaptive filters that are used in ART circuits.

After ART was introduced in order to analyse attentive learning and recognition, subsequent research by Grossberg and Mingolla focused on processes of preattentive vision. In this work, a new type of cortical cell, called a *bipole cell*, was predicted to exist (Grossberg, 1984, 1987a, 1987b; Grossberg and Mingolla, 1985a, 1985b, 1987). Bipole cells cooperatively link perceptual features into emergent boundary segmentations via cooperative-competitive feedback signals in a network called the CC Loop. The CC Loop is part of a larger neural model, called the Boundary Contour System (BCS), which suggested new perceptual roles for cortical simple cells, complex cells, hypercomplex cells, and bipole cells (Figure 3). In addition, the BCS was used to explain and predict a variety of psychophysical and perceptual data, notably data about texture segregation, subjective contours, filling-in of brightness and color, and 3-D surface perception.

The bipole cell receptive field was predicted to consist of two long, thin independent flanks which non-linearly sum inputs from cells with orientation preferences similar to the orientation of the long axis of the bipole (Figure 4). Bipole cell output signals can be activated if and only if both flanks are sufficiently activated. These signals feed excitatory input back to model hypercomplex cells in a lower network layer which have the same orientation preference and are positioned near the middle of the bipole cell. Through this cooperative feedback cycle, two disconnected but colinear contours can induce a boundary completion between them.

Although the bipole cell was predicted on perceptual grounds, its existence was soon supported by neurophysiological data. Recording from Area 18 of alert monkeys, von der Heydt, Peterhans, and Baumgartner (1984) found cells that responded to moving illusory contours. That is, with no local luminance information to suggest a contour and only with colinear inducing lines lying beyond the receptive fields of the cells, cells responded strongly when the global percept of the stimulus suggested an illusory contour. When the stimulus was altered so that an illusory contour was no longer perceived, the cells did not respond. Inducing lines on both sides of the site were necessary for the perception of the illusory contours by both the cells and human observers. These data indicate that some cells in visual cortex respond well to subjective contours, and that cells which are not directly activated by bottom-up signals require input from at least two colinear flanking regions in order to be activated.

In addition to this electrophysiological data, Gilbert and Wiesel (1989) provided ana-

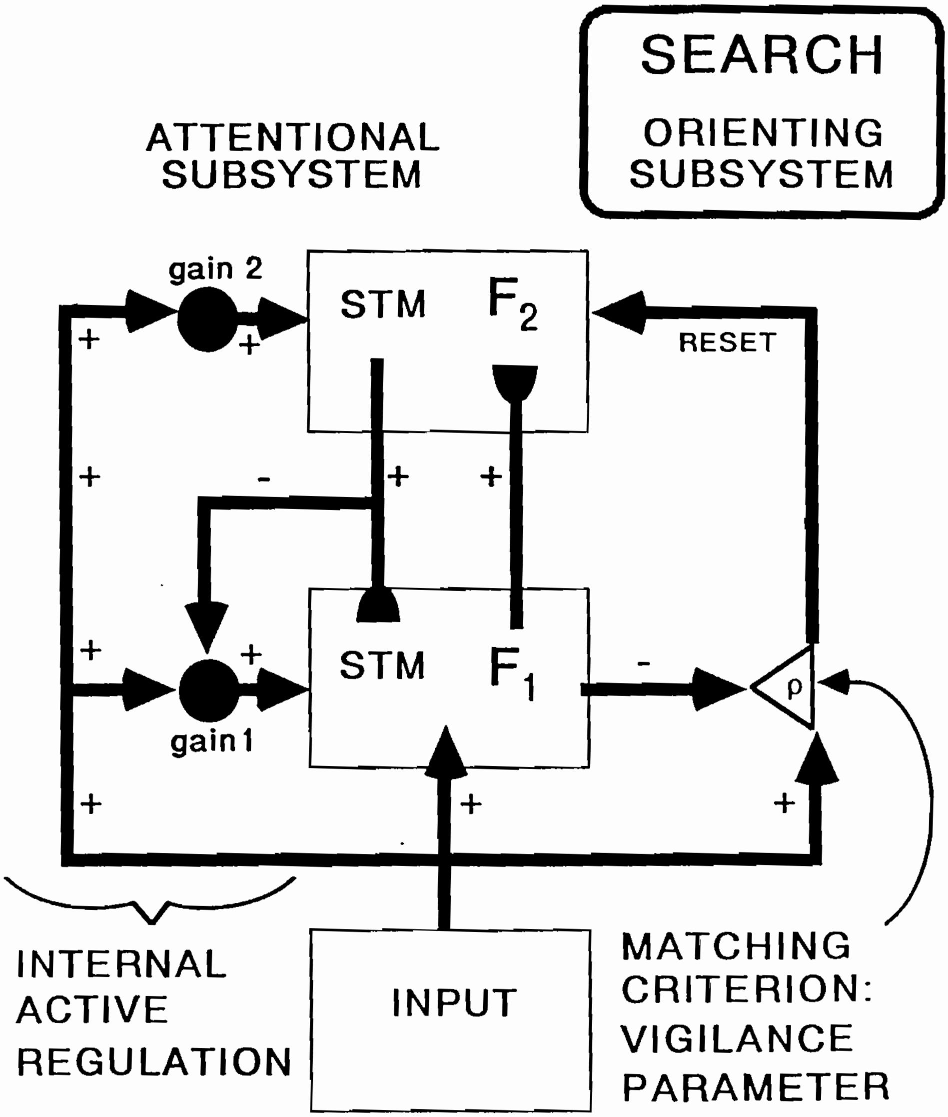


Figure 2: ART 1 system: Two successive stages, F_1 and F_2, of the attentional subsystem encode patterns of activation in short term memory (STM). Bottom-up and top-down adaptive filter pathways between F_1 and F_2 contain trainable long term memory (LTM) traces which multiply the signals in these pathways. The remainder of the circuit modulates these STM and LTM processes. Modulation by gain control enables F_1 to distinguish between bottom-up input patterns and top-down priming, or expectation, patterns, as well as to match these bottom-up and top-down patterns by the 2/3 Rule. Gain control signals also enable F_2 to react supraliminally to signals from F_1 while an input pattern is on. The orienting subsystem generates a reset wave to F_2 when sufficiently large mismatches between bottom-up and top-down patterns occur at F_1. This reset wave selectively and enduringly inhibits previously active F_2 cells until the input is shut off, and triggers a bout of hypothesis testing or memory search for a better F_2 representation. (Reprinted with permission, Carpenter and Grossberg, 1990.)

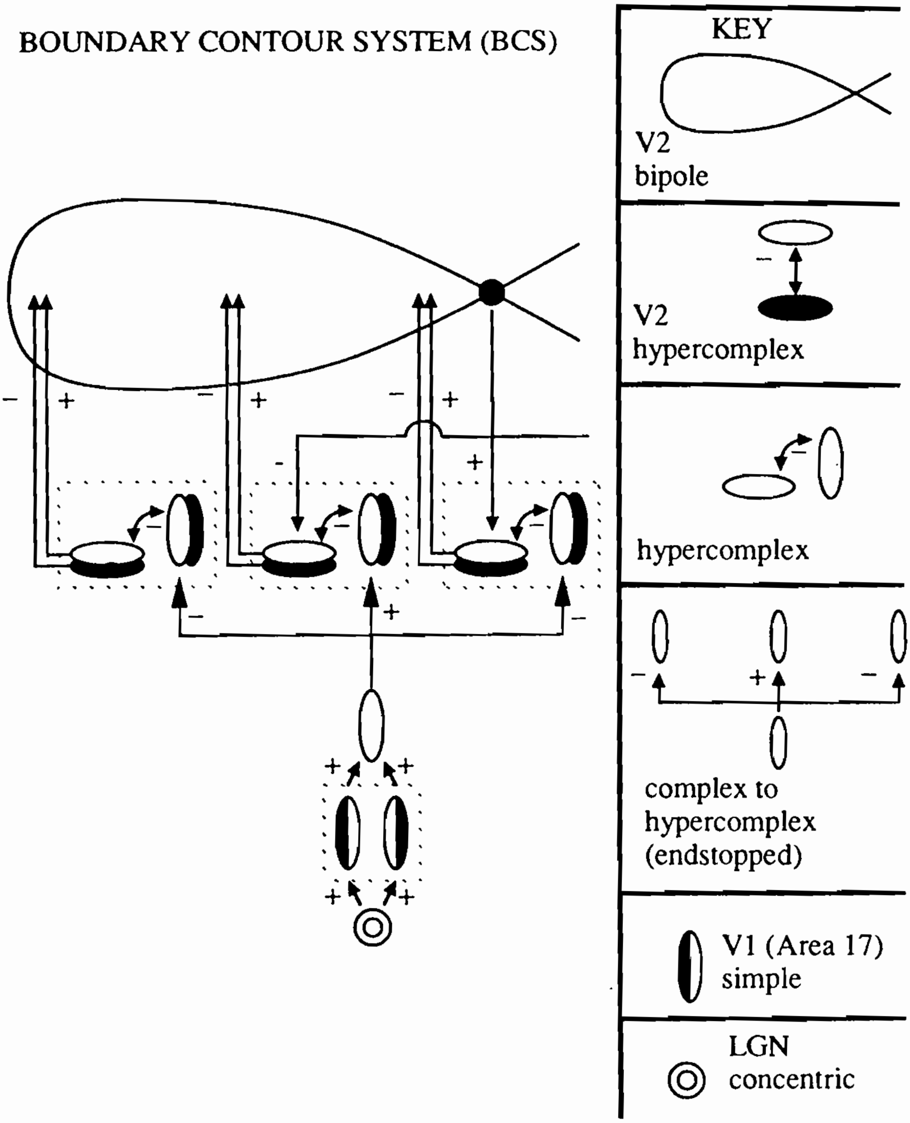


Figure 3. The static Boundary Contour System circuit described by Grossberg and Mingolla (1985a). The circuit is divided into an oriented contrast-sensitive filter (SOC Filter) followed by a cooperative-competitive feedback network (CC Loop). Multiple copies of this circuit are used, each corresponding to a different range of receptive field sizes of the SOC Filter. The depicted circuit has been used to analyse data about monocular vision. A binocular generalization of the circuit has also been described (Grossberg, 1987b; Grossberg and Marshall, 1989).

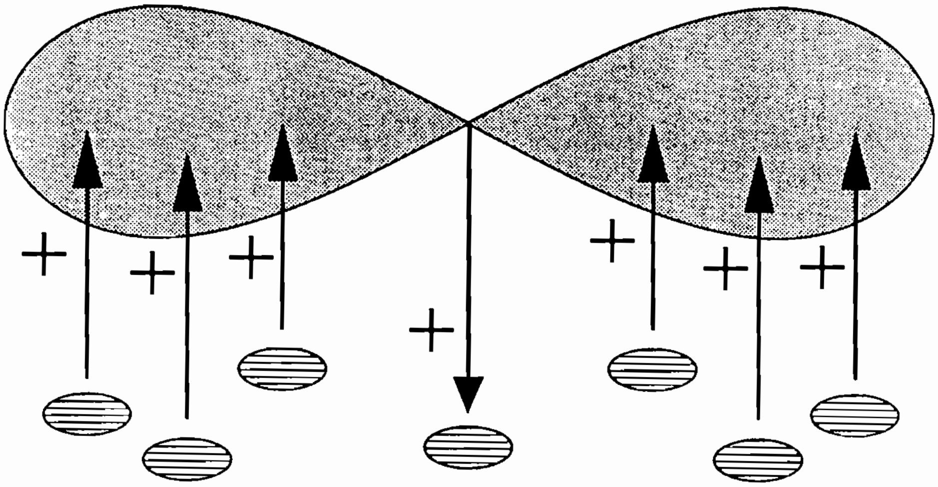


Figure 4. A bipole cell fires only if it is activated by sufficient input of similar orientation and/or direction to both of its receptive fields. It then delivers positive feedback signals to the layers of cells by which it was activated.

tomical evidence from Areas 17 and 18 of the cat. They remarked that "a prominent and stereotypical feature of cortical circuitry in the striate cortex is a plexus of long-range horizontal connections running for 6–8 mm parallel to the cortical surface". Using retrograde labeling, they found that these connections run between cortical columns of similar orientation preferences. Individual cells tended to have long and narrow receptive fields and greater than 90% of the connections appeared to be excitatory. Gilbert and Wiesel noted that while like orientation was necessary to achieve labelling, it was not sufficient. They speculated that there were "subthreshold contextual influences" at work. However, from these labeling techniques they were unable to determine a consistent relation between the orientation of the axis of the axonal fields and the orientation preferences of the columns to which they connected. While such evidence is not conclusive proof of the existence of long-range cooperative bipole cells in visual cortex, it does seem to strongly support the biological plausibility of the bipole mechanism.

The present article demonstrates that both the CC Loop and ART circuits can cooperatively link cells into stimulus-specific standing waves wherein cell activities oscillate in phase with each other. More generally, we show that Cooperative Bipole Coupling, Adaptive Filter Coupling, Nearest Neighbor Coupling, and Random Connection Coupling can all generate synchronous oscillations, but typically not within one or two processing cycles.

Finer differences between the global structure of these oscillations may be used to infer their different functional roles, while also testing predictions of the preattentive BCS theory and the attentive ART theory. In particular, a preattentive BCS resonance is predicted to complete across gaps in two stimulus inducers, as during the Gray *et al* (1989) two bar experiments and the perception of illusory contours (Grossberg and Mingolla, 1985a, 1985b). In contrast, an attentive ART resonance is predicted not to complete across gaps in stimulus inputs. It can "confirm the hypothesis" that input features are present and can bind them into coherent recognition codes, but it does not activate new features that are not already represented in the input data (Carpenter and Grossberg, 1991; Grossberg, 1987c; Grossberg and Stone, 1986). Synchronized oscillations may thus be generated in different parts of the brain by circuits that carry out different functional tasks, such as preattentive vision and attentive visual object recognition. The existence of synchronized oscillations in two different parts of the brain does not, imply that they carry out similar functions. Rather, they are suggested to share a basic computational format for the efficient processing of spatial patterns.

4. Specification of the Model

The source of the 40–60 Hz oscillations that have been reported has yet to be identified. With an average period of 16–25 ms, such oscillations may arise from local network effects, such as a feedback loop between an inhibitory interneuron and an excitatory cell, or the oscillations may be due to single cell membrane effects, such as the influence of a slow channel or second messenger. In the present simulations, we investigated how neural circuits that have already been shown to have strong behavioral and neural predictive value could act to synchronize their cell activations in a stimulus-specific manner.

The starting point for our work is the analysis by Ellias and Grossberg (1975) of oscillations within a neural network of excitatory potentials X_i and inhibitory interneuronal potentials Y_i which obey the equations

$$\frac{d}{dt}X_i = -AX_i + (B - X_i)[\sum_{k=1}^{n} f(X_k)C_{ki} + I_i] - X_i \sum_{k=1}^{n} f(Y_k)D_{ki} \tag{3}$$

and

$$\frac{d}{dt}Y_i = -EY_i + \sum_{k=1}^{n} X_k F_{ki}. \tag{4}$$

Each excitatory potential X_i in (3) obeys a membrane, or shunting, equation (Grossberg, 1973; Rall, 1955a, 1955b, 1956; Sperling and Sondhi, 1968), whereas each inhibitory interneuronal potential Y_i is approximated by an additive equation in (4). In equation (3), parameter A is the passive decay rate, B is the excitatory saturation point, C_{ki} is the excitatory path strength from cell k to cell i, I_i is an external input, and D_{ki} is the inhibitory path strength from cell k to cell i. In (4), parameter E is the passive decay rate, and F_{ki} is the excitatory path strength from cell k to cell i. A case of particular interest is the 2-dimensional E-G network

$$\frac{d}{dt}X = -AX + (B - X)(C[X - \Gamma]^+ + I) - DX[Y - \Gamma]^+ \tag{5}$$

and

$$\frac{dY}{dt} = E(X - Y), \tag{6}$$

where $[w]^+ = \max(w, 0)$, which was shown (Ellias and Grossberg, 1975) to undergo a series of Hopf bifurcations from equilibrium to frequency-dependent oscillations as the arousal level I is parametrically increased. This input-dependent oscillatory behavior is representative of visual cortical neurons that fire repetitively only when stimulated.

The parameters used in the present simulations were chosen as follows: $A = 1$, $B = 1$, $C = 20$, $D = 33.3$, $\Gamma = 0.4$, $E = F = 0.025$. These values were prescribed in Ellias and Grossberg's original work. The choice $E = 0.025$ was made to give the oscillator strong relaxation properties due to the relative time scale differences between the passive decay rates A and E of the excitatory and inhibitory cells. These parameters also produce a desirable "spike-like" waveform. For these parameter choices, the (X, Y) unit in (5) and (6) exhibited stable limit cycle oscillations for inputs between $I = 0.7$ and $I = 2.25$. The present results are consistent with the hypothesis that relaxation oscillators couple more rapidly and more reliably than sinusoidal oscillators for a variety of architectures (Somers and Kopell, 1991).

The simulations reported here utilized a one-dimensional array of 64 (X, Y) units organized, as in Ellias and Grossberg (1975), in a ring to avoid boundary effects. In order to connect these oscillatory units, a cooperative feedback loop among the potentials X_i was implemented. Thus each excitatory-inhibitory unit (X_i, Y_i) in the array obeys the equations:

$$\frac{d}{dt}X_i = -AX_i + (B - X_i)(C[X_i - \Gamma]^+ + \alpha C[Z_i - \Gamma]^+ + I_i) - DX_i[Y_i - \Gamma]^+ \tag{7}$$

and

$$\frac{d}{dt}Y_i = -EY_i + FX_i. \tag{8}$$

In (7), Z_i is the activity of the ith coupling unit. This term will be specified below. Parameter α calibrates the size of the excitatory coupling strength relative to that provided by the self-excitatory term $C[X_i - \Gamma]^+$. In these simulations, α was parametrically increased from 0—the no-coupling case—to test the effects of excitatory interneuronal coupling on the coherence of the oscillations.

5. Cooperative Coupling Mechanisms

Several coupling architectures were investigated; namely, Cooperative Bipole Coupling, Adaptive Filter Coupling, Nearest Neighbor Coupling, and Random Connectivity Coupling (Figure 5). This analysis illustrates the robust nature of the synchrony phenomenon. Each coupling unit Z_i could be interpreted biologically as either the output signal from the dendritic tree of an X_i cell, or as another cell that sends an excitatory connection to the X_i cell. For example, the Cooperative Bipole Coupling (Figure 5a) could be interpreted as a bipolar dendritic tree in which both compartments must be sufficiently activated to provide input to the X_i cell. Alternately, this coupling unit could be interpreted as a distant cell, perhaps lying in Area 18 (Grossberg and Mingolla, 1985a; von der Heydt, Peterhans, and Baumgartner, 1984), having the same dendritic properties and making a monosynaptic connection with the X_i cell. The coupling units are made explicit in the following equations:

Cooperative Bipole Coupling

$$Z_i = \left[\frac{P(\text{Right}_i)^n}{Q^n + (\text{Right}_i)^n} + \frac{P(\text{Left}_i)^n}{Q^n + (\text{Left}_i)^n} - \Gamma_{cpl}\right]^+ \tag{9}$$

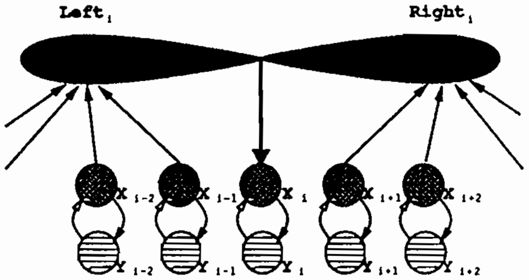
where

$$\text{Right}_i = \frac{1}{\text{width}} \sum_{j=1}^{\text{width}} [X_{i+j} - \Gamma]^+ \tag{10}$$

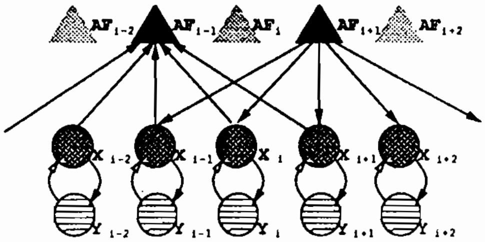
and

$$\text{Left}_i = \frac{1}{\text{width}} \sum_{j=-1}^{-\text{width}} [X_{i+j} - \Gamma]^+. \tag{11}$$

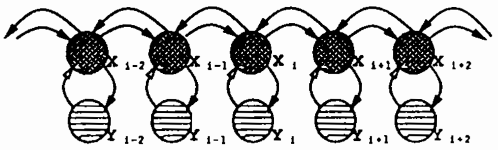
Parameters P,Q, and n in (9) characterize a sigmoidal, or S-shaped, response curve that indicates a typical nonlinear summation within each cell compartment (Grossberg, 1973, 1982b; Rall, 1955a, 1955b, 1956). For these simulations, the values $P = 1$, $Q = 0.10$, and $n = 5$ were chosen. Parameter Γ_{cpl} is the coupling threshold. The choice $\Gamma_{cpl} = P$ was made in order to guarantee that both compartments or flanks needed to be sufficiently activated



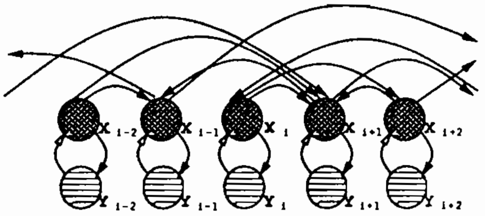
A) BIPOLE COUPLING



B) ADAPTIVE FILTER COUPLING



C) NEAREST NEIGHBOR COUPLING



D) RANDOM COUPLING

Figure 5: Coupling architectures. Figures A–D show the connectivities characteristic of the four coupling architectures implemented in the simulations. Each (X, Y) pair represents a single oscillator and the lines indicate typical connections. In (A) the bowtie-shaped symbol represents a single bipole cell. Coupling inputs from the right of oscillator i feed exclusively into the right half of the bipole. Coupling inputs from the left feed exclusively into the left half of the bipole. The two halves of the bipole are combined and the rectified, thresholded coupling signal that results feeds to oscillator i. There is a single bipole cell corresponding to each (X, Y) oscillator pair. In (B) the triangle-shaped symbols represent adaptive filter (AF) elements. Each adaptive filter element may receive coupling input from many oscillator units, and in turn may feed coupling output back to many oscillator units. In these simulations there are as many adaptive filter elements as there are oscillator units. In (C) each oscillator unit is connected reciprocally and equally with its immediate neighbor on either side and with no other oscillator units. In (D) each oscillator is connected with a fixed number of randomly chosen oscillators. All oscillators send out the same number of coupling outputs, but typically receive different numbers of coupling inputs. The filled arrowheads indicate excitatory connections, while unfilled arrowheads indicate inhibitory connections. The only inhibitory connections are from the Y cells to the X cells.

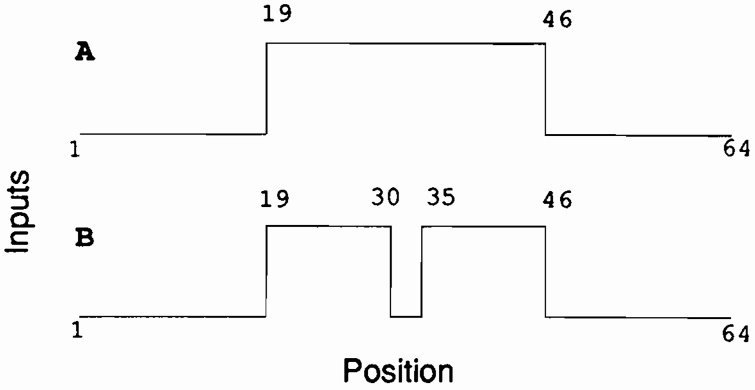


Figure 6: Single bar and double bar system inputs. Simulations were run on two different input images: a single, long bar (A); or two short bars separated by a slit (B). The values of I_i are displayed for each position i along the 64-position ring. Each high value ($I_i = 1.0$) represents a position on a bar in the image and is sufficient to drive an uncoupled (X, Y) pair into its oscillatory regime. Each low value $I_i = 0.05$ represents part of the background of the image and is not sufficient to drive oscillations in an uncoupled (X, Y) pair; rather, an equilibrium value is approached. Within the course of a simulation run, all input values were constant and did not themselves oscillate.

before Z_i could be activated, and thus before coupling feedback from Z_i to X_i could be generated. The width of the flanks was parametrically varied in the simulations.

Adaptive Filter Coupling

$$Z_i = \left[\frac{1}{\text{fan out}} \sum_{j=-\text{fan out}/2}^{+\text{fan out}/2} AF_{i+j} - \Gamma_{cpl}\right]^+ \tag{12}$$

where

$$AF_i = \frac{1}{\text{fan in}} \sum_{j=-\text{fan in}/2}^{+\text{fan in}/2} [X_{i+j} - \Gamma]^+. \tag{13}$$

The Adaptive Filter coupling (Figure 5b) assumes that many inputs fan-in, bottom-up, to each coupling compartment AF_i, and that these AF_i's fan-out, top-down, to many compartments Z_i. In the general case (fan in > 1, fan out > 1), this coupling can be realized, for example, by letting each Z_i collect signals in the excitatory dendritic tree that feeds X_i. In the case fan out = 1, AF_i and Z_i may be collapsed into the same dendritic structure, and it is not necessary to postulate intervening cells.

Nearest Neighbor Coupling

$$Z_i = 1/2[X_{i-1} - \Gamma]^+ + 1/2[X_{i+1} - \Gamma]^+ \tag{14}$$

Nearest Neighbor coupling (Figure 5c) is defined by excitatory signalling between each cell and its two immediate neighbors.

Random Connection Coupling

$$Z_i = \left[\frac{1}{\text{num conn}} \sum_{\text{random } j}^{\text{num conn}} [X_{i+j} - \Gamma]^+ - \Gamma_{cpl}\right]^+. \tag{15}$$

Random coupling (Figure 5d) sums the active inputs of a number of random connections. If the total input is sufficiently great, an excitatory signal to X_i is activated. Note that while the coupling is chosen randomly, the same random connections remain in effect throughout the course of a simulation run.

6. Methods

The typical paradigm for the simulations is as follows. At the start of each simulation, the (X, Y) units were given random initial conditions and the coupling variables Z were set equal to zero. The test stimuli were either long single bar images or short disconnected double bar images (Figure 6). For the single bar stimulus, the central region ($i = 19$ to $i = 46$) was set to the target value. The double bar stimulus differed in that a central slit region ($i = 31$ to $i = 34$) was set to the background value. Input array positions corresponding to part of a bar were given values sufficient to generate stable limit cycle oscillations in an uncoupled unit [equations (5) and (6)]. At positions not on a bar, the input value was insufficient to sustain oscillations in its unit. For a given simulation run, the inputs and parameters were chosen and held fixed. Within a series of runs, a parameter or pair of parameters, such as the synaptic coupling strength α and/or the widths of coupling interaction, were varied in order to determine their effects.

7. Results

The primary control experiment for these simulations is the uncoupled ($\alpha = 0$) case. In the uncoupled case, units receiving sufficient input exhibit stable limit-cycle oscillations, while units receiving insufficient input quickly approach a low equilibrium value (Figures 7 and 8). Since the initial values were chosen randomly, the units oscillated in random phase with respect to one another. If all ON inputs were the same, these phase relationships did not change over the time course of the simulation, since their frequencies were the same.

Using the Cooperative Bipole Coupling Architecture in (9)–(11), coherent oscillations emerged rapidly (approximately one cycle or less) for both the one bar (Figure 9) and two bar (Figure 10) stimuli. In the two bar case, oscillations were induced in the slit between the two bars and these oscillators could be almost instantly synchronized with the others. In both stimulus cases, the bipole architectures did not induce a spreading of oscillatory activity to the outer regions beyond the stimuli. Inward boundary completion without outward spreading of oscillatory activity was found to be a robust property of bipole coupling.

Adaptive Filter coupling also yielded rapid synchronization for single bar stimuli (Figure 11). As shown in Figure 12, the disconnected regions that were activated by a double bar stimulus were synchronized with respect to each other. This is a robust property of adaptive filter coupling. If the fan-in and fan-out are chosen broadly enough to include only one bar, then the cellular units corresponding to that bar become synchronized. If the fan-in and fan-out are chosen broadly enough to also include the region spanned by both bars, then units corresponding to both bars are synchronized. Depending upon cell parameters, the intervening units may undergo synchronized subthreshold or suprathreshold oscillations. There is also a strong tendency for cells flanking the exteriors of the bars to undergo analogous oscillations.

Nearest neighbor coupling and random coupling could also cause synchronized oscillations to emerge, although this synchrony did not occur as rapidly, nor for as robust a set of initial conditions, as it did for the bipole and adaptive filter architectures. See Grossberg and Somers (1991) for examples of these oscillations.

Figures 8 and 10 together with Figures 13 and 14 present two different perspectives of the synchronized behavior for double bar stimulus, using the bipole architecture. Figures 8 and

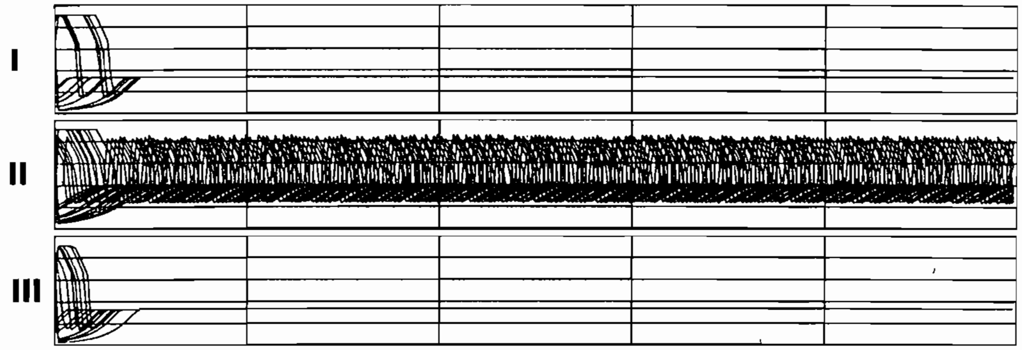


Figure 7: Uncoupled ($\alpha = 0$) case for single bar input. Three windows are displayed in which plots of X_i versus time are overlayed. In window I, positions $i = 1$ thru $i = 18$ are overlayed. In window II, positions $i = 19$ thru $i = 46$ are plotted. Positions $i = 47$ thru $i = 64$ are shown in window III. The positions displayed in windows I and III correspond to the image background, while window II displays activity of X_i along the bar. In this uncoupled case, the activities at positions corresponding to the background quickly approach the same steady-state value, while positions along the bar oscillate in random phase. This uncoupled case represents the control simulation for single bar input.

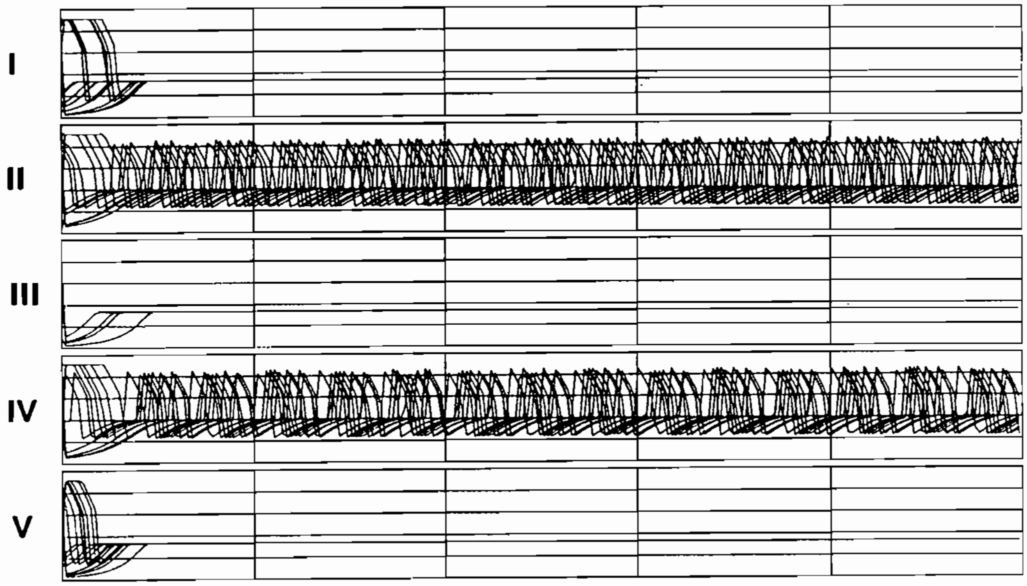


Figure 8: Uncoupled ($\alpha = 0$) case for double bar input. Five windows are displayed in which plots of X_i versus time are overlayed. In window I, positions $i = 1$ thru $i = 18$ are overlayed, while in window II, positions $i = 19$ thru $i = 30$ are plotted. Windows III and IV display positions $i = 31$ thru $i = 34$ and $i = 35$ thru $i = 46$, respectively, and positions $i = 47$ thru $i = 64$ are shown in window V. The positions displayed in windows I and V correspond to the image background, while window III displays activity in the slit between the two bars. Windows II and IV display activity of X_i along the left and right bars respectively. In this uncoupled case, the activities at positions corresponding to the background and the slit quickly approach the same steady-state value, while the activities at positions along both bars oscillate in random phase. This uncoupled case represents the control simulation for double bar input.

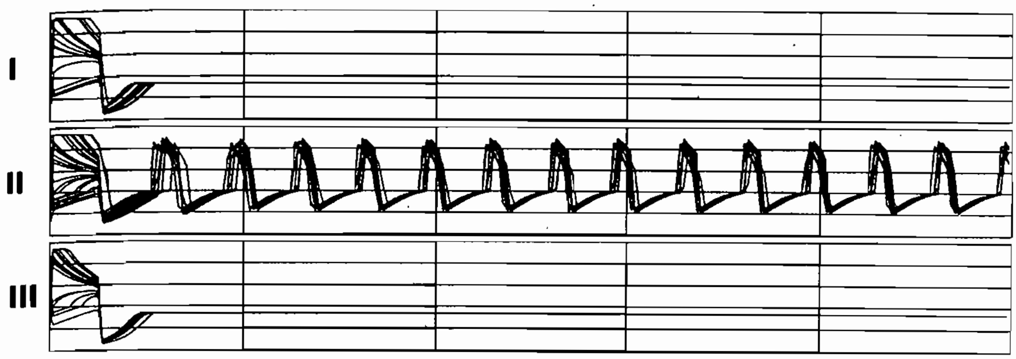


Figure 9: Bipole coupling for single bar input. Using the same inputs and initial conditions which were used to generate Figure 7, bipole coupling with $\alpha = 0.25$ yielded rapid and sustained synchronization of oscillatory activity at positions along the bar without inducing oscillatory activity at positions corresponding to the background. Each bipole flank received input from six neighboring positions (width = 6).

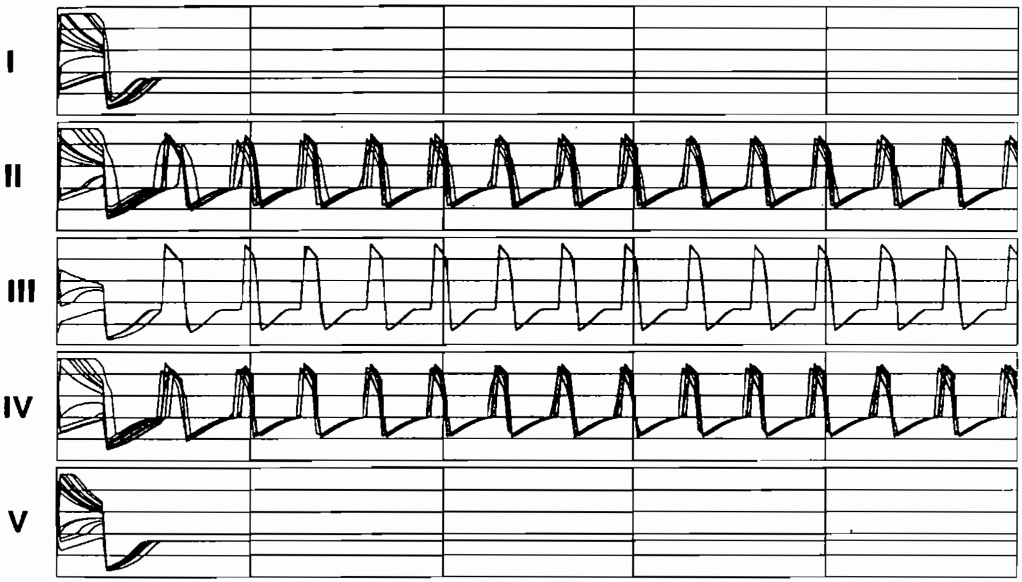


Figure 10: Bipole coupling for double bar input. Using the same inputs and initial conditions which were used to generate Figure 8, bipole coupling with $\alpha = 0.25$ yielded rapid and sustained synchronization of oscillatory activity at positions along both bars and induced synchronous oscillatory activity at the slit positions $i = 31$ thru $i = 34$ but did not induce oscillatory activity at positions corresponding to the outer background regions. This may be interpretted as the completion of a disconnected image boundary, resulting in the perception of a single long bar. Each bipole flank received input from six neighboring positions (width=6).

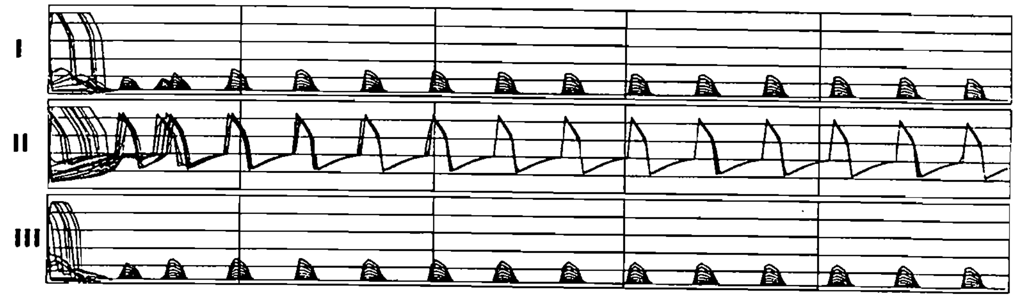


Figure 11: Adaptive filter coupling for single bar input. Shown here with $\alpha = 0.10$ and fan-in and fan-out widths of 9, adaptive filter coupling yielded rapid synchronization of oscillatory activity along the bar. While some small oscillatory activity was induced at background positions, this activity was well below the firing threshold of 0.4. The inputs and initial conditions were identical to those used in generating Figure 7.

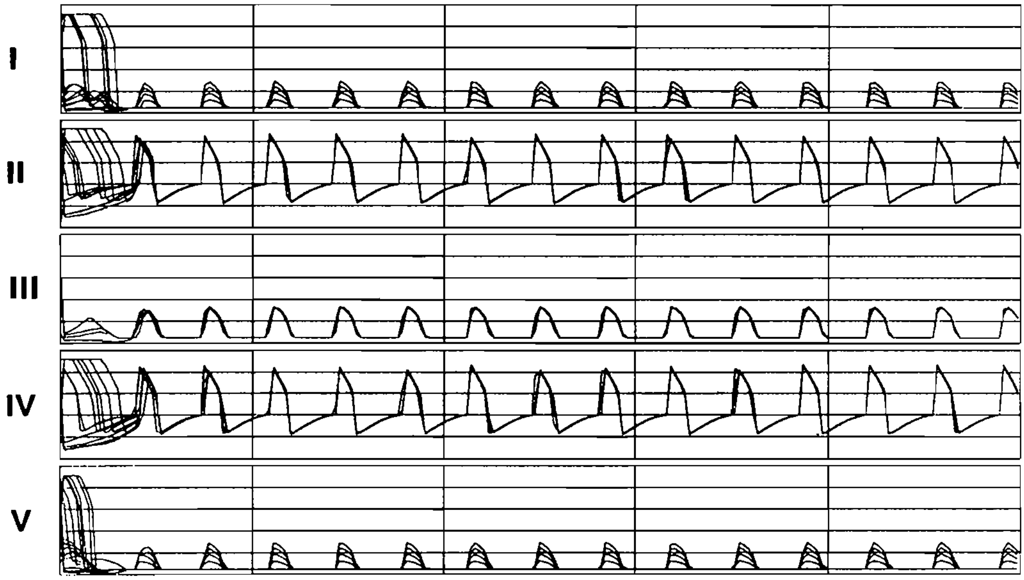


Figure 12: Adaptive filter coupling for double bar input. Shown here with $\alpha = 0.10$ and fan-in and fan-out widths of 9, adaptive filter coupling yielded rapid synchronization of oscillatory activity along each bar and synchronized the bars with respect to each other. While some small oscillatory activity was induced at background positions and in the slit, this activity was subthreshold. The inputs and initial conditions were identical to those used in generating Figure 8.

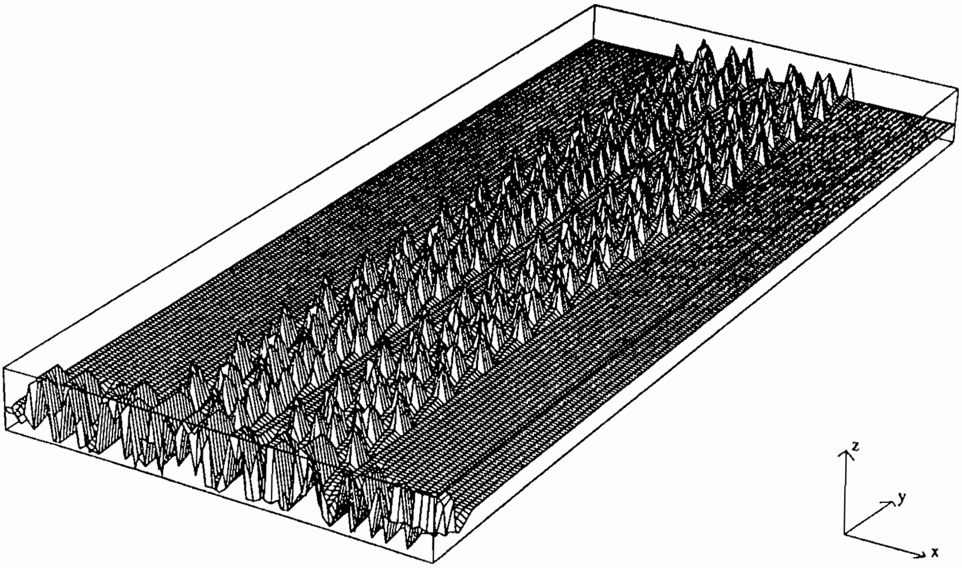


Figure 13: 3-D perspective of uncoupled case for double bar input. The data of Figure 8 is replotted in three dimensions in order to demonstrate the positional structure of the activity. The X-axis represents the position, i, of the $X - Y$ unit; the Y-axis represents time; and the Z-axis represents the activity, X_i. This perspective more clearly displays two regions of incoherent oscillatory activity separated by a slit of region that quickly approaches equilibrium. The larger background regions to the outsides also quickly approach equilibrium from their random initial conditions.

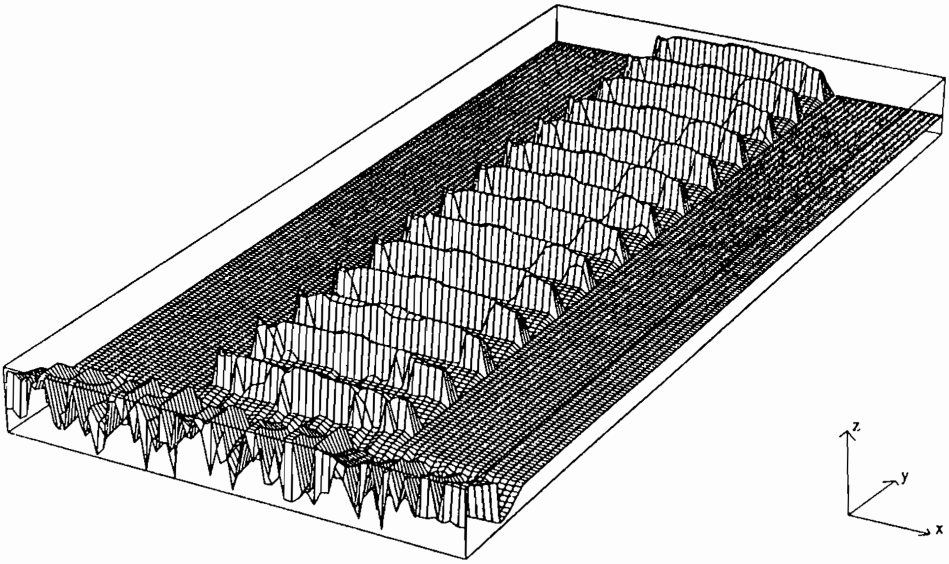


Figure 14: 3-D perspective of bipole coupling for double bar input. By implementing bipole coupling for the inputs and initial conditions shown in Figure 13, two nearby regions of incoherent oscillatory activity are very rapidly synchronized and oscillations are induced in the slit region and these oscillations very rapidly synchronize with the bar regions. This represents a successful boundary completion between the bars which results in a single coherent contour of oscillatory activity that does not spread to the outer background positions. The data plotted is the same that is shown in the overlay plots of Figure 10.

13 display the uncoupled ($\alpha = 0$) case and Figures 10 and 14 display the tight synchrony ($\alpha = 0.25$) of the bipole coupling. Not only are the two bars synchronized, but also synchronized oscillations were induced in the slit region between the two bars, indicating that a subjective contour was generated across the slit and that the features were linked across the "occluding" region, as was also ascribed to bipole cells in the equilibrium point version of the BCS (Grossberg and Mingolla, 1985a, 1985b). A quantitative measure of oscillator coherence as a function of the coupling parameter α in (7) is described in Grossberg and Somers (1991).

8. Discussion

The present results indicate that a wide variety of nonlinear cooperative feedback networks, whose cell units obey shunting or additive equations, can undergo synchronous oscillations if their coupling strength is sufficiently high, and if at least one slow variable, here a slow inhibitory interneuron, exists. These synchronous oscillations can, for example, support a preattentive boundary completion process, as occurs during visual boundary segmentation; an attentive resonant state, as occurs during visual object recognition; and either preattentive or attentive adaptive filtering operations during more general processes of cortical feature detection and short term memory representation.

These results illustrate how the brain may overcome the temporal "jitter" inherent in multi-level processing of spatially distributed data. Such compensatory processing enables mechanisms of short term memory and long term memory to process the coherent spatial patterns of spatially distributed features that are used to represent the events with which we deal in the external world.

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