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Reentrant signaling among simulated neuronal groups leads to coherency in their oscillatory activity

(visual cortex/orientation columns/neuronal oscillations/cross-correlations/neural networks)

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ABSTRACT **Recent experiments have revealed tightly synchronized oscillatory discharges in local assemblies of cortical neurons as well as phase coherency of oscillations at distant cortical sites. These findings are consistent with the theory of neuronal group selection, a population theory of brain function that is based on the properties of local groups of neurons. A set of computer simulations shows that cooperative interactions within and among neuronal groups can generate the observed phenomena. In the simulations, oscillations within neuronal groups are generated through local excitatory and inhibitory interactions. Different groups in general oscillate in an uncorrelated fashion. Coherency of the oscillatory activity of different neuronal groups depends crucially on reciprocal reentrant signaling and can reflect the spatial continuity of a stimulus. Separated or discontinuous features of a given stimulus can be transiently associated in a temporally coherent pattern through reentrant signaling between groups in networks responding to different aspects of that stimulus. A simulation of reentrant activity between arrays of neuronal groups selective for oriented lines and pattern motion displays cross-correlations between groups that are responsive to different parts of a stimulus contour if these parts move together. Such coherency among neuronal groups might be used in the discrimination of a stimulus from other stationary or differentially moving elements in a visual scene.**

The theory of neuronal group selection (1, 2) proposes that the basic functional unit of cortical processes is the neuronal group, a local collective of strongly interconnected neurons. The borders between groups as well as the receptive field properties of their constituent cells are a function of local neuroanatomy but can change dynamically under varying input conditions (3, 4). Groups compete with each other for the incorporation of additional cells, some only during a sensitive or critical period, others throughout the adult life of the organism. The cooperative effects resulting from local excitatory interactions between neurons in a group lead to a tendency for temporally correlated, synchronous firing. Indeed, groups are stabilized against competitive influences by such firing (4). Neurons belonging to different groups in general show asynchronous and uncorrelated firing.

Signaling between neuronal groups occurs via excitatory connections that link cortical areas, usually in a reciprocal fashion (5, 6). According to the theory of neuronal group selection, selective dynamical links are formed between distant neuronal groups via reciprocal connections in a process called "reentry." Reentrant signaling establishes correlations between cortical maps, within or between different levels of the nervous system. It is more general than feedback in both connectivity and function in that it is not simply used for error correction or cybernetic control in the classical sense. Instead, reentrant interactions among multiple neuronal maps can give rise to new properties. Indeed, a recent computer model simulating reentry in visual cortex demonstrates that such interactions might serve as bases for complex visual illusions (7) achieving figural synthesis by recursion while competitively resolving conflicts between segregated cortical areas. This reentrant cortical integration model emphasized the reentrant circuits themselves and for economy represented groups as single units with fixed properties rather than as actual populations. It is the aim of the present study to investigate further the mechanism of reentrant cortical integration by making explicit use of the population properties of neuronal groups. At the same time, we wish to relate our analysis to results of recent experiments on visual cortex (8–10) indicative of group behavior.

Gray and Singer (8, 9) have observed oscillatory neural activity within orientation columns in cat visual cortex. Appropriate stimulation produced rhythmic, temporally correlated discharges in areas 17 and 18 in adult cats and kittens, awake or under varying conditions of anesthesia. In many cases, it was found that multiunit activity as well as local field potentials oscillate at a frequency of about 40 Hz when a light bar of optimal orientation, velocity, and direction of movement is passed through the receptive field of one of the recorded neurons. Oscillatory activity decreased in the absence of a stimulus or during presentation of a light bar at other than the optimal orientation. Recordings from the lateral geniculate nucleus (LGN) showed no evidence of oscillations within the frequency range of 20–70 Hz. Gray and Singer concluded that the observed cortical oscillations are generated by local excitation and recurrent inhibition within the cortex. As previously predicted (1), these results show "that groups of adjacent cortical neurons, when activated appropriately, engage in cooperative interactions" (ref. 8, p. 1702).

Cross-correlation of multiunit recordings from spatially separate sites in area 17 revealed that oscillatory responses in orientation columns with similar specificity but with nonoverlapping receptive fields are synchronized if a single long light bar is moved across both receptive fields (9). This synchronization of oscillatory activity in remote columns may be mediated by intracortical, cross-columnar connections or by long projections from other cortical areas. An independent study (10) confirmed intracolumnar correlations and correlations between neighboring hypercolumns; in addition, synchronization of oscillatory activity was observed between different cortical areas. During the presentation of an appropriately oriented light bar, coherent and oscillatory local field potentials appeared in columns both in area 17 and area 18. These reports (9, 10) not only prompt the idea that the observed temporal correlations between spatially separate cortical sites in response to linked stimulus features may be of importance in the transient association of such features

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Abbreviations: LGN, lateral geniculate nucleus; OR, orientation network; MO, motion network; AAF, average activity function.

but also provide evidence for the existence of neuronal groups and are suggestive of the role of reentry in correlating the behavior of different groups.

To demonstrate the consistency of these observations with the theoretical concept of reentry, we present here a simplified computer model of groups in two interconnected visual areas. Models that generate oscillatory phenomena have previously been proposed (11, 12) but are not based on local populations of neurons and do not deal with their interactions and coherent behavior. The model described here lends support to the theory of neuronal group selection by generating phenomena similar to those observed (8–10) without the addition of special assumptions.

DESCRIPTION OF THE MODEL

The model is implemented using the Cortical Network Simulator program (for details see ref. 13), and run on an IBM 3090 at the Cornell National Supercomputer Facility. Full-scale simulations of 25,600 cells and over 3.5 million connections required up to 5 hr for 9,000 iterations (cycles). The model consists of two separate visual areas (Fig. 1): "OR" which contains 32 orientation- and direction-selective neuronal groups consisting of 200 excitatory and 120 inhibitory units; and "MO" which contains 64 pattern-motion-selective neuronal groups consisting of 160 excitatory and 80 inhibitory units. Each unit corresponds to a single neuron. Unit activity is calculated as

$$s_i(t) = (\sum_j c_{ij}s_j)\phi(D) + N + \omega s_i(t-1), \qquad [1]$$

with s_i, s_j = states of units i, j; t = time (in cycles); c_{ij} = connection strength from unit j to unit i ($-1 \leq c_{ij} \leq 1$); j = index over individual afferent connections; $D = \upsilon_D s_i(t-1) + \omega_D D(t-1)$ = depression term, υ_D = growth coefficient for D, ω_D = decay coefficient for D, $\phi(D) = 0$ for ρ cycles (refractory period) when $D > \theta_D$ (refractory threshold), $\phi(D) = 1 - 2D^2 + D^4$ otherwise; N = gaussian noise; and ω = decay coefficient. All units are updated synchronously and without time delay. After maximal activation, the individual units enter a refractory period ($\rho = 2$) during which firing of the unit is not possible (depression parameters: $\theta_D = 0.8$, $\upsilon_D = 0.3$, $\omega_D = 0.25$). This prevents prolonged bursting of individual units.

Simulated neuronal activity is evaluated by computing auto- and cross-correlation functions of both single units and entire neuronal groups during stationary firing periods. Continuous $s_i(t)$ values for single units were subjected to a threshold condition (if $s_i > 0.875$, then s_i set to 1, otherwise

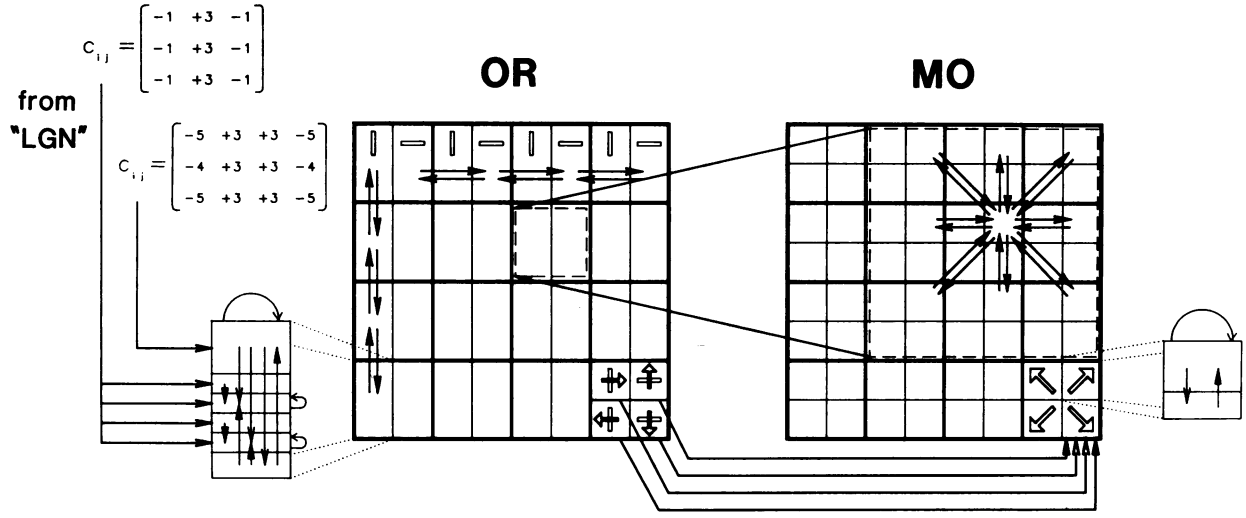

FIG. 1. Schematic overview of the model showing the visual areas OR and MO with their response selectivities and the reentrant connections between them that give rise to coherent oscillations. Units in OR, which is the primary visual area in the model, respond preferentially to oriented line segments. Units in MO, a higher area receiving input from OR, respond with large receptive fields to overall motions of contours. Repertoires OR and MO (large squares) are divided into arrays of groups (delineated by grid lines). Each group in OR contains units responding to stationary oriented bars (indicated by small open rectangles across the top of OR) and units responding to moving bars (open rectangles with arrows at the lower right of OR). Groups in OR are arranged in vertical stripes; all the units in each stripe respond to bars with the same orientation (rectangle at the top of the stripe). Pairs of groups encompassing both orientation preferences form clusters (enclosed in heavier grid lines; OR contains 16 such clusters in a 4 × 4 array). OR receives topographically mapped input from the simulated LGN (not shown). The inset at the lower left is a more detailed view of one OR group. Each such group contains six kinds of units (separated by horizontal lines). In order from top to bottom, these are: 160 excitatory orientation-selective neurons, two sets of 20 direction-selective neurons with 20 associated inhibitory interneurons, and 80 inhibitory neurons. Connections are indicated by arrows: connections within a group in the *Inset* and those between groups in the main diagram (open arrowheads represent excitatory connections and filled arrowheads represent inhibitory connections). Orientation-selective units receive 12 connections from the "LGN", and direction-selective units receive 9 such connections (arrows entering inset at far left). These connections arborize over arrays of 4 × 3 and 3 × 3 "LGN" cells, respectively. The strengths of these connections (c_{ij} in Eq. 1) determine the orientation selectivities of the units; sample c_{ij} matrices for units that respond to vertically oriented bars are shown. Each unit receives additional connections from units in its own group in the same (curved arrows at edges of the inset) or different (vertical arrows within the inset) layers. There are also 32 weak excitatory connections between orientation-selective units of the same orientation specificity in neighboring groups (vertical and horizontal pairs of arrows in the main OR diagram). Groups in MO respond to motion in one of four oblique directions (open arrows at the lower right of MO). Groups with all four directional specificities form clusters (as with OR, there are 16 such clusters forming a 4 × 4 array). Each MO group contains two layers of units (see lower right *Inset*): 160 excitatory (top) and 80 inhibitory units (bottom). Three sets of connections join units within a group (arrows at the top edge and within the *Inset*). In addition, excitatory MO units receive 16 connections from neighboring units in each of eight directions (pairs of arrows at the upper right of MO). Long-range reentrant connections are indicated by arrows between OR and MO. Each orientation-selective unit in OR receives 32 excitatory connections from motion-selective units in MO, and each unit in MO receives 32 excitatory connections from units in OR selective for two different directions of motion whose vector sum corresponds to the directional preference of the MO unit. In addition, MO units receive 32 inhibitory connections from the remaining two directions of motion in OR (an example is shown on the lower right of the OR and MO areas). Reentrant projections in both directions are divergent, each group projecting to a 3 × 3 area in the target network. The total number of connections per group is 14,040 within OR, 23,120 within MO, 5,120 reentrant from MO to OR, and 20,480 reentrant from OR to MO.

s_i set to 0) to obtain discrete spikes. An average activity function (AAF) is computed as the sum of s_i over all units within a group that are active (s_i = 1) at a given time and serves as an analogue for the local field potential (8).

A simulated visual stimulus (such as an oriented light bar) in the input array (model retina) activates a network (referred to as "LGN") containing ON-center units (modeled as single neurons) analogous to those in the LGN. Input to OR is provided by an anatomically ordered topographical projection from the "LGN". The preferred stimulus of an orientation-selective unit is a stationary or moving oriented bar; the angle depends on the pattern of input from the "LGN". Each group in OR contains 160 orientation-selective units that receive inputs from randomly chosen but overlapping positions in the "LGN". Units within a group are coupled by sparse local excitatory and inhibitory connections, in a pattern that is based on observed anatomical and functional interactions among cortical neurons (14, 15). Adjacent groups with the same orientation specificity are reciprocally interconnected.

Units selective for the direction of movement of an oriented bar also receive anatomically ordered inputs from the "LGN". In every group of direction-selective units, there is a subpopulation of inhibitory units that stay active for some time after activation (ω = 0.99). They provide time-delayed inputs to the direction-selective units, which fire only in response to a concurrence of movement in their preferred direction *and* appropriate input from the orientation-selective layer. The direction-selective units in OR project to MO, which contains groups of units (very similar to those in the orientation network) that are selective for pattern motion (16, 17). Pattern motion of a complex contour in general differs from the direction of movement of local parts of the contour (component motion). In the model, pattern-motion selectivity is generated by combining two excitatory inputs from different directions of motion and two inhibitory inputs from the opposite directions (see also ref. 7). For simplicity, the model is not sensitive to line orientations other than horizontal and vertical or pattern motion other than in the four oblique directions. None of our conclusions is dependent on this simplification. The pattern-motion-selective groups, reentrantly coupled among themselves, signal back to the orientation-selective groups. These signals are usually below firing threshold. The projections between orientation and motion networks are divergent in both directions, such that the receptive fields of motion-selective units are large and back-projections to OR influence activity in a large part of that network. The response properties of orientation-, direction-, and motion-selective units are partially determined by their intragroup connections and thus do not depend solely on the pattern of anatomical input from the "LGN".

RESULTS

We describe first the behavior of only the orientation-selective units of OR in response to stimulation with a moving oriented bar. Presentation of the stimulus results in nonoscillatory activity of ON-center units in the "LGN" network and in oscillatory activity in neuronal groups in OR. Oscillations are generated by activity of relatively sparse local excitatory and inhibitory connections and occur independently of intergroup coupling. Entry of excitatory cells into a refractory period after strong firing contributes to (but is not sufficient for) the oscillatory activity of the network. Oscillatory behavior of this kind is a population phenomenon and does not require inherent oscillatory properties of individual neurons (18). Most units seem to discharge fairly irregularly (Fig. 2*A Upper*), although subthreshold oscillations of unit activity are more robust. The AAF of a neuronal group exhibits clear rhythmicity (Fig. 2*A Lower*). Auto- and cross-correlation functions for single units show statistically significant oscillations (Fig. 2*B*) at levels comparable to those experimentally observed (8). That oscillations are not due to some hidden periodicity in the stimulation is indicated by the flat "shifted" autocorrelation function (Fig. 2*B Bottom*).

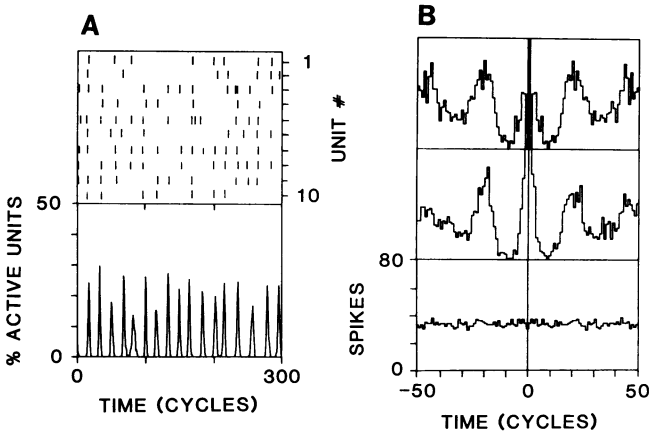

FIG. 2. (*A*) Single unit activity (*Upper*) and average activity function (AAF) (*Lower*) of orientation-selective units in OR responding to a simulated light bar in preferred orientation moving through the unit's receptive field. Ten different orientation-selective units within the same group are recorded simultaneously (*Upper*) and their activity is compared to the AAF of that group (*Lower*). Note that few single units appear to discharge at regular intervals, making identification of oscillatory behavior without the use of statistical techniques difficult. (*B*) Autocorrelation, cross-correlation, and shifted autocorrelation (from top to bottom, respectively) for single-spike data (as in *A*, responses are accumulated for 10 trials). The autocorrelation shows a characteristic oscillatory waveform. Cross-correlation is between two simultaneously recorded units within the same group and also shows an oscillatory waveform. "Shifted" autocorrelation is averaged over all nine possible shifts; flatness indicates that correlations are not due to stimulus-induced effects.

Interactions through reciprocal, excitatory connections between adjacent groups of the same specificity in OR give rise to coherent oscillations in neighboring as well as distant groups with a near zero phase lag, as is evident from cross-correlation functions of single unit activity (Fig. 3). In the model as well as in the experiment (9), correlations are found between units in groups that have nonoverlapping receptive fields if a long, continuous moving bar is presented. If two colinear short bars are moved separately but with the same velocity, these distant correlations disappear. In the model, local reentrant connections are only present between adjacent groups in OR, thus directly linking only groups that have overlapping receptive fields. If connections are added between more distant groups, their mutual interaction and correlation in response to a spatially continuous stimulus is stronger but still decreases or disappears if a spatially discontinuous stimulus is presented. Given the limited extent of cross-columnar connections (19), it is unclear whether the experimentally observed correlations over 7 mm of cortex (9) require direct coupling; the model demonstrates that it is possible for correlations to be generated via multiple and even indirect paths.

These observations show that oscillatory activity, correlated activity in groups, and stimulus-driven cross-correlations can be modeled. However, the key point of this paper is to present an example of the constructive properties of reentry among maps based on the population properties of neuronal groups. The ability of reentry to create coherency between groups in different segregated areas was studied in simulations of OR and MO responding to moving contours (Fig. 4). When a moving stimulus such as the corner of an object is presented, orientation- as well as motion-selective groups exhibit oscillatory activity, roughly within the same

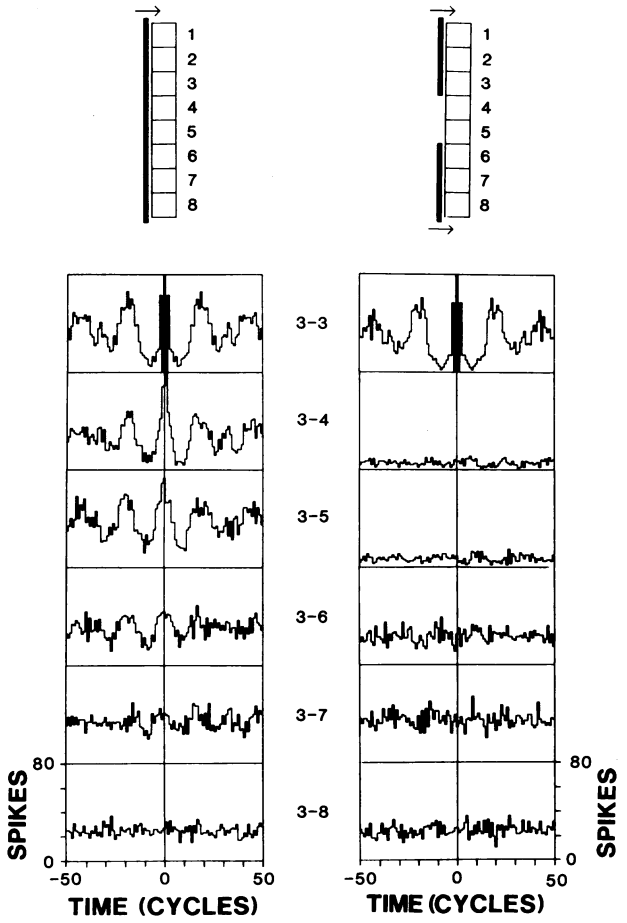

FIG. 3. Auto- and cross-correlations of single unit activity recorded from orientation-selective groups arranged in a 1 by 8 array (*Upper*) when a single long bar (*Upper Left*) or two short aligned bars (*Upper Right*) of appropriate orientation are moved through their receptive fields. Receptive field areas of adjacent groups overlap by about 60%. (*Lower*) Correlations between units in groups with overlapping receptive field areas (3–4) directly linked by local reentrant connections and with nonoverlapping receptive fields (3–6) only indirectly linked are present in the case of a single continuous stimulus (*Lower Left*) but are not present in the discontinuous case (*Lower Right*).

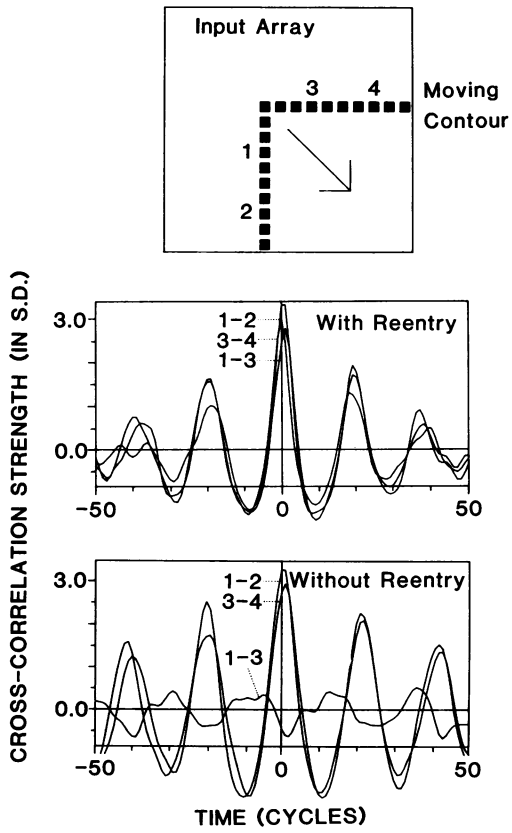

FIG. 4. The effect of long-range reentrant connections between OR and MO in response to a simulated moving contour. The diagrams show the cross-correlation of the AAF of neuronal groups in OR in the presence (*Middle*) and absence (*Bottom*) of reentrant connections from MO to OR. Parts of the moving contour to which neuronal groups 1, 2, 3, and 4, located in OR, respond are indicated (*Top*). Cross-correlation strength is expressed in standard deviations (SD) above the background computed from scaled cross-correlation functions.

frequency range. Oscillations within MO are driven by the direction-selective units, whereas oscillations in OR do not depend upon oscillations in MO. In the presence of long-range reentrant connections, coherency develops between groups responding to differently oriented parts of the contour moving together as one pattern. If connections reentering OR from MO are cut (leaving connections from OR to MO intact), coherency of oscillations in OR exists only between groups of the same orientation preference and is due to reciprocal coupling via local reentrant connections (see above, and Fig. 3). Thus, the dynamic linkage of responses in OR depends on signals arriving from another area, MO. Reentrant interactions between areas resembling OR and MO in the model might allow the discrimination of a moving stimulus from a background (20) by higher cortical areas capable of detecting phase coherencies in primary visual cortex.

It is of interest to compare the temporal properties in these modeled systems. The oscillation frequency of an isolated neuronal group depends on a variety of factors, including intensity of the stimulus; strength or density of intragroup connections; decay rate of inhibitory protentials ($\omega = 0.85$ for a period of 20 cycles); length of refractory period; etc. All of these parameters are likely to vary among collections of neuronal groups. In the model such variability prevents accidental phase-locking of unrelated groups and for short observation times results in significant and largely unpredictable shifts in the peak frequency of the power spectrum of the AAF (see also ref. 10). A significant shift of the peak frequency averaged over many stimulus trials occurs when reentrant coupling is introduced, however. Consistently, the oscillation period lengthens (the frequency decreases), sometimes by as much as 10% (data not shown). This is presumably due to slightly prolonged activity during the time of interaction. A similar shift might be observable in cortical groups if the reentry between identified areas were disrupted (e.g., by cooling).

In the model, transmission delays in reentrant connections longer than about 25% of the oscillation period result in significant phase shifts in the cross-correlation function (data not shown). Slow conduction velocities in actual corticocortical fiber systems (21) could thus limit the spatial extent of phase coherencies. To establish coherencies with the observed (9, 10) near-zero phase lag, interactions between distant cortical areas would seem to require fast-conducting (10–100 m/s) fibers.

DISCUSSION

The network model is consistent with the idea that reentry between neuronal groups links responses in distributed cortical systems and thus causes coherent firing. Transient correlations between neuronal groups located in distant cortical maps might allow the combination and recombination of

features of different visual submodalities in a great number of ways. Such linkage might be particularly important if one feature is topographically mapped and another is not, or a feature is mapped with large receptive fields (as is the case for many extrastriate visual areas, and, in the model, MO). In such cases, the transient linkage mechanism may provide a way for featural responses that are not well localized to be linked to corresponding stimulus objects at a particular location in space. Thus, reentry "guarantees that continuity in the neural construct is an obligate consequence of the spatiotemporal continuity of objects" (ref. 1, p. 76).

As demonstrated in the network model, coherent oscillations can be found among distinct neuronal groups that are responding to a single, coherent stimulus. In extension of this idea, two or more distinct stimuli could give rise to *cohorts* of neuronal groups, such that groups within a cohort oscillate in phase but groups within different cohorts do not. Such cohorts would be formed by partitioning cortical maps into transient functional subsets of neuronal groups, bound together by selectively activated subsets of their interconnections. Reentry between oscillating groups thus can establish a dynamic network of functional linkages, the configuration of which will, in primary visual cortex, depend largely on the momentary correlations present in the stimulus.

It is possible, of course, that oscillatory cross-correlations are nothing more than indicators of underlying cooperative effects within groups of neurons or their reentrant interactions. However, the experiments (8–10) as well as the above theoretical considerations suggest to us a number of possible functions for oscillations *per se*:

(*i*) Oscillations could act to isolate or sharpen coherent responses to a particular stimulus. While a neuronal group is engaged in cooperative discharges, other inputs to that group arriving out of phase or at a different frequency would be less efficient in exciting the group or would be suppressed altogether.

(*ii*) The oscillatory properties of neuronal groups may interact in a variety of ways with biochemical or cellular processes involving synaptic modification and different transmitter systems ("transmitter logic", see ref. 2, chapter 7). Long-term potentiation, mediated by *N*-methyl-D-aspartate receptors, for example, has been shown experimentally to depend on the frequency and timing of afferent impulses (22).

(*iii*) The spatiotemporal pattern of cortical oscillations might play a critical role in guiding early morphogenetic events in the brain, such as the migration of growth cones, neurite extension and branching, cell death, synaptogenesis, dendritic spine formation, and the formation of reentrant anatomy itself.

We predict that similar oscillations and phase coherencies will be found in other regions of the visual cortex, in areas devoted to other sensory modalities, and in motor areas—all of which contain strongly reentrant connections. Moreover, it seems possible that the activity of neurons engaged in sustained firing during visual memory tasks (23, 24) might be based on excitatory impulses among reentrantly connected neuronal groups exhibiting oscillatory properties similar to those found in the cat's visual cortex. The detailed analysis of oscillatory properties might provide a method by which functional connectivities between distant cortical areas can be detected.

The previous reentrant cortical integration model (7) demonstrated the rich possibilities and emergent properties that arise from reentrant interactions among multiple segregated areas. The present model includes more realistic local neuronal populations in each group and provides another example of the emergence of new properties as a result of reentry. The two studies together lead us to believe that reentry between neuronal groups in cortical maps is essential to reflect spatiotemporal continuity in the stimulus world as well as to construct complex response properties by recursive synthesis. This suggests an important and general functional role for the large proportion of vertebrate neuroanatomy consisting of reentrant structures.

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