

Interareal synchronization in the visual cortex

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Abstract

The primary visual cortex (V1) is part of a highly interconnected network of cortical areas, hierarchically organized but operating concurrently across hierarchical levels. The high degree of reciprocal interconnection among visual cortical areas provides a framework for their interaction during the performance of visual scene analysis. The functional interdependency of visual cortical areas which develops during scene analysis can be investigated by techniques which measure interareal correlated activity. Evidence from monkeys performing a visual pattern discrimination suggests that synchronization of aperiodic activity from neuronal ensembles in cortical areas at different hierarchical levels is a relevant aspect of visual function. The near-periodic nature of the synchronized response to moving light bars in earlier studies may have been a result of the type of stimulus used. Various models of visual cortex are discussed in which interareal synchronization plays a functional role.

Keywords: Visual cortex; Visual perception; Local field potential; Correlated activity; Synchronization; Oscillation

1. Introduction

Photonic energy impinging on the retina produces an intensity distribution that varies with retinal position, time, and wavelength. Photonic excitation initiates a series of events along segregated parallel pathways extending from the retina, through the lateral geniculate nucleus (LGN) and primary visual cortex (V1 in primates). Because of the crucial role of these pathways in conveying information from the retina, it has often been assumed that sequential activation along a serial chain continues beyond V1, and is the primary means by which all cortical areas receive and transmit information. However, visual areas are extensively interconnected by pathway convergence and divergence, as well as by lateral and feedback projections [55]. Furthermore, visual responses in cortical areas are observed to overlap in time [7,22,37,100]. These considerations argue against a strictly serial activation scheme for visual processing [55,82], suggesting instead that processing in each area depends on concurrent interactions with other areas. Therefore, although each area has a degree of functional autonomy, visual scene analysis is an integrated process which must be understood by con-

sidering the interactions between areas as well as their individual functions.

Interareal interactions are thus crucial to an understanding of visual cortex as an integrated system. As a visual cortical area engages in its own local processing, interactions allow it to draw information from, and provide information to, other areas to which it is connected. In practice, it is not possible to monitor the pulse traffic on all of the axonal pathways connecting the visual areas of the cortex in order to directly measure their interactions. Instead, the distribution of areas that function together while an animal is processing visual information can be mapped by spatial imaging of optical, metabolic, or electrophysiological signals. Then, the functional interdependency of active areas can be inferred from the covariation of their active states. A state of functional interdependency, sometimes called a *functional connection* [2,39,58,146], may develop between different areas that are jointly engaged in visual processing. The functional connection of two areas depends on the existence of monosynaptic or polysynaptic anatomical connections between them.

The sign of functional connection between areas may appear in part as a concurrent increase in the activity of cells in each area. More information though is potentially available in the temporal patterns of neuronal activity than in changes of intensity alone, and there is

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growing evidence that the temporal activity patterns of neurons in the visual cortex do contain information [37,77,81,90,96,100,116,138]. It is possible, therefore, that functional connections are manifested by a shared temporal activity pattern [23,128,131], as well as by a shared increase in activity. Much attention has been given in recent years to the possibility that temporally correlated activity in V1 reflects the 'binding' of processes that are spatially separate, but related to a single object in the visual field [27,28,53,70,103,157]. Long-range horizontal connections running parallel to the cortical surface have been proposed as the anatomical basis for correlated activity in V1 [67,133]. But long-range interareal connections also exist, suggesting that functional connections between visual areas may also be observed in the form of correlated activity [24,131,165,166].

This review will consider recent experimental, theoretical, and computational results relating to functional connections between cortical areas in the visual system. In order to first establish an anatomical and physiological framework for the discussion of functional connections, segregated pathways underlying the functional specialization of extrastriate areas will be described (Section 2), and the organization of visual cortex as a hierarchical, interactive network will be discussed (Section 3). Then evidence for temporal correlation in the visual system will be reviewed, with particular attention given to recent findings of task-dependent interareal correlated activity (Section 4). Finally, the possible roles played by interareal correlated activity in visual information processing will be explored (Section 5).

2. Segregated pathways in visual cortex

A large body of evidence indicates that the primate visual system contains at least two [21] parallel segregated pathways from the retina, through the LGN, to V1 [94]. Cells in the M pathway, which passes through the magnocellular subdivision of the LGN, are distinguished by their high luminance contrast sensitivity, transient responses, and lack of wavelength sensitivity. Cells in the P pathway, which involves the parvocellular subdivision, show lower luminance contrast sensitivity, sustained responses, and pronounced wavelength sensitivity [35]. In area V1, the M pathway thalamocortical fibers terminate in layer 4C α on spiny stellate neurons which project to layer 4B, and the P pathway terminates in layer 4C β on spiny stellate neurons which project to layers 3B and 4A [95]. The P pathway projections to 4A also contribute collaterals to more superficial layers [11].

Continuation of the M and P pathways is defined by the tangential patterning in areas V1 and V2 produced by staining for the mitochondrial enzyme cytochrome

oxidase (CO). The M pathway continues in V1 through layer 4B neurons to thick CO-staining stripes in V2, and through projections from both V1 layer 4B neurons and V2 thick-stripe neurons to area MT [34,93,98]. The antibody Cat-301 also selectively labels layer 4B, the V2 thick stripes, and area MT [36]. These paths to MT are associated with motion analysis because of a large proportion of cells showing direction selectivity and binocular disparity sensitivity in V1 layer 4B, V2 thick stripes, and area MT [102]. The lack of P input to this pathway can account for the wavelength insensitivity of MT neurons [99]. Motion specificity of MT neurons is consistent with the heavy projections from MT to the visual parietal areas, which are specialized for analyzing spatial relations of objects and for visual guidance of movements toward objects in space [31,148,149].

The M and P pathways both project to CO-staining blobs in the superficial layers (4A, 3B, 3A, 2) of V1 [102]. The blobs receive input from layers 4C α and 4B (M pathway) as well as layer 4C β (P pathway) [57]. The interblob regions of the superficial layers receive input from layer 4C β neurons (P pathway). M pathway projections have not been described, but pathway inactivation studies show that they too receive an M pathway contribution [110]. Wavelength-selective neurons are found in both V1 blobs and interblobs, although they predominate in the blobs [93]. Blob and interblob neurons both project to V2, with blob projections terminating in thin CO-staining stripes and interblob projections terminating in interstripe regions [92]. Both the thin-stripe and interstripe regions of V2 project to V4 [129]. There is also a direct projection from the superficial layers of V1 to V4, although it has not been determined whether the projection originates solely in blobs or interblobs [161,163].

Pathway inactivation studies confirm the dependence of visual responses in area V4 on both P and M input [56]. The P contribution is evident in the wavelength selectivity of neurons in the V1 blobs and V2 thin stripes, the V1 interblobs and V2 interstripes, and in V4 [35,102]. Both the high spatial resolution of the P input and the high contrast sensitivity of the M input may contribute to the selectivity for orientation and binocular disparity that is found in the pathway through the V1 interblobs, V2 interstripes, to V4. Area V4 projects heavily to the visual areas of the inferotemporal cortex which are implicated in shape and pattern recognition [31,148,149]. The utilization of a wide variety of sensory cues by these functions is consistent with the range of neuronal sensitivities of neurons along the paths through V4 to inferotemporal cortex.

In addition to segregated, parallel, feedforward connections, there are at least three other types of connection in the visual pathways [55,102]. First, the feedforward pathways diverge, as in the projection of cells in layer 4B of V1 to area V3 as well as to V2 and MT. Area V3

in turn projects to both V4 and MT, while V4 projects to parietal as well as inferotemporal areas. Then there are also lateral connections: between layer 4B and the superficial layers of V1; between the thick and thin stripes of V2; and between V4 and MT. Finally there are feedback projections, such as from area MT to layer 4B and the superficial interblob regions of V1, as well as to both to the thick and thin stripes of V2 [87]. These interconnections suggest that there is considerable 'cross talk' between pathways.

3. Network properties of visual cortex

The system of cortical areas having visual function has characteristics of both an interconnected network and a structured hierarchy. The system has a multiplicity of interconnections, but not all areas are connected equivalently, nor are they functionally equivalent. Each area has a unique set of connections that is used to assess its hierarchical level. The comprehensive 1991 review by Felleman and Van Essen [55] summarized the connectivity among visual cortical areas as was known in the macaque monkey. According to that report, area V1 projects to eight other visual cortical areas in addition to V2, and area V2 projects to twelve others in addition to MT and V4. In all, 25 neocortical areas are predominantly visual in function, and an additional seven areas have heavy visual inputs. From this set of 32 areas, 121 reciprocally interconnected pairs were known. Another 58 unidirectional pathways were known for which a clear-cut test of the reverse direction had not been made at the time of that report. Only a few other pairs had been specifically tested and found not to be reciprocally connected. In all, roughly 40% of the total number of pairs of areas had been tested and found to be connected. (Another 30% had not yet been tested). Each area has, on average, about ten inputs and ten outputs. Although not fully interconnected, then, the visual cortical areas form a highly integrated system.

The hierarchical organization of visual cortex has been determined from the ordering of areas based on interareal laminar connectivity patterns [55,117,152]. The concept of hierarchical levels is supported by single-cell response characteristics [79]. Compared to V1, where neurons are selective for features such as stimulus orientation, direction of movement, and binocular disparity [123–125], neurons at higher levels have larger receptive fields and more complex selectivities [31,97]. Examples are cells in MT that are selective for movement of a complex pattern rather than the orientation of its components [108], inferotemporal cells that are selective for the appearance of complex patterns [32,121,126], and posterior parietal cells that are selective for optical flow motion [106].

The 'near ubiquity' [55] of reciprocal connections

between cortical areas suggests that the most common informational transaction may be the recursive exchange of information between areas rather than its unidirectional transfer from one area to another. Even though they are hierarchically organized, cortical areas do not process visual information sequentially, one after the other, in any fixed order. Rather, the observation of temporally sustained and overlapping responses to patterned stimuli of neurons in multiple visual areas indicates that visual processing proceeds in parallel in those areas [7,22,37,100]. Divergence and convergence in feedforward pathways provide ample grounds for a high degree of mixing of the information that is conveyed to higher levels, and feedback pathways provide the opportunity for higher-level information to be transmitted down to lower levels. In short, the cortical system for higher visual function consists of a spatially distributed, hierarchically organized network of highly interconnected cortical areas, processing information in parallel [151].

4. Correlated activity in visual cortex

The hypothesis that visual perception involves the formation of functional connections in visual cortex has motivated the investigation of correlated activity between spatially separate cortical sites. Recent experimental studies of the visual system in non-human primates and lower mammals have revealed correlated activity between sites both within and between cortical areas. Although the emphasis here is on interareal correlation, studies on intraareal correlation will also be reviewed since they comprise most of the work in the field, and, from what is known of interareal correlation, it shares many of the properties of intraareal correlation.

For the activity at two locations to be correlated implies a tendency to show similar variation in time (with possible delay). Correlated activity is measured as the statistical interdependence between the time series recordings from two sites. The experimental observation of correlated activity between cortical sites implies that processing at those sites is being coordinated, but it does not specify a particular coordinating mechanism since correlated cortical activity could, in general, arise by way of different cortical and subcortical pathways [75].

A common approach to the recording of correlated activity is to measure the occurrence of coincident spikes (with possible delay) from pairs of single neurons [145,150]. The cross-correlation histogram is commonly used to detect coincident spikes in simultaneously recorded spike trains [1,3,65,114]. Correlated neuronal firing has been observed both between neuron pairs in the same area, and between neurons located in different areas (see below).

Although this approach has been popular, the rele-

vance of correlated activity between individual cortical neurons for the establishment of long-range functional connections has also been questioned [40,53,113,139]. The probability of finding significantly correlated single-cell spike trains is typically low, particularly for cells that are separated by millimeters or more, rather than microns [39,88,89,150]. This is because a cortical neuron receives synaptic contacts from thousands of other neurons, with very few synapses originating from any single neuron [12,13,38]. Also, over the fraction-of-a-second time span that correlated activity must occur during visual processing, single cortical neurons typically generate only a few pulses. The resulting effect of a pulse from one cortical neuron on the pulse train of another is estimated to be on the order of only 1:1000 or smaller [1,150].

A second approach emphasizes the neuronal ensemble [46,47,58,76,107,137] as a more relevant functional unit than the single neuron for the establishment of correlated cortical activity [26,139]. In visual cortex, the relevant ensemble structure may correspond to the hypercolumn. One argument for the importance of ensemble activity concerns the greater effectiveness of the ensemble than the single neuron in influencing a postsynaptic neuron, as seen in the non-linear relationship between presynaptic firing rate and EPSP magnitude. The joint firing of an ensemble of presynaptic neurons can produce a larger effect on a target neuron than the sum of their individual effects. It is only when tens of neurons fire together that the firing probability of the target neuron is significantly altered [1].

A second argument for the importance of ensemble activity derives from studies of receptive field properties in extrastriate cortex. Both the receptive field size and response complexity of neurons in the visual pathways increase with distance from the retina [5,78,108,162,164], and neurons in different visual cortical areas vary in their response properties, cells in each area having preferences for a particular set of stimulus characteristics [165–167]. However, the cells in an area do not respond in all-or-none manner to a single stimulus feature, but give responses that are graded along several different stimulus dimensions [31,159]. For example, face-selective neurons in the cortex of the superior temporal sulcus do not uniquely code for individual faces, but rather convey information as a population that can allow discrimination of faces [120]. Findings such as this suggest that visual information in an area is contained in the response of neuronal ensembles, rather than that of any single neuron.

Ensemble activity is typically recorded in either one of two related forms. Since local interactions in the ensemble involve both axonal pulses and postsynaptic dendritic potentials, the local intensity of ensemble activity can be characterized either by the pulse density [59], measured as the local multiunit activity (MUA), or by

the dendritic current density [135], measured as the local field potential (LFP). The LFP in V1 has been shown to display the same spatial, orientation, and chromatic tuning properties that are well-established by single-unit studies [156]. Interareal correlation may be most robust for the LFP, which is an instantaneous spatial average of ensemble activity [61], because spatial averaging is inherent in the communication between areas. The spatial averaging of activity from many neurons in an ensemble, as manifested in the LFP, may approximate that which takes place in the interactions between areas due to axonal spatial divergence and dendritic integration. A corresponding summation is only achieved by the experimenter measuring single neuron correlations by summing over long periods of time.

4.1. *Intraareal correlated activity*

Most studies of correlation in the visual system have focussed on interrelations within the primary visual cortex of the anesthetized cat or monkey. Single neuron spike-train correlation studies have revealed local shared input and intracortical functional relations over distances of 1 mm or less (i.e., within a hypercolumn) with respect to laminar location, ocular dominance, orientation selectivity, and response class [4,88,143,144]. Functional connections have been identified between cells in superficial [147] and infragranular layers [127] having the same orientation specificity, but separated in the horizontal direction by up to several millimeters. Greater correlation has been found between nearby neurons activated by a single light bar than by two independent bars presented together [147]. Functional connections have also been observed between neurons in the inferotemporal cortex of awake monkeys fixating on a light spot [68].

The investigation of correlated activity at the ensemble level has concentrated on quasi-periodic γ (30–90 Hz) frequency [14] oscillations [19,70,73,80]. Correlated ensemble activity is usually referred to as *synchronization*. Most reports on synchronized γ -frequency oscillations have involved MUA and LFPs recorded from sites in the primary visual cortex of the anesthetized cat [42,49–51,72,84], although many of their properties have recently been confirmed in the alert cat [71]. These properties include stimulus dependence, variability in frequency, and lack of locking to stimulus onset. Synchronization occurs in variable duration episodes lasting on the order of hundreds of milliseconds [74].

On a spatial scale of less than 2 mm, quasi-periodic MUA and LFP γ -frequency oscillations from columns with overlapping receptive fields synchronize in response to a moving light bar regardless of orientation preference. For columns having non-overlapping receptive fields, and separated by from 2 to 7 mm, MUA synchronization

occurs primarily between activated columns having similar orientation preferences. In keeping with the result from single cells [147], MUA synchronization is greater in response to a single light bar than to two independent bars [72]. LFP synchronization, on the other hand, occurs between activated columns even with dissimilar orientation preferences and even with separations greater than 7 mm [49]. Stimulus-related γ -frequency synchronization has also been reported between MUA from spatially separate sites in V1 of the anesthetized squirrel monkey [91], and in the caudal superior temporal sulcus of the anesthetized [86] and awake [85] macaque monkey, when those sites are activated by a single moving light bar. Finally, it has been reported between LFPs from spatially separate sites within V1 of the awake macaque [62] in response to checkerboard reversal stimuli.

4.2. Interareal correlated activity

Correlated activity involving extrastriate areas is generally similar to that observed within striate cortex in terms of stimulus dependence, frequency variability, and lack of stimulus-onset locking. Even though the spectral peaks of individual episodes of synchronization vary over the γ range, the variation occurs in parallel in the two synchronized areas. Moving light bar stimulation induces synchronization that is strongest when the receptive fields of the cells in both areas overlap and the orientation preferences are similar. Binocular stimulation is more effective than monocular for inducing synchronization [39]. Stimulus-induced correlated neuronal firing occurs between neuron pairs located one each in areas 17 and 18 of the anesthetized cat [111], and V1 and V2 of the anesthetized monkey [20,118]. Also in the anesthetized cat, stimulus-induced interareal γ -frequency synchronization takes place between LFPs and MUA from areas 17, 38 and 19 [39–44], and between area 17 and the PMLS (posteromedial lateral suprasylvian) area [52]. Synchronization occurs between area 17 of the left and right hemispheres, and can be abolished by transection of the corpus callosum, indicating that it is mediated by cortico-cortical connections [50]. Stimulus-induced synchronization of LFP and MUA γ -frequency oscillations has also recently been reported between V1 and V2 of an awake monkey [63].

4.3. Aperiodic interareal correlated activity

Several groups have proposed that synchronization of periodic γ -frequency oscillations serves a functional role in the visual system by uniquely 'binding' the distributed neuronal activity related to individual entities in the visual scene [27,28,39,53,130,131]. This hypothesis has been controversial, and counter-evidence has been presented indicating that periodic γ -frequency oscillations

do not have a functional role in the visual cortex [142]. For example, in contrast to the studies cited above, moving stimuli have been found not to be effective in inducing such oscillations in single-unit spike trains from area 17 of the anesthetized cat [66], or in LFPs from V1 or MT of the anesthetized monkey [160]. In the awake monkey, static visual images are ineffective at inducing them in single-unit and multi-unit activity from the inferior temporal cortex or cortex of the superior temporal sulcus [141], or in LFPs from the inferior temporal cortex [64]. And moving dot patterns are reported to be ineffective at inducing periodic γ -frequency oscillations in single-unit activity from area MT [8]. In contrast to these findings has been a recent report that stimulus-induced γ -frequency oscillations occur in V1 of the awake monkey, but in a higher part of the γ range (70–80 Hz) than in the cat [45].

In attempting to resolve this controversy, it is necessary to disambiguate the concepts of 'synchronization' and 'oscillation'. Proponents on both sides of the issue agree on this [54,141]. The phenomenon of synchronization refers to a joint tendency of two signals to have similar waveshapes, irrespective of the specific shape. The proposals in favor of synchronization have largely invoked mechanisms involving periodic oscillations having a relatively narrow spectral peak centered at a frequency in the γ range. The counterarguments have consequently focussed on the absence of periodic oscillations, without directly addressing the issue of synchronization. Central to this discussion is the fact that, in general, oscillations may be *aperiodic* as well as periodic [83]. Aperiodic activity may have multiple spectral peaks, or a broad spectral distribution without clear-cut peaks. Synchronization may be important for cortical integration in the visual cortex, regardless of whether the oscillations are periodic or aperiodic. Broad-band synchronization may be a general phenomenon, with synchronization of narrow-band, near-periodic γ oscillations being a special case under certain conditions or in certain species [60]. Relevant in this regard is the report that synchronization between areas 17 and 18 in the cat reverts to a broad-band from a narrow-band pattern after a moving stimulus becomes stationary [39].

A number of lines of evidence support a functional role for aperiodic activity in the visual cortex of the monkey. The power spectrum of the population response (LFP) in V1 has a broad-band, approximately '1/f' distribution, which includes but is not limited to the γ range [62]. Information about stimulus attributes is distributed in the LFP dynamics in V1 across a broad frequency band including at least part of the γ range [156]. Stimulation with moving light bars has been found to induce a broad-band increase in LFP power in areas V1 and MT [160], and aperiodic synchronization of MUA between sites in the cortex of the superior temporal sulcus [85].

Furthermore, visual pattern discrimination involves aperiodic LFP synchronization among many widespread neocortical sites in the monkey, including those in visual areas such as striate, prestriate, inferotemporal, superotemporal, and posterior parietal cortices [15–18]. Fig. 1 shows three recording sites in visual areas of the left hemisphere in a monkey trained to discriminate between two different static dot patterns. The three areas, striate, prestriate, and inferotemporal cortices, represent different hierarchical levels [55]. Stimulus presentation initiates multiple episodes of interareal synchronization, lasting on the order of 50–200 ms, which follow a different time course for the different site pairs (Fig. 2). Synchronization is measured by spectral coherence, which establishes that the occurrence of synchronization during pattern discrimination is statistically reliable over hundreds of trials. The significant increases in coherence following stimulus onset for all three site pairs indicate that visual pattern discrimination involves synchronization of areas at three different hierarchical levels.

Although similar in duration to previously observed episodes of intraareal and interareal synchronization in the cat and monkey [39,74,85], these episodes involve a broad frequency band including but not limited to the γ range. The temporal patterning of the episodes is very similar at all observable frequencies. There is also a tendency for the LFP amplitude to increase over this broad band following stimulus presentation [17], consistent with the report [160] that the cortical response to static visual stimuli is a broad-band increase in power rather than the emergence of a single narrow-band spectral peak. The broad-band nature of the interdependency between visual areas while the animal performs the pattern discrimination indicates that synchronization of aperiodic activity may be an information processing mechanism in visual cortex. The narrow-band, near-periodic nature of the synchronized response to moving light bars that has been previously reported

[39,45,49,74] may be a peculiarity related to that particular type of stimulus.

5. Putative functions of interareal correlated activity in visual processing

As discussed above, visual scene analysis involves interdependent processing in multiple cortical areas at the same and different hierarchical levels. A basic necessity in cortical systems is for access by neurons in each part of the system to information from other parts [9]. In the visual system, scene analysis may depend on interactions that distribute information across areas and hierarchical levels [115]. Theoretical studies, many using computer simulations, have begun to determine how interareal interactions may operate in scene analysis. Accounts of interactions based on correlated activity will be reviewed in this section. Perhaps the most well-known example of interareal interaction is the feedforward convergence of inputs from areas processing low-level cue information onto hierarchically higher areas. But feedback effects from higher to lower levels are beginning to be understood as well. Moreover, because of the large number of reciprocal interconnections, there is growing interest in the processing advantages afforded by recursive interactions between areas at multiple levels.

5.1. Feedforward convergence

Structural information implicit in the retinal image is made explicit by the visual system using many computational strategies to infer high-level perceptual attributes from low-level sensory cues [31,35]. High-level functions, such as object identification, can depend on different combinations of low-level cues, such as orientation, velocity, color, or binocular disparity [35,121]. An edge in a complex scene, for example, may be indicated only weakly by any one of these cues taken alone, but may be strongly indicated by correlated changes in several of them. In general, low-level cues contribute to the computation of many different perceptual attributes, and perceptual processes can employ different cues, alone or in combination [153].

The detection of covariation among sensory cues may be fundamental to the computation of high-level attributes [9,10,76,115]. This would imply that neurons at any hierarchical level in extrastriate cortex can detect covariances in their inputs from neurons at lower levels. The anatomical basis for this detection may be found in the topical convergence of projections from a large part of a lower area to a smaller part of a higher area [166,167]. Covariation in time of stimulus-related activity at the lower level is a potentially powerful way to convey covariation in sensory information over converging projections to the higher level. Although the full

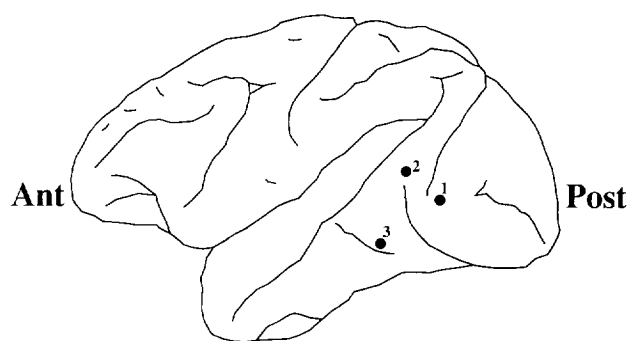


Fig. 1. Left hemisphere of rhesus macaque monkey TI, showing positions of cortical recording sites in Striate (1), Prestriate (2), and Inferotemporal (3) regions. At each site, the field potential was localized by differential transcortical recording from a pair of microelectrodes.

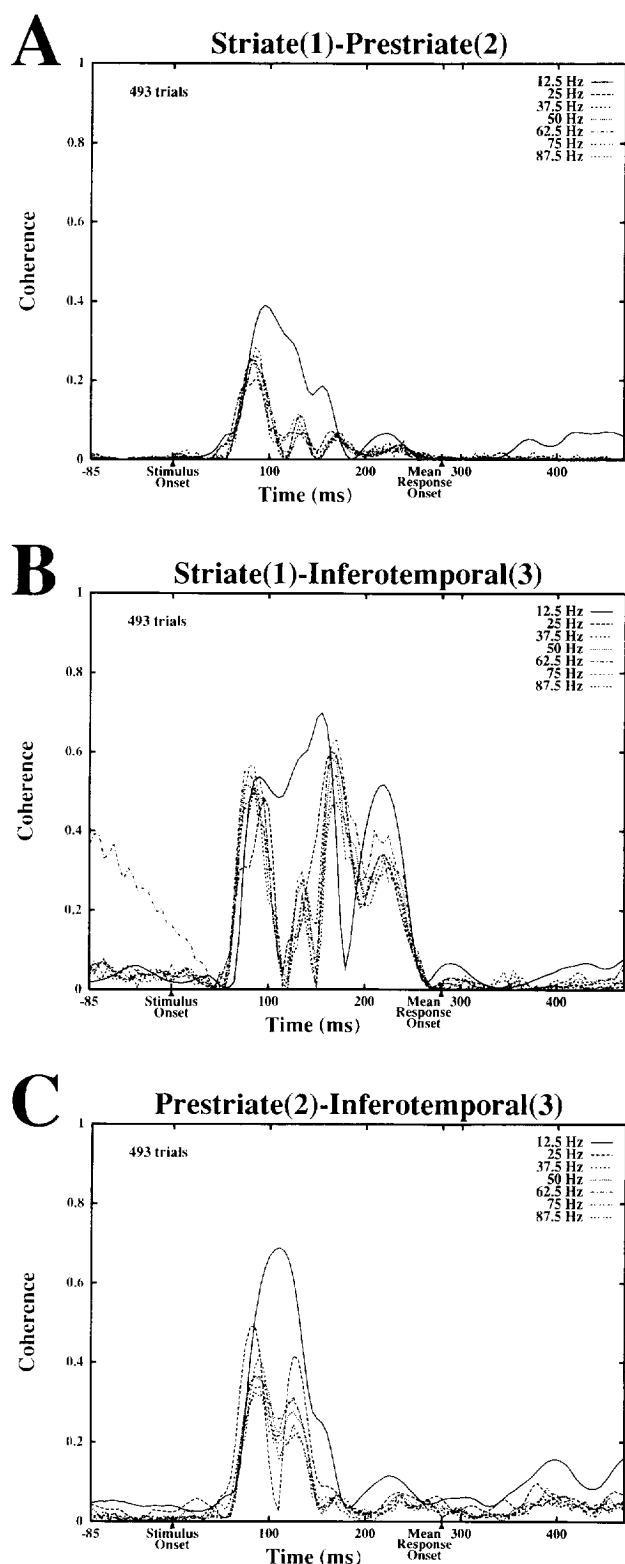


Fig. 2. Local field potential (LFP) synchronization was measured with the spectral coherence, which provides a statistically reliable index of correlated activity as a function of frequency. Monkey TI performed a visual pattern discrimination task which involved identifying one of two types of static dot pattern presented for 100 ms on a display screen. Spectral coherence measures were derived from a total of 493 trials in which the monkey correctly identified one pattern type, and signified it with a hand response. (For further experimental

spectral range of stimulus-related correlated activity in visual cortex has not yet been ascertained, it appears to cover the γ range [17,53], and may even extend to the kilohertz range [111,134].

It was argued above that significant effects of one cortical area on another are exerted at the level of the local neuronal ensemble rather than the single neuron. It is known that stimulus-specific information is carried in the broad-band temporal patterning of ensemble activity in V1 [156]. Therefore, synchronization of activity in different local ensembles of V1 may be optimal for the conveyance of covarying feature information to higher levels because synchronous dendritic activation is more effective than asynchronous for altering the firing rate of the target neuron [1]. The synaptic effect of synchronized output from the cells of each ensemble, when transmitted over multiple axonal branches to the dendritic trees of higher-level neurons, is greater than that of a single neuron, and is augmented even further by the convergent synchronous arrival of inputs from different lower-level ensembles.

5.2. Feedback divergence

Feedback projections from higher to lower areas are common in the visual system, but the termination patterns of these projections typically are more diffuse than those in the forward direction [167]. Thus, for example, whereas the forward projection from V2 to MT originates in the thick stripes, the feedback projection covers not only the thick stripes, but the thin stripes and interstripes as well. Likewise, the feedback projection from MT to V1 layer 4B encompasses cells projecting to both V3 and MT. Although the functional role of feedback projections has not been adequately explored experimentally, speculation has focussed on the ability of feedback to provide a matching of concurrent activity in different areas both with respect to time [24] and retinotopic position [82]. Thus, feedback may allow all the different attributes of a visual stimulus to be brought into precise spatio-temporal registration.

Again, synchronization may be involved in this process. Suppose, for example, that visual input consists of

(details see Refs. [16] and [17].) To track the change in coherence with time, an 80-ms-long analysis window was progressively stepped across the length of the trial. Coherence spectra (frequency resolution = 12.5 Hz, i.e., 1 cycle per 0.08 s), computed at each step, are plotted as a function of time on task. Coherence time series are displayed for each pairwise combination of the three recording sites shown in Fig. 1. (A: Striate with Prestriate; B: Striate with Inferotemporal; and C: Prestriate with Inferotemporal). Coherence time series for all seven available frequencies are superimposed in each plot. Task-related episodes of elevated coherence, lasting on the order of 50–200 ms, followed the stimulus onset. The change in coherence with time was similar at all available frequencies for each site pair, but differed considerably among the three pairs.

line segments forming the outline of a square moving across the visual field. Cells in different parts of V1 will respond to the local motion within their small receptive fields. Cells in MT, however, with much larger receptive fields, will respond to movement of the entire square. It is possible that MT cells feed back information about the pattern as a whole to V1. This distributed feedback may interact with ongoing activity in V1 to bring the activity of the V1 neurons that were already responding to the various parts of the pattern into temporal synchrony. In fact, computer simulations have been performed which model this phenomenon. In those models, severing the feedback projection from MT to V1 disrupts the synchronized activity of units in V1 which process the pattern contour [140].

5.3. Recursive interactions

From the fact that most projections between visual cortical areas are reciprocally arranged, functional effects have been considered not just in terms of feedforward or feedback, but also in terms of ongoing, recursive interaction. That is, if two areas are reciprocally connected, then it is likely that under certain circumstances they may interact by sending and receiving information from each other at the same time. This dynamic process has been termed *re-entry* [46]. Several groups have explored the computational properties that result from re-entry, some by constructing computer models, and others from a strictly theoretical perspective.

In one study [158], a computer model was constructed in which one network of coupled non-linear oscillators, representing V1, received patterned visual input, and was reciprocally connected to a second network, representing an extrastriate area which stored patterns of elementary features. Synchronized oscillations which emerged in the first network served to organize coherent figures from the discrete input features. Recursive interaction between the two networks led to the emergence of synchronized oscillations in the second network, representing a stored memory pattern, which, when fed back to the first network, then provided constraints that allowed separation of the figure from the background.

In another study [122], a network of coupled non-linear oscillators was also constructed, this one consisting of three modules, each representing a visual area for processing either stimulus disparity, orientation, or color information. The representations of a single object in the three feature domains were associated by re-entrant interactions between modules, manifested as synchronized oscillations. Segregation of two different stimuli was achieved by desynchronization of their representations. Even in the case where ambiguities existed in distinguishing the two stimulus representations in one feature domain, correct segregation was accomplished

by using information conveyed through re-entrant interaction with the other feature domains.

In a third study [140], in which a computer model represented nine functionally distinct visual areas, re-entry also served to associate the representations of features of an object across areas. Synchronization was observed between units in an area, as well as between different areas, both across hierarchical levels and at the same level. Synchronized units representing features of one object were distinguished from those of another object by a consistent phase difference. A foveation response as output of the model provided a basis for discrimination behavior, and the modification of connection strengths in the model by a saliency system allowed conditioned discriminations among multiple objects. Successful discrimination among objects was based on the correct conjunction of form, color, and position, and depended critically on synchronization of active units representing these features in different areas.

Each of these three studies may be said to have followed a 'bottom-up' approach, in which different aspects of visual function arise from the interactions of large numbers of processing units. A 'top-down' approach, on the other hand, considers how high-level operations may be implemented at the systems level, without necessarily constructing explicit network models. In one such treatment, recursive interactions between cortical areas, manifested as synchronized oscillations, were considered to be a general mechanism by which visual cortical areas communicate with each other [109]. This communication, according to the hypothesis, takes the form of an iterative relaxation algorithm. Spatial activity patterns, initially representing visual images, are transmitted from a hierarchically lower to a higher area over forward projecting pathways, and other patterns, representing stored templates, are conveyed back from the higher to the lower area over feedback pathways. As the iterative process proceeds, the lower area continues to transmit residual patterns, representing deviations from the down-projected templates, and the higher area continues to transmit templates which have been modified by the residual information it receives. This looping continues until the patterns in each area stabilize, signifying that the system has reached a state of recognition.

5.4. Global interactions

Interareal synchronization may play a role in global interactions between the visual system and other brain systems. A prime candidate for this type of interaction is the transfer of visual output to the motor system. The potential to effect behavior through cortical and sub-cortical [69] projections to the motor system may be an advantage of having multiple visual areas in the extrastriate cortex [25]. Visual areas have been observed to

engage in episodes of synchronized activity with motor cortex, as well as other areas in the frontal lobe, during visual pattern discrimination performance [17]. Multiple visual cortical areas may act in concert to influence target motor structures. Synchronized output from multiple visual areas could be particularly potent at conveying excitation to target neurons on which their projections all converge.

Synchronization may also play a role in the storage and recall of perceptual information. One postulate is that neuronal ensembles (referred to as convergence zones) at each hierarchical level within the extrastriate cortex retain records specifying the sets of lower-level ensembles from which they receive synchronized convergent input during visual perception [30]. The retrieval of perceptual information from memory is proposed to occur when the convergence zone ensemble uses its stored information to re-activate and re-synchronize the same distributed set of lower-level ensembles that were originally synchronized during perception. Convergence zones may also organize function on a larger scale, retaining records of interactions between visual areas and those of other modalities [29]. The parahippocampal region, for example, receives projections from many cortical areas, including high-level visual areas, is interconnected with the hippocampal formation, and projects back to widespread cortical areas [6,48,136,155]. Feedback from this region may be used to re-synchronize visual cortical areas for visual recall, based on relations with other modalities [119,120].

Finally, it has been observed that in a system which allows a large number of interactions among its components, there is a need for control mechanisms to constrain and coordinate the active functional connections at any instant in time [112,154]. In other terms, local interactions in an unsupervised system must be constrained by global function [119]. Evidence for global constraints in the visual system comes from experiments on attention showing that the large receptive fields of neurons in extrastriate regions, such as V4 and IT, can effectively contract in size as a result of attentional demands [31,33,104]. V1 and V2 neurons exhibit spatial attentive effects as well [105]. A central role in one model of visual attention is played by control neurons which dynamically modulate the effective functional connections in visual cortex in order to route information from V1 to a select set of higher cortical areas [112,154]. Control neurons in the model are likened to cells in the pulvinar complex, which is reciprocally connected with all the visual cortical areas involved in the analysis of form. Visual attention has been proposed to also involve the transient synchronization of neuronal assemblies in different cortical areas [26–28]. The effect of control neurons may be to selectively enhance the synchronization of particular sets of visual areas on an instant-to-

instant basis, perhaps by dynamically controlling the level of excitability of cortical pyramidal cells [132]. In this way, the routing of information across hierarchical levels in extrastriate cortex may be analogous to constraining the system to form functional connections among a particular set of areas at multiple hierarchical levels.

6. Conclusions

This review has emphasized the importance of functional connections between areas of visual cortex for the processing of visual information. It has been argued that correlated activity is an important feature of visual function. Although interactions between individual neurons may be most important within a small local region such as the hypercolumn, it is argued that interactions between visual cortical areas are best viewed as occurring at the level of the neuronal ensemble. Detailed knowledge of the dynamic functional relations between interacting neuronal ensembles is seen as essential for understanding the visual cortex as an integrated network.

According to this view, it is no longer sufficient to characterize the operating characteristics of activity in each visual area as if it were only one stage in a relay chain. What is required is the advancement of experimental techniques for simultaneous microelectrode recording of the ensemble electrical activity from different areas of alert animals. Subcortical and limbic cortical areas must be monitored along with visual cortical areas for the investigation of global operations and modulatory control processes. Also needed is the development of more powerful analytic techniques for assessing cooperative interactions among areas. Understanding of these interactions should be aided by insights gained from the field of non-linear dynamics, which deals with complex systems of interacting elements [101]. When fully implemented, this mesoscopic approach should prove itself as a useful complement to other approaches at the microscopic (e.g., unit recording) and macroscopic (e.g., EEG, MEG, PET) levels. Mesoscopic analysis can provide useful insights into the neural basis of visual perception that are not available by any other means.

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