

Functional Connections of the Visual Cortex Studied by Cross-Correlation Techniques

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Abstract. The cross-correlation technique has been one of the most powerful tools for investigating structure-function relations in the visual cortex. It can demonstrate the connectivity between two cells, fundamental to their photic responsiveness, in terms of their interaction during response to photic stimulation. This has never been possible by simply analyzing the responses evoked by electrical or photic stimulation. A number of important findings have emerged from cross-correlation studies with respect to geniculocortical, corticogeniculate, and intracortical connectivities and their functional significance. However, the application of the cross-correlation technique has been limited to strong and local, cell-to-cell connections, while diffuse and weak, area-to-area connections still remain undetected by the cross-correlation technique. An additional problem is the low sensitivity of the cross-correlation technique with respect to inhibitory interactions. The solution to these problems will provide further insight into the structure-function relations of the visual cortex.

CROSS-CORRELATION TECHNIQUES USED AS A TOOL IN THE STRUCTURE-FUNCTION PROBLEM

Visual cortical cells exhibit a variety of responsiveness which are highly selective for some features of visual stimuli. Two basic response types have been identified: the simple cell whose receptive field consists of ON and OFF subareas and whose responsiveness is predictable from linear integration of the ON and OFF responses, and the complex cell whose receptive field consists of superimposed ON and OFF subareas and whose responsiveness can be explained by nonlinear interactions between the ON and OFF responses (Hubel and Wiesel 1962, 1965). Analysis of the postsynaptic responses evoked by electrical stimulation of the visual pathway (Stone and

Dreher 1973; Toyama et al. 1974; Mitzdorf and Singer 1978), and analysis of dendritic and axonal morphology of the cortical cells (Gilbert 1983) has demonstrated four basic principles of organization in the circuitry of cat visual cortex (area 17). First, the geniculate (both X- and Y-) axons terminate in layers IV and VI, and feed monosynaptic excitation to somata or dendrites of layer III-VI cells. Second, some of the layer III and IV cells convey excitation to layer II cells through their main axonal trunks or axon collaterals, while others transmit inhibition to layer III-VI cells. Third, some of the layer II cells are inhibitory, and transmit trisynaptic inhibition to other layer II cells or to themselves. Fourth, besides these basic cortical pathways there are abundant pathways interconnecting cells of layers II-VI, which probably transfer excitation or inhibition in a rather diffuse fashion.

The question of how the visual cortical circuitry generates characteristic neuronal response properties is a central problem in visual physiology. To this end, numerous studies have been undertaken to determine the neuronal connectivities underlying cortical responses. The cross-correlation technique first introduced into neurophysiology by Perkel et al. (1967a, b) presented a new approach to this problem. It reveals interactions between two simultaneously recorded cells and identifies the type of neuronal connectivity between them. Although cross-correlation analysis is a more indirect way of demonstrating synaptic connections than analysis of postsynaptic potentials evoked by electrical stimulation, there are some advantages over the latter method. First, cross-correlation analysis demonstrates a cell-to-cell interaction that may not be demonstrable by electrical stimulation. Second, it is free of the problems of current spread, activation of passing axons, and stimulus artifacts which are frequently associated with electrical stimulation. Third, it reveals the ongoing interaction between the cells during their visual responses, and determines the contribution to the responses if the analysis is made during visual stimulation. Given these advantages, cross-correlation analysis provides a powerful tool for studying the structure-function problem in the visual cortex (Toyama and Tanaka 1984).

EXPERIMENTAL TECHNIQUES FOR CROSS-CORRELATION ANALYSIS

Cross-correlation analysis requires simultaneous recording of extracellular impulse discharges from at least two cells. This has been done in several laboratories. In some studies (Lee et al. 1977; Tsumoto et al. 1978; Toyama et al. 1981a, b; Tanaka 1983; Ts'o et al. 1986), a two-channel recording with a pair of microelectrodes was used. This allows sampling from pairs of neurons in any relative location, either from the same (Toyama et al. 1981a, b) or different functional columns of the visual cortex (Ts'o et al. 1986), or

analysis of neuronal pairs of different brain structures (e.g., those in the geniculate nucleus or the retina versus the visual cortex (Lee et al. 1977; Tsumoto et al. 1978; Tanaka 1983)). In other laboratories (Michalski et al. 1983), a multi-channel recording with a multiwire electrode assembly was employed. This allows sampling of more than two neurons but within restricted regions (Michalski et al. 1983).

For the compilation of reliable cross-correlograms (CCGs), sampling of a large number of impulses (more than several thousand) is required. This has been achieved in two ways. Visual stimulation is one commonly used method. Neurons under investigation are activated by repeated visual stimulation. The neurally related CCG representing the true synaptic interactions between the neurons is determined by subtracting the stimulus-related CCG which represents stimulus-dependent coactivation, and is compiled after shuffling the impulse trains (Perkel et al. 1967b).

The second method is chemical stimulation by electrophoretic ejection of a chemical stimulant, such as glutamate, from the microelectrode (Tsumoto et al. 1978; Toyama et al. 1981a). Double-barrel microelectrodes are used for this purpose—one barrel for recording and the other for chemical stimulation. Both methods have their respective advantages and are selected according to experimental purposes (Toyama and Tanaka 1984). The first method reveals neuronal interactions resulting from common inputs as well as interactions between cells, which are frequently otherwise difficult to discriminate, while the second method discloses only the latter interaction. The contribution of the interactions to visual responses of the recipient cell can of course be determined only by the first method.

BASIC NEURONAL INTERACTIONS DEMONSTRATED BY CROSS-CORRELATION ANALYSIS

Three basic types of neuronal interactions have been demonstrated by cross-correlation analysis of neuronal discharges in the geniculate nucleus and visual cortex: common excitation, serial excitation, and serial inhibition.

Common Excitation

The first type of interaction represents synchronized excitation of two neurons. The CCG of Fig. 1A, determined for impulse discharges in two cortical cells (C_1 and C_2), represents a sharp positivity extending only for a millisecond around zero time, indicating that the C_1 and C_2 are excited in precise synchrony. Common excitation may occur if the two cells receive a common input, either excitatory or inhibitory, and tend to discharge conjointly (Perkel et al 1967b). However, the precise synchronization of their activation indicates that they share potent excitatory inputs.

Serial Excitation

The second type of interaction represents excitation of one cell by another. The CCG of Fig. 1B represents serial excitation exerted by C_2 onto C_1 . The positivity is asymmetric around zero time. It occurs with a negative delay (-0.6 ms), attains a maximum after a millisecond, and declines gradually after a few milliseconds, indicating that C_1 is activated by C_2 .

Serial Inhibition

The third type of interaction is inhibition of one cell by another. The CCG of Fig. 1C represents a negativity occurring with a delay of -1 ms and continuing for several tens of milliseconds, indicating that C_1 is inhibited by C_2 .

GENICULOCORTICAL CONNECTIVITY

Parallel Geniculate Inputs

Retino- and geniculocortical connectivity has been studied in two laboratories (Lee et al. 1977; Tanaka 1983). Tanaka (1983) performed simultaneous recordings from geniculate cells of both the X- and Y-type and from the cortical cells including Eon (subtype of simple cells with exclusively ON response area), Eoff, simple, standard, and special complex cells (Table 1). Cross-correlation analysis during visual stimulation revealed serial excitation in about one-third (79/214) of the geniculocortical pairs with overlapping receptive areas. The analysis also indicated transfer of the geniculate inputs onto all types of cortical cells: pure Y-geniculate inputs to the special complex cells, mixed X- and Y-inputs (but predominantly X-inputs) to the simple cells and their subtypes, and mixed X- and Y- inputs (but predominantly Y-inputs) to the standard complex cells (Table 1).

Double-line Hypothesis

Another important finding is the correspondence between the response polarity in the geniculate vs. Eon/Eoff cells and simple pairs that exhibited excitatory connections: the ON-center area of the geniculate cells overlapped with the ON-response area of the cortical cells, and the geniculate OFF-center area with the cortical OFF-response area. These findings are consistent with the double-line model, assuming that the ON- and OFF-response areas of simple and Eon/Eoff cells are constructed by convergence of ON- and OFF-center geniculate cells respectively. Since the diameter of the ON- or OFF-center area of geniculate cells is approximately the same as the width

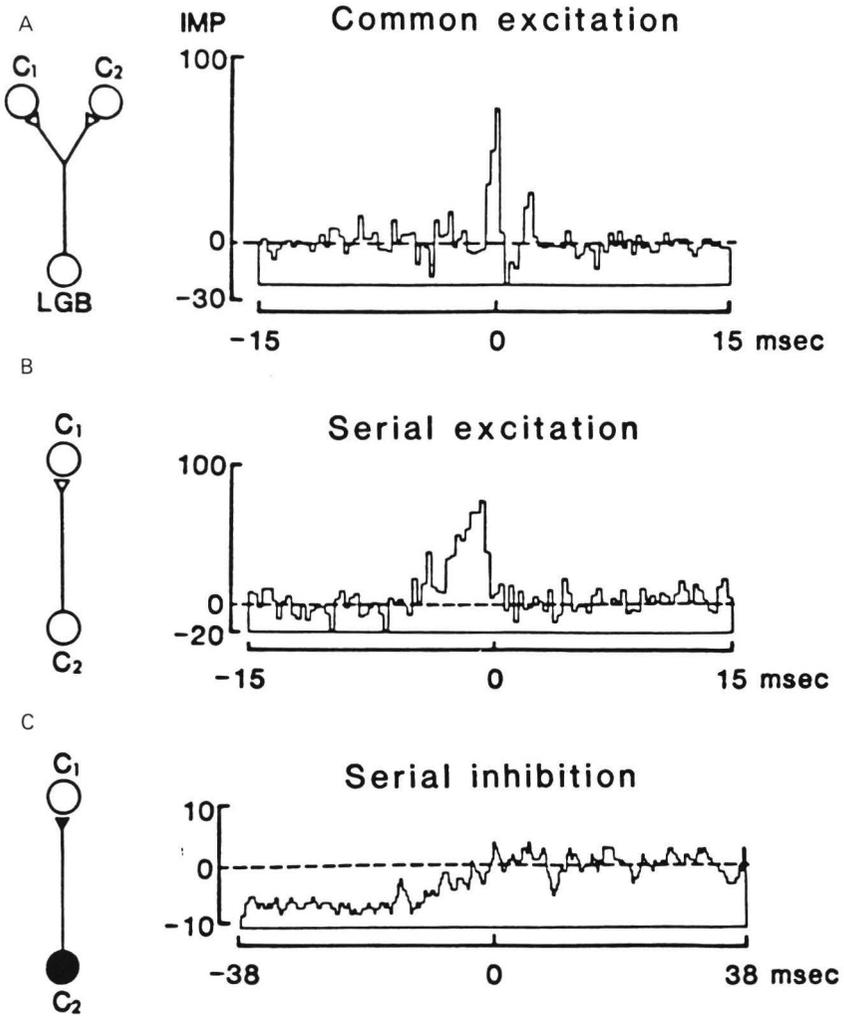


Fig. 1—Basic patterns of interneuronal interactions demonstrated by cross-correlation analysis (From Toyama 1984).

of the ON- or OFF-response area of cortical cells, the elongated response areas of cortical cells may be constructed by the convergence of excitation from several or more geniculate cells whose receptive areas are lined up along the axial orientation in the receptive area of cortical cells.

The following evidence supports this idea: first, in the simple cells and their subtypes (Table 2), the contribution of serial excitation to the response of cortical cells, as determined by the ratio of the number of impulses

TABLE 1. Frequency of occurrence of geniculocortical connections

Geniculate cells	Cortical cells				Total
	Eon/Eoff	Simple	Standard complex	Special complex	
X	8/22	18/49	17/45	0/16	43/132
Y	1/6	4/14	20/33	11/29	36/82
Total	9/28	22/63	37/78	11/45	79/214

Denominators represent number of the geniculate-striate pairs studied and numerators represent number of pairs exhibiting the serial correlation (modified from Table 1 in Tanaka 1983).

TABLE 2. Genulocortical contribution

From	To			
	Eon/Eoff	Simple	Standard complex	Special complex
X	0.10 (0.05–0.17)	0.11 (0.04–0.25)	0.03 (0.01–0.07)	
Y	0.03	0.11 (0.06–0.13)	0.04 (0.01–0.08)	0.03 (0.02–0.06)

Values are means and ranges of contribution determined for responses to stimulation by a moving stimulus (from Tanaka 1983).

resulting from serial excitation to those contained in the response to visual stimulation, was roughly 0.1. This indicates that approximately 10 geniculate axons converge onto these cells. The contribution was much smaller (about 0.03) in the standard and special complex cells, suggesting greater geniculate convergence (about 30) onto the latter types of cells.

Second, cross-correlation analysis of multiple geniculate versus single cortical cell pairs demonstrated convergence of excitation to a single cortical cell from multiple geniculate cells whose receptive areas were lined up along the axial orientation of the cortical cell's receptive area (Tanaka 1983).

A similar observation was made in the cross-correlation study of Lee et al. (1977) between retinal ganglion cells and simple cells. Cross-correlating the neuronal pairs with overlapping receptive areas during visual stimulation produced a positive CCG in about one-fifth of the pairs (6/29) including

both X- and Y-retinal cells. The CCGs closely resembled those found by Tanaka in the geniculocortical pairs except for longer delay (4-5 ms) and longer duration. This difference may be attributed to the longer conduction distance and an additional synaptic relay at the geniculate nucleus. Interestingly, the contribution of the CCG to visual responses (determined by the author from their figures) was roughly the same (0.2-0.3) as that reported by Tanaka for geniculate-simple pairs, which is consistent with the finding in the cross-correlation study of Levick et al. (1972) that an almost one-to-one connection is established between retinal ganglion cells and geniculate cells representing the central visual field.

CORTICOGENICULATE CONNECTIVITY

Although Tanaka (1983) did not detect a cross-correlation indicative of corticogeniculate synaptic action, Tsumoto et al. (1978) reported serial excitation from cortical cells to geniculate cells with overlapping receptive areas (18/114), and serial inhibition to those with slightly separated receptive areas (8/114).

INTRACORTICAL CONNECTIVITY WITHIN ADJACENT FUNCTIONAL COLUMNS

The intra- and intercolumnar connectivities between adjacent columns were studied in the two laboratories using cross-correlation analysis (Toyama et al. 1981a, b; Michalski et al. 1983). The results are in agreement in spite of considerable differences in the cross-correlation techniques used.

Common Excitation among Neurons with Different Response Properties

Toyama et al. (1981a, b) studied neuronal interactions by sampling a number of cells with a microelectrode vertically advanced along the column, while holding a single reference cell in the same or adjacent column, with another microelectrode advanced obliquely. The neuronal interaction most frequently found (51%, 95/185) was common excitation. Common excitation was characterized by synchronized activation of neuronal pairs within a few milliseconds. These pairs were distributed over a wide cortical space extending over a vertical distance of several hundred microns around layer IV. The sharp synchronization and the spatial distribution around layer IV indicate that common excitation represents excitation by shared geniculate inputs. Common excitation was most frequently found between neuronal pairs with the same response types. However, it also occurred in neuronal

TABLE 3. Frequency of occurrence of common excitation

To Cell	Eon/Eoff	From Cell Simple	Complex	Hypercomplex
Eon/Eoff	8/12	6/16	8/17	0/2
Simple		21/35	26/36	0/6
Complex			23/45	2/13
Hyper-complex				1/3

Figures in the table represent frequency of occurrence of common excitation using the same conventions as in Table 1 (from Toyama et al. 1981b).

pairs with different response types (i.e., Eon/Eoff versus simple, simple versus complex, etc; see Table 3), and in those with different orientation and directional preference, but never in those with different ocular dominance.

Similar observations were also made by Michalski et al. (1983) who investigated the interactions in neuronal pairs sampled with multichannel tungsten electrodes. Common excitation was found in about two-thirds (61%) of the 286 neuronal pairs tested, including all combinations of simple and complex cells, even if they were separated by a horizontal distance of 1 mm and probably located in different functional columns. The findings in the two laboratories indicate that single geniculate axons terminate on cortical cells of diverse response types in a large cortical space, extending horizontally across many orientation columns throughout the whole extent of a single ocular dominance column and vertically throughout layers III–V. This view is consistent with the findings of Tanaka (1983) that Eon/Eoff, simple, and complex cells all received excitation from X-geniculate cells.

Serial Excitation Transferred to the Same Response Types

In contrast to the frequent occurrence and broad distribution of common excitation in a large cortical space, Toyama et al. (1981b) reported a rather rare incidence (10%) and limited spatial distribution of serial excitation—it was mediated by complex cells located at the border area between layers III and IV to complex or hypercomplex cells located superficially in the same orientation column at distances of a few hundred microns. Therefore, intracortical excitation does not seem to extend across orientation columns.

Slightly more frequent serial excitation (20%) was reported by Michalski et al. (1983), but it was also limited to neuronal pairs in the same functional column. One reason for the more frequent occurrence may be that serial

excitation was identified by Michalski et al. on the basis of cross-correlation of neuronal activities during visual stimulation, while Toyama et al. based their identification on cross-correlation during visual and chemical stimulation. The serial excitation demonstrated during visual stimulation was frequently contaminated by strong common excitation, and identification was therefore difficult. In such cases, interactions were accepted as serial excitation only if it was confirmed by analysis during chemical stimulation. Serial excitation was studied by Michalski et al. in relatively few neuronal pairs of different response types, but one case of slight serial excitation from simple-to-complex cells was found superimposed on strong common excitation.

Serial Inhibition between Different Response Types

Serial Inhibition was found by Toyama et al. in approximately the same proportion (10%) of neuronal pairs as for serial excitation. However, it occurred in neuronal pairs of different response types and with different (up to thirty degrees) as well as the same orientation preference. Therefore, cortical inhibition occurs between cells in different orientation columns and with different response types. Serial inhibition was found in four combinations: between Eon and Eoff, from Eon/Eoff to simple, from Eon/Eoff to complex, and from simple to complex cells. Therefore, cortical inhibition is sequentially transferred from cells with a simpler receptive area to those with a more complex receptive area.

Serial inhibition was reported by Michalski et al. (1983) but was not related to neuronal response types. Serial inhibition was slightly less frequent (7%) and much weaker than that demonstrated by Toyama et al. This variation may also be accounted for by differences in the experimental methods. The serial inhibition determined by Michalski et al. was based on cross-correlation analysis during visual stimulation. Toyama et al. analyzed correlations during chemical stimulation; the latter demonstrates serial inhibition in isolation from common excitation, which almost always contaminates serial inhibition during visual stimulation.

Contribution of Connectivity to Visual Responses

The contribution of neuronal interactions to visual responses was also studied by Toyama et al. (1981b) and Michalski et al. (1983). In Toyama et al.'s study, the contribution of common excitation varied according to response types. In general, it was larger between the same response types than between different response types. In cell pairs with the same response types, common excitation was largest for Eon/Eoff, modest for simple, and smallest for complex cells (Table 4).

TABLE 4. Contribution of common excitation

To Cell	Eon/Eoff	From Cell Simple	Complex
Eon/Eoff	0.76 (0.38–0.92)	0.11 (0.01–0.29)	0.07 (0.03–0.09)
Simple		0.3 (0.02–0.81)	0.05 (0.01–0.17)
			0.15 (0.01–0.58)

Conventions are the same as in Table 2 (from Toyama et al. 1981b).

The contributions of a similar order of magnitude were found for serial excitation (0.1–0.3) and inhibition (0.1–0.2). Contributions of the same magnitude (0.1–0.6) were also reported by Michalski et al.

INTRACORTICAL CONNECTIONS ACROSS DISTANT FUNCTIONAL COLUMNS

Ts'o et al. (1986) studied neuronal correlation between supragranular cells in distant columns. A number of cells were sampled by advancing one microelectrode horizontally across many columns while holding one reference cell with another electrode. Cross-correlation analysis revealed that during visual stimulation, common and serial excitation often occurred together, and the magnitude of the correlation peak depended on the horizontal separation of cortical cells, their ocular dominance, and orientation preference, and was relatively independent of their directional preference (Table 5). Excitatory interaction was detectable between pairs at distances less than 2 mm, and with orientation preferences differing as much as 90°, but it was much stronger between pairs where the difference was smaller than 30° (Table 6).

Although common excitation may be partly accounted for by common inputs through geniculate axons which extend horizontally over a few millimeters (Humphrey et al. 1985), serial excitation is entirely attributed to the horizontal transfer of cortical excitation by axon collaterals of supragranular cells. Therefore, excitatory signals are transferred between supragranular cells in distant columns with the same ocular dominance and with the same or similar orientation preference. Interestingly, a similar dependence (on vertical distance, ocular dominance, and orientation preference) was found for common excitation mediated by geniculate axons (see above).

TABLE 5. Relationship of ocular dominance and directionality with correlation strength

	Correlation strength groups			
	0	1	2	3
Ocular				
Dominance				
opposite	2	1	0	0
same	5	0	6	2
Directionality				
opposite	3	1	5	2
same	4	1	8	5

Figures represent number of neuronal pairs included in the correlation strength groups. The analysis was made for 45 pairs which were distanced at least 500 μm and exhibited an orientation preference difference of less than 30° (Modified from Ts'o et al. 1986).

TABLE 6. Relationship of orientation preference with correlation strength

Orientation difference	Correlation strength groups			
	0	1	2	3
0–10°	0	2	10	9
20–30°	4	1	7	11
40–50°	10	6	4	3
60–70°	17	7	0	0
80–90°	18	6	0	0

Figures represent number of neuronal pairs for combinations of correlation strength and orientation difference groups (Modified from Ts'o et al. 1986).

It would be interesting to know the relative strength of transcolumar and intracolumar interactions. Direct comparison of their strength is difficult, because Ts'o et al. (1986) used a measure other than the relative contribution to express the strength of transcolumar interactions. Transcolumar interactions, however, appear to be at least one order of magnitude smaller than intracolumar interactions, as judged from the number of impulses used to determine the interactions. Roughly 5 times as many impulses were used for assessment of transcolumar than for the determination of intracolumar interactions (about 15,000 in Ts'o et al. 1986, versus 3,000 in Toyama et al. 1981a, b), and the strength of cross-correlation increases as a function of the product between the numbers of impulses used for the analysis.

CONCLUDING REMARKS

Cross-correlation studies have provided a number of important findings concerning structure-function relations in the visual cortex. Studies of geniculocortical interactions revealed parallel geniculate channels (Xon/Xoff and Yon/Yoff) connected with a variety of cortical cells. There are mixed X- and Y-inputs (but predominantly X-inputs) to simple cells and their subtypes (Eon/Eoff), pure Y-inputs to special complex cells, and mixed X- and Y-inputs (but predominantly Y-inputs) to the standard complex cells. Therefore, X- and Y-geniculate inputs are not completely specific, but may still significantly contribute to the generation of various response types of cortical cells. In support of the double-line hypothesis, evidence shows that ON and OFF response areas of cortical cells are constructed by convergence from ON- and OFF-center geniculate cells, respectively. The receptive area of cortical cells is constructed by convergence of several to up to thirty geniculate axons, as estimated by analysis of the relative contribution.

Cross-correlation analysis of corticogeniculate interactions demonstrated positive feedback of excitatory signals to geniculate cells with overlapping receptive areas and negative feedback of inhibitory signals to those with nonoverlapping receptive areas. Since layer VI cells are mostly binocular, positive feedback may enhance visual signals with binocular disparities within the fusion range, while negative feedback may depress those beyond the fusion range (Schmielau and Singer 1977). Positive feedback may also contribute to the end-stop properties of lateral geniculate cells (Sillito, personal communication).

One of the most remarkable findings revealed by studies of intracortical interaction is that a single geniculate axon extends across many orientation columns to the entire extent of an ocular dominance column, and feeds signals to cortical cells of diverse response types with the same or opposite directional preference. Therefore, geniculate inputs are specific neither to orientation nor directional selectivity. In contrast, cortical excitation and inhibition are restricted to a rather small cortical space, probably including a single or several orientation columns, and are specific to both response type and orientation preference. Evidence shows that geniculate excitation provides the basis for response selectivity of cortical cells, such as ocular dominance, orientation and directional selectivity, and that the selectivity is refined by cortical inhibition, which probably works across at least several orientation columns. The established response selectivity may be transferred along a single orientation column by cortical excitation.

Another remarkable finding is that cortical signals are transferred across a horizontal distance of a few millimeters, corresponding to a retinotopic distance of several degrees, through axon collaterals of supragranular cells. The transfer of signals is specific to orientation and ocular preference (it is

restricted to cells with the same or similar orientation preference and the same ocular dominance), and therefore it may work as an excitatory feedback to enhance orientation selectivity.

In summary, cross-correlation studies have provided a great deal of important information concerning the structure-function relation of visual cortical circuitry. However, the application of cross-correlation analysis has been restricted to the basic circuitry of the visual cortex which probably is constructed of focal, point-to-point, axonal projections. However, many neural connectivities suggested by morphological studies (Gilbert 1983) still remain undetected by cross-correlation. These pathways probably consist of diffuse, area-to-area, axonal projection, whose effects are small and difficult to detect through the present technique of cross-correlation analysis. The study of single-fiber-evoked excitatory postsynaptic potentials (EPSPs) in the spinal motoneurons indicates that the EPSPs below 80 μV produced no significant cross-correlation peaks (Cope et al., in press). A slow rise time of EPSPs could also reduce the detectability through cross-correlation techniques, particularly if synaptic noise is high (Fetz and Gustafsson 1983). Although the effect of a single axonal projection may be small, the convergence of many axons could eventually have a significant effect on the response selectivity of cortical cells and information processing in the visual cortex. Another problem may be the relatively low sensitivity of cross-correlation analysis in detecting inhibition, as suggested by a simulation study of interneuronal interaction (Aersten and Gerstein 1985). However, the conclusion should be reviewed in light of the strong shunting action of cortical inhibition demonstrated by spike-triggered averaging (see below).

In an attempt to overcome these problems in cross-correlation analysis, spike-triggered averaging, which is supposed to be a more sensitive method than cross-correlation analysis (Kirkwood 1979), was applied to slice preparations of visual cortex (Komatsu et al. 1988). The study confirmed all intracortical connectivities suggested by the cross-correlation studies (excitatory and inhibitory connections from juxtgranular to supragranular cells), and demonstrated two additional excitatory connections (from supragranular to layer V and from layer V to supragranular cells). Convergence and divergence were found in the already identified connections, but never in the newly-disclosed pathways. The unitary EPSPs produced through the former connections had larger amplitudes (a few hundred microvolts versus 100 μV or less), quicker rise times (1.7 versus 2.4 ms) and shorter half-widths (5 versus 14 ms) than those of the latter connections. Another interesting finding is that unitary inhibitory postsynaptic potentials (IPSPs) were smaller in amplitude (less than 100 μV), but exhibited much larger shunting conductance (probably more than 10-fold) than the unitary EPSPs of the old connections.

Altogether, spike-triggered averaging is superior to cross-correlation analysis in detecting weak and diffuse intracortical connectivities and is a promising technique for solving structure-function relations in the visual cortical circuitry.

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