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Quantitative procedures were developed for testing block-structured models for multi-input nonlinear visual circuits studied with spatio-temporal white noise. A linear-nonlinear (LN) model test index was found to be suitable for classifying cells as simple versus complex. Although simple cells were better modeled as LN systems than complex cells, most simple cells deviated considerably from LN behavior. A nonlinearity of cortical origin would appear to be responsible, possibly activated more strongly by broadband noise than by sinewave grating stimuli. Also, two classes of binocular complex cells were identified. Whereas all binocular complex cells necessarily have a non-zero second-order "same-eye" interaction kernel, their second-order "cross-eye" interaction kernel could, it was found, be either non-zero or identically zero. The two binocular complex cell classes are thought to be the monkey equivalents of the "phase

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Report

NON-LINEAR ANALYSIS OF VISUAL CORTICAL NEURONS – FINAL REPORT

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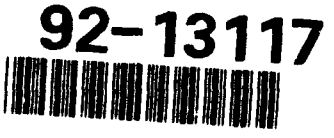

SUMMARY.

Quantitative procedures were developed for testing block-structured models for multi-input nonlinear visual circuits studied with spatiotemporal white noise. A linear-nonlinear (LN) model test index was found to be suitable for classifying cells as simple versus complex. Although simple cells were better modeled as LN systems than complex cells, most simple cells deviated considerably from LN behavior. A nonlinearity of cortical origin would appear to be responsible, possibly activated more strongly by broadband noise than by sinewave grating stimuli. Also, two classes of binocular complex cells were identified. Whereas all binocular complex cells necessarily have a non-zero second-order "same-eye' interaction kernel, their second-order "cross-eye" interaction kernel could, it was found, be either non-zero or identically zero. The two binocular complex cell classes are thought to be the monkey equivalents of the "phase specific" and "phase non-specific" cells previously discovered by Ohzawa and Freeman (1986b) in the cat. A random-jitter disparity tuning model suggested by Ohzawa and Freeman was found to be inconsistent with "phase non-specific" cells in the monkey, rather they must linearly combine nonlinear monocular inputs—as alternatively suggested by Ohzawa and Freeman. The left and right eye filters of simple cells in the monkey were found to have broadly varying phase relationships. Finally, a quadrature correlation model for stereo depth estimation was developed to account for recent new findings by ourselves, and others.

RESEARCH OBJECTIVES.

The major objectives of the project were as follows:

I. Develop quantitative procedures for testing block-structured models for multi-input nonlinear visual circuits. These methods would be used in the fullfillment of further objectives described below.

II. Determine if binocular simple cells in the monkey are well modelled by a spatiotemporal linear-nonlinear (LN) cascade model. Previous work, reviewed in Pollen, Jacobson and Gaska (1989), had long established that monocular simple cells in the cat and monkey could be well modelled by a linear filter followed by a threshold nonlinearity. Ohzawa and Freeman (1986a) had recently extended these results in the cat by observing that binocular simple cells in the *cat* combine left- and right-eye inputs linearly prior to response truncation. The techniques developed in objective 1 were to be used to similarly evaluate the LN model for binocular simple cells in the *monkey*.

III. Determine if the two classes of binocular complex cells, "phase-specific" and "phase non-specific," previously identified by Ohzawa and Freeman (1986b) in the

cat cortex, are also present in the monkey cortex. These two complex cell classes were distinguished by their sensitivity (or lack thereof) to the relative phase of a pair of dichoptically presented spatial sinewave gratings. If these two binocular cell classes were also found to exist in the monkey, we wished to obtain improved models of these cells as discussed below.

IV. Determine if "phase-specific" complex cells in the monkey can be well modelled by a straightforward binocular generalization of the Pollen and Ronner (1981) 4-cell quadrature model, where the phase-specific complex cell would receive inputs from four binocular simple cells whose phase relation is quadrature with respect to each eye individually. Such a phase-specific complex-cell model had been previously proposed by the investigators (Gaska *et al.*, 1988), (and implemented by them in a system for estimating disparity), and essentially the same 4-cell binocular model was later independently proposed by Ohzawa, DeAngelis and Freeman, (1990).

V. Determine if "phase non-specific" cells in the monkey are better modelled (a) by assuming that they sum two or more monocular complex cells—each sensitive to inputs from a different eye, or rather, (b) by assuming that their insensitivity to the relative phase of extended dichoptic gratings results from a random jitter of binocular disparity tuning throughout the receptive field. Both types of models had been proposed by Ohzawa and Freeman (1986b) to be consistent with their data from the cat. Experiments to differentiate between these models had not yet been performed in either the cat or monkey species.

VI. Determine how the phase differences of the left- and right-eye spatial filters of simple cells in the monkey are distributed. In particular, do the phases of the left- and right-eye spatial filters of simple cells differ by 0 and 180 degrees exclusively, as in the model previously proposed by the investigators (Gaska *et al.*, 1988), or do the phase differences distribute more broadly.

VII. Incorporate major new physiological findings into a model, previously proposed by the investigators, for binocular simple and complex cells and their respective roles in disparity estimation.

RESEARCH STATUS

New systems analysis methods

In this section we describe results we have developed, under this contract, for testing block-structured models for multi-input nonlinear visual circuits. These new methods were developed subject to the following important constraints and objectives:

1) The specific block-structured models of interest could be described by an interconnection of (a) linear time-invariant filters, and (b) memoryless (static) nonlinearities. Most monocular and binocular models that have been proposed for simple and complex cells fall into the above class of block-structured models. For example, consider a linear-nonlinear (LN) cascade system that operates on spatiotemporal inputs to produce a temporal output. Such a model is commonly attributed to *simple cells* in the visual cortex, where L is the spatiotemporal receptive field profile of the cell, and N is the threshold nonlinearity that relates the cell's output spike rate to its somal potential.

2) The structural model testing procedures were to be based solely on experimental stimulus–response data. Such data would generally be obtained during electrophysiological recording experiments which seek to characterize the input–output relationship of a visual neuron.

3) It was assumed that the multi-input stimuli used to evoke photic responses from visual neurons would be computer-generated approximations to spatiotemporal white noise. Such a stimulus generally consists of multiple spatial regions (bars, squares, etc.) whose luminances are varied randomly and independently as a function of time. Spatiotemporal white noise stimuli are relatively easy to generate, and there are well developed analytic methods for summarizing the measured white noise stimulus–response relation of a time-invariant nonlinear systems as a set of functional expansion kernels. For such reasons, many of the major laboratories studying cortical vision (Emerson at U. Rochester, Freeman at Berkeley, Palmer at U. Penn, Pollen at U. Mass. Med. (our group), Shapley at NYU) have utilized white noise stimuli in recent experiments.

4) To simplify their application, the procedures for testing block-structured models would be designed so as not to depend on the parameterization of the multi-input nonlinear visual circuit under study. This would therefore enable one to test, with a single application of the procedure, a large class of circuits whose members have a common structural design, but an infinity of parameterizations. Such a class of systems with

a common structure is illustrated by the set of all linear-nonlinear (LN) cascade systems with spatiotemporal inputs. As mentioned above, such a model is commonly attributed to simple cells. Using the structural testing procedures to be developed in this first objective, we hoped, for example, to be able to test simple cells for consistency with a spatiotemporal LN model without regard for the shape of the cell's linear spatiotemporal filter or the form of its output nonlinearity. Such a parameter independent LN test would be analogous to using the principal of superposition to test a system for linearity. Namely, the superposition test for consistency with the 'L' structural class does not presuppose any specific parametric form for the linear filter of the system under test.

Overview of results. During the present three-year contract, we have developed nonlinear structure classification and parameter identification methods that are applicable to a broad class of multi-input / single-output (MISO) neural networks of relevance to cortical visual processing (Chen, Jacobson, and Gaska, 1990; Chen, Jacobson, Gaska and Pollen, 1989). These methods are applicable to data from stimulus-response studies that use white noise stimuli consisting of *multiple* independent spatial inputs including random bar and random checkerboard stimuli. Given the growing use of such multi-input stimuli, the methods discussed in the above papers are likely to find wide application during coming years. The new analysis methods are fairly easy to apply to multi-input neural systems as illustrated by our recent paper submitted to Vision Research (Jacobson, Gaska, Chen and Pollen, 1992).

The new methods employ the low-order kernels of a multi-input system which can be estimated using standard approaches (Marmarelis and Marmarelis, 1978). Properties of the individual kernels and their mathematical relationship are exploited in a fashion that largely avoids dependence on the parameterization of the nonlinear system under study. **All of our objectives on this task were met or exceeded.**

Prior work. The approach we have developed for analyzing data from multi-input studies builds upon previous work that was concerned with testing and identifying single-input systems (Korenberg, 1973a,b; Billings and Fakhouri, 1978; Marmarelis and Marmarelis, 1978; Shapley and Victor, 1980; Victor and Shapley, 1980). These earlier methods made use of estimated Wiener (or Wiener-like) *self-kernels* to test and parameterize LN and LNL models for systems investigated with *single-input* stimuli (e.g., luminance modulation of a uniform spatial field or a single spot of light, or contrast modulation of a single spatial sinewave grating). Korenberg (1985) had also developed an important result for multi-input LN and LNL systems; namely, he established that existing single-input methods could be applied separately to each spatial input in a multi-input stimulation study.

New Methods. The new methods we have developed for testing multi-input nonlinear systems are described in a paper that appeared in Biological Cybernetics (Chen, Jacobson and Gaska, 1990), and further results are described in an IEEE conference paper (Chen, Jacobson, Gaska and Pollen, 1989). For details on the new methods refer to these two papers.

The prior work described above was formally extended by us in two principal ways as discussed below:

(1) Systems with parallel nonlinear channels: First, we enlarged the class of identifiable system structures to include multi-input models with parallel LNL paths. These include, for example, the classic feedforward complex cell models in which a complex cell summates the outputs from multiple simple-like mechanisms that are themselves modeled as multi-input LN systems. The extensions also encompass the half-phase and full-phase Reichardt motion detection models (Reichardt, 1961). We have also developed multi-input extensions, yet to be published, that treat special subclasses of a large class of bilinear models that were introduced by Rugh (1981), as well various specializations of feedforward and feedback shunting models previously investigated by Sperling & Sondhi (1968), Pece *et al.* (1990), Pinter (1983, 1989), Grossberg (1988), and Yasui (1982).

(2) Cross kernel utilization: Second, we have developed methods which incorporate the Wiener *cross-kernels*, as well as the self-kernels, when testing and parameterizing multi-input systems. The cross-kernels characterize the nonlinear interaction between multiple stimulus inputs—as reflected in the nonlinear response of a neuron. These interactions are the foundation of many visual models including, for example, the Reichardt motion detection model (Reichardt, 1961). Moreover, the cross-kernels provide a far stronger constraint on models than the self-kernels; they generally simplify the system identification process; and they are critical to the identification of some systems, (like Reichardt motion systems), whose self-kernels are identically zero.

The strong constraint offered by the cross-kernels derives from the observation that the complete Ith order kernel of an N-input system consists of N^I I-dimensional temporal subparts of which only N are self-kernel components and the other $N^I - N$ are cross-kernel components. Hence the self-kernel components only represent $1/N^{I-1}$ of the total kernel. Therefore, for a system studied with 100 inputs falling on the receptive field (typical of physiological experiments we perform), the cell's second-order kernel will be 1 percent self kernel and 99 percent cross kernel. The cross kernel components dominate even more as the kernel order is further increased. Therefore, if there are nonlinear interactions between the inputs to a system, the preponderance of data in the system's kernels of order two and higher is contained in the cross-kernels.

Practical Applications. In a recent paper submitted to Vision Research (Jacobson, Gaska,

Chen, and Pollen), we make extensive use of the cross kernels to test simple and complex cells in the striate cortex of the monkey for consistency with multi-input LN and LNL models. This same paper also describes many practical matters related to the application of the new methods to noisy physiological data. Such topics include (1) the benefits of cropping the support region of multi-dimensional kernels to eliminate excess background noise from regions outside of the receptive field, (b) statistical methods for quantifying the results from structural tests, (c) epochal kernel calculation methods for accurately estimating rates of eye drift from white noise stimulus-response data, and (d) a demonstration of the feasibility of relating structural test indices to traditional indices that are used for cell classification (we specifically describe the empirical relation between the LN index and the modulation index).

Experimental results

A number of major tasks had to be completed in order to obtain the results reported in this section:

1) Integrate a new graphics workstation (a Silicon Graphics 4D/120 GTX purchased under funding from this contract) into our experimental laboratory facilities. The SG workstation was to be used for both white noise stimulus generation and presentation of traditional drifting bar and grating stimuli.

2) Develop the software needed to apply the new structural model testing procedures developed in this project to the stimulus-response data collected during experiments. This software is described in an appendix to this report.

3) Carry out a series of electrophysiological experiments to record the responses of cortical cells to monocular and binocular spatiotemporal white noise stimuli, (as well as to traditional bar and grating stimuli as needed for comparative analyses and for classifying cells as *simple* versus *complex*). White noise studies each ran anywhere from 10 minutes to 2 hours.

4) Estimate the first- and second-order spatiotemporal kernels of each cell studied. The low-order kernels serve to summarize the white noise stimulus-response relationship as recorded during each cell study.

5) Perform data analyses to meet specific experimental objectives previously outlined in the Research Objectives section.

Overview of results. During the present three-year contract, we have carried out a series of electrophysiological experiments using monocular and binocular presentations of random bar

and checkerboard stimuli. In these experiments, we have collected more than 100 continuous hours of white noise stimulus-response data from more than 70 cells in V1 and V2. Most cells were also studied with traditional stimuli (drifting bars and gratings) to facilitate classification by conventional criteria, and to directly determine preferred spatial frequency, orientation, temporal frequency, directionality, and other relevant characteristics including the degree of end-stopping. These data have provided us with a rich characterization of the monocular and binocular stimulus-response relationships of a broad sample of unoriented cells, simple cells, and complex cells.

The stimulus-response data from these studies were initially used to estimate both the first- and second-order kernels that parameterize the best (with respect to the presented noise stimulus) linear and quadratic models for the input-output relationship of each cell. The 3D first-order kernels describe, for about 10 - 200 distinct spatial stimulus input positions, the spatiotemporal impulse response of the best linear model. As such, the first-order kernel data characterize the transmission delay from the retinae to the cortex as well as the detailed substructure and time evolution of the spatiotemporal receptive field(s) in one or both eyes. The 6D second-order kernels describe, for all possible pairs of spatial stimulus positions and temporal delays, the quadratic impulse response correction associated with the best second-order model. Accordingly, the second-order kernels characterize the transmission delay from retinae to cortex as well as the detailed temporal evolution of two-point nonlinear interactions as they affect the neuron's response. In effect, the second-order kernels summarize the results from a complete two-point interaction study, analogous to the response profiles obtained in the seminal two-bar interaction studies carried out by Movshon, Thompson and Tolhurst (1978b) which led them to a greatly improved understanding of complex cells.

Preliminary analyses of the collected data have been reported in abstract form (Jacobson, Gaska, Chen & Pollen, 1989; Gaska, Jacobson, Chen & Pollen, 1989), and a major paper is in review at *Vision Research* which describes our first physiological application of the structural testing methods described in the previous section. A copy of this paper entitled "Structural testing of multi-input linear-nonlinear cascade models for cells in macaque striate cortex" was previously sent to the Air Force on January 1, 1992, and another copy is included as an appendix to this report. The paper describes results from quantitative testing of multi-input feedforward *LN* and *LNL* structural models for simple and complex cells. Results from both monocular and binocular cells are described in the paper, but all analyses are characterizations of the monocular properties with respect to the dominant eye. Full binocular model analyses of these same cell data are still in progress and proceeding well.

Monocular modeling results. With respect to the monocular properties of simple and complex cells in the monkey, we have obtained the following results. First, we found that V1 cells can be divided into two major groups based on the degree to which their first- and second-order kernels are consistent with a multi-input LN (or LNL) model; the resulting classification was highly correlated with the simple cell versus complex cell distinction as determined by using a conventional modulation index computed from each cell's responses to drifting gratings. The general agreement between these measures validates the statistical methods we have developed for testing a cell's kernels against the predictions of the LN and LNL structural models.

However, the structural model test indices are substantially more informative than a simple modulation index. First, they are not specific to a particular stimulus orientation, direction, spatial frequency, or temporal frequency, but are in general based on a fine grain analysis of dynamic first- and second-order interactions throughout the receptive field. Second, although we describe in the paper results from tests of multi-input LN and LNL models, the approach generalizes to the testing of arbitrary models for which kernel relations can be derived. We have already developed tests for a large class of feedforward nonlinear models (Chen, Jacobson, and Gaska, 1990), and similar tests have been derived by ourselves and others for nonlinear models that include feedback (e.g., Pece *et al.*, 1990).

Judging from their structural test indices, complex cells deviated more strongly from LN behavior than did simple cells, a result we certainly anticipated. However, as described in our paper in review, no simple cell in our sample was fully consistent with an LN model even under the steady-state stimulus conditions employed. On average, only about 60 percent of the first- and second-order white noise stimulus-response relation of simple cells was consistent with LN behavior. Only 20 percent of the simple cells we studied with both white noise and gratings had an LN consistency level that was 80% or greater.

The substantial deviation of many simple cells from LN behavior was a surprising result which only became apparent to us as we proceeded to refine our statistical analysis of the data. Most simple cells in the macaque striate cortex clearly include additional nonlinearities in a feedforward or feedback path that have a strong effect on cell responses even during steady-state stimulation with spatiotemporal white noise.

Evidence concerning the spatiotemporal filter properties of the mechanisms that underlie the additional nonlinearities is contained in the first- and second-order kernels of these cells. Our subjective observations of the kernels suggest that these nonlinear mechanisms have the signature of units that fail to encode contrast sign, possibly resulting from subcortical nonlinearities or, perhaps resulting from feedback from simple and/or complex cells. Examples illustrating the nature of the deviations from LN model behavior are included in the paper in review. Further

consideration will be given to the interpretation of such clues as we continue to analyze our existing database.

Binocular modeling results. Although we are still in the process of analyzing data from binocular studies of simple and complex cells, several conclusions that relate to our stated objectives have already become apparent.

First, we discuss results that are relevant to Objective II in the Research Objectives section. Since as described above, many simple cells deviate substantially from LN behavior with respect to their *monocular* response properties, we should perhaps not be surprised to discover similar deviations from LN behavior with respect to their *binocular* summation properties. This has indeed proven to be true for binocular simple cells that have been analyzed thus far. The binocular LN model tests we are using involve the relationship of the left- and right-eye components of a cell's first-order kernel and the cross-eye component of the cell's second order kernel. The latter cross-eye data characterizes much of the nonlinear interaction between inputs from the two eyes.

Unfortunately, we are still not far enough along with these analyses of binocular simple cells to determine whether monocular or binocular deviations from LN behavior differ in degree. Nevertheless, our results to date showing deviation of binocular summation from LN behavior clearly contradict, to some extent, the results obtained by Ohzawa and Freeman (1986a) for binocular simple cells in the cat, since they concluded that dichoptic summation was linear prior to truncation at the output of binocular simple cells. Indeed, even our monocular results would seem to contradict past studies of the linearity of monocular summation by simple cells is the cat (Movshon, Thompson and Tolhurst, 1978a; Andrews and Pollen, 1979; Pollen, Gaska and Jacobson, 1987).

Quite possibly, results using stimuli with a narrow spatial-frequency passband fail to invoke certain types of nonlinear behavior that would become apparent with broadband stimulation such as is characteristic of spatiotemporal white noise. This is not an unreasonable hypothesis since nonlinear interactions between paired gratings of different spatial frequencies, believed to be of cortical origin, are well established in the cat, and may also be present in the cortex of the monkey, although the monkey has been studied far less in this regard. Alternatively, the strong local contrast of white noise stimuli may strongly evoke nonlinearities at subcortical levels since, for example, LGN cells are known to exhibit substantial response truncation at higher contrasts. It is presently not known whether nonlinearities arising in the separate ON and OFF channels of the LGN are effectively compensated for by mechanisms at the cortical level.

In either case, LGN nonlinearities can't explain our observed deviations from LN behavior with respect to dichoptic summation. This conclusion is reached as follows. First, we know that the initial point of convergence of dichoptic signals onto single neuronal target cells occurs within the cortex. But, in general, if two channels are combined linearly at some stage, then the cross-channel kernel measured at that stage must be identically zero even for highly nonlinear input channels. In the present context, nonlinear subcortical channels could not lead to nonzero cross-eye kernel unless a cortical nonlinearity follows convergence of the dichoptic signals at the cortical level. This certainly bolsters the argument in favor of a cortical origin for the apparent failure of dichoptic summation during white noise stimulation.

With regard to Objective III, we strongly believe that we have found two classes of complex cells that are the monkey equivalents to the two classes of binocular complex cells discovered by Ohzawa and Freeman (1986b) in the cat. They refer to these as phase-specific and non phase-specific complex cells, as describes their sensitivity to the relative phases of dichoptically presented pairs of gratings.

Although dichoptic grating stimuli have not been specifically used in the present investigation, analysis of our binocular data has demonstrated that two subclasses of binocular complex cells exist also in the *monkey* visual cortex. As anticipated in the grant application, one subclass (presumed to be phase-specific) have non-zero second-order cross-eye kernels—hence, as argued above, a fundamental nonlinearity occurs after the convergence of inputs from the two eyes. In contrast, a second subclass of complex cells (presumed to be phase non-specific) have second-order cross-eye kernels that are identically zero—hence all nonlinearities must occur *before* the convergence of inputs from the two eyes.

A binocular complex cell whose second-order cross-eye kernel, (as well as all other higher-order cross-eye kernels), is identically zero would be insensitive to the phase of a pair of dichoptically presented gratings. This fact supports the investigator's presumption that that the second subclass of complex cells described in the above paragraph, having a zero cross kernel, is likely to correspond to the phase non-specific subclass identified by Ohzawa and Freeman (1986b). If this association is correct, then, as discussed above, phase independence of this class of complex cell is a straightforward consequence of the structure of the underlying network.

However, as discussed in Objective V, Ohzawa and Freeman (1986b) also suggested an alternative model for non-phase specific complex cells in which a lack of phase specificity to pairs of *extended* gratings could result from a random jitter of binocular disparity tuning throughout the receptive field. However, a random jitter model predicts a non-zero second-order cross-eye kernel whose binocular interaction phase varies randomly across space. But, of the binocular complex cells with non-zero second-order cross-kernels studied by the present investigators,

none exhibited such randomness in their interaction phases. Rather, they exhibit an essentially constant (non-random) interaction phase which would lead to phase-specific responses to pairs of dichoptically presented gratings. (This is apparent from the stated properties of the kernel together with the form of the multi-input Wiener G-functional expansion term of second order which can together be used to predict the response contribution of the cross-eye kernel). In short, a random phase model for phase non-specific complex cells in the monkey is rejected by our data. This therefore answers Objective V which sought to determine the proper model for phase non-specific cells.

With respect to Objective IV, the feasibility of modeling phase-specific cells in the monkey using a straightforward binocular generalization of the Pollen and Ronner (1981) 4-cell quadrature model, our results clearly show that this is a reasonable model. In particular, the second-order cross-eye kernels have essentially the same appearance as the second-order same-eye kernels, consistent with a straightforward binocular generalization of the monocular 4-cell model by supposing that the underlying simple cells are binocular. Of course, Ohzawa, DeAngelis, and Freeman (1990a) have already arrived at the same conclusion based on their experiments employing white noise to study binocular encoding by complex cells in the cat.

With respect to Objective VI, we have analyzed enough first-order kernels from binocular simple cells to conclude that the restriction to 0 and 180 degree relative phase relations for the left- and right-eye spatial receptive field profiles predicted by our disparity estimation theory (Gaska, *et al.*, 1988) must be wrong. The relative phases of binocular simple cells in the monkey are more variable than our model would predict. The variability of the binocular phase difference was first emphasized by Ohzawa, DeAngelis and Freeman at ARVO (1990) where we also presented our first preliminary data on the relative phases of binocular filters in the monkey (Jacobson and Gaska, 1990).

In retrospect, given our familiarity with the seminal findings of Poggio and Fischer (1977) on near, far, tuned inhibitory, and tuned excititory binocular mechanisms in the cortex, we should have ourselves anticipated widely varying phase relations between the left- and right-eye filters of binocular simple cells. It is interesting to note that binocular simple cells whose binocular filters have a 0 or 180 degree phase relation could operate directly on a sum or difference image representation derived by mechanisms presynaptic to the binocular simple cell. However, binocular cells with more general phase relations must, in effect, apply independent filters to the inputs from the two eyes.

Finally, with regard to Objective VII, the simple cell component of our original model for cortical disparity estimation must clearly be modified to incorporate the results on relative inter-eye phase variability described above. Such binocular phase results obtained first (for the

cat) in Freeman's laboratory have led them (Ohzawa *et al*, 1990a,b, DeAngelis *et al.*, 1991) and Nomura *et al.* (1990) to independently suggest that the filter envelopes of all simple cells may be in retinal correspondence (ie. have no spatial disparity shift) and that disparity tuning may result solely from relative phase differences in the left and right eye filters. This represents a radical departure from previous binocular theories in which position differences were emphasized as a basis for disparity tuning. As shown by Nomura *et al.* (1990), phase differences in the left and right eye filters of simple cells certainly have a profound influence on their disparity tuning curves, producing near, far, tuned excititory, and tuned inhibitory responses such as those described by Poggio and Fischer (1977) for real monkey visual cells. However, we have recently developed an alternative interpretation of the inter-eye phase variations which is motivated by functional considerations.

Briefly, complex-like units in our modified theory for disparity estimation encode not only the *in-phase* component of inter-eye Gabor signal correlation (tuned inhibitory or tuned excititory response behavior) as in our original theory, but also a *quadrature* correlation component (near or far response behavior). **This is an important point.** In effect, a phase-dependent complex cell in the cortex (we're talking about real cells here!) effectively acts to encode a cross-correlation between two complex-valued spectral coefficients (Gabor or whatever), each derived with respect to a different eye. Mathematically, such a correlation only yields a real-valued result if the spectral coefficients are identical (such as when the left and right eye image patches, as seen by the cell, are non-disparate); otherwise the correlation result is complex-valued. If the entire correlation is to be encoded, then there must be both in-phase and quadrature mechanisms to encode the real part and imaginary part of the correlation, respectively. Returning again to a discussion of our modified theory, the addition of the new quadrature correlation component therefore causes the binocular correlation representation to become informationally complete. It can also help to control vergence movements, and can be used together with the in-phase correlation component to normalize network activity to discount *contrast differences* in the two eyes—something not possible in our original theory.

The completeness of the new binocular representation relates to the fact that the response of a binocular mechanism (simple or complex cell) with an arbitrary inter-eye phase relation can be obtained as a linear combination of binocular in-phase and quadrature-phase mechanisms. Therefore, a considerable redundancy of information is inherent in most theories that postulate that disparity information is encoded by a population of cells (> 2) that differ only in their inter-eye phase differences. In practice, any linear combination of the in-phase and quadrature-phase components could be used a representational basis for the inter-eye correlation function. Local orthogonality of inter-eye phase differences is predicted by the modified theory for a small

cluster of cells that would encode the binocular correlation at a single position, orientation and spatial-frequency. However, the choice of basis could still vary across the cortex, consistent with the empirical finding that, when data are pooled across all cells, the inter-eye phase differences of simple cells appear to be distributed quite uniformly.

Freeman's group and Nomura *et al.*, (1990) as discussed above, are promoting the idea that disparity estimation might be achieved strictly on the basis of mechanisms whose left and right eye receptive field *envelopes* are in strict retinal correspondence.

In contrast, our modified model for disparity estimation still retains spatial displacements of the left- and right-eye receptive fields to estimate non-zero disparities in an image. Phase differences in the left- and right-eye spatial filters of simple cells would only be present to permit the encoding of both in-phase and quadrature-phase inter-eye correlation components at a single disparity—providing therefore a parsimonious explanation for the existence of tuned excititory, tuned inhibitory, near, and far disparity-tuned cells. However, the presence of such mechanisms would in no way negate the importance of using displaced cortical filters as a means for encoding non-zero disparities.

Unfortunately, as pointed out by DeAngelis *et al.* (1991), there is still insufficient empirical evidence to decide between a pure phase model (such as they are promoting) or a combined displacement and phase model (such as ours) for binocular filtering by simple cells. This very fundamental question concerning the encoding of disparity certainly ranks as one of the most important unresolved issues facing the cortical vision community today.

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PROJECT PERSONNEL.

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NEW DISCOVERIES.

Quantitative procedures were developed for testing block-structured models for multi-input nonlinear visual circuits studied with spatiotemporal white noise. The new methods were used to test multi-input structural models for the monocular and binocular filtering by simple and complex cells in the striate cortex of the macaque monkey. A linear-nonlinear (LN) model test index was found to be suitable for classifying cells as simple versus complex. Although simple cells were better modeled as LN systems than complex cells, most simple cells deviated considerably from LN behavior. A nonlinearity of cortical origin would appear to be responsible, possibly activated more strongly by broadband noise than by sinewave grating stimuli. Also, two classes of binocular complex cells were identified. Whereas all binocular complex cells necessarily have a non-zero second-order "same-eye' interaction kernel, their second-order "cross-eye" interaction kernel could, it was found, be either non-zero or identically zero. The two binocular complex cell classes are thought to be the monkey equivalents of the "phase specific" and "phase non-specific" cells previously discovered by Ohzawa and Freeman (1986b) in the cat. A random-jitter disparity tuning model suggested by Ohzawa and Freeman was found to be inconsistent with "phase non-specific" cells in the monkey, rather they must linearly combine nonlinear monocular inputs—as alternatively suggested by Ohzawa and Freeman. The left and right eye filters of simple cells in the monkey were found to have broadly varying phase relationships. Finally, a quadrature correlation model for stereo depth estimation was developed to account for recent new findings by ourselves, and others.

APPENDIX: SOFTWARE DESCRIPTION

ND : A C-callable function library for multi-dimensional array processing.

A library of 'C' callable functions has been developed to facilitate the storage and processing of multi-dimensional arrays of data. This function library, denoted hereafter as "ND", enables one to manipulate arrays with arbitrarily many dimensions, including also zero-dimensional arrays (ie. scalars).

Each array in ND can contain data of type "int", "float", "double", "complex int", "complex float", or "complex double." In addition, an "array" data type is included to permit arrays of arrays of ... to any depth. Functions are also included that permit the user to dynamically add new data types which can then be allocated, deallocated, and otherwise manipulated by many of the basic ND functions.

Various ND functions can be used to create child arrays that define alternative multi-dimensional mappings into all or part of an existing parent array's data field. Any child array can also have children of its own which continue to refer to the original ancestral array's data field. Trees of array dependencies are automatically maintained by link fields so that a parent array with "living" children can be deallocated by the user at any time; such a parent array is simply flagged as dormant and the actual deallocation of the parent array's data is automatically deferred until all of its descendent arrays have themselves been deallocated.

ND allows the user to "attach" an array of binary data located in a file on a system disk; the data in the file is mapped into the user process's virtual memory space and the data in the file can then be read/written or both like any other ND array that resides in main memory. The file is automatically unmapped and closed when the attached array is deallocated.

ND currently includes functions for: element-by-element sums and products of arrays, outer sums and products of arrays, inner products of arrays, element-by-element polynomial expansion of an array, array smoothing and integration, array interpolation and decimation, array transpositions, array duplication and copying, subarray mappings and data extractions, array data type conversions, array storage and retrieval from disk, array statistics calculation, and multi-dimensional array index manipulations. All functions minimally accept array arguments whose data type conforms to one of the six fundamental real and complex data types mentioned earlier. When a function receives two or more array arguments with different data types, automatic type conversion is performed as necessary on the inputs and the function returns a result whose data type is automatically promoted.

The ND function library exemplifies a programming philosophy that is crucial to the rapid prototyping and development of multi-dimensional signal processing applications. Namely,

rather than implementing an algorithm (e.g., an FFT) as multiple routines, each specific to data of a different array dimensionality and type, one should instead seek to write a single routine that is applicable to arrays of arbitrary dimensionality and data type. With careful design, such generality can be achieved with little sacrifice in computational efficiency.

The ND C-callable function library serves as the basis for most data analysis software that was developed during the present project. We next describe a module that builds on the capabilities of the ND function library to make it possible to interactively view ND arrays.

Although the original and most capable version of the ND library was developed to run on Silicon Graphics workstations, a portable version of the ND library with most of the capabilities of the original version is also now available. The portable version is suitable for use on PCs or any other platform on which a C compiler is available.

LOOK : A C-callable software module for interactive viewing of ND arrays.

As previously discussed, the nonlinear network analysis methods developed during this project make use of estimated first- and second-order kernels of a neuron. For a 2D spatial noise study, the first order kernel is a three-dimensional function and the second-order kernel is a six-dimensional function (See Fig. 1). These functions must be viewed and interactively manipulated by the experimenter at several stages of analysis.

For example, the second-order kernel of a neuron is generally non-zero only over a limited region of its six-dimensional space. Only by viewing the computed kernel estimate can the experimenter determine the actual location and extent of this 6D region. In some cases, the estimated kernel is observed to be so corrupted by noise that it must be completely discarded. However, when the kernel is discriminable from the noise, the experimenter must determine whether the kernel power is wholly contained within the region over which the estimate was computed. If not, the region of computation must be expanded and the kernel recomputed. Once the full support of the kernel is included in the estimate, the experimenter must then crop the kernel in six dimensions so as to eliminate regions consisting entirely of noise. Such cropping greatly enhances the sensitivity of the methods we have developed to evaluate various nonlinear models for a neuron's network.

Also, with a little practice, one acquires the ability to infer many properties of a neuron by merely viewing its kernels. For example, it becomes quite easy to subjectively determine from a neuron's kernels whether it is orientation tuned, whether it is directionally selective, or whether it should be classified as simple or complex.

To make these interactive tasks possible, a C-callable software module, hereafter referred to as "LOOK", has been developed during this project. LOOK enables the experimenter to

view a multi-dimensional array of data with arbitrarily many dimensions. The user can view all dimensions simultaneously or, alternatively, view the data contained within an arbitrary rectangular subvolume of the multi-dimensional space.

Multi-dimensional data viewing is accomplished in LOOK by first partitioning an N-dimensional data array into three-dimensional rectangular subarrays, and then recursively nesting these blocks in 3D space so as to encompass the remaining input dimensions. The resulting 3D volume mosaic image can then be viewed one 2D (x, y) slice at a time on the computer screen, using a scroll bar to move through the third (z) dimension.

The user can use LOOK to manipulate the viewed data in several ways. First, the original ND array can be interactively cropped to include any desired rectangular subvolume of data. Second, each dimension $(1, ..., N)$ of the cropped data array can be independently assigned to one of the x, y, or z dimensions of the volume mosaic image. Third, one can specify the desired nesting order of the input dimensions assigned to each output dimension (x, y, z) of the volume mosaic image. Optionally, all input dimensions can be assigned to output dimensions x and y, enabling the experimenter to instantaneously view the entire ND array on the screen in the form of a recursively nested mosaic of two-dimensional images. Finally, LOOK permits the user to save any cropped subregion of an ND array to a new file, and both 2D and 3D contour plots can be interactively generated from the data in the LOOK window.

LOOK was invaluable to this project. It provided a window into the operation of kernel analysis software during development and debugging, and it is extensively used now to perform routine data analysis tasks. (An example of the appearance of the LOOK user interface is shown in the figure attached at the end of this report. Illustrated in the LOOK data window in that figure is a mosaic view of all six dimensions of the second-order kernel of a simple cell from monkey V1.) LOOK currently runs on Silicon Graphics Workstations using the SGI-standard GL graphics library.

KCAL: Nth-order monocular and binocular kernel calculation.

Another application developed during this project is a program for kernel calculation, hereafter referred to as "KCAL". KCAL is used to compute the self- and cross-kernels of multi-input visual neurons driven through either one or both eyes. Owing to its use of the ND function library, KCAL can be employed to estimate system kernels of any order. To use KCAL, the experimenter must specify the names of stimulus and response description files, and the root name of the output kernel file(s). The user is then prompted for additional information including the order of the desired kernel, and the region over which the kernel is to be computed. The region of computation is specified by a time-delay interval together with a rectangular spatial

support region that is separately specified for each eye.

KCAL can be used to compute kernels associated with binary, ternary, or general N-ary stimuli. Kernels can also be computed with respect to modulation along multiple axes in color space, including nonlinear response interactions arising between stimulus components directed along these color axes. KCAL also provides an option to compute multiple estimates of the system kernels, each computed from a distinct epoch of the stimulus response record. This capability is currently used to assess the degree of stationarity in each neuron's response properties. In particular, conditions such as significant eye movement or loss of spike discrimination are readily detectable on the basis of systematic changes in such epochal kernel estimates.

To facilitate rapid calculation of higher order kernels, KCAL automatically detects the number of CPUs in the host computer (any Silicon Graphics Power Series Multi-processor machine) and spawns additional threads to distribute the computation among all available CPUs. (The computer used in this project was a Silicon Graphics 4D/120 GTX which has two CPUs).

subheadingNonlinear structure testing software

The last category of software includes programs that are used to test candidate structural models for a neuron's underlying multi-input nonlinear network. Each structural model (e.g., a multi-input L-N or L-N-L model) is associated with one or more necessary conditions. These necessary conditions are multi- dimensional equations, (involving the system kernels), that must hold if the associated structural model is valid.

In practice, each necessary condition is evaluated in two principal stages: First, a system's estimated kernels must be substituted into an equation that defines the necessary condition. Second, statistical methods must be employed to test the hypothesis that the resulting multi-dimensional equation is satisfied. If this hypothesis is rejected by the data, then the corresponding structural model is also rejected; otherwise, the corresponding structural model is deemed to be consistent with the kernel data.

Software has been developed to generate each multi-dimensional term comprising the necessary conditions associated respectively with the multi-input L-N and L-N-L models. (Coverage of additional models is in the works). The same software also resolves a free parameter (a scale factor) in each resulting equation by employing a minimum mean square error (MMSE) criterion. There results a multi-dimensional error residual which is retained for subsequent statistical analysis.

Software has also been written to estimate the statistics of the multi-dimensional noise process that corrupts each term in the above-mentioned equations. Estimation of the noise process statistics is facilitated by computing estimates of the system kernels over non-causal time intervals where the signal component is necessarily zero. The estimated noise statistics also take

into account the fact that the necessary conditions generally involve nonlinear transformations of the kernels, resulting therefore in a nonstationary noise process. The term-by-term noise statistics are subsequently combined to produce an estimate of the statistics of the multi-dimensional noise process that corrupts the residual obtained during evaluation of each necessary condition.

Finally, software has been developed to apply several statistical tests to each multi-dimensional residual. In particular, hypothesis testing is used to determine if the difference between each residual and its corresponding estimated noise process is too large to be accounted for by chance. If the differences are too great, then the multi-dimensional residual is judged to contain a systematic error. This implies that the corresponding necessary condition is not satisfied, and hence the associated structural model must be rejected. Otherwise, the structural model is deemed to be consistent with the estimated low-order kernels of the neural system under study. As the spatiotemporal resolution and signal-to-noise ratio of the kernel estimates improve, increasingly precise model discriminations can be made.

Readers of this report who have an interest in obtaining any of the software described above should feel free to contact:

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Note: The ND library is available in a portable version that is in a ready-to-ship state, although documentation is still somewhat sparse. LOOK, currently specific to Silicon Graphics platforms, will probably go through a major revision in the forseeable future to make it compatible with X window enviornments. A portable version of KCAL could be developed in a short time if there is a demand for it. The structural test software is the least refined and is not entirely self-contained since it uses some functions from the "Recipes in C" library.

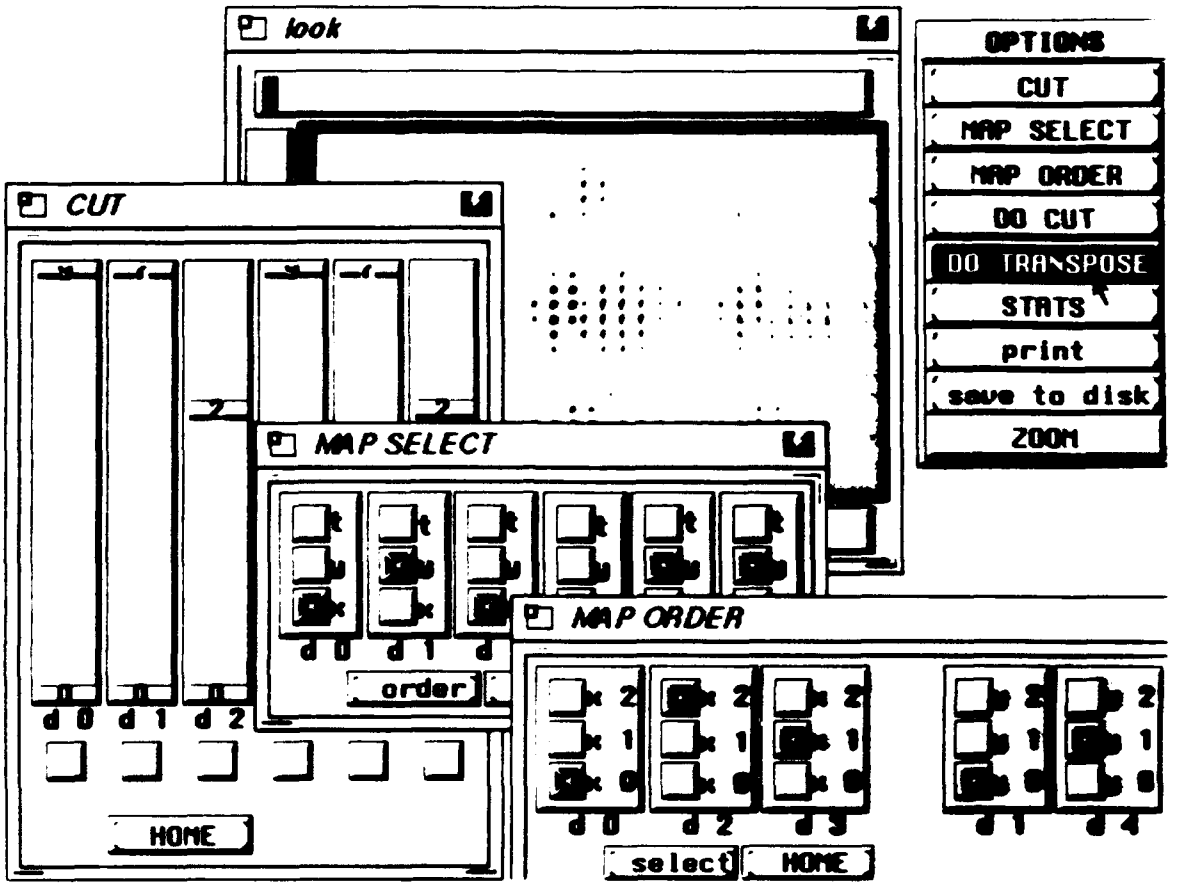

Figure 1. Appearance of the LOOK user interface As was described in the Appendix, LOOK was developed to facilitate interactive viewing of data arrays with arbitrarily many dimensions. Illustrated in the LOOK window above are all six dimensions of a (10 x 8 x 3 x 10 x 8 x 3) slice CUT from the second-order kernel estimated for a simple cell from monkey V1.

The six dimensions shown in the LOOK window correspond to the (2D) spatial position and (1D) delay of test ($d0, d1, d2$) and reference ($d3, d4, d5$) stimulus spots; the stimulus spots constitute a two-dimensional, 60 Hz noise movie that was presented on a $10x8$ grid which covered the cell's receptive field. The interpretation of the data is as follows. At (6D) coordinates where

the kernel appears bright, paired stimuli caused net excitation (inhibition) of the cell's response when the spots were of the same (different) polarity. Conversely, at coordinates where the kernel appears dark, paired stimuli caused net inhibition (excitation) when the spots were of the same (different) polarity. [Note: Same polarity: B–B or D–D, Different polarity: B–D or D–B, where B = bright spot, D = dark spot relative to mean background luminance.] The excititory/inhibitory sensitivity of the cell to paired spots, as revealed by the second-order kernel, is not all or nothing, but rather is continuously distributed.

Note that via the SELECT and ORDER control windows, the user has instructed LOOK to display all six array dimensions simultaneously in the form of "a 2D mosaic of 2D mosaics of 2D images." The innermost $x - y$ dimensions in the LOOK window correspond to $d0 - d1$ (spatial coordinate of test spot), the next outer $x - y$ dimensions are $d3 - d4$ (spatial coordinate of reference spot), and the outermost $x - y$ dimensions are $d2 - d5$ (time delays since presentation of test and reference spots). The spatial and temporal resolution of the illustrated kernel are 0.1 deg/sample and 16.7 msec/sample, respectively.