The Classification of Spatial, Chromatic, and Intensity Features of Simple Visual Stimuli by a Network of Retinal Ganglion Cells

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ABSTRACT

We are investigating the representation of simple visual objects by groups of retinal ganglion cells and are simultaneously recording the responses of ganglion cells in the isolated turtle retina with 15 out of an array of 100 penetrating microelectrodes. Stimulation is with circular spots of light of various intensities, diameters and colors. We have trained a three layer artificial neural network to estimate the stimulus parameters and have challenged it to classify the color, size and intensity of test stimuli. Individual ganglion cells are poor encoders of stimulus features, but the 15 cells in our sample allow one to classify intensity, color and spot diameter to within 0.6 log units, 61 nm, and 0.68 mm, respectively.

INTRODUCTION

There is considerable preprocessing of visual information that takes place by the vertebrate retina before it is sent to higher visual centers. The preprocessing begins in the photoreceptors and is elaborated by each of the neurons in the radial and lateral retinal pathways. Before the retinal visual signals reach the first synapse, they have already been substantially preprocessed. Each cone transduces the local light incident upon the retina into an electrical signal. The phototransduction process has an “automatic gain control” whereby cone gain (mV/photon) is set by the flux of light that strikes each cone. This gives the cone both high contrast sensitivity and good dynamic range over a very wide range of ambient illumination conditions (1). The mosaic of cones, and the different absorption spectra of the three types of photopigments found in the red, green and blue cones separates the incident colored light image into three superimposed primary images. Thus, cones perform a spatial, chromatic and intensity decomposition of the incident light stimulus.

The cones also begin the process of spatial band pass filtering. This spatial filtering is augmented by the triad synapse composed of the cones, horizontal cells and the bipolar cells. The horizontal cells have large receptive fields that provide an inhibitory surround for the bipolar cells. Light that excites cones that are presynaptic to a bipolar cell produces a direct response in the bipolar cell (the “center” response), while light some distance away excites cones that inhibit the direct response (the “surround” response) (2). This spatial antagonism, called lateral inhibition, produces a band pass spatial filtering of the visual image. By the time this filtering has reached the second order retinal neurons, the spatial, temporal and intensity filtering of the stimuli striking the retina, as well as the orientation selectivity of the receptive fields of these cells, have all been achieved.

These observations on retinal anatomy and physiology have established that retinal signal processing. By the time that a retinal ganglion cell is reached, the visual stimuli have already experienced signal processing in the retina that has encoded many aspects of the visual stimuli, the spatial orientation, spatial frequency, color, form and intensity of visual stimuli. These retinal ganglion cells are stimulated by visual stimuli and respond to their repeated presentation. The responses of individual ganglion cells to patterns of light have been studied extensively using multi-electrode array techniques. However, the identity and the parameters of the stimulus can be identified only if the parameters of the stimulus can be identified by the individual ganglion cells. The identification of the stimulus parameters has been limited by a lack of a suitable method for recording the responses of large numbers of cells. Our understanding of how the retina encodes the visual input has been made possible by the use of multi-electrode arrays that can record the responses of individual ganglion cells to patterns of light. We have used multi-electrode arrays to record the responses of individual ganglion cells to patterns of light.

We have used a high density array of penetrating microelectrode to study the responses of simple visual stimuli by ganglion cells. The study has focused on two questions: how the retina encodes visual stimuli from the patterns of firing of the ganglion cells; and, to what degree does the visual system encode the spatial, temporal and intensity properties of the visual stimuli.

The network (4), trained with back propagation, contains two layers of simultaneously recorded ganglion cells to perform a spatial, temporal and intensity decomposition of the visual stimuli. The network able to classify the intensity, color and orientation of visual stimuli into three superimposed primary images. The network is able to classify the intensity, color and orientation of visual stimuli into three superimposed primary images.
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In order to encode visual objects by groups of retinal ganglion responses of ganglion cells in the isolated turtle microelectrodes. Stimulation is with circular visual information that takes place by the visual centers. The preprocessing begins in each of the neurons in the radial and lateral signals reach the first synapse, they have the first transduces the local light incident wave. The phototransduction process has an input (mV/photon) is set by the flux of light both high contrast sensitivity and good of ambient illumination conditions. The absorption spectra of the three types of red, blue and green cones separates the incident colored light space. Thus, cones perform a spatial filtering of the visual image. By the time that the encoded visual image has reached the second order retinal neurons, it has lost information about the absolute light intensities striking the retina, as well as the very low spatial frequencies in the image.

These observations on retinal anatomy and physiology illustrate the complexities of retinal signal processing. By the time that the visual image has reached the ganglion cell level, it has experienced additional transformations. Each ganglion cell in this network is encoding many aspects of the visual image: color, space, intensity, temporal, etc. As a consequence, the identification of the color, intensity or shape of the visual stimuli should be possible by examining the firing patterns of the group of ganglion cells that are stimulated by the visual stimuli. We have begun a systematic examination of this notion.

The variability of ganglion cell responses is expected to confound the process by which the parameters of the stimulus can be identified from a set of responses. Ganglion cells do not have a stationary transfer function but manifest considerable variability in their responses to repetition of simple stimuli. This variability can be extreme in some cells and is less significant in others.

Further, the study of the representations of complex stimuli by groups of ganglion cells has been limited by a lack of a suitable means to sample the simultaneous activity of large numbers of cells. Our understanding of the biophysics of the individual ganglion cells has been made possible by the use of single microelectrodes to record the responses of individual ganglion cells to simple patterns of light. How these cells interact in a network to encode all the features of a complex image can best be understood using multiple microelectrodes. The recent development of high density microelectrode arrays has provided the tools that can be used to begin the study of these network properties.

We have used a high density array of penetrating microelectrodes to investigate the representations of simple visual stimuli by a small network of ganglion cells. Our study has focused on two questions: how accurately can we classify simple visual stimuli from the patterns of firing of the groups of neurons sampled by our electrode array, and, to what degree does the variability in the ganglion cell responses complicate this classification process. We have used a three level perceptron neural network (4), trained with back propagation to classify the responses of 15 simultaneously recorded ganglion cells to circular spots of various colors, intensities and diameters. Our multielectrode data at this point must be regarded as being of a preliminary nature, and we are presenting our findings as “work in progress”. We have found that while individual ganglion cells are quite poor classifiers of the general color, form, and intensity of visual stimuli, individual ganglion cells have response specializations: some are better classifiers of intensity, others are better at colors. However if the classification is performed using all fifteen recorded responses, the network is able to classify the intensity, color, and form of the stimulus to within 0.6 log units, 61 nm, and 0.62 mm, respectively. Correlations of 0.65-0.8 were observed between the estimated stimulus parameters and the actual parameters.
METHODS

Our extracellular ganglion cell recordings were made in the isolated superfused turtle retina preparation (5) using an array of 100, 1.5 mm long needles (The Utah Electrode Array). Our manufacturing techniques have been described elsewhere (6). The needles penetrate into the retina and record from groups of ganglion cells. They are built from silicon on a square grid with a 400 micron pitch. The distal 50 microns of each needle is metalized with platinum and forms an active electrode. The remaining parts of the silicon array are insulated with polyimide. In about ½ of the electrodes, we can use template generation and matching (7) to isolate single units from the multunit responses typically recorded with the array.

In this study we have selected electrodes that had the highest signal-to-noise ratios, and have isolated 1 to 2 units from the multiunit responses with the expedient of high thresholds. We refer to these as “single units” throughout this paper. While stable recordings could be made in this preparation in retinas that had been isolated for over eight hours, the retinas we used in our experiments were typically limited to four hours post isolation. The retinas were isolated from the pigment epithelium, and mounted photoreceptor side down and perfused with a physiological solution (5). The light stimuli were delivered to the photoreceptor surface, and the electrode array was inserted into the retina from the ganglion cell side.

Light stimuli were produced from a tungsten lamp with wavelength selection by narrow band interference filters. Intensities were controlled with neutral density filters. Responses were amplified with a 16 channel 25,000 gain bandpass differential amplifier (low and high corner frequencies of 250 and 7500 Hz). Fifteen channels of data plus one stimulus channel were digitized with a commercial multiplexed A/D board and data was stored in a Pentium based computer.

The electrophysiological data was presented to a variety of neural network models for training and subsequent classification of the test data. The neural networks were three layer perceptron models, with 330 input nodes (15 neurons with 22 time bins for each neuron), a hidden layer with from 25 to 35 nodes, and three output nodes. Training was with back propagation with momentum and adaptive learning rates. The training and data sets were obtained by random selection of two subsets of the ganglion cell data: a training subset composed of 1046 sets of 15 simultaneously recorded responses (22 time bins long), and 523 test sets of 15 simultaneously recorded responses.

RESULTS

Response recordings: The goal of this experiment was to learn how well recordings from a network of ganglion cells could be used to predict the shape, color, and intensity of the visual stimulus that evoked the set of responses. Eight sets of 15 simultaneously recorded responses from 15 electrodes to progressively dimmer flashes of 633 nm, 3.4mm diameter, light are shown in Figure 1. The stimulus duration was 0.2 seconds, and it was followed by a 0.24 second period of darkness. The data is displayed as a gray level two dimensional plot. Time is plotted on the abscissa (in terms of 20 msec time “bins”), unit number in spikes/sec (calculated from the number of spikes per unit represented in gray levels. All of the units have the same type. It is noted that while the individual responses are unique in terms of the number and timing of spikes in the temporal sequence during the response.

Figure 1-Dependence of 15 ganglion cell responses to dim stimuli in upper left, dimmest in lower right.

To illustrate how color and spot diameter influence the response patterns, we show in Figure 2, three sets of averaged responses to spots of light of various diameters and intensities. Figure 2A shows the set of averaged responses to 633 nm, 3.4mm diameter spot, with light intensity approximately 3 log units above the detection threshold, evoked responses in 1/3 of the units. Figure 2B shows responses to 546 nm flashes, again, about 3 log above detection threshold. The dependence of the set of neuronal responses to these flashes was decreased from 3.4 mm to 1.13 mm spot diameters. The central regions whose receptive fields were not well stimulated produced a smaller response, while others produced a larger response. To further illustrate this point, the three figures and Figure 1 illustrate the patterns that are taken as a whole, there are clearly asymmetrical differences in the response to various parameters of the stimulus.
were made in the isolated superfused turtle retina. The 0.15 mm long needles (The Utah Electrode have been described elsewhere) (6). The needles were inserted into the ganglion cells. They are 100 micron pitch. The distal 50 microns of the needle forms an active electrode. The remaining 50 microns is polyimide. In about 1/2 of the electrodes, latching (7) to isolate single units from the rest of the array.

Those had the highest Signal-to-Noise ratios, or Multiunit responses with the expedient of high Signal-to-Noise ratios) throughout this experiment. While stable recording in retinas that had previously been isolated for over 24 hours, the experiments were typically limited to four hours from the pigmented epithelium, and mounted in a physiological solution (5). The light was focused on the surface, and the electrode array was mounted on the cell side.

A tungsten lamp with wavelength selection by filter plates was used to control neutral density. A channel 25,000 gain bandpass differential amplifier with a low pass filter of 250 and 7500 Hz). Fifteen channels of the amplifier was digitized with a commercial multiplexed A/D converter.

Data were collected with a variety of neural network models for the test data. The neural networks were three layers (15 neurons with 22 time bins for each layer, 8 neurons, and three output nodes. Training was performed with adaptive learning rates. The training set was a set of 15 simultaneously recorded responses from the same cell.

The experiment was to learn how well recordings could be used to predict the shape, color, and darkness of the set of responses. Eight sets of 15 individually dimmer flashes were used to give the data in Figure 1. The stimulus duration was 24 second period of darkness. The data is plotted on the abscissa (in terms of 20 msec time "bins"). Unit number is plotted on the ordinate, and the firing rate in spikes/sec (calculated from the number of spikes in a 20 msec time interval) is represented in gray levels. All of the units shown in this figure are of the "on-off" type. It is noted that while the individual responses share certain kinetics, each response is unique in terms of the number of action potentials and their relative temporal sequence during the response.

Figure 1: Dependence of 15 ganglion cell firings on stimulus intensity (brightest stimuli in upper left, dimmest in lower right). Time (represented in bin numbers) on abscissa, unit number on ordinate and firing rate in gray levels.

To illustrate how color and spot diameter are represented in ganglion cell firing patterns, we show in Figure 2, three sets of 15 simultaneously recorded ganglion cell responses to spots of light of various diameters and colors. Figure 2a shows a reference set of averaged responses to 633 nm, 3.4 mm diameter circular spots of light, of an intensity approximately 3 log units above threshold (defined as the intensity that evoked responses in 1/3 of the units). Figure 2b shows how the photon set responded to 546 nm flashes, again, about 3 log above threshold. Finally, Figure 2c shows the dependence of the set of neuronal responses on spot diameter. Here, the spot diameter was decreased from 3.4 mm to 1.13 mm diameter. As expected, some units (those whose receptive fields were not well stimulated by the smaller spot) produced a smaller response, while others produced a slightly more vigorous response. These three figures and Figure 1 illustrate the point that when the neural response set is taken as a whole, there are clearly aspects of the units that seem to respond differentially to various parameters of the stimulus.
Figure 2-Effect of color (b) and spot size (c) on a reference set of 15 ganglion cell responses (a). Time (represented in bin numbers) on abscissa, unit number on ordinate and firing rate in gray levels.

Response Variability: Ganglion cell responses manifest considerable variability in sequential presentations of a fixed stimulus. The number and timing of the action potentials that make up the response vary from stimulus to stimulus. Thus, the differences seen in the responses of Figures 1 and 2 could reflect differences in the coding of various stimulus parameters, or they could simply reflect this nonspecific response variability.

An example of this variability is illustrated in Figure 3 where each panel is a plot of the responses of one of the 15 simultaneously recorded ganglion cells to a sequence of seven 633 nm, 3.4 mm diameter, 0.2 second long flashes that were about 3 log units above threshold. In each panel, time (reflected in 20 msec bin numbers) is plotted on the abscissa, and individual trial number is plotted on the ordinate. Firing rates (calculated from the 20 msec bins) are represented in gray level. These responses were recorded consecutively over a 3.5 second period, and were preceded by a 3.5 second sequence of flashes that were about 0.5 log units less intense. It is seen that some ganglion cells manifested considerable variability, while others had a more constant response. This figure illustrates the well known observation that ganglion cell responses to a repetitive stimulus vary substantially between cells and between responses. We conclude from these figures that while the intrinsic variability of responses from stimulus to stimulus could make discrimination of two very similar stimuli problematic, this will be less of a problem for classifying stimuli that are substantially different from each other.

Is Variability Global or Local? If the variability shown in Figure 3 were of a global nature, then the firing rates in all cells would wax and wane as a group and the changes in ganglion cell activity would not have a major effect on the encoding and our subsequent differential classification of the stimulus. However, if the variability were very local (i.e., some units increased their responses while adjacent units decreased their responses), the variability would make stimulus classification much more error prone.

Our results here are preliminary, and consist at this point of plots (not shown) of the total number of action potentials evoked by the stimulus in each of the fifteen cells for each of the seven successive presentations. This plot shows little consistent change in the number of spikes in each cell for each stimulus. Some increased their firing while other decreased their firing. Clearly, variability is a local phenomenon. Clearly, we can draw a significant conclusion.

Figure 3-Responses of 15 ganglion cell plots the responses of each cell to the 7 flash stimuli. Abscissa, stimulus number on ordinate.

Optimization of the neural network was implemented that contained from 25 to 35 units. It was trained and tested on their ability to classify responses. The number of training epochs was correlated to test stimulus parameters.

For the data used in this study, hidden units were found to only subtly affect the performance. Therefore, we focused our work on networks containing 25 units. The network models were also trained only for the responses expected from the response kinetics (Figure 4) and the highest correlations at time bins 3 and 7.

Classifications using entire data set: The training of our neural network model is to fully specify a randomly selected test stimuli when the model
the number of spikes in each cell for each presentation. Some cells increased their firing while other decreased their firing. Our tentative conclusion is that the response variability is a local phenomenon. Clearly however, more work is needed before one can draw a significant conclusion.

![Graph with data points and labels](image)

The variability shown in Figure 3 were of a global nature, but would wax and wane as a group and the individual cells have a major effect on the encoding and decoding of the stimulus. However, if the variability increased their responses while adjacent units increased their activity would make stimulus classification much more difficult.

![Graph with data points and labels](image)

Figure 3—Responses of 15 ganglion cells to 7 sequential flashes of light. Each panel plots the responses of each cell to the 7 flashes. Time (represented in bin numbers) on abscissa, stimulus number on ordinate and firing rate in gray levels.

Optimization of the neural network: Neural network architectures were implemented that contained from 25 to 35 nodes in the hidden layer. The models were trained and tested on their ability to classify the stimuli that evoked the set of test responses. The number of training epochs was optimized to produce the highest correlations between test stimulus parameters and neural network classifications.

For the data used in this study, hidden layers containing from 25 to 35 nodes were found to only subtly affect the performance of the models. Thus, for most modeling, we focused our work on networks containing 25 nodes in the hidden layer. Neural network models were also trained only to specific time bins in our response set. As expected from the response kinetics (Figures 1-3), classifications of test data showed the highest correlations at time bins 3 and 13, the times of maximal neural activity.

Classifications using entire data set: The most challenging classification problem for our neural network model is to fully specify the color, intensity, and spot diameter of randomly selected test stimuli when the network has been trained using a subset of the
entire data set. The classification capabilities of the optimized network architecture were tested by presenting input nodes with fifteen simultaneously recorded responses from our test data set. The classifications were made over the full range of 8 intensities, 9 colors and 6 spot diameters used in our stimulus set. Performance of the network was judged with histograms of the number of classifications of the stimulus parameter at each value of the test parameter.

The capabilities of the network to classify the intensity of the test stimulus is given in Figure 4a. The 8 histograms were constructed for 8 different test intensities. The value of each column is the classification of the neural network, and its height is the number of classifications. Perfect classifications would be represented as 8 single columns, running from the lower left to the upper right. Figure 4a illustrates two important features. First, as the intensity of the test stimulus was lowered, the network generally predicted that a lower intensity was used to evoke the responses. Second, the network often miscalculated the test intensity as judged by the width and mean value of each histogram.

<table>
<thead>
<tr>
<th>Correlation Coefficient</th>
<th>0.74</th>
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<tr>
<td>Standard Deviation</td>
<td>0.59 log units</td>
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Classification and training with variations in the first classification task we have given the neural network a very challenging task, especially true when one considers that the stimuli all share inherent inconsistencies (bright 700nm flashes, 400 nm flashes, both wavelengths only excite L cones to a very small extent). To make the classification task more difficult, we restricted both the training and test sets to contain only variations in one parameter. Thus, the training set only contains our largest diameter spots, and the test set only contains our largest diameter spots. The overall classification accuracy was only slightly improved. Greater than 70% of the classifications of 0.77 were obtained. Greater accuracy was found for the colors and spot diameters, but the reduced size of the training data set restricted how well individual ganglion cells are able to classify stimulus differences in the test data set. Fifteen separate tests were conducted and trained with our training data set; each neuron was tested with a different single unit. The number of training epochs for each neuron was determined by the greatest correlations between the predicted and actual classifications. The correlation coefficients for all fifteen neural network classifications are shown in Figure 4c (middle row), and spot diameter (bottom row).

Not surprisingly, the individual neural network completed the color and diameter task. Also not surprising, some neurons were better at classifying intensity (units 6 and 11), while others were better at color and diameter. Not surprisingly, the network performed best at the classification parameters: intensity, color, and spot diameter.
made misclassifications of the color and diameter of the stimuli, but generally, the histogram of the network responses were centered around the actual test values.

Figure 4 indicates that the neural network is able to classify the parameters of the test stimuli, but it does so with some errors. We have performed a linear regression between the test parameters predicted by the neural network and the actual parameters, and have used the correlation coefficients and standard deviation as a quantitative index of the classification performance of the neural network. These performance criteria are presented below.

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<th></th>
<th>Intensity</th>
<th>Color</th>
<th>Spot Diameter</th>
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<tbody>
<tr>
<td>Correlation Coefficient</td>
<td>0.74</td>
<td>0.65</td>
<td>0.81</td>
</tr>
<tr>
<td>Standard Deviation</td>
<td>0.59 log units</td>
<td>60.7 nm</td>
<td>0.62 mm</td>
</tr>
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Classification and training with variations in only one stimulus parameter: The classification task we have given the neural network is admittedly daunting. This is especially true when one considers that the dimensions of the training set contain inherent inconsistencies (bright 700 nm flashes are indistinguishable from dimmer 633 nm flashes, both wavelengths only excite long wavelength cones to any significant extent). To make the classification task more tractable, we have restricted our training and test sets to contain only variations in one stimulus parameter. When the stimulus set only contains our largest diameter spots, and only 633 nm stimuli, the network classification was only slightly improved. Correlation coefficients for intensity classifications of 0.77 were obtained. Greater correlation coefficients were expected, but the reduced size of the training data set resulted in this value.

Classifications by individual neurons: We have used neural networks to learn how well individual ganglion cells are able to classify the color, intensity and diameter of the stimuli in our test data set. Fifteen separate neural networks were implemented and trained with our training set; each neural network was trained with data from a single unit. The number of training epochs for each network was optimized to provide the greatest correlations between the predictions for the test data sets. The correlation coefficients for all fifteen neural network classifications for color (top row), intensity (middle row), and spot diameter (bottom row) are shown in Figure 5.

Not surprising, the individual neural networks performed poorly in the classification task. Also not surprising, some neurons were better classifiers of color than others (units 6 and 11), while others were better at classifying intensity units (5 and 13). As can be seen from Figure 5, none of the neurons were good classifiers of all three stimulus parameters: intensity, color, and spot diameter.
The data set that was used in our neural network was larger to allow us to train the network with a larger parameter. The isolated retina preparation of the retina is stripped away from the pig and at best minimal and in some cases, non-existent with a poor initial and gets poorer with each try. It is quite bright in order to evoke superthreshold responses.

In summary, the use of high density, silicon-based arrays to begin to get a glimpse of how more complex firing patterns of networks of ganglion cells to input stimuli allows one to better understand selective groups of neurons, and how this works over time. The techniques described here have been shown to reduce noise and variability in ganglion cell responses, and the role of coincident firing of groups of neurons.

REFERENCES


DISCUSSION

Figure 5-Correlation coefficients for classifications by each of all 15 units. Top, middle and bottom rows show results of single unit classifications of color, intensity, and spatial diameter, respectively. Ordinate is unit number.

This study was motivated to verify the intuitive notion that since spatial, temporal, chromatic and intensity information about visual stimuli is encoded in the spatial/temporal firing pattern of networks of ganglion cells, reliable estimates of the parameters of visual stimuli could be made from the responses of subsets of ganglion cells. We have been able to show that a neural network is able to use the temporal firing pattern of fifteen simultaneously recorded ganglion cells to classify the color, size, and intensity of a circular test spot with greater precision than was possible using individual single unit responses.

Unfortunately, the neural network performed this task with considerable error. Many of the errors were anticipated, and, as described earlier, were a simple consequence of the classification conflicts inherent in the original data set. Specifically, in some cases, we trained the network and challenged it to classify the color and size of spots that were of intensities below threshold (in this situation, the ganglion cells were "unaware" that any stimulation had occurred). In other cases, as seen in Figure 1, the responses to bright lights were often very similar: the network would have a particularly hard time distinguishing saturating intensities from supersaturating intensities. Finally, the network was expected to classify the spot size and intensities of short wavelength stimuli, a region of the spectrum where our incandescent lamp emitted minimal energy. Considering the number and size of these inherent "potholes" in the road that leads to accurate classification, it is not surprising that the neural network classified with less that total precision.

We have pointed out that we regard this study as "work in progress" and look forward to refining our physiological techniques so we can have greater confidence in our data.
The data set that was used in our neural networks, while large, should have been even larger to allow us to train the networks for stimulus variations in only one stimulus parameter. The isolated retina preparation also has another major difficulty; because the retina is stripped away from the pigment epithelium, photopigment regeneration is at best minimal and in some cases, nonexistent. This means that photosensitivity is poor initially, and gets poorer with each test stimulus and that test stimuli must be quite bright in order to evoke superthreshold responses.

In summary, the use of high density, silicon based microelectrode arrays is allowing us to begin to get a glimpse of how more complex visual stimuli are represented by the firing patterns of networks of ganglion cells. The use of neural networks to classify input stimuli allows one to better understand the extent of coding that occurs in selected groups of neurons, and how this encoding takes place, in terms of both space and time. The techniques described herein should provide us with new insights into noise and variability in ganglion cell responses, the stationarity of the coding process, and the role of coincident firing of groups of neurons in visual feature representation.

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(4) Perceptron neural networks obtained from MATLAB Neural Network Toolbox.