Lateral Geniculate Neurons in Behaving Primates

I. Responses to Two-Dimensional Stimuli

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SUMMARY AND CONCLUSIONS

1. Using behaving monkeys, we studied the visual responses of single neurons in the parvocellular layers of the lateral geniculate nucleus (LGN) to a set of two-dimensional black and white patterns. We found that monkeys could be trained to make sufficiently reliable and stable fixations to enable us to plot and characterize the receptive fields of individual neurons. A qualitative examination of rasters and a statistical analysis of the data revealed that the responses of neurons were related to the stimuli.

2. The data from 5 of the 13 “X-like” neurons in our sample indicated the presence of antagonistic center and surround mechanisms and linear summation of luminance within center and surround mechanisms. We attribute the lack of evidence for surround antagonism in the eight neurons that failed to exhibit center-surround antagonism either to a mismatch between the size of the pixels in the stimuli and the size of the receptive field or to the lack of a surround mechanism (i.e., the type II neurons of Wiesel and Hubel).

3. The data from five other neurons confirm and extend previous reports indicating that the surround regions of X-like neurons can have nonlinearities. The responses of these neurons were not modulated when a contrast-reversing, bipartite stimulus was centered on the receptive field, which suggests a linear summation within the center and surround mechanisms. However, it was frequently the case for these neurons that stimuli of identical pattern but opposite contrast elicited responses of similar polarity, which indicates nonlinear behavior.

4. We found a wide variety of temporal patterns in the responses of individual LGN neurons, which included differences in the size of the pixels in the stimuli and the size of the receptive field or to the lack of a surround mechanism (i.e., the type II neurons of Wiesel and Hubel).

INTRODUCTION

Recently, researchers from this laboratory reported that the temporal patterns of the response waveforms of neurons in the inferior temporal and striate cortices can vary with the stimulus presented (Richmond et al. 1987, 1990; Richmond and Optican 1987) and that this variation in the temporal pattern of the response carries stimulus-related information (Optican and Richmond 1987; Richmond and Optican 1990). These findings raised the question of whether this sensitivity of the temporal pattern of the response to the stimulus arises in the cortex or is seen at earlier precortical stages of the visual system, such as the lateral geniculate nucleus (LGN).

Traditional approaches

The responses of LGN neurons are governed by the spatial and temporal characteristics of their receptive fields. The receptive fields of most LGN neurons are modeled as two concentric regions, the center and the surround, that have different spatial extents and that act in opposition to each other in governing the response of the neuron. Rodieck (1965) proposed a difference-of-Gaussians model for cat retinal ganglion cells, in which the receptive field consists of two circular mechanisms shaped like Gaussian surfaces having a common center but opposite polarities and differing widths. This model can successfully predict the magnitude of the responses of one class of LGN neuron in cat and monkey, the linear summatons or “X-like” neurons, to one-dimensional sine wave gratings (Derrington and Fuchs 1979; Kaplan and Shapley 1982; Shapley et al. 1981; Shapley and Hochstein 1975; So and Shapley 1979). In addition to having different spatial extents, the center and surround mechanisms have different temporal properties (Dawis et al. 1984; Giclen et al. 1982; Ikeda and Wright 1972; Shapley et al. 1985). To account for these findings, Enroth-Cugell et al. (1983) and Dawis et al. (1984) modified the difference-of-Gaussians model to give the center and surround mechanisms different temporal properties.

A central assumption in previous studies is that only the strength of the response contains stimulus-related information (Barlow 1972). The temporal properties of the response waveforms have been used primarily to distinguish among classes of neurons—on the basis of either response transience (Derrington and Fuchs 1979; Ikeda and Wright 1972; Marrocco 1972, 1976) or the linearity of spatial summation (Enroth-Cugell and Robson 1966; Hochstein and Shapley 1976)—or to draw conclusions concerning the dynamics of how neurons integrate their inputs (Dawis et al. 1984; Enrogh-Cugell et al. 1983; Ikeda and Wright 1972). As a consequence, a major emphasis of previous studies of LGN neurons has been to determine how the center and surround mechanisms interact to affect univariate measures reflecting the strength of the response, such as the number of spikes elicited by flashed stimuli (DeValois et al. 1966; Hammond 1973; Marrocco 1972; Wiesel and Hubel 1966) or the depth of modulation to a time-varying stimulus (Dawis et al. 1984; Derrington and Fuchs 1979; Enroth-
Limitations of traditional approaches

Despite the progress that has been made, there are four ways in which the approaches described above remain limited in their ability to describe LGN neuronal function. 1) The bulk of the studies on the LGN have used spots, annuli, or one-dimensional gratings as stimuli. However, the use of these types of stimuli may obscure important details of the receptive field (Daugman 1980; Marmarelis and Marmarelis 1978), such as the anisotropies reported by Rodieck and Stone (1965b) for cat retinal ganglion cells. 2) The spatial frequency analysis that was so successful in substantiating the difference-of-Gaussians models of the LGN is most appropriate for linear systems (Shapley and Lennie 1985). However, even X-like neurons, the most linear neurons seen thus far in the mammalian visual system, show spatial linear summation only when stimulus contrast is low (Enroth-Cugell and Robson 1966; Enroth-Cugell et al. 1983; Hochstein and Shapley 1976); and the Y-like neurons in the LGN do not show linear spatial summation even in the low-contrast condition (Shapley and Hochstein 1975; Shapley et al. 1981; So and Shapley 1979). 3) The spatial patterns of the response waveforms of cat ganglion cells (Ikeda and Wright 1972) and monkey geniculate neurons (Marrocco 1976) can be changed by varying the stimulation of the center and surround regions. In addition, the magnitude of the second harmonic of the responses of cat retinal ganglion X-cells as function of the stimulus contrast (Enroth-Cugell et al. 1983), and the relative magnitudes of the first and second harmonics of the responses of retinal ganglion and LGN Y-cells, vary as a function of spatial frequency (Hochstein and Shapley 1976; Kaplan and Shapley 1982; So and Shapley 1979). These findings suggest that stimulus-related information may be carried in the temporal pattern of the response waveform (Bullock 1967; Lestienne and Strehler 1987; Mountcastle 1967; Perkel 1970), information that would not be recognized if only response amplitudes were measured. 4) Previous experiments in the LGN have been done by paralyzing and anesthetizing the animal to eliminate eye movements. Although paralysis ensures ocular stability and accurate alignment of the stimulus with the receptive field (Shapley and Lennie 1985), experiments conducted in this manner ignore the effects of arousal on the function of the LGN and the effect of anesthesia on neuronal responses (Coenen and Vendrik 1972; Maffei and Rizzolatti 1965; Sakakura 1968; Sestokas and Lehmkuehle 1988; Sherman and Koch 1986; Uhlich et al. 1989).

Communication channel paradigm

In their experiments on the visual neurons in inferior temporal cortex, Richmond and Optican introduced a paradigm that overcomes these limitations of the traditional approaches (Optican and Richmond 1987; Richmond et al. 1987; Richmond and Optican 1987). This paradigm treats neurons as communication channels and focuses on the messages neurons transmit about visual stimuli. The goal of the paradigm was to determine the relation between visual patterns that were neither moving nor flickering and both the number and temporal distribution of spikes in the response, rather than to measure the fidelity with which a neuron could respond to stimuli that are changing over time, either by moving or flickering them. Using this paradigm, Richmond and Optican studied the relationship between a set of two-dimensional stimuli and the responses of neurons in both the inferior temporal and striate cortices in behaving monkeys. The stimuli constitute a complete basis set for patterns, i.e., they can be used to construct any arbitrary, two-dimensional picture with a resolution of one part in eight or less on an 8- × 8-pixel grid. The analysis used a complete set of orthogonal waveforms, the principal components, extracted from the data to quantify both the strength and the temporal pattern of the response waveform. Because the stimuli were mathematically complete for representing any two-dimensional picture, they were ideal for studying neurons with rotationally anisotropic receptive fields. Because the quantification considered the contributions of both the number and the temporal distribution of spikes in the response when the temporal properties of the input were held constant, it was possible to assess whether independent information concerning the spatial pattern and the luminance of the stimulus was present in the temporal properties of the response waveform. Finally, because the experiments were conducted in behaving monkeys, the contaminating effects of low arousal and anesthesia were eliminated.

In these three papers we will show that this new paradigm can offer new insights into the function of neurons in the LGN. In this first paper we demonstrate the feasibility of studying single neurons in the LGN in awake monkeys, describe our findings, and relate them to previous studies. In the second paper we demonstrate the superiority of multivariate temporal codes over univariate codes in representing the stimulus-dependent features of the neuronal responses. In the third paper we present a model of parvocellular X-like neurons that accurately reproduces the shapes of the response waveforms of neurons to the stimuli in the basis set of patterns and that predicts the shapes of the response waveforms to arbitrarily constructed black and white stimuli. A series of preliminary reports describing these findings has been presented (Gawne et al. 1988; McClurkin et al. 1988; Richmond et al. 1988).

METHODS

Two adult male rhesus monkeys (Macaca mulatta) were used in these experiments. Data were collected from one hemisphere of each monkey.

Surgical protocol

A head fixation device, recording cylinder, and scleral search coil were implanted in each monkey. Implant surgery was carried out with standard sterile surgical techniques while the animal was under pentobarbital sodium anesthesia in a veterinary operating room. During the surgery, a socket to fix the head and a single unit recording chamber that allowed access to the LGN were attached to the skull with dental acrylic. Fifteen self-tapping stainless steel
bone screws were embedded in a circle around the top of the skull, and the skull was covered with cyanoacrylate tissue cement to aid in anchoring the acrylic pedestal. A magnetic-field search coil was implanted around the sclera of one eye (Judge et al. 1980). The search coil connector was embedded in the dental acrylic on the skull. Both of the monkeys used in this study recovered from the implant surgery without complications and remained healthy for the duration of the experiments.

Behavioral protocol

The monkeys were initially trained to obtain a drop of water by releasing a bar when a small fixation spot changed luminance slightly ("fixation-bar release"). When the monkeys were able to make 90% correct responses, the head fixation device, recording cylinder, and scleral magnetic search coil were implanted as described above. After the monkeys had recovered from the surgery, they were trained to perform a different fixation task. In this new task, the monkey's head was rigidly fixed, its eye position was monitored using the magnetic-field search coil technique (Robinson 1963), and it was rewarded intermittently with a drop of water (see below) for keeping its eyes positioned within a 2° square window surrounding the fixation point ("fixation only"). After a week of training on this new task, the monkeys were able to maintain their eye position within the fixation window for long periods of time and were able to make repeated fixations with <2° of error. Experiments were begun after the monkeys had learned the "fixation only" task.

Experimental protocol

During the initial experiments, the location of the LGN in relation to the recording cylinder was mapped by the use of glass-coated platinum-iridium electrodes. After this mapping, a guide tube was inserted into the brain to within 3 mm of the dorsal surface of the LGN and held in place by a grid positioned in the cylinder (Crist et al. 1988). The guide tube was placed to allow access to neurons with receptive fields within 10° of the fovea. The guide tube and positioning grid were left in place for up to 2 wk. Data collection was begun immediately after the mapping experiments.

For each data collection experiment, a tungsten electrode was lowered through the guide tube until a neuron in the LGN was isolated. The activity recorded by the electrode was amplified with an AC-coupled preamplifier. The amplified signal was then passed through an active Butterworth filter to remove the signals generated by the magnetic-field coils and any 60-Hz AC noise. The low-frequency shoulder of the Butterworth filter was set at 100 Hz, and the high-frequency shoulder was set at 10 kHz. The signal was then passed through a time and level waveform discriminator. For each spike that passed through both the time and amplitude windows, the discriminator generated a discrete pulse that was fed into a PDP 11 computer, which collected the data and controlled the experiment. The computer coded the arrival of the pulses; and these codes, together with the times of their arrival, were stored on a disk for later analysis.

The neurons were characterized by the use of a series of stimuli, presented on a video monitor, which reversed contrast at the rate of 2 Hz in a square-wave fashion. The positions of the stimuli were controlled with a joystick, and the minimum movement possible with our display was 0.03°. The stimuli alternated between black and white against a gray background. The characterizations of the neurons were made by listening to the responses on an audiomonitor. The location of the center of the receptive field of each neuron was plotted with horizontal and vertical 2 × 0.25° contrast-reversing bars. The polarity of the center mechanism was determined by stimulating the neuron with a contrast-reversing 0.25° square positioned in the center of the receptive field and noting which luminance of the stimulus, black or white, elicited an excitatory response. After determining the polarity of the center mechanism, we verified the location of the receptive field by moving the contrast-reversing 0.25° square to the previously determined edges of the center and listening for the response of the center mechanism. Finally, the linearity of the neuron was assessed by slowly moving a contrast-reversing bipartite (½ black and ½ white), 2° square back and forth across the receptive field. Hochstein and Shapley (1976), (cf. p. 248, Fig. 5, row 3, histograms 4, 5, 10, and 11) and Kaplan and Shapley (1982) (cf. p. 137, Fig. 6, row 2, histogram 1) have shown that the responses of Y-like neurons exhibit frequency doubling when a contrast-reversing grating of low spatial frequency is positioned so that the division between the light and dark parts of the grating bisects the receptive field center. The responses of X-like neurons, on the other hand, cease to modulate in this condition. This stimulus can be thought of as one cycle of a square-wave grating having a spatial frequency of 0.5 cycles/deg. We determined whether our bipartite flickering stimulus could be positioned so that either the modulation disappeared or it responded to each phase of the flicker (frequency doubled). For the neurons we recorded, we were always able to position our contrast-reversing bipartite square so that the neuron failed to show response modulation to the contrast reversal. After characterizing the neuron, we positioned on the receptive field a grid that defined the pixels in the stimulus such that the pixel immediately below and to the left of the center of the picture stimulated the center mechanism of the receptive field (see Fig. 1).

After a single neuron's activity was isolated and the visual receptive field characterized, the behavioral task was initiated. The time course of a trial is diagramed in Fig. 2. The fixation target was turned on 50 ms after the start of the trial and remained on for 300 ms, during which time the monkey had to begin fixating. If the monkey achieved fixation, the target was turned off, and the stimulus was presented 220 ms later and remained on for 256 ms. The onset of a stimulus was synchronized to the start of the vertical scan of the video monitor. The fixation target was turned on again 192 ms after the stimulus was removed and remained on for 300 ms. The reward, a drop of water, was delivered during this poststimulus fixation period on a variable interval schedule every one to five trials. The rewards were never delivered while the stimulus was on. The fixation target was then removed for 100 ms. If the monkey looked away from the fixation point at any time during the trial, the trial was aborted, an error code was inserted in the data file, and the experiment was halted for 800 ms before the next trial was started. The length of a trial ranged from 1.4 to 2.2 s, depending on whether and when the monkey made fixation errors. Only data from successful trials were used in the analysis.

The degree of synchronization between the PDP 11 computer and the video display was checked with a high-speed photometer (EG & G model 550). The PDP 11 was programmed to send a signal to a digital port when it received a signal from the video display indicating that the stimulus had been turned on. The analog output from the photometer was sent to an oscilloscope that was triggered with the signal from the digital port. There was no appreciable variation in the time between the triggering pulse from the PDP 11 and the analog signal from the photometer that indicated that the stimulus had turned on.

The order of presentation of the stimuli was shuffled, i.e., randomized without replacement. The list of elements was reshuffled for each presentation cycle. A presentation cycle consisted of the whole set of stimuli presented once each. The stimuli from trials that were aborted because of fixation errors were placed in a recycle list. If the recycle list contained >10 elements at the completion of a cycle of stimuli, these elements were reshuffled and presented again before the next cycle of stimuli. If the recycle list contained ≤10 elements at the completion of a cycle, the elements
were shuffled into the next cycle. This method of presentation guaranteed that the order of the stimuli would be random but did not guarantee that each stimulus would be presented the same number of times. However, the maximum difference in the number of times each stimulus was presented was never greater than two. Each experiment continued until the monkey was no longer interested in performing the fixation task, typically 2,000–3,000 correct trials.

**Stimulus set**

The stimuli used in these experiments included a complete, two-dimensional set of black and white patterns based on Walsh functions (Fig. 3). The set of Walsh functions is a linear basis for any function with the same resolution (Ahmed and Rao 1975). Therefore patterns derived from these Walsh functions constitute a complete, linear basis for any picture with the same resolution.

Further, each Walsh function is orthogonal to all others; therefore no pattern derived from these Walsh functions can be generated by a linear combination of the others. Because of completeness and orthogonality, each Walsh pattern can be thought of as one letter of an alphabet for pictures (Richmond et al. 1987).

To form the Walsh patterns, we first generated eight Walsh functions with increasing sequency, sequency being the Walsh equivalent of frequency (Ahmed and Rao 1975; Hammuth 1977; Richmond et al. 1987). The Walsh functions take values of -1 and 1, and the sequency of a function describes the number of times it changes sign. One-dimensional patterns were generated by assigning black to -1 and white to 1, resulting in a series of black and white gratinglike patterns. Two-dimensional patterns were generated by multiplying, pixel by pixel, each member of a vertical one-dimensional set of functions by each member of a horizontal one-dimensional set of functions. Initially, the resolution of the Walsh set was 4 pixels along each dimension, each pixel being 0.5° square, and the patterns were 2° square. This low-resolution Walsh set consisted of 16 normal-contrast and 16 reverse-contrast Walsh patterns for a total of 32 basis stimuli. In later experiments, the resolution of the basis set was increased to 8 pixels along each dimension, with each pixel being 0.25° square. The high-resolution patterns were also 2° square. This high-resolution Walsh set consisted of 64 normal-contrast and 64 reverse-contrast Walsh patterns for a total of 128 basis stimuli.

The Walsh series, rather than the Fourier series, was originally chosen as a basis for our stimuli because the luminances of neighboring pixels in the Walsh set are not correlated with each other, whereas the luminances of neighboring pixels in the Fourier series are correlated. Thus patterns based on Walsh functions can be used to study nonlinear interactions among the various parts of a receptive field, making Walsh patterns better suited than sine wave stimuli for studying the nonlinear activity of neurons (Marmarelis and Marmarelis 1978). A two-dimensional set was chosen over a one-dimensional set because a two-dimensional set is more likely to reveal anisotropies in the receptive field (Daugman 1980). Because neurons cannot fire negatively and because the stimulus-response relationship cannot be assumed to be linear, a contrast-reversed version of each Walsh pattern was also used.

To provide a means of testing the ability of the model presented in the third paper in this series (Gawne et al. 1991) to predict responses to arbitrary stimuli, we also included in the stimulus set

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**FIG. 1.** Relationship between the stimulus and the receptive field for stimuli that had a resolution of 1:8 pixels. A similar alignment was used for stimuli with a resolution of 1:4 pixel, i.e. the pixel just below and to the left of the center of the pattern was centered on the receptive field. Stimulus was placed off-center in this fashion so that the dividing line between pixels never bisected the receptive field center, thus avoiding null responses from X-like neurons.

**FIG. 2.** Time course of a trial. The 3 traces represent time courses of the fixation point (FP), the stimulus (Stim), and the reward, respectively. Dashed lines at the right ends of the traces represent the time-out period if the monkey made eye position errors. Upward deflections of the fixation point and stimulus traces represent intervals when the fixation point and the stimulus were turned on, and the upward deflection of the reward trace represents the time that a drop of water was delivered to the monkey. Timing marks are presented on the lowest trace. Tick marks on the timing trace represent 400-ms intervals.
30 test patterns drawn on the same grid as the Walsh patterns. Two of the test patterns were annulus-like figures consisting of a 0.5° white square centered on a 1.5° black square or a 0.5° black square centered on a 1.5° white square (see Fig. 6). These annuli could be decomposed into weighted combinations of 16 Walsh patterns. The other 28 test patterns were linear superpositions of 2 Walsh patterns. The responses to these superposition patterns are analyzed in the third paper in this series.

To study the luminance sensitivity of the neurons in our sample, we presented the patterns at each of seven luminance combinations (Fig. 4). In the experiments with the low-resolution basis set (4 × 4), all of the basis and annulus patterns were presented at each of the luminance pairs. With 32 Walsh patterns (16 normal and 16 reverse-contrast), 2 annuli (1 normal and 1 reverse-contrast) presented at each of 7 luminance pairs, and 28 superposition patterns, the entire low-resolution stimulus set consisted of 266 elements. In the experiments with the high-resolution basis set (8 × 8), only the Walsh patterns on the diagonal of the basis set extending from the lower left–most to the upper right–most pattern (see Fig. 3) and the annulus patterns were presented at each of the seven luminance pairs. The remaining 112 Walsh patterns were only presented at the brightest luminance combination. With 16 Walsh patterns (8 normal and 8 reverse-contrast), 2 annulus patterns presented at 7 luminance pairs, 112 Walsh patterns (56 normal and 56 reverse-contrast) presented at the brightest luminance combination, and 28 superposition patterns, the entire high-resolution stimulus set also consisted of 266 elements.

When presenting stimuli on a videomonitor, it is important to ensure that the stimuli are not so large or are not presented at such a range of luminances that the screen voltage power supply be-
whether they fall in the center or near the edge (Richmond et al. 1990). They assign spikes to the center of bins equally, regardless of the exact position of the neuron. The probability of spike occurrence at any instant is estimated from the density functions. Rasters were formed by marking each spike occurrence with a dot and using the stimulus onset time to align the trials.

Data analysis

The spike data were displayed as rasters and as spike-density functions. Rasters were formed by marking each spike occurrence with a dot and using the stimulus onset time to align the trials. Note that this method synchronized the rasters to the beginning of a video frame. Responses were quantified by counting the number of spikes that occurred during a period that started 20 ms after the onset of the stimulus and extended for 256 ms, the time that the stimulus was on. The spike-density function, a continuous function that estimates the probability of spike occurrence at any instant, was used in place of the histogram to sum rasters because histograms are biased by bin edge, or quantization, artifact, i.e., they assign spikes to the center of bins equally, regardless of whether they fall in the center or near the edge (Richmond et al. 1990; Sanderson and Kobler 1976). Spike-density functions were formed by replacing each spike with a Gaussian kernel and averaging the individual density functions across trials (Richmond et al. 1987, 1990). The initial width of the Gaussian kernel was 3 ms. The width was then adjusted from that starting width depending on the local density of the data points (Silverman 1986). Details concerning the calculation of the kernels can be obtained from Richmond et al. (1990).

In summing the spike densities within each stimulus condition, we adjusted the latency of each response to account for the variability in response latency to that stimulus (Richmond et al. 1990; Sanderson 1980). The maximum that any response could be adjusted was ±25 ms. The computational details of the latency adjustment can be obtained from Richmond et al. (1990).

The effect of the adaptive kernel technique and the latency adjustment can be seen by comparing the rasters and spike-density functions in Fig. 5. For this figure, the responses of one neuron to the stimuli were summed with a fixed kernel and latency adjustment, with a fixed kernel and latency adjustment, with an adaptive kernel and latency adjustment, and with both an adaptive kernel and latency adjustment. Use of a fixed kernel and fixed latencies blurs the response to the video raster and might also have blurred the temporal patterns of the response waveforms. When the widths of the kernel and the latencies of the spike-density functions are adjusted before summing, the response of the neuron to the 60-Hz raster of the videomonitor becomes apparent in the summed spike-density function. Thus the adapted and shifted spike-density function most accurately preserves the temporal patterns of the responses, the chief subject of these experiments.

We used a bootstrap Monte Carlo technique to determine whether or not the responses we obtained were related to the stimuli (Efron 1982; Richmond et al. 1987). In using this technique, we sampled the responses in the original data set with replacement and assigned them to stimuli at random (Richmond et al. 1987). The sampling of the original data set was repeated until the shape of the resulting distribution of mean spike counts for the various stimulus conditions became stable, usually after 10–13 passes. The random distribution of spike counts obtained in this way was then compared with the distribution of spike counts existing in the data by the Kolmogorov-Smirnov test (Siegel 1956). We also used parametric statistical tests to analyze our data. Differences between pairs of responses were assessed by the use of Student’s t test.

All experimental protocols described above were approved by the National Eye Institute Animal Care and Use Committee and complied with National Institutes of Health policy on the humane care and use of laboratory animals.

RESULTS

These results are based on 10 neurons recorded from one monkey and 3 neurons recorded from another. The experiments were carried out on the first LGN neuron encountered that could be isolated and held for the length of time needed to present each stimulus a minimum of five times, a period of 1–1.5 h. All neurons were located in layers 5 and 6. The locations of the receptive field centers were plotted to within 0.25°, and all receptive fields were located in the lower contralateral visual quadrant between 3 and 8° of the fovea. The sizes of all receptive field centers were <0.25° in diameter, as measured with manually controlled stimuli. The test of linearity described in METHODS classified all of the neurons in our sample as X like.

Previously it has been reported that many neurons in the parvocellular layers in the monkey LGN respond to the 60-Hz field rate of videomonitors (Rodieck 1983). We
FIG. 5. Effect of adaptive kernels and latency shifting. In this and all subsequent data figures, the top records are summed spike-density functions showing the probability of spike occurrence; bottom records are response rasters. Vertical lines indicate the time at which the stimulus was turned on, and the thick horizontal lines indicate the 256-ms duration of the stimulus. In the rasters each dot represents a single spike, and each line of dots represents a single trial. This figure shows responses of 1 neuron to the white square in 4 different conditions. Top left: effect on the spike-density function when the Gaussian kernel was fixed at 4 ms and the latencies of the rasters were not shifted. Top right: effect of a Gaussian kernel fixed at 4 ms but with shifted rasters. Bottom left: effect of the adaptive Gaussian kernel with an initial width of 4 ms and fixed rasters. Bottom right: effect of the adaptive Gaussian kernel combined with the latency shift. The adaptive kernel and the latency shift procedure allow this neuron's response to the 60-Hz video raster to be seen in the summed spike-density functions.

found that all of the neurons in our sample were capable of following the raster of the monitor to some extent. The response to the video raster could be heard clearly on an audiomonitor and can be seen clearly in the spike-density functions presented in the figures throughout this paper.

Reliability of fixation

There are two concerns in studying the visual responses of LGN neurons in awake monkeys. First, the eye must be stable during fixation, and second, the monkey must make consistent repeated fixations. If these conditions cannot be met, stimuli cannot be accurately positioned with respect to the receptive field.

As can be seen by examining the individual response rasters, we found that consistent responses could be obtained over periods extending to 1.5 h. The responses of an on-center and an off-center neuron to two annuli of opposite contrast are presented in Fig. 6. The outer dimension of the annulus was 1.5° and the size of the center was 0.5°. Examining the rasters shows that, whereas there are individual trials that appear to be out of place in a particular raster, the response was quite consistent over the period of the experiment. The excitatory and inhibitory responses are easily distinguished and are appropriate to the luminance of the pixel that stimulated the receptive field center. Because the size of the center pixel was 0.5°, these data show that the monkeys were able to maintain eye position much more accurately than was enforced by the 2° behavioral window.

A statistical analysis supported our qualitative evaluations. A comparison of the random distribution of responses generated by the bootstrap technique with the distribution of responses to all stimuli obtained for one neuron is presented in Fig. 7. The probability that the responses were distributed randomly was <0.001 for this neuron. For no neuron was the probability of random distribution >0.01. Thus the different responses we obtained were determined by the different stimuli and not just by random fluctuations or variations in fixation.

Responses to squares and annuli

One of the Walsh patterns in our stimulus set, number 0, was a 2° square of uniform luminance. Another type of stimulus was a 1.5° annulus with a 0.5° square center. These stimuli allowed us to examine the luminance sensitivity and the center-surround balance of the neurons in our sample. We used stimuli of the same size for all neurons.

We measured the luminance sensitivity of the neurons in our sample by presenting the 2° square at 10 different luminances. For 10 neurons the stimulus luminances ranged from 0.5 to 43.8 cd/m², with a background luminance of
FIG. 6. Responses of on-center and off-center neurons. Icons above each spike density in this and all subsequent data figures represent the stimuli. A: responses of an on-center neuron to an annulus with a bright center and dark surround (left) and to an annulus with a dark center and a bright surround (right). Both rasters contain 8 trials. Ripple in the response of the on-center neuron is the neuron’s response to the 60-Hz video raster. B: responses of an off-center neuron to same stimuli. Both rasters contain 6 trials. Data in rasters in A were collected over a period of 80 min, and data in rasters in B over a period of 60 min. Average interval between trials in a single raster was 8–10 min. If the monkey had made errors in fixation >0.5°, excitatory and inhibitory trials would have been intermixed in each raster. Because all successive trials in each raster exhibit the same polarity, excitation or inhibition, this figure is a graphic indication that the monkey was able to achieve sufficiently reliable fixation to allow accurate placement of the stimuli with respect to the receptive field.

FIG. 7. Statistical test of stimulus-response dependence. Mean numbers of spikes per trial are plotted against the percentage of times that that number occurred in the data set for 1 neuron. Solid line is a plot of the expected percentage of spike count occurrence given a random distribution of responses among the 266 stimulus conditions. Dashed line is the obtained percentage of spike count occurrence. Expected and observed distributions of spike counts were significantly different by the Kolmogorov-Smirnov test (P < 0.001), suggesting that the responses of the neuron were related to the stimuli.

8.6 cd/m². For the remaining three neurons the stimulus luminances ranged from 0.1 to 61.0 cd/m², with a background luminance of 4.5 cd/m². The response strength of an on-center neuron to the latter luminance series is presented in Fig. 8. A plot of the average number of spikes per trial obtained at each luminance for this neuron (Fig. 9) shows that the relationship between luminance and response is saturated at both high and low luminances. This saturation may be a reflection of the contrast gain control mechanism that has been described for retinal ganglion cells and LGN neurons (Kaplan et al. 1987; Shapley and Victor 1978). This neuron exhibited a well-behaved but nonlinear relation between luminance and response that is typical of that seen for all of the neurons we studied over the range of luminances used in these experiments.

Most LGN neurons have spatially opponent receptive fields. We used Student’s t test to examine the center-surround balance of the neurons in our sample by comparing the number of spikes in the responses to the 2° square with the number of spikes in the responses to the annulus. For on-center neurons we compared the responses to the brightest square with the responses to the annulus with the brightest center and darkest surround. For off-center neurons we compared the responses to the darkest square with the response to the annulus with the darkest center and
FIG. 8. Luminance sensitivity. Spike densities and rasters are the responses of a neuron to a 2° square stimulus presented at a series of luminances. Stimulus luminance increases from bottom left to top right. Icons symbolizing the luminance of each stimulus are presented above each response. Numbers above each icon indicate the luminance of the stimulus in cd/m². Background luminance was 4.5 cd/m². Ripple in the sustained portions of the responses to 2 brightest stimuli is the response to the 60-Hz video raster.

brightest surround. In this comparison, an antagonistic surround is manifested by a larger response to the annulus than to the square (Fig. 10). Using this measure, we found evidence for surround antagonism in five neurons (4 on-center and 1 off-center). The \( t \) values for these neurons ranged from 2.41 with \( P < 0.05 \) to 3.57 with \( P < 0.005 \).

The remaining eight neurons (5 on-center and 3 off-center) did not show this evidence of surround antagonism when we used the spike count as a measure of neuronal response. One of the on-center neurons gave equal-size responses to the square and to the annulus (\( t = 0.06, df = 17, P > 0.9 \), Fig. 11A). The remaining seven neurons gave significantly larger responses to the squares than to the annuli (Fig. 11B). The \( t \) values for these neurons ranged from 2.22 with \( P < 0.05 \) to 10.10 with \( P < 0.0001 \). Although we found no evidence of antagonistic surrounds when we compared only the total number of spikes in each response, there were clear differences in the temporal patterns of the response waveforms to the two different stimuli (see Fig. 11A). The differences in the temporal pattern of the response will be discussed in more detail later.

FIG. 9. Mean number of spikes per trial as a function of stimulus luminance; a graphic representation of responses shown in Fig. 8. Vertical bars through each data point indicate SE. There is saturation of response at both low and high luminances. Thus the luminances used here spanned the sensitivity range of this neuron.
FIG. 10. Neurons with antagonistic surrounds. Responses of an on-center (A) and an off-center neuron (B) to a 2° square stimulus and to an annulus with a 0.5° square center are presented. A: square was presented on 9 trials and annulus was presented on 7 trials. B: both square and annulus were presented on 6 trials. Responses of both neurons to annuli contained significantly more spikes per trial than did responses to squares (A, t = 3.57, df = 14, P < 0.005; B, t = 2.41, df = 10, P < 0.05), suggesting that both neurons have antagonistic surrounds. Clear responses to the 60-Hz video raster can be observed in A.

Three possible explanations for the lack of evidence for antagonistic surrounds are 1) variations in fixation among trials, 2) a poor match between the sizes of the receptive field center mechanisms and the annulus center pixels, and 3) recording from neurons that had no surround mechanism.

The first explanation, artifacts due to variations in fixation, can be ruled out by examining the response rasters. Because the annuli had 0.5° inner widths and 1.5° outer widths compared with the 2.0° widths of the squares, variations in fixation would produce more variability in the responses to the annuli than to the squares (Gur and Snodderly 1987). However, the increased variability in the responses to the annuli would not necessarily cause the mean response to the annuli to be smaller than the mean response to the squares. Indeed, in Fig. 10A, the responses to the annulus were clearly more variable than the responses to the square; nonetheless, the mean response to the annulus is significantly larger than the mean response to the square. In Fig. 11B, the response to the annulus is less variable than the response to the square. Finally, the responses to the annulus in Fig. 11A were far too consistent to have been caused by variations in fixation. Thus eye movements are not likely to be responsible for the lack of evidence for an antagonistic surround.

As to the second explanation, if these neurons had center-surround receptive fields with center mechanisms >0.5°, the surround of the annulus would fall on the outer edges of the center mechanisms, thus producing less than maximum excitation of the neuron. The 2° square would also produce less than maximum excitation because part of the square would fall on the surround mechanism of the receptive field and evoke some inhibition. However, unless the surround mechanism were very strong, the reduced excitation from the annulus would more than offset the inhibition from the square, causing a smaller response to the annulus. Alternatively, if these neurons had center-surround receptive fields that were very small, the outer edges of the square would excite the outer disinhibitory surround, reducing the inhibition of the neuron (Hammond 1973). The surround of the annulus, on the other hand, would decrease the excitation of the outer disinhibitory surround, increasing the inhibition of the neuron.

Previous studies have reported that the diameters of receptive field centers in the LGN at the retinal eccentricities of the neurons in our sample are considerably smaller than the 0.5° center of the annulus used in these experiments (Wiesel and Hubel 1966). This would suggest that we failed to find evidence of an antagonistic surround because our stimuli were very large in comparison with the receptive fields and were affecting the outer disinhibitory surrounds of these neurons. However, one must exercise caution in using results obtained from paralyzed, anesthetized monkeys to draw conclusions about results obtained from awake, behaving monkeys. McClurkin and Marrocco (1984) have reported that manipulation of the corticogeniculate feedback pathway alters the sizes of LGN receptive fields. Thus it would not be surprising if changes in arousal also caused changes in the sizes of LGN receptive fields.

Addressing the third explanation, if these neurons had
FIG. 11. Neurons without antagonistic surrounds. Responses of an on-center (A) and an off-center neuron (B) to a 2° square stimulus and to an annulus with a 0.5° square center are presented. A: square was presented on 9 trials and annulus was presented on 10 trials. B: square was presented on 7 trials and annulus was presented on 5 trials. In contrast to the 2 neurons presented in Fig. 10, responses of both of these neurons suggested a lack of an antagonistic surround. There was no significant difference in the number of spikes per trial between the response to the square and the response to the annulus for the neuron presented in A (t = 0.06, df = 17, P > 0.95). However, note that there was a large difference in the distribution of those spikes within the response interval. The response of the neuron presented in B to the black square was significantly larger than the response to the annulus (t = 10.10, df = 10, P < 0.0001). It is also clear from inspection that in no trial did the number of spikes elicited by the annulus exceed the maximum number of spikes elicited by the square. The response of the on-center neuron in A to the white square contains a strong 60-Hz component contributed by the video raster.

uniform receptive fields >0.5°, the annulus would be a sub-optimal stimulus and so would produce less than maximum excitation. The 2° square would evoke greater excitation because it would stimulate more of the receptive field. In either the second or the third case, the responses should be consistent from trial to trial, which is the result we obtained. Thus our failure to find evidence of surround antagonism in eight neurons was due either to a poor match between the sizes of the receptive field center mechanisms and the annulus center pixels or to a lack of antagonistic surround mechanisms.

Responses to Walsh patterns

According to traditional models of LGN receptive fields, the polarities of the responses to the series of Walsh patterns we used should depend solely on the luminance of the pixel stimulating the receptive field center. Only the responses to the highest-contrast Walsh patterns were used in this analysis. We found that the response polarity was determined solely by the luminance of the pixel centered on the receptive field for six of the nine on-center and for two of the four off-center neurons. In each case, the black pixels were darker than the background luminance and the white pixels were lighter than the background luminance (see Fig. 4). The on-center neurons gave excitatory responses to all stimuli that had a white pixel centered on the receptive field and inhibitory responses to each of the opposite-contrast stimuli. The reverse was true for the off-center neurons. This pattern of responses is presented for an on-center neuron in Fig. 12. The 16 responses on the left are to those Walsh patterns that had a white pixel centered on the receptive field (Fig. 12A). The 16 responses on the right are to the opposite-contrast Walsh patterns (Fig. 12B). Note that all the responses on the left are excitatory and all the responses on the right are inhibitory.

For the remaining three on-center and two off-center neurons, the polarity of the response was not always determined by the contrast of the pixel centered on the receptive field. Some Walsh patterns elicited excitatory responses and other Walsh patterns elicited inhibitory responses regardless of whether the pixel centered on the receptive field was lighter or darker than the background. The responses of an on-center neuron to the two opposite-contrast versions of two Walsh patterns are presented in Fig. 13A. Because each pixel in the stimulus on the left is opposite in contrast to the pixels in the stimulus on the right, one of these two responses should have been excitatory and the other inhibitory. This was the case for the bottom two responses. However, both of the top two stimuli evoked nearly identical excitatory responses. The responses of an off-center neuron to the two opposite-contrast versions of two Walsh patterns
FIG. 12. Linearity of responses. Responses of a neuron to the brightest, low resolution, normal, and reverse-contrast Walsh patterns are sorted so that responses to patterns that had a white pixel centered on the receptive field are presented in A, and responses to patterns that had a black pixel centered on the receptive field are presented in B. All responses in A are excitatory and contain the same average number of spikes per trial ($F = 1.04, df = 15/114, P > 0.4$). All responses in B are inhibitory and contain the same average number of spikes per trial ($F = 0.68, df = 15/113, P > 0.8$). Thus, for this neuron, the polarity and magnitude of the response depend only on the luminance of the pixel stimulating the receptive field center and not on the distribution of pixels in the surround. Response to the video raster is apparent in all of the excitatory responses.

are presented in Fig. 13B. Again, because each pixel in the stimulus on the left is opposite in contrast to the pixels in the stimulus on the right, one of these two responses should have been excitatory and the other inhibitory. As in A, this was the case for the bottom two responses. However, both of the top two stimuli evoked inhibitory responses. At this point we must reiterate that all of these neurons were classified as linear summators; their responses clearly stopped modulating when a contrast-reversing, bipartite, black and white stimulus was positioned so that the black-white boundary bisected the receptive field. Furthermore, the left patterns in Fig. 13, A and B, produced luminance increments, and the right patterns produced luminance decrements, on the receptive field centers.

One explanation for the fact that the top pairs of responses in Fig. 13 were of the same polarity is that the mean luminances of the top pairs of patterns were higher than the background; thus the excitatory responses in the top of A and the inhibitory responses in the top of B reflect responses to changes in the mean luminance of the stimuli. However, we feel that this explanation is unlikely because the mean luminances of the bottom pairs of patterns in Fig. 13 were also higher than the background, and these responses were opposite in polarity. Thus we believe that these data suggest that—even though these neurons appeared to show linear spatial summation to our small test stimulus, i.e., failed to show response modulating to a contrast-reversing bipartite stimulus—they do have some nonlinear mechanisms, probably in the surround (Hochstein and Shapley 1976).

**Temporal properties of the responses**

By the criteria of previous studies, all the neurons in our sample were sustained neurons. That is, all neurons in our sample produced an initial transient burst of spikes when the stimulus was presented, followed by a period of elevated activity that lasted for the duration of the stimulus presentation (Derrington and Fuchs 1979). The relative amplitude
FIG. 13. Nonlinearity of responses. Responses of an on-center (A) and an off-center neuron (B) to 2 pairs of opposite contrast patterns. A: stimulus on the top left was presented on 9 trials and that on the top right was presented on 8 trials. Bottom 2 stimuli were each presented on 7 trials. B: stimuli on the top left and bottom right were each presented on 6 trials, the stimulus on the top right was presented on 5 trials, and the stimulus on the bottom left was presented on 7 trials. Top 2 stimuli in A evoked excitatory responses even though the pattern on the left had a white pixel centered on the receptive field and the pattern on the right had a black pixel centered on the receptive field. Bottom 2 stimuli in A evoked responses of opposite polarity. B: both of the top 2 stimuli evoked inhibitory responses, even though the pixels centered on the receptive field were of opposite contrast. Bottom 2 stimuli evoked responses of opposite polarity. Thus these 2 neurons responded in a nonlinear fashion to some pairs of contrast-reversed stimuli but not to others.
form luminance could affect the size and shape of both the initial and later portions of the response (Fig. 14A). The later portions of the response could remain at a constant level (Fig. 14, A, C, and D) or could wax or wane during the time the stimulus was on (Fig. 14B). Indeed, the response of this neuron to an annulus became exceedingly transient compared with its response to a square (Fig. 11A). The responses to some patterns had a single transient burst of spikes at stimulus onset, whereas the responses to other patterns had two bursts (Fig. 14, B and C). These transients contained more than one cycle of the 60-Hz component of the response and so reflect more than changes in the neuron's ability to follow the video raster. Finally, responses could have one or two initial bursts, depending on the luminance of the stimulus (Fig. 14D). These results show clearly that the use of a large set of spatially complex, two-dimensional patterns presented at a wide range of luminances can reveal significant stimulus-related complexities in the temporal properties of the responses of X-like neurons.

DISCUSSION

The results we presented in this paper show that 1) reliable data can be recorded from the precortical visual system in behaving monkeys; 2) the responses of LGN neurons are saturated at very high and very low luminances, indicating that models (such as difference-of-Gaussians) that require linear summation of inputs would be limited in their ability to account for the responses of these neurons (Rodieck 1965); 3) the use of a large set of complex, two-dimensional, black and white stimuli presented at a wide range of luminances reveals large variations in the shapes of neuronal response waveforms, suggesting that, even in the precortical visual system, the temporal pattern of neural activity may be as important an aspect in the encoding of visual stimuli as is the amplitude of the response.

Use of behaving monkeys

Because of the small sizes of the receptive fields in the LGN and the apparent susceptibility to stimulus alignment, it might be difficult to study the visual properties of LGN neurons in behaving monkeys (Gur and Snodderly 1987). Despite these concerns, an effort to study these neurons in a behaving animal is warranted, both because of the direct effects of anesthesia on the function of geniculate neurons and because of possible effects of anesthesia on the nonretinal inputs that have been shown to govern geniculate neuronal responses (Sherman and Koch 1986; Uhlrich et al. 1989). The spontaneous activity and the responsiveness of LGN neurons change with changes in arousal (Maffei and Rizzolatti 1965; Sakakura 1968; Sestokas and Lehmkuehle 1988). Furthermore, the number of ganglion cell spikes required to elicit one geniculate neuron spike varies markedly with changes in arousal (Coenen and Vendrik 1972). Thus important aspects of neuronal function may be missed when animals are paralyzed and anesthetized. It is not possible to eliminate all sources of artifact from an experiment. One must then ask, if artifact is unavoidable, which is less serious—that which is part of the normal visual behavior of an animal (such as small errors of fixation or eye-motion tremor) or that which results from anesthesia?
In this paper we presented evidence that the visual properties of LGN neurons can be studied in awake monkeys. We monitored eye position data but did not save them for further analysis. However, we know we controlled eye position. What we need to address is whether the control was accurate enough to study these neurons. The reliability of fixation was accurate enough so that we were able to plot the location of the receptive field center to within 0.25°; to hear the null phase responses of X-cells to a contrast-reversing, black and white stimulus; to see the inhibitory contributions of the surround mechanism to the responses of neurons; and to obtain responses with polarities determined by the luminance of the pixel stimulating the center across many trials. There were individual trials in many data sets that were clearly different from the others in that condition. These could have been caused by a difference in fixation or accommodation for that trial, eye blinks, or variations in the spike-generating mechanisms of the neuron (Gur and Snodderly 1987). Nonetheless, statistical analysis showed that, across the whole data set, the responses were related to the stimuli presented. Thus our results show that any residual inaccuracies in the retinal location of the stimulus that might be due to variability of eye position from one trial to the next were not serious enough to prevent studying the stimulus-response relations for LGN neurons. At worst, errors of fixation would tend to cause a blurring or loss of resolution in our data but would not indicate phenomena that do not exist. If fixation were totally uncontrolled, then our data would be random and unrelated to the stimuli, which was clearly not the case.

Luminance nonlinearity

The traditional difference-of-Gaussians model of X-like LGN receptive fields assumes that the neuron sums light linearly across the receptive field (Shapley and Hochstein 1975; Shapley et al. 1981; So and Shapley 1979). This linearity of summation requires that the neuron respond in a linear fashion to changes in the luminance of a stimulus (Rodieck 1965). Thus most investigators have chosen to study these neurons by the use of stimuli with restricted luminance ranges to avoid nonlinear behavior (Enroth-Cugell et al. 1983), e.g., a sine wave grating of 45° contrast and a mean luminance of 20 cd/m² (So and Shapley 1981), representing a luminance range of 0.42 log units. However, in our experiments, the range of luminances spanned 2.78 log units, enough to produce response saturation at the low and high luminances. Therefore we conclude that any model that requires a linear luminance function would not be able to adequately predict the responses of a neuron to the range of luminances we used.

Nonlinearity of the surround

Despite its explanatory power, the difference-of-Gaussians model proposed by Rodieck (1965) for retinal ganglion cells only approximates the actual receptive field. In particular, Rodieck reported that the model could not describe responses to stimuli with very long or very short durations, that it could not reproduce the nonlinear summation that he had observed in the receptive field (Rodieck and Stone 1965a), and that it ignored rotational anisotropics that he and others observed in the centers and surrounds of retinal ganglion cells (Cleland and Enroth-Cugell 1968; Hammond 1974; Kuffler 1953; Levick and Thibos 1982; Rodieck and Stone 1965b). Furthermore, nonlinear surrounds in cat retinal ganglion X cells have been demonstrated that cannot be explained by the difference-of-Gaussians model (Enroth-Cugell and Robson 1966; Hochstein and Shapley 1976). These latter studies reported that some X-like cells give weak on-off responses to the presentation and withdrawal of an edge that bisects the receptive field (Enroth-Cugell and Robson 1966) and to the contrast reversal of sine wave gratings of very low spatial frequencies placed at the null position (Hochstein and Shapley 1976).

In accord with previous studies, we also found some X-like neurons in our sample that exhibited nonlinear behavior, i.e., the polarity of response did not vary with the contrast of the pixel stimulating the receptive field center. However, our results represent an extension beyond previous findings for two reasons. First, we were able to observe nonlinear behavior even though our stimuli had a pixel of uniform luminance centered on the receptive field, with no edges bisecting the receptive field. Second, we did not see on-off responses; rather, stimuli of the same pattern but opposite contrast elicited responses of the same polarity, temporal pattern, and strength, which is evidence of nonlinear behavior.

The most likely explanation for the differences between our observations of nonlinear behavior in X-like neurons and those described in previous results lies in our choice of stimuli. The previous studies that demonstrated nonlinearities in X-like neurons used low-contrast, one-dimensional stimuli, either an edge with a contrast of 20% (Enroth-Cugell and Robson 1966) or a low-frequency sine wave grating with a contrast of 55% (Hochstein and Shapley 1976). Our stimuli, on the other hand, were two-dimensional, had a contrast of nearly 100%, and had sharp edges between pixels. This type of stimulus is optimal for stimulating the nonlinearities of a system (Marmarelis and Marmarelis 1978).

Temporal patterns of response

In previous studies, the temporal pattern of the response waveform has been seen principally as a characteristic with which to classify neurons (Cleland et al. 1971; Derrington and Fuchs 1979; Gouras 1969; Ikeda and Wright 1972; Marrocco 1976) or as a measure of the fidelity with which a neuron can transmit a temporal input to its output (Enroth-Cugell and Robson 1966; Enroth-Cugell et al. 1983; Hochstein and Shapley 1976). However, Ikeda and Wright (1972) have shown that certain aspects of the shape of retinal ganglion cell responses, such as the relative strengths of the transient and sustained components, depend on which part of the receptive field is stimulated. Furthermore, a few sustained neurons in the monkey LGN can be made to produce transient responses by activating the surround mechanism (Marrocco 1976).

By the criteria of Derrington and Fuchs (1979), all the neurons in our sample were sustained. However, details of the temporal patterns of the response waveform were determined in large measure by the stimulus patterns presented. Some of the variations we observed were similar to those
observed by Ikeda and Wright (1972) and Marrocco (1976). In addition, we also observed that the number of initial transient bursts varied according to the stimulus presented. We also observed great variety in the shapes of the response waveform after the initial bursts of spikes. This rich variation in the shapes of the response waveforms is most probably a consequence of our use of a rich set of two-dimensional stimuli.

Previous results from our laboratory have demonstrated that neurons in the inferior temporal and striate cortices encode information about stimuli in the temporal distribution of spikes in their responses (Optican and Richmond 1987; Richmond and Optican 1990). The results presented in this paper show that the temporal patterns of the response waveforms of neurons in the LGN vary with the stimulus presented, suggesting that these neurons might also encode information in the temporal distribution of spikes in their responses. However, to know whether these temporal patterns contain stimulus-related information, we first need to be able to quantify them. In the next paper of this series, we analyze these temporal patterns and show that they carry stimulus-related information. In the third paper we develop a model of X-like parvocellular neurons that predicts the temporal characteristics of their responses to novel stimuli.

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