Cortical feedback increases visual information transmitted by monkey parvocellular lateral geniculate nucleus neurons

JOHN W. McCLURKIN,1 LANCE M. OPTICAN,1 AND BARRY J. RICHMOND2
1Laboratory of Sensorimotor Research, National Eye Institute, Bethesda
2Laboratory of Neuropsychology, National Institute of Mental Health, Bethesda
(RECEIVED April 19, 1993; ACCEPTED December 2, 1993)

Abstract
We studied the effect of cooling the striate cortex on parvocellular lateral geniculate nucleus (PLGN) neurons in awake monkeys. Cooling the striate cortex produced both facilitation and inhibition of the responses of all neurons, depending on the stimulus presented. Cooling the striate cortex also altered the temporal distribution of spikes in the responses of PLGN neurons. Shannon's information measure revealed that cooling the striate cortex reduced the average stimulus-related information transmitted by all PLGN neurons. The reduction in transmitted information was associated with both facilitation and inhibition of the response. Cooling the striate cortex reduced the amount of information transmitted about all of the stimulus parameters tested: pattern, luminance, spatial contrast, and sequential contrast. The effect of cooling was nearly the same for codes based on the number of spikes in the response as for codes based on their temporal distribution. The reduction in transmitted information occurred because the differences among the responses to different stimuli (signal separation) were reduced, not because the variability of the responses to individual stimuli (noise) was increased. We conclude that one function of corticogeniculate feedback is to improve the ability of PLGN neurons to discriminate among stimuli by enhancing the differences among their responses.

Keywords: Corticogeniculate feedback, Temporal encoding, Transmitted information

Introduction
Previously, we reported that neurons in the parvocellular layers of the lateral geniculate nucleus (PLGN) encode unambiguous information about both the pattern and the luminance of a stimulus in the number and temporal distribution of spikes in their responses (McClurkin et al., 1991b). In this study, we investigated the contribution of feedback from the striate cortex to this encoding process. The feedback from the striate cortex constitutes a major input to the mammalian LGN (Lund et al., 1975; Hendrickson et al., 1978). Indeed, LGN relay neurons receive more synapses of cortical than of retinal origin (Robson, 1983). Previous studies have reported that cortical neurons may excite LGN neurons, inhibit LGN neurons, or both (Geisler et al., 1981; Ahsen et al., 1982; McClurkin & Marrocco, 1984; Murphy & Sillito, 1987; Sillito & Murphy, 1988; Gulyas et al., 1990). This diversity of results makes it difficult to define a general role for cortical feedback to the LGN.

For the experiments reported here, we adapted the communications channel paradigm we have used previously (Richmond et al., 1990; Richmond & Optican, 1990; Gawne et al., 1991; McClurkin et al., 1991a,b). The stimuli consisted of a set of two-dimensional, black-and-white patterns based on Walsh functions presented at nine different luminance combinations. We considered the temporal distribution as well as the number of spikes in our analysis of the neuronal responses. In addition to these analyses of the responses, we used information theory to quantify the stimulus-response relationship. We conducted the experiments using awake monkeys to eliminate any obscuring effects of anesthesia and low arousal (Iwama et al., 1965; Maffei & Rizzolatti, 1965; Sakakura, 1968; Coen & Vendrik, 1972; Sherman & Koch, 1986; Sestokas & Lehmkuhle, 1988; Uhlrich et al., 1989).

Methods
Two adult, male rhesus monkeys were used in these experiments. Data were collected from one hemisphere of each monkey. All stimuli were presented on a video monitor placed 171 cm from the monkey's eyes. The monitor operated at 60 Hz with noninterlaced raster lines.

Surgical protocol
The surgical protocol used in these experiments is largely the same as that described in a previous report (McClurkin et al., 1991a). Briefly, a magnetic-field search coil was implanted.

Reprint requests to: John W. McClurkin, LSR/NEI, Bldg. 49, Room 2A30, 9000 Rockville Pike, Bethesda, MD 20892, USA.
around the sclera in each eye (Judge et al., 1980), and a pedestal made of dental acrylic was implanted on the skull. The pedestal contained a recording chamber positioned over the right LGN, a chamber positioned over the right striate cortex to allow cryogenic manipulation of the corticogeniculate feedback pathway, a socket for fixing the position of the head, and plugs connected to the search coils. Implant surgery was carried out under isoflurane inhalation anesthesia using sterile procedures in a veterinary operating room. Both monkeys recovered from the surgery without complications and remained healthy for the duration of the experiments.

 Behavioral protocol

The behavioral task used in these experiments was similar to those described in a previous report (McClurkin et al., 1991a). Briefly, monkeys were trained to fixate a 0.2 deg black square while stimuli were presented on the neuron's receptive field. The monkeys were required to keep their eyes within a 0.6 deg x 0.6 deg window centered on the fixation point. The monkeys maintained steady fixation for several seconds at a time and were able to make repeated fixations with less than 0.2 deg error, which was within the measurement noise of the eye movement monitor.

 Experimental protocol

The method used to collect data has been described in a previous report (McClurkin et al., 1991a). After isolating a neuron, the position of the receptive-field center was mapped using horizontal and vertical 1.6 deg x 0.2 deg bars which could be switched from white to black. The polarity of the center mechanism, on or off, was determined using a 0.2 deg x 0.2 deg square which could also be switched from white to black. Color opponency was determined by flashing 1.6 deg red, green, and blue squares on the receptive field, and listening for excitation or inhibition. The intensity of these colored squares was the same as the background. Neurons were classified as color-opponent if they were excited by at least one and inhibited by at least one of these three colors. Broadband neurons were those that were either excited or inhibited by all three colors. Ocular dominance was determined by occluding first one eye, then the other, and listening for stimulus-evoked activity. Linearity of spatial summation was determined using two stimuli which reversed contrast at the rate of 2 Hz in a square-wave fashion: one stimulus was a 1.6 deg bipartite square containing 1 cycle of a square-wave grating, and the other was a 1.6deg square containing 4 cycles of a square-wave grating. These stimuli were placed at a series of successive locations relative to the receptive field while we listened for the disappearance of stimulus-evoked modulation or for frequency doubling in the response. Neurons were classified as linear summators if these stimuli could be placed on the receptive field in such a way that the stimulus-evoked modulation disappeared.

Data collection was begun after a neuron's receptive field had been mapped and characterized. For each neuron, the position of the driving eye was monitored, and a trial was begun if the eye was inside the 0.6 deg window surrounding the fixation point. If the monkey looked away from the fixation point during a trial, the trial was aborted, and the experiment was halted for 800 ms. Only responses from successful trials were used in the data analysis. The onset of the stimuli was synchronized to the start of the vertical scan of the video monitor. Each stimulus was presented for 256 ms and the interstimulus interval was 256 ms, except when the monkey broke fixation. The order of presentation of stimuli was randomized, without replacement, by shuffling. The list of stimulus conditions was reshuffled for each cycle. A stimulus cycle consisted of the presentation of each stimulus once. The stimuli from aborted trials were placed in a recycle list. If the recycle list contained ten or fewer elements at the end of a cycle, those elements were added to the list for the next cycle. If the recycle list contained more than ten elements, those elements were reshuffled and presented again before the start of the next cycle.

 Stimulus set

The stimuli (Fig. 1) consisted of a set of two-dimensional, black-and-white patterns based on Walsh functions (Ahmed & Rao, 1975; Richmond et al., 1987). The resolution chosen for the Walsh patterns was 8 x 8, resulting in 64 different patterns. The size of each stimulus was 1.6 deg x 1.6 deg, and the size of a pixel was 0.2 deg x 0.2 deg. These patterns constitute a complete, linear basis for the description of any picture with the same or lower spatial resolution; thus, they can be thought of as a picture alphabet. Since neurons cannot fire negatively, the contrast reversed version of each of these patterns was also used.

For the 64 normal-contrast and 64 reverse-contrast patterns, the luminance of the black pixels was 0.054 cd/m², and the luminance of the white pixels was 62.72 cd/m² against a background luminance of 20.43 cd/m² (Fig. 2, LCI). To study the luminance sensitivity of neurons, eight of the normal-contrast Walsh patterns and the eight reverse-contrast versions of those patterns (cf. Fig. 9) were presented at eight additional luminance combinations (Fig. 2, LC2-LC9). There were 144 Walsh stimuli used in the analysis of the ability of neurons to encode information about stimulus pattern and luminance, and a total of 256 Walsh stimuli altogether. All stimuli were positioned so that the edges of the pixels did not bisect the receptive-field center (Fig. 3).

 Cortical cooling

Each experimental session consisted of two blocks of trials. In the first block, the striate cortex was at normal temperature. The striate cortex was then cooled and the second block of trials was administered. Usually, 10 min were required to reduce the temperature of the cortex, during which time the monkeys were allowed to continue working at the fixation task. To ensure that the data from both blocks of trials were from the same neuron, receptive fields were remapped and recharacterized (as described above) at the end of the normal temperature block of trials, again just prior to beginning the cool block of trials after the cooling process had been completed, and finally at the end of the cool block of trials. Furthermore, the shape of the spike waveform on the oscilloscope was monitored. Only data from experiments in which the gross receptive-field properties and spike waveform shape of the neuron remained constant through both blocks of trials were used. Of the 93 neurons which were isolated and characterized, 34 passed our criteria for constancy of receptive-field properties and spike waveform shape through both blocks of trials.

To control the temperature of the striate cortex, a variable-speed gear pump was used to circulate ethyl alcohol through
Fig. 1. Walsh patterns. This figure shows the 64 normal-contrast Walsh patterns we used. All patterns are orthogonal to the others in that none can be constructed from a linear combination of the others. Thus, each pattern can be considered a letter in an alphabet for pictures. Because neurons cannot fire negatively and because the linearity of the stimulus response relation cannot be assumed, we also used the reverse-contrast version of each of these patterns.

A sealed, stainless-steel chamber secured inside the cylinder over the striate cortex. The cryogenic chamber was stored in cetlycide between experimental sessions to ensure sterility. Because the chamber was sealed, the alcohol never came in contact with the monkey's tissues. Care was taken to ensure that this cryogenic chamber was in contact with, but did not depress, the dura. The recording cylinder was flooded with sterile saline to eliminate air pockets under the cryogenic chamber. The temperature of the dura was continuously monitored with a thermocouple inserted through a port in the center of the cryogenic chamber. For the normal temperature condition, alcohol heated to 40°C with a temperature controller was circulated with the pump rate set so that the temperature of the dura as measured by the thermocouple was maintained at 37°C. For the cool temperature condition, alcohol cooled to -70°C with dry ice was circulated with the pump rate set so that the temperature of the dura was maintained at 0°C. Neither monkey exhibited any behavioral signs of discomfort when the dura was cooled, or when it was brought back to normal temperature. Both monkeys were as willing and able to work at the fixation task when the dura was cooled as when the dura was at normal temperature.

We did not make any subdural temperature measurements because previous work in monkey has shown that a 2°C cooling probe can produce a temperature gradient of 3.9°C/mm under the center of the probe (McCurtain & Marrocco, 1984). Furthermore, we did not attempt to measure the lateral spread of cooling because the structure of the acrylic implant and recording chamber made such recordings impossible without surgery, and thus very difficult to do in awake animals.

In any paradigm in which the experimental conditions are presented in blocks of trials, one must always be alert to the possibility that differences between blocks of trials arise from
factors not related to the experimental manipulations. One means of identifying such uncontrolled factors is to present the baseline conditions before and after the experimental manipulations. In these experiments, we attempted to identify such uncontrolled factors by collecting data during a third block of trials after the striate cortex had been returned to normal temperature (Baker & Malpeli, 1977; Marrocco et al., 1982; McClurkin & Marrocco, 1984; Marrocco & McClurkin, 1985). However, the neuronal isolation always deteriorated, either during the rewarming process or during the third block of trials. Thus, we were unable to make comparisons between the data collected during the third block of trials and data collected during either of the first two blocks of trials. We are not able to explain this loss of isolation.

As an alternative method of identifying uncontrolled factors and to assess the possibility that cooling had global effects on the behavior of the monkeys that were not directly related to the removal of feedback, we recorded from two groups of PLGN neurons, experimental and control (Baker & Malpeli, 1977). The experimental neurons had receptive fields in the visual space represented in that part of the striate cortex under the cooling cylinder. The control neurons had receptive fields outside this space (Fig. 4). To determine the extent of visual space represented under the cooling cylinder, we plotted the receptive fields of cortical neurons encountered in penetrations into the striate cortex near the rostral, caudal, medial, and lateral edges of the cooling cylinder. The cortical mapping was done prior to recording from the PLGN. Because of the retinotopy of the projection from the striate cortex to the LGN (Hollander, 1970; Hendrickson et al., 1978; Tsutsumo et al., 1978), any differences in the responses of these control neurons between the normal and cool blocks of trials would not be due to the elimination of cortical feedback. Rather, differences in the responses of the control neurons would reflect uncontrolled sources of variances. If we assume that these uncontrolled factors are the same for both the experimental and control neurons, the effects of cortical feedback can be separated from those arising from uncontrolled factors by comparing experimental and control neurons. Previous work has suggested that neurons serving as controls can have receptive fields as close as 1.0 deg to the edge of the space represented in the striate cortex under the cooling cylinder and not be affected by the cryogenic blockade of the striate cortex (Marrocco et al., 1982).

**Fig. 2.** Luminance combinations of the Walsh patterns. Each pair of points connected by a vertical bar represents one of the pairs of luminances used in the Walsh patterns. The dashed line represents the background luminance of the screen. The upper points indicate the intensities of the "white" points, and the lower points indicate the intensities of the "black" points.

**Fig. 3.** Alignment of stimuli on the receptive field. The small circle represents the receptive-field center, and the large circle represents the receptive-field surround. The 8 × 8 grid shows the locations of the pixels in the Walsh patterns.

**Quantification of responses**

The methods used to quantify the number and temporal distribution of spikes in the responses, and the statistical tests used to measure the stimulus dependence of the responses, were the
To determine whether the spike count and the coefficients of the K-L transform depended on the stimulus conditions or simply reflected noise, we randomly assigned responses to stimulus conditions using a Monte Carlo bootstrap technique to obtain an estimate of the distribution of response measures one would expect if there was no relationship between the stimulus conditions and the responses. These estimates of random distributions were then compared with the distributions of response measures obtained in our experiments with the Kolmogorov-Smirnov test (Efron, 1982; Richmond et al., 1987; McClurkin et al., 1991a,b).

Transmitted information

The bootstrap procedure described above gives the probability that the stimulus-response pairs we obtained were due to chance, but does not give the degree to which the responses could be used to tell which stimulus had been presented (Gawne et al., 1991). To address this question, we measured the amount of information transmitted by each neuron about the stimuli using the method developed by Optican et al. (1991), and described in Appendix 2. Transmitted information is defined as the reduction in uncertainty regarding which stimulus was presented given the signal that occurred (Shannon, 1948). In our paradigm, the signals of information theory are the neuronal responses. Transmitted information will be greatest if each stimulus evokes a unique response which is the same on all trials. Transmitted information will be lower if a stimulus evokes different responses on different trials, or if several stimuli evoke the same response. When one stimulus evokes different responses on different trials, transmitted information will be low because the neuronal signal contains noise. When several stimuli evoke the same response, transmitted information will be low because that neuronal signal cannot be used to separate the stimuli.

Statistical analysis

We used the Student’s t test, linear regression, and the analysis-of-variance programs in the BMDP statistical package to compare the responses of neurons in the normal and cool conditions, and to compare the responses of the experimental and control neurons. For the t-tests and linear regression, one-tailed comparisons were made because, in each case, the effects we observed could be attributed to the removal of cortical feedback only if the cooling effect was greater for experimental neurons than for the control neurons (Welkowitz et al., 1976; Hogg & Tanis, 1977).

Analysis of variance yields three measures that are useful in evaluating data. First, analysis of variance provides an F ratio which can be compared to a table of critical values to determine whether the experimental manipulations have significant effects on the neuronal response. Second, analysis of variance provides the within-groups-variance, which is a measure of how much the responses obtained on each trial to each stimulus differ from the average response to each stimulus. Third, analysis of variance provides the between-groups-variance, which is a measure of how much the average responses to different stimuli differ from the grand mean, i.e. the average of all responses.

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

Neuronal classification

The results in this paper are based on the analysis of the responses of 34 neurons, 26 of which were in the experimental group and 10 of which were in the control group. Nineteen neurons (14 experimental, five control) were recorded from one monkey and 15 neurons (ten experimental, five control) were recorded from a second monkey. Fifteen neurons (nine from the first monkey, six from the second) were driven by the ipsilateral eye and the remaining 19 neurons were driven by the contralateral eye. Fifteen neurons (eight from the first monkey, seven from the second) had ON-center receptive fields and the remaining 19 neurons had OFF-center receptive fields. All of the neurons were classified as linear summators using the linearity tests described in Methods. All of the neurons were clearly color-opponent. Eleven neurons exhibited +G −R opponency, eight exhibited +R −G opponency, 11 exhibited +B −Y opponency, and four exhibited +Y −B opponency. Based on the linearity and color-opponency test, we concluded that all 34 neurons were in the parvocellular layers of the lateral geniculate (Wiesel & Hubel, 1966; De Valois et al., 1966; Shapley et al., 1981).

Effect of cortical cooling on PLGN responses

Response strength

When we considered the effect of cooling the striate cortex on the number of spikes elicited by each stimulus from the experimental neurons, we found facilitation, inhibition, or no effect, depending on the stimulus presented (Fig. 5, left). There was much less variability between normal and cool conditions in the responses of the control neurons (Fig. 5, right). A more general view of the effect of cortical cooling on these two neurons is given in scatter plots of the effects of cortical cooling on the average responses to the 64 normal-contrast Walsh stimuli (Fig. 6).

To assess the significance of the effects of cortical cooling on the neuronal responses, we used a two-way analysis of variance with stimulus type as the first factor and cortical cooling as the second factor. Because cooling the striate cortex could produce both facilitation and inhibition, we considered both the main effects of cooling and the stimulus-by-cooling interaction. These analyses showed that all 34 experimental neurons had significant main effects of cooling or stimulus-by-cooling interactions. Furthermore, eight of the ten control neurons also had significant main effects of cooling or stimulus-by-cooling interactions.

The significant effects on the control neurons indicate sources of response variability manifested through our blocked experimental design that were not related to the projection from the

**Fig. 5.** The effect of cortical cooling on the responses to three Walsh patterns. Each tick mark in the rasters represents one spike, and each line of tick marks represents one trial. The vertical lines represent the time of stimulus onset, and the thick horizontal lines represent the 256-ms epoch of the response used in the data analysis. The height of the vertical line in the spike density functions represents a firing rate of 100 spikes/s. The Walsh pattern above each column of spike densities and rasters indicates the stimulus that elicited the responses shown in that column. The top row of spike densities and rasters were collected in the normal condition, and the bottom row of spike densities and rasters were collected in the cool condition. Data from an experimental neuron are shown on the left, and data from a control neuron are shown on the right.
Fig. 6. The effect of cortical cooling on the magnitude of the responses to the 64 normal-contrast Walsh patterns. The average number of spikes in each response in the normal condition is plotted on the abscissa, and the difference between the cool and normal conditions in the number of spikes is plotted on the ordinate. The horizontal dashed lines represent no change between normal and cool conditions. The positions of the Walsh patterns in the figure indicate the average number of spikes in the response to that pattern in the normal condition, and the effect of cortical cooling on that response. Responses above the dashed line represent facilitation, and responses below the dashed line represent inhibition. Data from an experimental neuron are plotted on the left, and data from a control neuron are plotted on the right.

Striatic cortex (Baker & Malpeli, 1977). Sources of such uncontrolled variability include differences in fixation between normal and cool conditions, long-term changes in responsiveness, and changes in the monkey's motivation due to satiety or boredom. To determine whether the changes observed in the responses of the experimental neurons were due solely to these uncontrolled factors, we compared the between-groups mean squares for the main effect of cooling and the cooling-by-stimulus interaction for the experimental and control neurons using one-tailed t-tests. (The between-groups mean squares indicate the magnitude of the cooling effect, one-tailed tests were made because only a larger effect on the experimental neurons would allow us to conclude that we had successfully removed cortical feedback.) The between-groups mean squares for both the main effect of cooling and the cooling-by-stimulus interactions for the experimental neurons were larger than those for the control neurons (Table 1. Spikes). Thus, the changes in the number of spikes in the responses of the experimental neurons

<table>
<thead>
<tr>
<th>Response measure</th>
<th>Mean squares source</th>
<th>Average mean squares</th>
<th>Student's t (Exp-Con)</th>
<th>df</th>
<th>P (one-tailed)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spikes</td>
<td>Cooling</td>
<td>5666.21</td>
<td>1136.59</td>
<td>2.013</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>Cooling by stimulus</td>
<td>183.18</td>
<td>95.38</td>
<td>1.930</td>
<td>32</td>
</tr>
<tr>
<td>( \phi_0 )</td>
<td>Cooling</td>
<td>571650.84</td>
<td>1121591.20</td>
<td>2.011</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>Cooling by stimulus</td>
<td>208468.12</td>
<td>100939.64</td>
<td>1.963</td>
<td>32</td>
</tr>
<tr>
<td>( \phi_1 )</td>
<td>Cooling</td>
<td>207291.49</td>
<td>67271.32</td>
<td>1.288</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>Cooling by stimulus</td>
<td>20923.97</td>
<td>13598.42</td>
<td>1.876</td>
<td>32</td>
</tr>
<tr>
<td>( \phi_2 )</td>
<td>Cooling</td>
<td>154856.57</td>
<td>38487.08</td>
<td>1.778</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>Cooling by stimulus</td>
<td>19950.29</td>
<td>6501.12</td>
<td>3.364</td>
<td>32</td>
</tr>
</tbody>
</table>
after cooling the striate cortex cannot be attributed solely to artifacts associated with the use of blocked trials.

Response waveform
Inspection of many of the responses of the neurons in our sample in the normal and cool conditions suggested that cooling the striate cortex might affect the temporal distribution as well as the number of spikes. This result is similar to that reported by Kalil and Chase (1970). Fig. 7 shows the rasters and spike density functions of the responses of an experimental and a control neuron to one of the Walsh patterns in both the normal and cool conditions. The response of the experimental neuron is larger in the cool condition than in the normal, but the distribution of spikes is clearly different as well. The differences between normal and cool conditions were not as great for the control neuron.

To assess the significance of the effects of cortical cooling on the temporal distribution of spikes, we first quantified the number and distribution of spikes using principal component analysis. We then used two-way analyses of variance with stimulus type as the first factor, and cortical cooling as the second factor. The dependent variables were the coefficients of the first three principal components. Across all neurons, the coefficient of the first principal component was highly correlated with the spike count, therefore we expected the analysis for the first principal component to be similar to that for the spike count, and this is the result we obtained. There were significant main effects of cooling or stimulus-by-cooling interactions on the coefficients of the first principal component for all 24 experimental neurons, and for eight of the control neurons. A comparison of the between-groups mean squares for the main effect of cooling and the stimulus-by-cooling interaction revealed that the magnitude of the cooling effect was greater for the experimental neurons than for the control neurons (Table 1, $\phi_0$).

The coefficients of the higher principal components were uncorrelated with the spike count and with the coefficients of the first principal component; therefore, any differences between blocks of trials would indicate an effect on the temporal distribution of spikes independent of that on the number of spikes. We found significant main effects of cooling or stimulus-by-cooling interactions on the coefficients of the second principal component for 20 experimental neurons, and five control neurons, and on the coefficients of the third principal component for 18 experimental neurons and four control neurons. The significant effects on the coefficients of the higher principal components for the control neurons indicate variability in the temporal distribution of spikes that is not related to cortical cooling. However, the between-groups mean squares for the main effect of cooling and the stimulus-by-cooling interaction were larger for the experimental neurons than for the control neurons (Table 1, $\phi_1$ and $\phi_2$).

One might be tempted to conclude from Table 1 that, because the differences between experimental and control neurons would not have been statistically significant if two-tailed tests had been used, these differences are not real. Had there been no real difference between experimental and control neurons, the between-

---

Fig. 7. The effect of cortical cooling on the response waveform. The spike density functions and rasters are drawn in the same manner as in Fig. 5. Data from an experimental neuron are shown on the left, and data from a control neuron are shown on the right. All responses were elicited by the same Walsh pattern, shown above.
VI feedback increases transmitted information in LGN

...groups mean squares for some of the principal components might have been larger for the control neurons than for the experimental neurons. This is because the coefficients of the three principal components are uncorrelated, and random factors might have had random effects on the different principal components. (Such random effects were observed for the control neurons on the amounts of information carried by the three principal components; see Table 2.) The similarity of the effect on all response measures adds confidence to our conclusion that the changes in the number and temporal distribution of spikes in the responses of the experimental neurons after cooling the striate cortex cannot be attributed solely to artifacts associated with the use of blocked trials.

Receptive-field eccentricity

The analyses described above show that there were greater differences between normal and cool conditions in the responses of the experimental neurons than in the responses of the control neurons. We have attributed this effect to a removal of cortical feedback from the experimental neurons. However, the control neurons tended to have more eccentric, and therefore larger, receptive fields than did the experimental neurons (cf. Fig. 4). Because the effects of eye movements on the responses of a neuron depend on the relative sizes of the eye movement, the receptive field, and the stimulus, an alternative explanation for our results could have been that eye movements caused the differences between the experimental and control neurons. To test this hypothesis, we computed the correlation between retinal eccentricity and the average absolute value of the difference in response between normal and cool conditions across all 34 neurons. These correlations were computed using the spike count and the coefficients of the first three principal components. (One-tailed tests of significance were made because only negative correlations would imply that the effect we attribute to cortical cooling was actually an artifact of receptive-field eccentricity.) Only the relationship between retinal eccentricity and the change in the coefficient of the third principal component was statistically significant ($r = -0.34, df = 32, P < 0.05$). There was no relationship between retinal eccentricity and the changes in the spike count, the coefficient of the first principal component, or the coefficient of the second principal component ($r = -0.24, df = 32, P > 0.05$, for all three response measures).

Thus, retinal eccentricity could account for only 11.8% of the change in the coefficient of the third principal component. Based on this result, we conclude that eye movements account for little of the difference between experimental and control neurons, and therefore, the effects we observed in the experimental neurons were largely due to removal of cortical feedback.

Functional consequence of cortical cooling

Transmitted information

The fact that PLGN neuronal responses are altered when feedback is removed suggests that cortical feedback plays a role in the encoding of messages in the LGN, but does not offer any clear picture of what that role is. Altered responses could reflect simple changes in the gain of the response, changes in the overall information content of the message, changes in the relative sensitivities to different stimulus parameters, or changes in the tuning characteristics to individual stimulus parameters, to mention just a few of the possibilities. To explore these questions, we examined the effect of cooling the striate cortex on the ability of geniculate neurons to transmit information about stimuli.

We first examined the effect of cortical cooling on the average information about all stimuli carried by a code based on the number of spikes in the response. To assess the effect of cortical cooling on information transmission, we normalized the information carried by the various codes in the cool condition by dividing them by the information carried in the normal condition. This normalization was done because of the large differences in information carried by the different codes and by different neurons. For the ten control neurons, there were no differences between normal and cool conditions in the average information carried by the spike count code. In contrast, for the 24 experimental neurons, the average information carried by the spike count code was reduced in the cool condition (Table 2, Spikes). In addition, the mean of the ratios of the spike count code for the experimental neurons was smaller than the mean of the ratios for the control neurons.

The result we obtained for a three-component temporal code based on the coefficients of the first three principal components was similar to that for the spike count code. For the ten control neurons, there were no differences between normal and cool conditions in the average information carried by the temporal code. For the 24 experimental neurons, the average information carried by the temporal code was reduced in the cool condition (Table 2, $\theta_{12}$). Furthermore, the mean of the ratios of the temporal code for the experimental neurons was smaller than the mean of the ratios for the control neurons.

The three-component temporal code represents both the number and the distribution of spikes in the response. Since the information carried by the spike count code was reduced

Table 2. The ratio of the information transmitted in the cool condition vs. the information transmitted in the normal (C/N) was significantly less than 1.0 for the experimental neurons, but not for the control neurons*

<table>
<thead>
<tr>
<th>Experimental (df = 23)</th>
<th>Control (df = 9)</th>
<th>Exp-Con (df = 32)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Code</td>
<td>N</td>
<td>C</td>
</tr>
<tr>
<td>Spikes</td>
<td>0.95</td>
<td>0.80</td>
</tr>
<tr>
<td>$\theta_{12}$</td>
<td>1.20</td>
<td>1.00</td>
</tr>
<tr>
<td>$\theta_{13}$</td>
<td>0.97</td>
<td>0.83</td>
</tr>
<tr>
<td>$\phi_1$</td>
<td>0.19</td>
<td>0.16</td>
</tr>
<tr>
<td>$\phi_2$</td>
<td>0.15</td>
<td>0.13</td>
</tr>
</tbody>
</table>

*Furthermore, the ratios of the experimental neurons were smaller than the ratios of the control neurons.
in the cool condition for the experimental neurons, it is possible that the reduction in information carried by the temporal code was due solely to the reduction in the information carried by the first component of that code, the component which reflects the number of spikes in the response. Therefore, we examined the effect of cooling the striate cortex on the information carried by each component of the temporal code separately. For the control neurons, there were no differences between normal and cool conditions in the amounts of information carried by the first (φ₁) and third (φ₃) principal components, and an increase in the amount of information carried by the second principal component (φ₂) in the cool condition (Table 2). For the experimental neurons, on the other hand, there were reductions in the amount of information carried by all three principal components in the cool condition (Table 2). Also, the means of the ratios of the higher-order temporal codes for the experimental neurons were smaller than the means of the ratios for the control neurons. Thus, cooling the striate cortex not only reduced the average information carried by codes based on the number, but also the average information carried by codes based on the temporal distribution of spikes in the responses of PLGN neurons.

Relation between changes in response and transmitted information

We observed considerable variation among the experimental neurons in the magnitude of the effect of cooling on the average magnitude of the responses and on the information carried by them. To determine whether there was any relationship between the change in the average response magnitude and the change in the average transmitted information associated with cortical cooling, we computed the correlation between the information ratios and the difference in average response magnitude for the experimental neurons. We found no significant correlation between the effect of cooling on average response magnitude and the average information carried by either the spike count code or the three-component temporal code. Thus, transmitted information was reduced regardless of whether the average responses were facilitated, inhibited, or did not change.

Comparability of experimental and control neurons

An examination of Table 2 reveals that the control neurons transmitted less information in the normal condition than did the experimental neurons. This result raises the possibility that the control neurons were not really comparable to the experimental neurons. Furthermore, the control neurons transmitted nearly the same amount of information in the normal condition as the experimental neurons did in the cool condition. This result opens the possibility that the difference between the experimental and control neurons in the effect of cortical cooling was due to some type of floor effect that prevented the information transmitted by the control neurons from dropping, rather than from a removal of cortical feedback from the experimental neurons. To test these hypotheses, we selected a subset of ten experimental neurons such that the average of the information transmitted by this subset in the normal condition was equal to the average of the information transmitted by control neurons in the normal condition. We then compared the effect of cortical cooling on the subset of experimental neurons with the effect of cortical cooling on the control neurons. For the subset of experimental neurons, the average information carried by each code was reduced in the cool condition (Table 3). Furthermore, the means of the ratios of cool vs. normal information for the subset of experimental neurons were less than those for the control neurons. Thus, the control neurons were comparable to the experimental neurons, and the lack of an effect on the control neurons was not due to a floor effect.

<table>
<thead>
<tr>
<th>Stimulus parameters</th>
</tr>
</thead>
</table>
| Decreases in the amount of information transmitted about a set of stimuli could be produced by a reduction in the information transmitted about only one of the parameters of the stimuli, say luminance, or by a reduction in the information transmitted about all of the parameters of the stimuli. To determine how cooling the striate cortex affected the information carried about the individual parameters of our stimuli, we presented 16 Walsh patterns (shown in Fig. 9) at each of nine different luminance combinations (shown in Fig. 2). To compute the information about pattern, independent of luminance, we pooled the responses to the 144 stimuli across luminance combinations according to stimulus pattern to obtain 16 stimulus codes. To compute the information about luminance, independent of pattern, we pooled the responses to the 144 stimuli across patterns according to the luminance of the pixel centered on the receptive field (cf. Fig. 3), to obtain 18 stimulus codes. We also pooled responses according to spatial contrast (whether the pixel centered on the receptive field was the lighter or the darker of the two pixels in the stimulus), and according to sequential contrast (whether the pixel centered on the receptive field was lighter or darker than the background) as described in our previous

<table>
<thead>
<tr>
<th>Table 3. A subset of the experimental neurons that transmitted, on average, the same amount of information as the control neurons, was selected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Experimental (df = 9)</td>
</tr>
<tr>
<td>-----------------------</td>
</tr>
<tr>
<td>Code</td>
</tr>
<tr>
<td>Spikes</td>
</tr>
<tr>
<td>φ₀₁</td>
</tr>
<tr>
<td>φ₀</td>
</tr>
<tr>
<td>φ₁</td>
</tr>
<tr>
<td>φ₂</td>
</tr>
</tbody>
</table>

*For this subset, the ratio of the information transmitted in the cool condition vs. the information transmitted in the normal (C/N) was also significantly less than 1.0. Furthermore, the ratios of this subset of experimental neurons were smaller than the ratios of the control neurons.*
report (McClurkin et al., 1991b). For both forms of contrast there were two stimulus codes for the information analysis. We then computed the amount of information transmitted about pattern (Pat), luminance (Lum), spatial contrast (Spa), and sequential contrast (Seq) in the normal and the cool conditions assuming two different response codes, one based on the spike count and the other based on the coefficients of the first three principal components (Fig. 8). There were no significant differences between the normal and cool conditions in the amount of information transmitted about any of the four stimulus parameters for the control neurons. However, the experimental neurons transmitted significantly less information in the cool condition than in the normal condition about all four stimulus parameters. Nearly identical effects were seen with both the spike count and the temporal codes. For the spike count code, the student's t values ranged from 3.56, df = 23, P = 0.0008 (one-tailed) to 5.43, df = 23, P = 0.000008 (one-tailed). For the temporal code, the student's t values ranged from 4.02, df = 23, P = 0.0003 (one-tailed) to 5.67, df = 23, P = 0.000004 (one-tailed). Thus, after the striate cortex was cooled, LGN neurons encoded less information about all of the stimulus parameters examined in this study.

**Signal and noise**

The amount of information transmitted by a neuron will decrease if either the variability of the neuron's response to individual stimuli increases (increased noise), or if the differences among the neuron's responses to different stimuli decreases (decreased signal separation). To determine the reason for the reduction in transmitted information associated with cooling the striate cortex, we used one-way analyses of variance with Walsh stimulus as the factor, with pattern independent of luminance as the factor, and with luminance independent of pattern as the factor. From these analyses, we obtained within-groups and between-groups variances in the normal and cool conditions for the experimental neurons. There were no differences between the normal and cool conditions in the within-groups variances (noise) for any of the response measures in any of the stimulus conditions when compared with one-tailed Student's t tests (Table 4). (One-tailed comparisons were used because only increases in the within-groups variances in the cool condition could account for the decreases in transmitted information associated with cortical cooling.) In contrast, the between-groups variances (signal separation) were significantly smaller in the cool than in the normal condition for all response measures in all of the stimulus conditions when compared with one-tailed Student's t test (Table 5). (One-tailed comparisons were used because only decreases in the between-groups variances in the cool condition could account for the decreases in transmitted information associated with cortical cooling.)

The decreased signal separation for stimulus pattern associated with cortical cooling is illustrated for one neuron in Fig. 9. For this neuron, the smallest responses were increased in the cool condition (thin lines) relative to the normal condition (thick lines), whereas the largest responses were unaffected. This selective facilitation of the smallest responses resulted in the set of responses becoming more similar (less separated) in the cool condition compared to the normal condition.

The decreased signal separation for stimulus luminance associated with cortical cooling is illustrated for one neuron in Fig. 10. For this neuron, some of the smaller responses were increased, and the larger responses were decreased in the cool condition (thin lines) relative to the normal condition (thick lines). The selective inhibition of the largest responses coupled with the facilitation of the smallest responses resulted in the set of responses becoming more similar (less separated) in the cool condition compared to the normal condition. These two figures illustrate how both facilitation and inhibition can cause a reduction in signal separation leading to a reduction in transmitted information.

The lack of a cooling effect on the noise in the responses serves as an additional control for our use of awake monkeys. When using awake animals to study visual processing, artifacts could arise from changes in the animal's behavior. In particular, in a blocked design such as ours there may have been increased variability in responses to individual stimuli due to a decrease in the monkey's ability to fixate reliably, resulting perhaps from satiety or fatigue. Because the normal condition was always run before the cool condition, such an artifact would have been reflected as an increase in noise in the cool cond-

---

**Fig. 8.** The effect of cortical cooling on the information transmitted about stimulus parameters. Information transmitted about four stimulus parameters is shown: luminance of the pixel centered on the receptive field (Lum); the Walsh pattern (Pat); spatial contrast, whether the pixel centered on the receptive field was the "white" or "black" pixel in the pattern (Spa); and sequential contrast, whether the pixel centered on the receptive field was lighter or darker than the background (Seq). The top row of graphs show the effect of cortical cooling on the information carried by the spike count code, and the bottom row of graphs show the effect of cortical cooling on the information carried by the three-component temporal code.
Table 4. There were no significant differences between normal and cool conditions in the within-groups variances (WG) for any of the response measures in any of the stimulus conditions

<table>
<thead>
<tr>
<th>Response measure</th>
<th>Stimulus condition</th>
<th>WG Variance</th>
<th>Student's t</th>
<th>df</th>
<th>P (one-tailed)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Normal</td>
<td>Cool</td>
<td>(Normal-Cool)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spikes</td>
<td>Walsh stimuli</td>
<td>71.80</td>
<td>75.92</td>
<td>0.90</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Pattern</td>
<td>72.84</td>
<td>73.30</td>
<td>0.10</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Luminance</td>
<td>60.55</td>
<td>71.40</td>
<td>1.58</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Walsh stimuli</td>
<td>76080.56</td>
<td>79826.36</td>
<td>0.79</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Pattern</td>
<td>76758.09</td>
<td>76723.08</td>
<td>0.01</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Luminance</td>
<td>64389.14</td>
<td>74691.30</td>
<td>0.92</td>
<td>23</td>
</tr>
<tr>
<td>(\phi_0)</td>
<td>Walsh stimuli</td>
<td>18683.73</td>
<td>17691.97</td>
<td>0.61</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Pattern</td>
<td>14428.20</td>
<td>13679.04</td>
<td>0.54</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Luminance</td>
<td>14436.88</td>
<td>13763.35</td>
<td>0.49</td>
<td>23</td>
</tr>
<tr>
<td>(\phi_1)</td>
<td>Walsh stimuli</td>
<td>10966.46</td>
<td>10780.70</td>
<td>0.35</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Pattern</td>
<td>8996.82</td>
<td>8680.78</td>
<td>0.65</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Luminance</td>
<td>8845.26</td>
<td>8595.96</td>
<td>0.51</td>
<td>23</td>
</tr>
</tbody>
</table>

Discussion

Previous studies have sought to understand the role of corticogeniculate feedback by examining the effects of manipulation of the striate cortex on the magnitudes of responses of LGN neurons, and a number of functions have been proposed. Corticogeniculate feedback has been shown to mediate binocular interactions in cat LGN, leading to the hypothesis that cortical feedback enhances the responses of LGN neurons to stimuli lying in the plane of fixation (Schmielau & Singer, 1977) and suppresses conflicting input from the two eyes (Varea & Singer, 1987). However, binocular interactions are not prominent in the primate LGN (Marrocco & McClurkin, 1979; Rodieck & Dreher, 1979), and therefore mediation of binocular interactions is probably not an important role for corticogeniculate feedback in the primate.

Early studies suggested that feedback served to gate the flow of visual information through the LGN (Kaill & Chase, 1970; Tsumoto et al., 1978). Later studies, however, have produced results that are difficult to reconcile with a simple gating hypothesis and have emphasized the effect of cortical feedback on the tuning properties of LGN neurons (Geisert et al., 1981; McClurkin & Marrocco, 1984; Murphy & Sillito, 1987; Gulyas et al., 1990). Of these studies, those using the smallest stimulus sets have yielded the clearest interpretations of corticogeniculate function, e.g. that feedback sharpens length tuning in the LGN (Murphy & Sillito, 1987), that feedback increases sensitivity to rapid movement (Gulyas et al., 1990), or that feedback improves the contrast sensitivity of LGN neurons (Ahlsten et al., 1982). However, despite the clarity of these individual interpretations, it is difficult to incorporate them into a general model of corticogeniculate feedback precisely because of the narrowness of focus dictated by their stimulus sets.

Studies with a broader range of stimuli have yielded more complex pictures of corticogeniculate function, e.g. that feedback may serve to broaden or to narrow the spatial tuning of LGN neurons (Geisert et al., 1981; McClurkin & Marrocco,

Table 5. The between-groups variances (BG) were significantly larger in the normal condition than in the cool condition for all of the response measures in all of the stimulus conditions

<table>
<thead>
<tr>
<th>Response measure</th>
<th>Stimulus condition</th>
<th>BG Variance</th>
<th>Student's t</th>
<th>df</th>
<th>P (one-tailed)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Normal</td>
<td>Cool</td>
<td>(Normal-Cool)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spikes</td>
<td>Walsh stimuli</td>
<td>719.74</td>
<td>558.05</td>
<td>2.62</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Pattern</td>
<td>2966.34</td>
<td>2195.62</td>
<td>2.91</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Luminance</td>
<td>3342.60</td>
<td>2022.62</td>
<td>4.12</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Walsh stimuli</td>
<td>779746.28</td>
<td>598019.40</td>
<td>2.72</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Pattern</td>
<td>3197725.44</td>
<td>2328184.39</td>
<td>3.09</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Luminance</td>
<td>3558035.59</td>
<td>2146889.42</td>
<td>4.23</td>
<td>23</td>
</tr>
<tr>
<td>(\phi_0)</td>
<td>Walsh stimuli</td>
<td>27459.00</td>
<td>23530.01</td>
<td>1.91</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Pattern</td>
<td>53171.39</td>
<td>36460.82</td>
<td>1.98</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Luminance</td>
<td>48671.25</td>
<td>28442.05</td>
<td>3.56</td>
<td>23</td>
</tr>
<tr>
<td>(\phi_1)</td>
<td>Walsh stimuli</td>
<td>15838.98</td>
<td>14048.82</td>
<td>1.74</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Pattern</td>
<td>21056.02</td>
<td>17944.78</td>
<td>1.80</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Luminance</td>
<td>28698.94</td>
<td>22129.00</td>
<td>2.41</td>
<td>23</td>
</tr>
</tbody>
</table>


Fig. 9. The effect of cortical cooling on the spike density functions for pattern. These spike density functions show the responses to the 16 Walsh patterns presented at all nine luminance combinations pooled on the basis of Walsh pattern. The spike densities in the normal condition are drawn with thick lines, and the spike density functions in the cool condition are drawn with thin lines. The Walsh patterns are indicated by icons.

1984), or to adjust the overall gain of LGN neurons (McClurkin & Marrocco, 1984). These results would have produced a coherent picture of corticogeniculate function if the changes in spatial tuning of the individual neurons had been such that the tuning of the lateral geniculate as a whole had been either narrowed or widened. However, this was not the case. The tuning of some neurons was shifted by increased responses to higher or lower spatial frequencies, but the tuning of others was shifted by decreased responses. Thus, it was not possible to tell if the average tuning of the LGN as a whole was changed at all. Consequently, although the fact that corticogeniculate feedback contributed to the spatial tuning of LGN neurons was clear, the underlying purpose of that contribution was not (McClurkin & Marrocco, 1984).

In considering the responses of the neurons in our sample to the stimuli we used, we obtained as diverse a set of effects of cortical cooling as has ever been observed. The average effects of cooling the striate cortex on individual neurons ranged from facilitation through no change to inhibition. However, when we evaluated the responses to individual stimuli, we found that cortical cooling produced the full spectrum of effects in all neurons. We can only conclude from these results that feedback affects the responses of LGN neurons to visual stimuli in a stimulus-dependent fashion.
In contrast with the picture of corticogeniculate function obtained from examining the effect of cortical cooling on neuronal responses, the picture of corticogeniculate function we obtain from assessing the effect of cortical cooling on transmitted information is clear and simple. Corticogeniculate feedback increases the amount of stimulus-related information that LGN neurons transmit. Corticogeniculate feedback increases the information carried by univariate codes based on the spike count or on individual coefficients of the K-L transform, as well as by a multivariate code based on the first three coefficients of the K-L transform. Corticogeniculate feedback increases the information that LGN neurons transmit about stimulus pattern, about stimulus luminance, about spatial contrast, and about sequential contrast. The means by which feedback increases transmitted information are also clear: corticogeniculate feedback increases transmitted information by increasing signal separation, i.e. by increasing the differences among the responses to different stimuli.
The analysis of the effect of cortical cooling on the signal and noise in the responses offers a resolution to the paradox between the diverse effects of cortical cooling on responses on the one hand, and the common effect of cortical cooling on the information carried by the responses on the other. The reduction in the between-groups variance indicates that the mean responses to different stimuli tended to become more similar when the cortex was cooled. An increase in similarity can be achieved by shifting all responses toward their original grand mean, by shifting all responses toward a new, lower grand mean, or by shifting all responses toward a new, higher grand mean. Thus, a reduction in transmitted information associated with a reduction in signal separation can be associated with an overall effect ranging from facilitation to inhibition.

The reduction in transmitted information carried by the three-component temporal code produced by cooling the striate cortex was statistically significant but small, only 0.20 bits. The small magnitude of this effect might lead one to ask: Would this reduction in transmitted information have any consequence for visual perception? We feel that the answer to this question is yes. If one considers the reduction of transmitted information as a percentage, our results indicate that cooling the striate cortex reduces the amount of visual information available by 15%. This would be as noticeable as a small amount of optical blur, and would be expected to affect perception.

Previous studies have noted that the temporal distribution of spikes in the responses of LGN neurons depends on the stimulus (Marrocco, 1976; Ikeda & Wright, 1972; Kallal & Chase, 1970), but little significance has been attached to this phenomenon. The effect of cortical cooling on the information carried by the higher-order principal components suggests that the temporal distribution of spikes is an important element of neuronal codes. Cooling the striate cortex reduced the information carried by the second and third principal components, parameters which reflect only the temporal distribution of spikes in the response. This was not a necessary outcome because there is no relationship between coefficients of the first and second or between the coefficients of the first and third principal components (McClurkin et al., 1991b; Optican & Richmond, 1987).

Thus, it is possible for information carried by the second and third principal components to have remained unchanged or even to have increased when the striate cortex was cooled, even though the information carried by the first principal component decreased. Indeed, the information carried by the second principal component for the control neurons increased in the cool condition whereas the information carried by the first and third principal components did not change. In light of this result one must ask: If the temporal distribution of spikes in LGN neuronal responses is not important to visual processing in the cortex, why would cortical feedback increase the information carried by the temporal distribution of spikes? Our answer is that temporal modulation of PLGN neuronal responses is indeed important for cortical visual processing.

Previous studies have shown that corticogeniculate feedback represents convergence onto LGN neurons; the receptive fields of the cortical neurons that project to the geniculate are larger than the receptive fields of LGN neurons (Gilbert, 1977) and LGN neurons are affected by feedback arising outside their classical receptive fields (Tsumoto et al., 1978; McClurkin & Marrocco, 1984). Taking this evidence of convergence together with our findings concerning the effect of corticogeniculate feedback on transmitted information, we can make a strong hypothesis about the role of corticogeniculate feedback: The purpose of corticogeniculate feedback is to provide global information that can be used to adjust local encoding mechanisms so that information transmission through the LGN is improved. This hypothesis predicts that the spatial sensitivities of LGN neurons must depend on the context in which they are measured. Specifically, the receptive field of a neuron when measured against an evenly illuminated background will be different than when measured against a textured background. Such background effects on the structure of the classical receptive field have been reported previously in cat (Li & He, 1987), and the results of McClurkin and Marrocco (1984) can be interpreted as demonstrating the importance of background on the structure of the classical receptive field.

In light of this hypothesis, one is led to ask: Why is global information needed for local encoding? We offer this speculative answer: The essence of object recognition is the discrimination of figure from background. Figure-ground separation depends, in turn, on the recognition of the boundaries which enclose objects. The boundaries which enclose objects are not local features, rather, they are global features, at least from the perspective of LGN neurons. Perhaps the visual system can better discriminate objects if the LGN neurons looking near the boundary of an object use different representations than those looking at the center of an object. If the receptive fields of LGN neurons are not large enough to determine whether an object boundary is present, it would not be possible to select the best representation using only local information. In this case, global information would be needed to select the best representation for LGN neurons to use.

References


Appendix I: Extraction of principal components

To extract the principal components, we converted the discrete spike train on each trial into a continuous function describing the probability of spike occurrence. Each spike was replaced with a kernel shaped like a Gaussian pulse. The initial width of the Gaussian kernel was set at 3 ms, and then adapted to reflect the local density of the data points (Silverman, 1986). Details concerning the calculation of the adaptive kernels can be obtained from Richmond et al. (1990). We used the spike density function rather than the peristimulus time histogram because the spike density function is not biased by bin edge artifacts, as is the histogram (Sanderson & Kobler, 1976). In summing the spike density functions within each stimulus condition, we adjusted the latency of each response by a small amount to account for the variability in response latencies across trials (Sanderson, 1980; Richmond et al., 1990; McCurkin et al.,...
VI feedback increases transmitted information in LGN

1991a). The maximum that any response could be adjusted was set to ±25 ms, although almost all adjustments were less than 3 ms.

The spike density function representing neuronal activity on each trial was sampled at 1-ms intervals and low-pass filtered with a nonrecursive digital filter (-3dB at 50 Hz) to eliminate the response to the 60-Hz video raster that was present in most of the responses we obtained (McClurkin et al., 1991a). The filtered spike density function for each trial was resampled at 4-ms intervals to obtain a response vector of 64 elements spanning the 256-ms stimulus duration. The average vector, obtained for each neuron by summing over all of the individual trial vectors, was subtracted from each of the individual response vectors in the data set. A 64 × 64 element covariance matrix was computed across all of the individual trials in the data set. The principal components that were the basis functions of the K-L transform were the eigenvectors of this covariance matrix (Richmond & Optican, 1987). This analysis allowed 64 uncorrelated principal components to be extracted from the data set. The K-L transform of a response is simply the set of coefficients needed to weight each of the principal components to reconstruct the spike density function on each trial.

Appendix 2: Calculation of transmitted information

To compute transmitted information, input and the output codes must be defined. The input codes were defined by assigning a number to each stimulus class. Output codes were defined by assigning the response measures into a series of 14 bins by a kernel estimation technique similar to that used to form the spike density functions (Silverman, 1986; Optican & Richmond, 1987). We tested five potential output codes. One code was based on the number of spikes elicited by each stimulus. Three codes were based on the coefficients of the first three principal components considered separately. The fifth code was based on the coefficients of the first three principal components considered jointly.

The conditional information transmitted about a particular stimulus is related to the conditional probability of obtaining each possible response given that stimulus summed over all possible responses:

\[ T(s_j; R) = \sum_k p(r_k \mid s_j) \log \frac{p(r_k \mid s_j)}{p(r_k)} \]  \hspace{1cm} (1)

where \( s_j \) is the \( j \)th member of the stimulus set, \( R \) is the set of all responses, and \( r_k \) is the \( k \)th member of the response set. Average transmitted information is obtained by averaging the conditional information transmitted about each of the stimuli in the stimulus set:

\[ T(S; R) = \sum_j p(s_j) T(s_j; R) \]  \hspace{1cm} (2)

Calculations of transmitted information from neuronal data are biased upwards due to response quantization, noise, and small sample size (Fagen, 1978). This upward bias is greater for multivariate codes than for univariate codes. To correct for this bias, we shuffled the data, randomly assigning responses to stimuli, and computed the average amount of transmitted information from these shuffled data sets:

\[ T_b = \frac{1}{N_b} \sum_{i=0}^{N_b-1} T_i \]  \hspace{1cm} (3)

where \( N_b \) is the number of shuffled data sets, \( T_i \) is the transmitted information calculated from the \( i \)th shuffled data set, and \( T_b \) is the estimated information bias. A stable estimate of the information bias could be obtained with five shuffles. This estimate of information bias, \( T_b \), was then scaled by an estimate of the noise to signal ratio, \( T_b / T \), and the product was subtracted from the raw information calculation, \( T \), to provide an improved estimate of transmitted information:

\[ \hat{T} = T - \frac{T_b}{T} \]  \hspace{1cm} (4)

This bias correction procedure has been shown to provide accurate estimates of transmitted information from neuronal data with as few as seven trials per stimulus with output codes containing as many as four components (Optican et al., 1991).