

Neural Correlates of Perceived Brightness in the Retina, Lateral Geniculate Nucleus, and Striate Cortex

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Brightness changes can be induced in a static gray field by modulating the luminance of surrounding areas. We used this induction phenomenon to investigate the neural representation of perceived brightness. Extracellular recordings were made in striate cortex, the lateral geniculate nucleus (LGN), and the optic tract of anesthetized cats using stimuli that produced brightness induction. While a cell's receptive field (RF) was covered by uniform gray illumination, the luminance of rectangular flanking regions was modulated sinusoidally in time, inducing brightness changes in the RF. We looked for a correspondence between the modulation of a cell's response and stimulus conditions that did or did not produce perceptual changes in brightness. We found that the responses of retinal

ganglion cell axons in the optic tract were never correlated with brightness. On the other hand, many neurons in striate cortex and a small fraction in the LGN responded in a phase-locked manner at the temporal frequency of the flank modulation, even though the flanks were 3–7° beyond the edges of the RF. Only in striate cortex were cells found that had responses correlated with brightness under all stimulus conditions. These findings suggest that brightness information is explicitly represented in the responses of neurons in striate cortex as part of a neural representation of object surfaces.

Key words: brightness; striate cortex; LGN; optic tract; surface perception; vision

Physiological studies of the visual system have demonstrated that beyond the initial photoreceptor level of the retina, neurons are primarily responsive to luminance contrast within their receptive fields (Kuffler, 1953; Hubel and Wiesel, 1962). This apparent bias toward contrast makes it unclear how the visual system determines the perceptual properties we attribute to areas bounded by contours, such as brightness and color.

Psychophysical studies have demonstrated that the perceived brightness and color of an area can be greatly influenced by the properties of neighboring and more distant regions. For example, in brightness induction, a gray patch on a bright background appears darker than the same gray patch on a dark background. If the background luminance is sinusoidally modulated in time, the brightness of the constant gray patch appears to change in antiphase to the background even though the patch is physically constant. This dynamic version of brightness induction is visible only at surprisingly low temporal frequencies of the background luminance modulation (below ~2.5 Hz), above which the central gray patch appears constant in brightness (DeValois et al., 1986; Rossi and Paradiso, 1996). The low temporal cutoff of dynamic induction is consistent with other studies (Paradiso and Nakayama, 1991; Paradiso and Hahn, 1996), suggesting that a relatively slow mechanism integrates information over large areas of the visual field to assign the brightness we perceive at a given location.

Brightness induction can be produced in test patches that are

much larger than receptive fields (RFs) in the retina, lateral geniculate nucleus (LGN), and striate cortex. If cells in these areas play a role in the perceptual effect, the underlying neural interactions presumably come from outside the small receptive fields. Numerous studies have shown that across visual areas the response of a neuron to contours within the RF can be significantly affected by stimuli presented outside the RF (Maffei and Fiorentini, 1976; Allman et al., 1985; Gilbert and Wiesel, 1990; DeAngelis et al., 1992; Sillito et al., 1995; Toth et al., 1996; Levitt and Lund, 1997). These surround effects suggest that individual neurons are capable of integrating information over large areas of the visual field in the determination of a response that is context dependent.

Virtually all of the previous studies examining surround interactions in striate cortex used gratings or bars of light as stimuli. This is consistent with the hypothesized role of V1 in form vision. However, recent work from our laboratory suggests that a significant percentage of neurons in striate cortex also integrate surface information over a spatial scale comparable to perceptual interactions (MacEvoy et al., 1998) and convey information about brightness (Rossi et al., 1996). Recent reports from other laboratories also support the hypothesis that surface information is represented in the responses of V1 neurons (Lamme, 1995; Komatsu et al., 1996; Lee et al., 1998). In the present study, we set out to further characterize brightness-associated responses in striate cortex and to assess whether such responses originate in the retina, LGN, or striate cortex.

A portion of the results from the cortical recordings has been published previously (Rossi et al., 1996).

MATERIALS AND METHODS

Animal preparation. Twenty-two adult cats, ranging in weight from 2.5 to 5.5 kg, were used for this study. All procedures were conducted in accordance with National Institutes of Health guidelines and were approved by Brown University's Institutional Animal Care and Use Com-

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mittee. Animals were initially sedated with an injection of acepromazine (0.11 mg/kg, i.m.) accompanied by atropine sulfate (0.05 mg/kg, i.m.), and a surgical level of anesthesia was achieved with sodium thiopental (initial dose 20 mg/kg, i.v., supplemented as needed). A tracheotomy was performed, and the animal intubated. The animal was then paralyzed with an intravenous infusion of atracurium besylate (initial dose 5 mg, 0.6–1.2 mg · kg⁻¹ · hr⁻¹) and artificially respired. The stroke rate and volume of the respirator were adjusted to maintain an end-tidal CO₂ between 3.5 and 4.0%. Rectal temperature was maintained near 38°C with a heating pad. Initially, sodium thiopental was infused continuously at the rate of 2 mg · kg⁻¹ · hr⁻¹. During the experiment, EKG and EEG (via epidural wires) were monitored, and adjustments in the rate of infusion were made to maintain the proper level of anesthesia. Pupils were dilated with 1% atropine sulfate, and the nictitating membranes were retracted with 10% phenylephrine. The accommodative power of the eyes was adjusted so that the eyes were focused on a tangent screen 57 cm away. This was accomplished by choosing the correct power contact lens that produced a sharp image of the retinal vasculature, which was back-projected on the tangent screen (tapetal reflection method). The positions of retinal landmarks were mapped on the tangent screen to estimate the eccentricity of receptive fields.

Recordings were made in three different components of the visual system: striate cortex, LGN, and optic tract. For the cortical recordings, a 2 × 2 mm craniotomy was made above the central visual field representation of striate cortex, and a small portion of the dura was resected. A glass-insulated tungsten electrode was then lowered to the cortical surface, and the craniotomy was filled with agar to minimize motion of the brain. For the LGN and optic tract recordings, a craniotomy was made around A9L6. Recordings of geniculate neurons were made in the A and A1 laminae. Recordings from axons of retinal ganglion cells were made by positioning the electrode in the optic tract ventral to the LGN.

Stimuli and procedure. A window discriminator was used to isolate the response of a single neuron based on the amplitude and slope of the action potential waveform. When the response of a neuron was isolated in striate cortex, LGN, or optic tract, the receptive field was mapped on the tangent screen using a hand-held stimulator. Boundaries of the receptive field were determined using moving and flashed bars and spots of light. In striate cortex, properties including orientation selectivity, ocular dominance, end-stopping, and direction selectivity were noted. In the LGN and optic tract, linearity was tested with counterphased sine-wave luminance gratings. All further visual testing was conducted with the automated presentation of computer-generated stimuli. Stimuli were generated by a Number Nine Graphics Board installed in a PC clone and displayed on a 27 inch monitor (NEC 4PG) with 640 × 480 pixel resolution and a refresh rate of 60 Hz. Stimuli were presented monocularly to the eye that responded best in previous testing. The key experimental stimulus configuration is shown in Figure 1A,B. A static gray central region was flanked on either side by regions where the luminance was modulated sinusoidally in time by lookup table animation. This produced brightness changes in the static center region, roughly in antiphase to the luminance modulation of the flanks (Fig. 1C). The luminance of the static, central portion of the stimulus was 30 cd/m². The luminance of the flanks was modulated about a mean of 30 cd/m² such that the stimulus had a 95% Michelson contrast $[(L_{\max} - L_{\min}) / (L_{\max} + L_{\min})]$ when the luminance was maximal and minimal. For all stimuli, the starting phase of the luminance modulation was a luminance increment from the mean value (i.e., sine phase). Photodiodes were used to confirm that the luminance of the static central portion of the stimulus remained constant while the luminance of flanking regions was modulated. After the receptive field of a cell was determined, the size of the stimulus was manipulated so that the central region was large enough to exceed the receptive field borders by at least 3° on each side. In preliminary experiments, we found that there was no significant effect of stimulus size on the response, so long as the flanking regions of the stimulus remained well outside the receptive field. Therefore, the largest stimulus size (center region of stimulus = 14 × 14°) was often used to assure that the luminance-modulated flanks were far outside the RF. Stimulus size was not scaled to reflect RF sizes in the optic tract, LGN, and V1, because we reasoned that any neural response associated with perceived brightness must occur in stimulus conditions known to yield perceptual brightness induction.

Within an experimental run, we presented several variations of the basic induction stimulus (Fig. 2) to assess the effects of the different components of the stimulus in isolation. In addition, several temporal frequencies of the luminance modulation were presented for each stim-

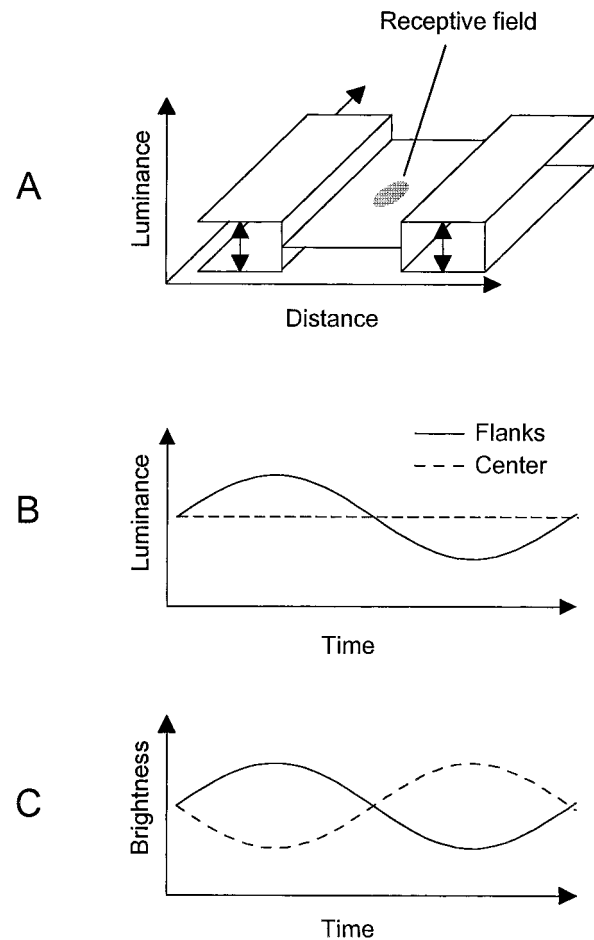


Figure 1. *A*, Luminance profile of the induction stimulus. The stimulus was composed of three rectangular regions of equal size. The luminance of the areas flanking the central gray area was modulated (arrows) sinusoidally in time (*B*), creating the perception that the brightness of the static center area varied in antiphase to the flanks (*C*). The static center region of the stimulus had a luminance equal to the time-average luminance of the modulated flanks.

ulus condition. The stimuli were presented in random order, and each condition was repeated 15–30 times within a given experimental run. The duration of the stimulus presentation was 4 sec, and the interval between stimulus presentations was 5 sec.

Data collection and analysis. The activity of a neuron was recorded as an event record of spike times relative to stimulus onset. These event records were converted to a time series with a resolution of 4 msec and displayed as peristimulus time histograms (PSTHs). To assess the degree of modulation in the PSTH, the neural response was multiplied by a sliding squarewave weighting function:

$$\text{activity} = \sum_{t=0}^{4 \text{ sec}} s(t) w(t),$$

where $s(t)$ = number of spikes in the 4 msec time bin, beginning at (t) , $w(t)$ = weighting function at (t) , and the summation is incremented in steps equal to the time bin width (4 msec). The weighting function is defined as a function of the initial squarewave phase θ , which varies from 0 to 2π :

$$w(t) = 0 \text{ for } t < \frac{\theta}{2\pi f} \text{ or } \frac{\theta + \pi(2i + 1)}{2\pi f} \leq t < \frac{\theta + 2\pi(i + 1)}{2\pi f} \quad i = 0, 1, \dots,$$

$$w(t) = 1 \text{ for } \frac{\theta + 2\pi i}{2\pi f} \leq t < \frac{\theta + \pi(2i + 1)}{2\pi f} \quad i = 0, 1, \dots,$$

where f = squarewave frequency.

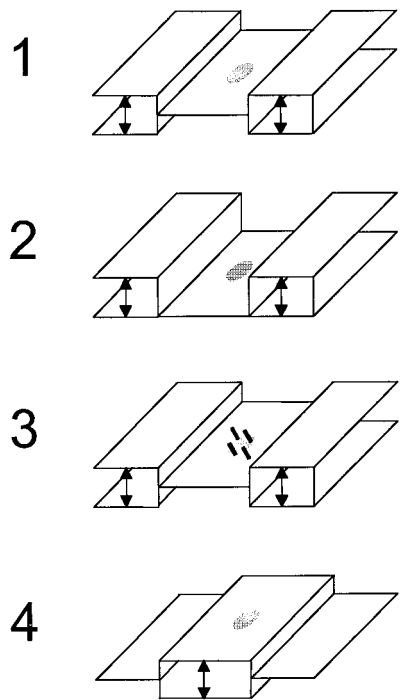


Figure 2. Spatial configurations of the stimuli. Stimuli were presented so that the central area of the stimulus was centered over the receptive field (shown as a gray oval). Stimuli consisted of the following: (1) constant gray center with luminance-modulated flanks (arrows) that resulted in the perception of brightness changes in the region corresponding to the receptive field and (2) black center with luminance-modulated flanks. There was no perceived brightness modulation in the central area containing the receptive field in this condition. (3) Same as (1) with the addition of drifting white (or black) bars over receptive field. Brightness induction was perceived in the area surrounding the bars. (4) Luminance modulation in center with static gray flanks.

This procedure yields a function that represents the summed activity of the neuron at incremental steps of phase in the luminance modulation of the stimulus. This function was then smoothed by means of the Savitzky-Golay filter (Press et al., 1988) with a space constant of 10 data points; each point corresponded to a 4 msec time bin. From the smoothed function, the amplitude and phase of the cell's response were determined at the luminance modulation frequency of the stimulus. This process is illustrated schematically in Figure 3. To determine the statistical significance of the response modulation, we performed simulations to estimate the probability that the modulation occurred by chance. A neuron was considered to have a significantly modulated response if the normalized measure of the response modulation satisfied the $p < 0.05$ level of significance. We found that this procedure gave more reasonable estimates of response modulation at the driving frequency than a fast Fourier transform, because the responses were usually rectified.

Histology. At the end of each electrode penetration, electrolytic lesions (5–10 μA , 5–10 sec) were made at selected locations along the electrode track to aid in the identification of recording sites. At the conclusion of each experiment, animals were given an overdose of thiopental sodium and perfused through the heart initially with saline and then with a mixture of 10% formaldehyde in 0.1 M phosphate buffer, pH 7.4. The brain was removed and kept for several days in a fixative solution with 30% sucrose. A freezing microtome was used to cut the tissue at 50 μm increments in the coronal plane. Sections were mounted and stained with cresyl violet. For cortical reconstructions, the laminar position of recording sites along a penetration was determined by criteria based on the relative size and density of cresyl-stained cell bodies (Garey, 1971).

RESULTS

Several configurations of the induction pattern composed the stimulus set that was used to examine the responses of neurons in striate cortex, LGN, and optic tract. The different stimulus con-

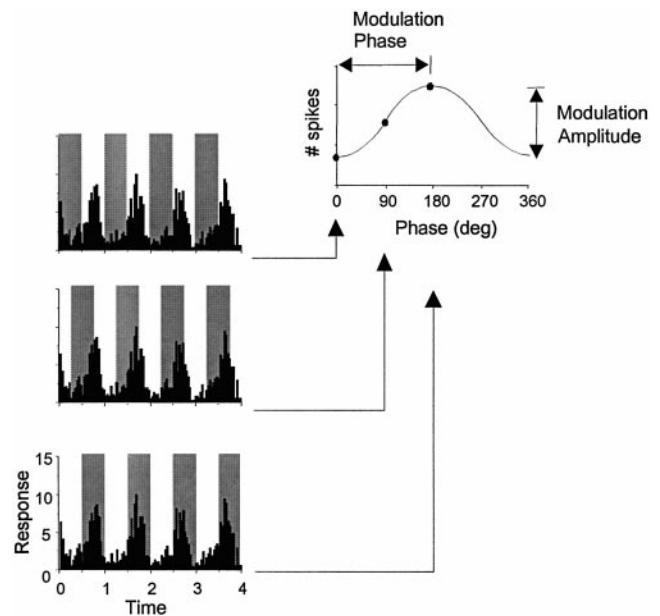


Figure 3. Schematic illustration of the procedure used to quantify the degree of modulation in the response histogram. On the left of the figure is the response of a neuron to the induction stimulus at a luminance modulation rate of 1 Hz. To assess the degree of modulation in the PSTH, the neural response was multiplied by a sliding squarewave weighting function having a period equal to the inverse of the modulation rate. The gray bands superimposed on the PSTH represent the weighting function in which the activity within the gray zones was summed. A plot of response modulation was constructed (top right) by incrementally shifting the weighting function across 360° of initial phase (left). The amplitude and phase of the response modulation sinusoid was then used to define the modulation amplitude and phase.

figurations will be referred to by their numerical designation in Figure 2. We recorded in the central visual representation of striate cortex and the LGN, where receptive field size was typically between 1 and 5°. To assure that stimulus flanks were well outside the RF, cells were not studied if the largest dimension of the receptive field exceeded 8°. The stimuli were presented so that the flanking regions were either to the left and right or above and below the RF. Receptive field boundaries were routinely remapped after the automated presentation of the stimulus set. All of the neurons described in this study responded significantly to spots of light or oriented bars presented within the RF.

Striate cortex

Effects of luminance modulation outside the RF

We reported previously that a significant percentage of neurons in striate cortex respond to luminance modulation outside the RF (Rossi et al., 1996). Here we will briefly review the key elements of the cortical results and provide additional analysis and comparison with recordings from the LGN and optic tract. Many cortical neurons were found to respond only in stimulus conditions that produced perceptual changes in brightness in the area corresponding to the receptive field. An example of this is shown in Figure 4. The third row of this figure shows the response of a neuron to the presentation of a constant gray field flanked on either side by luminance varying fields of equal size. The receptive field was 4° wide and was centered on the central gray area that was 14° across. The response of the neuron was phase-locked to the frequency of the luminance modulation in the stimulus

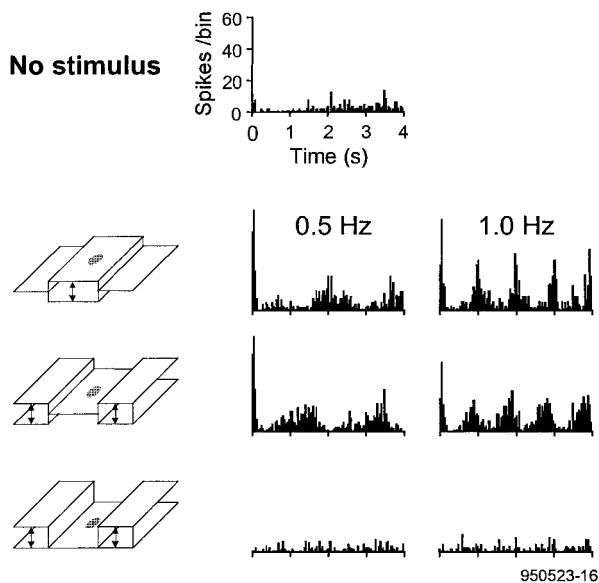


Figure 4. A neuron in striate cortex that responded to luminance modulation outside the RF. Stimulus configurations are shown on the *left* and the response of the neuron on the *right*. The RF was 4° wide \times 3.5° high, and the static gray central portion of the stimulus was 14° wide \times 14° high. At 0.5 and 1.0 Hz, the response was modulated in sync with luminance changes in the flanks, although the flanks were 5° beyond the RF on each side (*third row*). When the stimulus center was black, induction was perceptually lost along with the neuronal response modulation (*fourth row*). There was a clear shift in response phase in the induction condition (*third row*) compared with the condition with luminance modulation within the RF (*second row*).

flanks. There was no such response when the central portion of the stimulus was black (*fourth row*). This is an important distinction because there is perceptual induction of brightness changes in the stimulus with the gray center (*third row*) but not in the stimulus with the black center (*fourth row*).

In some neurons, the effect of surround modulation could only be brought out by adding a stimulus with contrast into the RF to raise baseline activity. The stimulus configuration used to test this (Fig. 2, stimulus 3) was identical to the induction stimulus (Fig. 2, stimulus 1) with the addition of bar stimuli that were drifted continuously through the receptive field. The color (black or white), orientation, speed, and direction of the bar stimuli were selected to produce the best response when presented within the RF in isolation. To human observers, the presence of the small drifting bars on the constant gray center did not appreciably affect the brightness modulation induced in the gray field surrounding the bars by the flanks of the stimulus. Figure 5 is an example of a striate neuron in which the effect of stimulation outside the RF was most apparent when the drifting bars were presented within the RF. For this neuron, the modest response to the bar stimuli within the RF (*second row*) was significantly augmented by the stimulation outside the RF (*fifth row*). Moreover, this increase in the response of the neuron was phase-locked to the rate of luminance modulation outside the RF. This neuron did not exhibit a modulated response to the induction stimulus when presented without the drifting bars (*third row*). In other words, this cell appeared to convey information about brightness, but only in concert with information about contrast within the receptive field.

In our sample of striate neurons we did not find a systematic relationship between classic receptive field properties (orienta-

tion selectivity, spatial tuning, simple vs complex) and the magnitude of the response to the brightness induction stimuli. We also did not find a significant effect of stimulus orientation (horizontal or vertical arrangement of flanks). In general, the response to the induction stimuli was less than the response to an optimal bar stimulus.

The effects of surround modulation were generally of two types: an overall increase in firing rate and modulation at the driving frequency. Using the procedure outlined in Materials and Methods, we quantified the degree to which responses showed general excitation or inhibition and/or modulation at the frequency of the flank modulation. Because low temporal frequencies (0.5–1.0 Hz) elicited the best responses on average to the induction stimulus (stimulus 1), we chose to examine the responses to 1 Hz luminance modulation. First, the total number of spikes that occurred during the stimulus presentation was taken as a measure of overall activity. To compare responses in conditions that do and do not give perceptual induction, we calculated an activity ratio as follows: activity ratio_{1,2} = total spikes (stimulus 1)/total spikes (stimulus 2).

Second, the amplitude of the modulation present in the response was determined at the temporal frequency of the luminance modulation (see Materials and Methods). The amplitude ratio of the neuron's response was given by: amplitude ratio_{1,2} = amplitude (stimulus 1)/amplitude (stimulus 2).

The amplitude and activity ratios obtained for the population of 160 striate neurons is shown in Figure 6A. Although there is considerable scatter in the population data, there is a tendency for neurons to show both increased overall activity and increased response modulation to effective stimuli.

The population was then examined with regard to how specific a neuron's response was to stimulus conditions that produce brightness induction in human observers (stimuli 1 and 3). Several criteria were adopted to make this determination. First, only neurons that exhibited a statistically significant amplitude of response variation ($p < 0.05$), with luminance modulation outside the RF, were included (see Materials and Methods). In our sample of 160 striate neurons, 120 (75%) satisfied this criterion. Second, comparisons of the responses to stimulus 1 (or stimulus 3) and stimulus 2 were made to establish whether the neuron's modulated response to stimulus 1 or 3 was lost when the central area was black, thus eliminating the perceptual induction (stimulus 2). The distribution of the amplitude ratio_{1(3),2} for 120 striate neurons is shown in Figure 7A.

This figure shows that a significant fraction of the population had ratios >1 , indicating that the amplitude of the response modulation to stimulation outside the RF was greater for those stimuli that produced brightness induction within the RF. We chose the conservative criterion that neurons were considered for further analysis only if the modulation amplitude in response to stimulus 1 or stimulus 3 was more than twice that of the response to stimulus 2. Forty-nine neurons had amplitude ratios_{1(3),2} that met this criterion. The 49 neurons (30% of total population) that satisfied this criterion appeared to reliably respond in a manner correlated with the perceptual induction of brightness. Because the response was significantly less in the center-black condition (stimulus 2), it is unlikely that the brightness-correlated responses resulted from scattering of light in the eye (see Discussion). A breakdown of how this subpopulation of neurons responded to stimuli 1 and 3 is shown in Table 1.

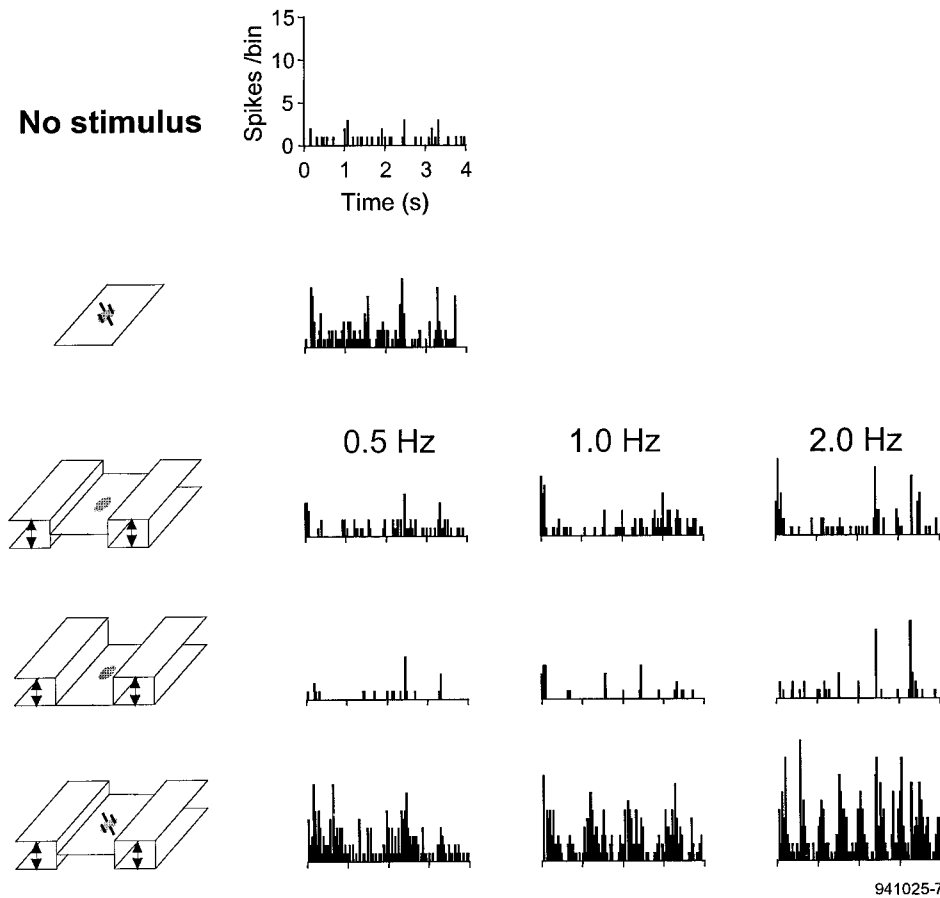


Figure 5. A neuron in striate cortex for which response modulation was most apparent when the baseline firing rate was elevated by drifting white bars of light through the RF (bottom row). Stimulus configurations are shown on the left with response of the neuron on the right. The second row shows the response of the neuron to drifting white bars on a static gray background. In the bottom three rows, there are three histograms for each stimulus condition for flank modulation at 0.5, 1.0, and 2.0 Hz. The bar stimuli were drifted through the receptive field at 6.6°/sec. Receptive field size = 4° wide × 3° high; stimulus center = 14 × 10°.

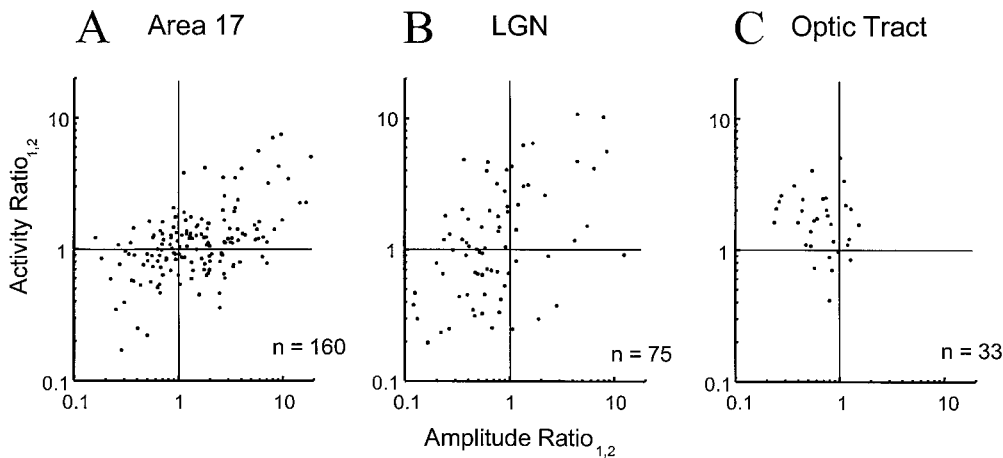


Figure 6. Comparison of the activity and amplitude ratios for the neurons recorded in striate cortex (A), the LGN (B), and the optic tract (C). Neurons with ratios >1 in either dimension indicate a larger response in the induction condition (stimulus 1) than the center-black condition (stimulus 2). For all neurons shown, the temporal frequency of the luminance modulation was 1.0 Hz.

Effects of luminance modulation within the RF

In the majority of the neurons tested, the response to luminance modulation within the RF was compared with the aforementioned effects of luminance modulation outside the RF. Surprisingly, it was not uncommon that striate neurons responded robustly to a uniform field of varying luminance that overlapped the RF by several degrees (stimulus 4), despite the lack of contours within the RF. For those neurons that exhibited amplitude ratios_{1(3),2} > 2, we wished to compare the response to the induction stimulus (stimulus 1 or 3) with that elicited by direct luminance modulation within the RF (stimulus 4). To describe this relation-

ship, the amplitude ratio_{1(3),4} was calculated: amplitude ratio_{1(3),4} = amplitude (stimulus 1 or stimulus 3)/amplitude (stimulus 4).

Figure 7B shows the distribution of the amplitude ratio_{1(3),4} for 42 striate neurons that met the criterion for amplitude ratio_{1(3),2} and were also fully studied with luminance modulation within the RF. It can be seen that the majority of these neurons had amplitude ratios >1, indicating that the degree of modulation in response to the 1.0 Hz induction stimulus was often equivalent to or greater than that produced by luminance modulation within the RF at the same rate. Neurons that exhibited a significantly

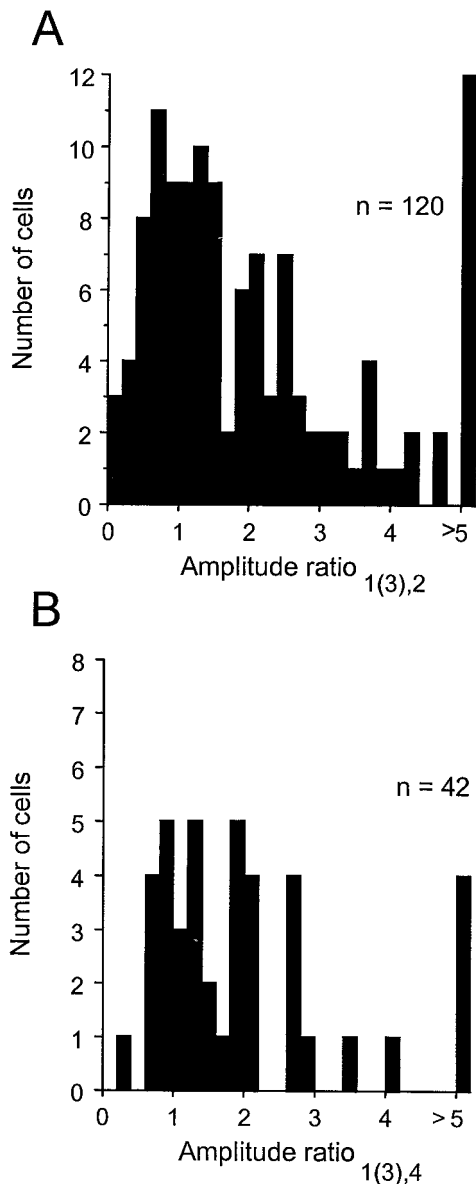


Figure 7. *A*, Distribution of the amplitude ratio $_{1(3),2}$ for 120 striate neurons. Ratios >1 indicate that the amplitude of the response modulation was greater for induction (stimulus 1 or stimulus 3) than for the center-black control (stimulus 2). *B*, Distribution of the amplitude ratio $_{1(3),4}$ for 42 striate neurons in which the amplitude ratio $_{1(3),2}$ was >2 . Ratios >1 indicate that the amplitude of the response modulation was greater for induction (stimulus 1 or stimulus 3) than for luminance modulation within the RF (stimulus 4). Both amplitude ratios were determined for responses to 1 Hz stimuli.

modulated response to luminance change within the RF (ratio $_{1(3),4} > 0.5$) and also satisfied the amplitude ratio $_{1(3),2}$ criterion are examined in greater detail in the following sections.

Effects of temporal frequency on response phase

One characteristic of the dynamic induction stimulus we used is that the induced brightness changes in the center of the stimulus occur in antiphase to the luminance modulation in the flanks. In many neurons there is a similar phase difference in the response to the induction stimulus (stimulus 1 or 3) relative to luminance modulation within the RF (stimulus 4). Examples of these phase differences can be seen in the responses of neurons in Figures 4

Table 1. Distribution of cells that responded to one or both of the induction stimuli

Stimulus	No. of neurons	% of population
1 only	18	11.3
3 only	11	6.9
1 and 3	20	12.5

These neurons showed a response amplitude at least twice as great in either induction condition than in the center-black condition (stimulus 4). Stimulus 3 was the same induction stimulus as stimulus 1 with the addition of small white bars at the optimal orientation, used to elevate the background firing rate.

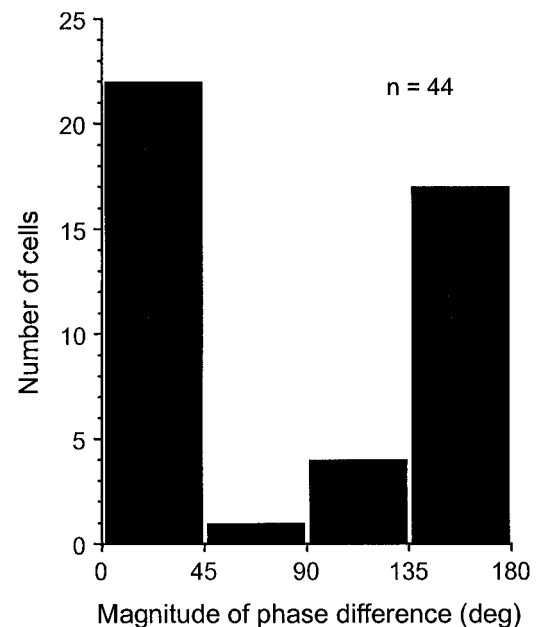


Figure 8. Distribution of phase differences in the response to induced (stimulus 1) versus direct (stimulus 4) brightness changes within the RF. The luminance modulation rate was 1.0 Hz.

and 9A. In both these examples, there was an approximate phase difference of 180° in the response to the induction stimulus (third row) relative to the response to direct changes in luminance within the RF (second row). As in the examples in the previous section, the response to luminance modulation outside the RF was greatly diminished when the gray center of the stimulus was removed (fourth row). The magnitude of the observed phase differences varied among neurons in our sample and is summarized in Figure 8. It can be seen in this figure that the greatest number of neurons exhibited either no phase difference or a phase difference near 180° . Because lower temporal frequencies (0.5–1.0 Hz) elicited the optimal response on average (see the following section), we chose to examine the population phase relationship of neurons at 1.0 Hz.

It was often the case that the observed phase differences were most pronounced at low temporal frequencies of the luminance modulation. It can be seen in Figure 9A that as the temporal frequency of the luminance modulation was increased above 1 Hz, there was a noticeable decrease in the phase difference between the induction and center-modulation responses. This shift in the phase of the response at higher temporal frequencies was observed only in neurons that had marked phase differences ($>100^\circ$) at lower temporal frequencies.

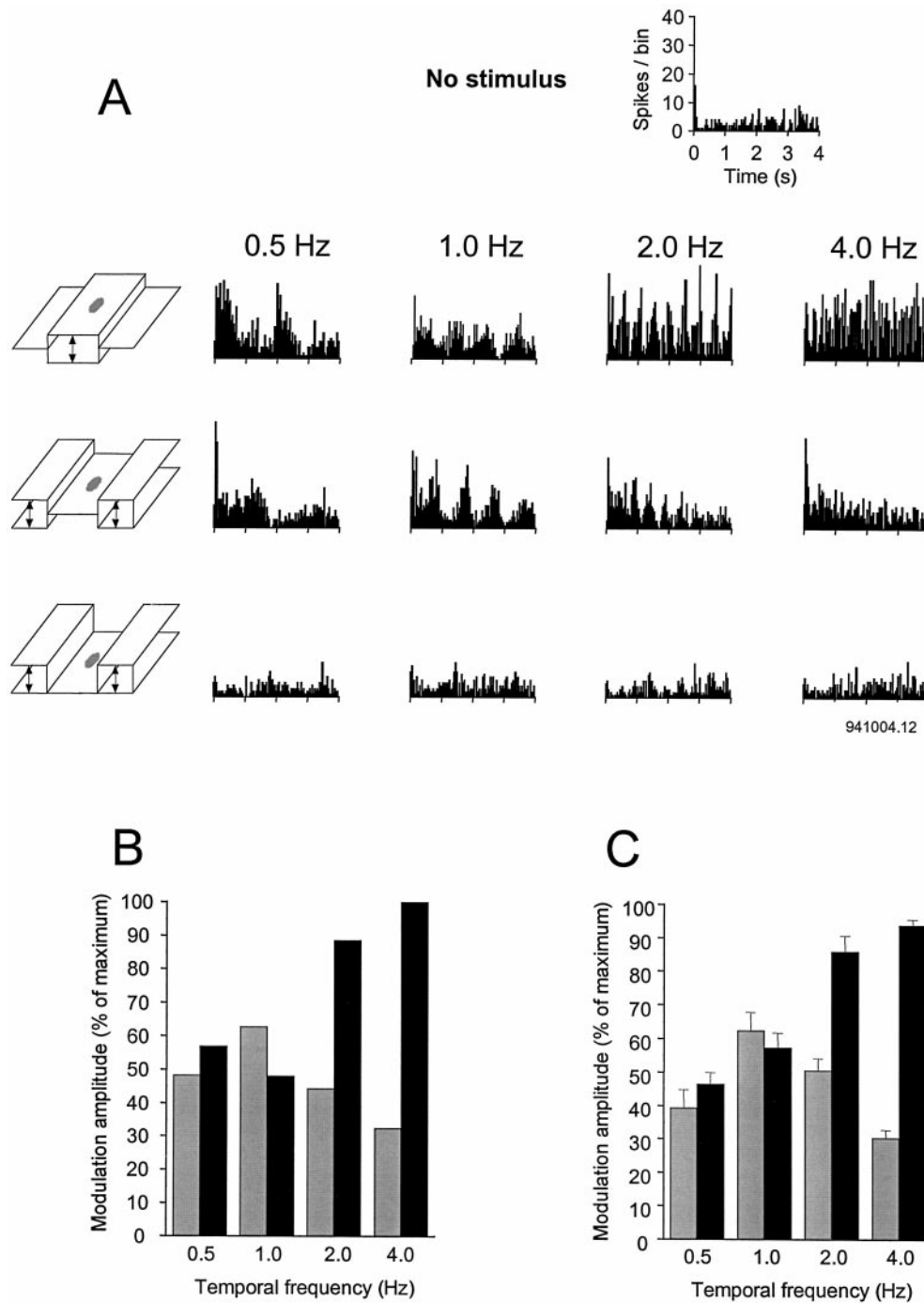


Figure 9. *A*, Temporal frequency of luminance modulation affects the response to induction and control stimuli differently. Responses to luminance modulation rates of 0.5, 1, 2, and 4 Hz are shown. *B*, The amplitude of response modulation plotted as a function of temporal frequency for the striate neuron shown in *A*. Gray bars represent the response to the induction stimulus (stimulus 1), and black bars represent the response to luminance modulation covering the RF (stimulus 4). The modulation amplitude is expressed as the percentage of the maximum response elicited by stimulus 4. *C*, Averaged normalized modulation amplitudes for 24 striate neurons plotted as a function of the rate of luminance modulation. The modulation amplitude is expressed as the percentage of the maximum response amplitude elicited by either stimulus 1 or stimulus 4. Gray bars represent the response to stimulus 1, and black bars represent the response to stimulus 4. Error bars are equal to 1 SEM.

Effects of temporal frequency on the response to luminance modulation

Psychophysical experiments (DeValois et al., 1986; Rossi and Paradiso, 1996) have shown that brightness induction occurs only when the luminance of the inducing stimuli is modulated at low rates (<3 Hz). Therefore, for those neurons that responded to both the induction stimulus and luminance modulation within the RF, we compared the responses at different rates of luminance modulation. Figure 9*A* is an example of a neuron that was tested at temporal frequencies of 0.5, 1.0, 2.0, and 4.0 Hz. It can be seen in this example that there was a reduction in the modulation amplitude to the induction stimulus with increases in temporal frequency above 1.0 Hz (third row). Conversely, this neuron

exhibited an increase in response modulation to luminance changes within the RF as the temporal frequency was increased (second row). The difference in the modulation amplitude for this striate neuron is quantified in Figure 9*B*, where the amplitude of the response modulation for these two conditions is plotted as a function of the temporal frequency. Figure 9*C* shows the relationship between response amplitude and luminance modulation rate for the group of neurons that were stimulated at all four temporal frequencies (*n* = 24). It can be seen in this figure that the degree of response modulation is comparable in the induction and “real” modulation conditions at 0.5 and 1.0 Hz. At temporal frequencies above 1.0 Hz, there was a steady decline in the modulation amplitude to luminance changes outside the RF (gray

Table 2. Laminar distribution of 27 neurons that had responses significantly more modulated by the induction stimulus than the center-black control stimulus

Lamina	No. of neurons	% of population
II, III	9	33
IV	10	37
V, VI	8	30

bars), whereas there was an increase in the modulation amplitude to luminance changes within the RF (black bars). This difference in the responses at higher temporal frequencies is striking because it correlates with perceived variations in brightness. At low temporal frequencies, brightness changes are perceived with both induced and “real” modulation, but at higher temporal frequencies, brightness variations are seen with the “real” modulation but are lost with induction.

Laminar distribution

Histological reconstructions were made of the electrode penetrations in six of the animals that were studied. Neurons that exhibited responses that were correlated with brightness changes were located in equal proportions in all laminae of striate cortex. Table 2 shows the laminar distribution of 27 striate neurons that had responses significantly more modulated by the induction stimulus than the center-black control stimulus (i.e., amplitude ratio_{1,2} > 2).

Lateral geniculate nucleus

In the previous section, we showed the effects of luminance modulation outside the RF on the response of cortical neurons. We found neurons in all cortical layers that responded to stimulation outside the RF in a manner correlated with perceptual changes in brightness. We wished to determine whether the brightness-correlated responses first occur in cortex or whether they are present at earlier stages of visual processing. Following the same procedure that was used in the study of cortical neurons, we examined the responses of 75 neurons in lamina A and A1 of the lateral geniculate nucleus.

Effects of luminance modulation outside the RF

The responses of the geniculate neurons that we studied did not correlate with perceived brightness as well as the responses in striate cortex. In total, 42 of the 75 (56%) geniculate neurons in our sample had responses that were significantly modulated ($p < 0.05$) and phase-locked to the luminance changes outside the RF. Figure 10A shows a geniculate neuron with a response that followed the modulation of light covering the RF (second row). The neuron was also excited by the induction stimulus with luminance modulation outside the RF (third row). However, the response to the induction stimulus was not significantly modulated.

To establish the degree to which the response of a geniculate neuron was specific to stimulus conditions that produced brightness induction, comparisons were made of the response to the induction stimulus (stimulus 1) and the black-center control (stimulus 2). Ratios of the overall activity and amplitude of modulation were calculated for each neuron as described previously for cortical neurons. A comparison of the amplitude and activity ratios for the population of neurons is shown in Figure 6B. The distribution of points in this figure indicates that most neurons had response amplitudes that were greater for stimulus 2

than for stimulus 1 (i.e., ratio < 1). Although approximately half of the neurons in our sample exhibited a greater overall response to stimulus 1 (activity ratio_{1,2} > 1), the modulation amplitude in response to stimulus 2 was usually greater (amplitude ratio_{1,2} < 1). This suggests that very few cells were modulated by the induction stimulus to a degree that exceeded that which might result from light scattering. Figure 11 shows the distribution of the amplitude ratio_{1(3),2} for 42 LGN neurons compared with the distribution for cortical neurons.

It can be seen in Figures 6B and 11 that a small fraction of our geniculate neurons had significantly greater response modulation to stimulus 1 (or stimulus 3) than to stimulus 2. As with the similar cortical neurons, the responses appeared to correlate with perceived brightness. Figure 10B shows an example of a geniculate neuron with an on-center/off-surround receptive field configuration that had a phase-locked response to luminance modulation outside the RF only when the center region of the stimulus was gray. Like many striate neurons, this LGN neuron showed a phase-locked response to luminance modulation within the RF (second row). It is important to note that the light modulation occurred outside the RF, not in the off-surround. Additionally, the phase of the response to stimulus 1 (third row) was in approximate antiphase to the response to luminance modulation within the RF. However, this antiphase response pattern was far less common in the LGN (2 of 75 neurons) than in cortex (Fig. 8).

Effects of temporal frequency on response amplitude

Approximately 10% of the geniculate neurons were significantly more modulated in the induction condition than in the center-black control condition. We have shown in Figure 9C that the amplitude of the striate response to the induction stimulus decreased as the temporal frequency of the luminance modulation was raised above 1.0 Hz. Figure 12 shows the same relationship between the response amplitude and the rate of luminance modulation for seven geniculate neurons stimulated at all four temporal frequencies. Similar to the response of striate neurons, the modulation amplitude of geniculate responses to luminance changes within the RF increased over the range of temporal frequencies tested. However, unlike our sample of striate neurons, the average modulation amplitude to luminance changes outside the RF did not decrease as the temporal frequency was raised.

Optic tract

With the same experimental procedure and analysis that were used in the study of cortical and geniculate neurons, we examined the responses of 33 retinal ganglion cells recorded in the optic tract. Similar to the responses of geniculate neurons, some retinal ganglion cells did respond in a phase-locked manner to luminance modulation within the RF, but most cells in the optic tract did not show modulated responses when the light level outside the receptive field was varied. Figure 13 shows the responses of an X-type ganglion cell to the basic stimulus set. It can be seen in the third row of this figure that there was a maintained elevation in the response of the cell to stimulus 1, but the effect of the luminance change outside the RF is not apparent in the response. The elevated response might have been caused by the presence of the static gray center in stimulus 1, because the response was greatly diminished when the region corresponding to the RF was black (fourth row).

The relationship between the overall activity and modulation amplitude of the response to stimulus 1 and stimulus 2 is shown

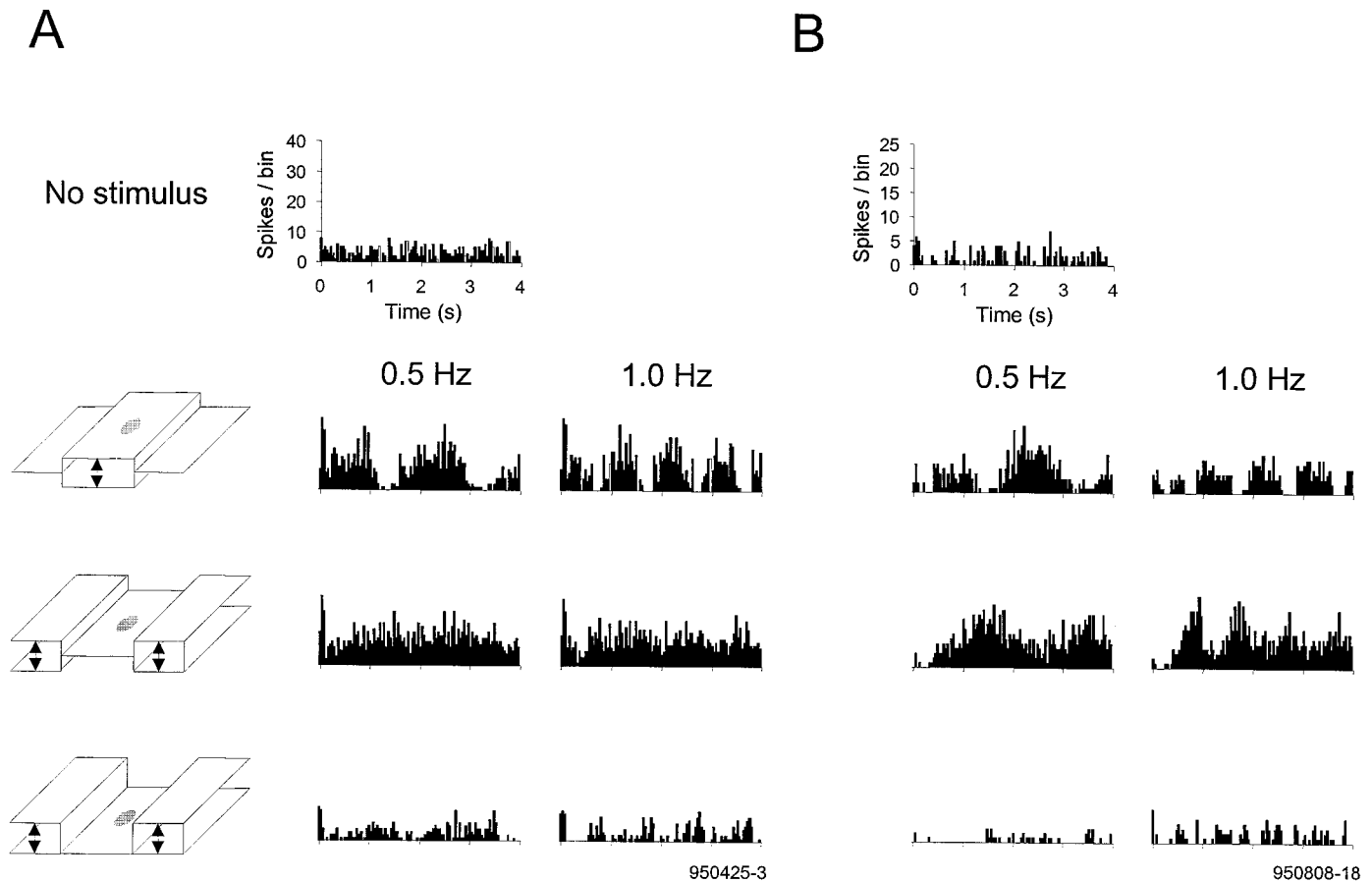


Figure 10. Responses of two geniculate neurons with on-center/off-surround receptive fields. *A*, A neuron that exhibited an elevated response in the induction condition, but little or no response modulation (*third row*). There was response modulation to luminance changes within the RF (*second row*). This cell's response did not correlate with perceived brightness. *B*, A neuron that exhibited a modulated response in the induction condition (*third row*) but no response in the center-black condition (*fourth row*). Note that there is a difference in the phase of the response to luminance modulation within (*second row*) and outside (*third row*) the RF. Although rare in the LGN, this response pattern was correlated with brightness.

in Figure 6C. It can be seen in this figure that most of the retinal ganglion cells studied had a greater modulation amplitude in response to stimulus 2, yet exhibited a greater overall response to stimulus 1. It is important to note that none of the 33 cells that were tested exhibited a significant degree of modulation in their response to luminance modulation outside the RF based on our minimum criterion ($p < 0.05$). Therefore, the measure of amplitude ratio_{1,2} for this population may not be meaningful because the degree of modulation observed in the responses of retinal ganglion cells was quite small.

DISCUSSION

At present, little is known about the neural representation of surfaces in general and brightness in particular. We examined neurons with a dynamic brightness induction stimulus because it allowed us to dissociate responses correlated with brightness from those correlated with actual light level. We found that some neurons in the optic tract, LGN, and striate cortex are affected by light outside the RF, often at distances up to 5–10°. This is comparable in scale to perceptual interactions involving brightness induction and constancy in humans (Land, 1959; Heineemann, 1972). We found significant differences in the responses of neurons in the three brain areas studied, suggesting that a brightness representation is developed at later stages of visual processing from the early contrast-based response.

Correlation of neural activity with perceived brightness

In the stimuli we used, the brightness of the area covering the RF was changed either by varying its luminance or by inducing a perceptual change by luminance modulation of the surround. Within the confines of the parameters we varied, a neural response correlated with brightness might be expected to have the following properties. (1) When the luminance of the area covering the RF is varied, the response should follow; (2) when the area covering the RF is static black, the response should not change despite modulation of the surround, because there is no perceptual change in the black area; (3) when the area covering the RF is static gray and the luminance of the surrounding area is modulated, the response should follow the induced changes in brightness; (4) in the center-gray induction condition, the response should phase shift 180° relative to the control condition in which the center luminance is varied, because that is what is perceived; and (5) response modulation in the induction condition should decline as the temporal frequency of the inducing surround increases above ~2.5 Hz, whereas response modulation to luminance changes in the RF should not decline. These temporal properties would correlate with the low cutoff rate for induction (DeValois et al., 1986; Rossi and Paradiso, 1996) relative to the critical flicker fusion rate, which is roughly 10 times higher.

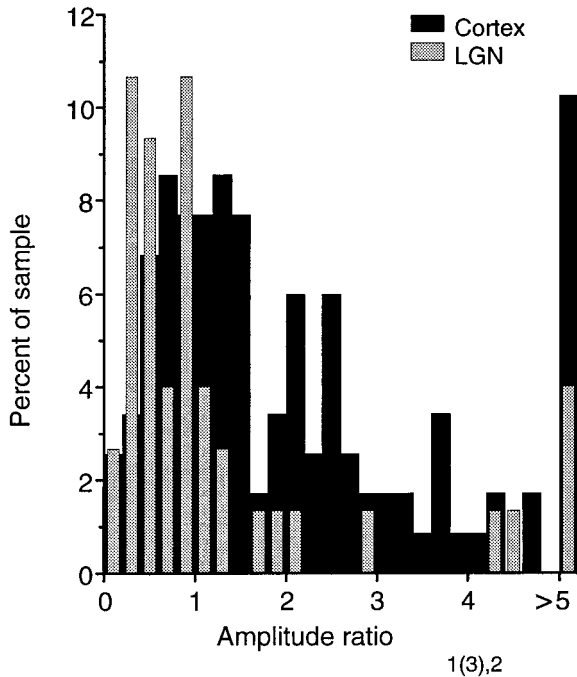


Figure 11. Distribution of the amplitude ratio $_{1(3),2}$ for neurons recorded in the LGN ($n = 42$) compared with striate cortex ($n = 120$). Note that the distribution of neurons for each group is represented as a percentage of the total number of neurons in that group. Ratios >1 indicate that the amplitude of response modulation was greater in the induction condition (stimulus 1) than in the center-black condition (stimulus 2). The amplitude ratios were determined for responses to 1 Hz stimuli. A larger percentage of neurons in striate cortex had ratios >1 , indicating that cortical responses were more often correlated with perceived brightness in the induction condition.

Each of the criteria above is open to question. Which assumptions are legitimate significantly impacts the assessment of whether activity in different visual structures is related to brightness. At one extreme is the retina, in which we found no cells that exhibited properties (3)–(5). In all cases, it appeared that responses were based on light level within the receptive field, with the occasional exception of an overall excitatory effect of surround illumination. Striate cortex is at the other extreme. Even with the strict criteria that we used (e.g., that response modulation to the induction stimulus must have at least *twice* the amplitude of the response in the center-black condition), 16 of our total population of 160 striate neurons were found that had all of the properties listed above. Although 16 neurons is not a large population, 10% of all neurons in striate cortex represents an impressive number of neurons that potentially carry information correlated with perceived brightness. Fittingly, the LGN was found to be intermediate in the degree to which the neurons had the properties above. Although no neurons were found that had all five properties, a handful did have the first four. It is possible that we have underestimated the number of neurons involved in representing brightness information, by insisting that a neuron possess all five properties listed above. For example, if a neuron in striate cortex showed appropriate response changes with temporal frequency, it might be involved in a brightness representation even if it did not show a 180° phase shift.

Do cells in the retina, LGN, and striate cortex represent brightness information in their firing rate? The lack of correlation between brightness and activity in the optic tract suggests that the

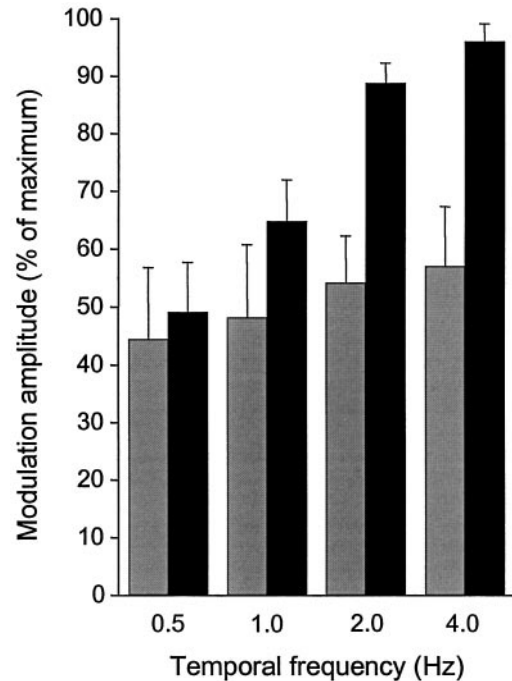


Figure 12. Average amplitude of response modulation plotted as a function of temporal frequency for seven LGN neurons. *Gray bars* represent the response to the induction stimulus (stimulus 1), and *black bars* represent the response to luminance modulation covering the RF (stimulus 4). With both stimuli, the modulation amplitude tended to increase with temporal frequency, although not significantly for the induction condition. The modulation amplitude is expressed as the percentage of the maximum response amplitude elicited by either stimulus for each neuron. Error bars are equal to 1 SEM.

answer is “no” for the retinal output. On the other hand, in striate cortex, there appears to be a sizeable population of cells that carries brightness information. Because these cells were selective for multiple visual attributes, it appears that brightness information is multiplexed with information about orientation, spatial frequency, and other stimulus properties. Both simple and complex cells spread across the cortical lamina were found to have brightness-correlated responses. There is always the possibility that additional tests might prove that the cortical responses do not entirely correlate with brightness. However, the correlations that we did observe showed intriguing subtleties, particularly the changes in response amplitude with “real” and induced brightness modulation as temporal frequency was increased above 1 Hz. As seen perceptually, induced modulation affected the neural response primarily at low temporal rates, whereas real luminance modulation evoked phase-locked responses at high rates.

It is more difficult to classify the LGN. Valberg et al. (1985) observed that steady surround illumination outside the receptive field can alter the sensitivity of geniculate neurons to receptive field stimulation in a manner suggestive of simultaneous contrast. DeValois and Pease (1971) did not observe induction in LGN neurons in the primate, but they used a static version of induction that might not have been as powerful a stimulus as ours. The dynamic induction stimulus that we used elicited responses that partially correlated with perceived induction in some cells. However, no LGN cells completely fit the profile of “brightness neurons” by possessing all of the properties listed above. Therefore, to summarize our findings, striate cortex is the first component of the visual system that has responses reliably correlated with

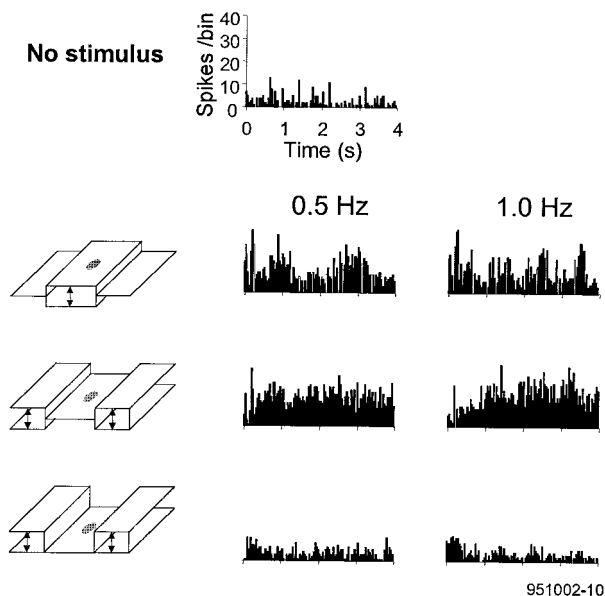


Figure 13. Response of an X-type retinal ganglion cell recorded in the optic tract. In the induction condition (*third row*) the cell's response was elevated above the spontaneous firing rate (*first row*), but the response was not modulated. The response was modulated by luminance changes within the RF (*second row*).

brightness. It appears that important computations take place at this level that make some cells respond in a manner better correlated with perceived brightness than with actual light level.

Possible concerns and artifacts

Conceivably, the interactions that we have reported as coming from beyond the receptive field might be caused by interactions within the receptive field. There are two ways this might happen. The first is by underestimating the size of the RF, thus having the surround stimuli actually within the RF. Although we used the most common technique of plotting receptive fields, there is no question that small differences in RF size result from different techniques. Nonetheless, it is quite unlikely that this was an important factor because the flanking regions of our stimuli were positioned at least 3° (and up to ~ 5 or 6°) beyond the conservatively estimated borders of the receptive fields. A second way in which RF stimulation might yield the results we obtained would be by light scattered within the eye. However, a number of observations suggest that scattered light did not cause the surround interactions we observed. First, the neuronal response to stimulation outside the RF was unaffected by the use of artificial pupils. Restriction of the angle of incident light would result in a reduced response if stray light from regions of the stimulus outside the RF illuminated areas of the retina corresponding to the RF. Second, increasing the ambient room illumination to alter the adaptation state of the retina did not reduce the effectiveness of the induction stimuli. Such a reduction would be expected if light scattered into the receptive field produced suprathreshold effects at low ambient illumination. Finally, we examined whether the responses in the center-black and center-gray conditions were consistent with light scatter. The effects of stray light on the response of a cell should be greater when the center of the stimulus is black than when the center is gray, because the photoreceptor gain would be higher in the former case. For this reason, we only considered neurons with greater responses in the center-gray condition. We took the conservative stance that a cell

showing a greater response in the center-black condition might carry artifacts resulting from scattered light.

Another concern is that we have compared the physiological data from cats with psychophysical data from humans. Although there are no behavioral data showing that cats perceive the brightness effects that we have described, there is considerable similarity in the visual systems of cats and humans up to the level of striate cortex (Sherman and Spear, 1982), and cats have been shown to see brightness effects associated with the perception of illusory figures (Bravo et al., 1988).

Contextual responses and surface perception

Several lines of evidence suggest that a general representation of surfaces first occurs in striate cortex and that this involves interactions from beyond the small receptive fields. Brightness appears to be first explicitly represented in striate cortex (Reid and Shapley, 1989; Rossi et al., 1996), and spatial interactions observed in this area are consistent with long-range brightness effects (Komatsu et al., 1996; MacEvoy et al., 1998). Striate cortex also appears to represent information about texture (Nothdurft and Li, 1985; Knierim and Van Essen, 1992; Kastner et al., 1997) and figure-ground segregation (Lamme, 1995; Zipser et al., 1996; Lee et al., 1998). Thus, aside from color, which appears to be handled more by extrastriate cortex (Zeki, 1980; Schein and Desimone, 1990), responses in striate cortex have been found that correlate with most attributes of surfaces. In general, it is not known whether these responses result from interactions within striate cortex or via feedback, but there is evidence that figure/ground segregation involves extrastriate feedback to V1 (Hupe et al., 1998; Lamme et al., 1998). Regardless of the mechanism, the first visual cortical area appears to be involved in far more than the detection of oriented contours, and its output conveys information that, in some ways, correlates with visual perception.

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