

Neural Representation of the Luminance and Brightness of a Uniform Surface in the Macaque Primary Visual Cortex

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Kinoshita, Masaharu and Hidehiko Komatsu. Neural representation of the luminance and brightness of a uniform surface in the macaque primary visual cortex. *J Neurophysiol* 86: 2559–2570, 2001. The perceived brightness of a surface is determined not only by the luminance of the surface (local information), but also by the luminance of its surround (global information). To better understand the neural representation of surface brightness, we investigated the effects of local and global luminance on the activity of neurons in the primary visual cortex (V1) of awake macaque monkeys. Single- and multiple-unit recordings were made from V1 while the monkeys were performing a visual fixation task. The classical receptive field of each neuron was identified as a region responding to a spot stimulus. Neural responses were assessed using homogeneous surfaces at least three times as large as the receptive field as stimuli. We first examined the sensitivity of neurons to variation in local surface luminance, while the luminance of the surround was held constant. The activity of a large majority of surface-responsive neurons (106/115) varied monotonically with changes in surface luminance; in some the dynamic range was over 3 log units. This monotonic relation between surface luminance and neural activity was more evident later in the stimulus period than early on. The effect of the global luminance on neural activity was then assessed in 81 of the surface-responsive neurons by varying the luminance of the surround while holding the luminance of the surface constant. The activity of one group of neurons (25/81) was unaffected by the luminance of the surround; these neurons appear to encode the physical luminance of a surface covering the receptive field. The responses of the other neurons were affected by the luminance of the surround. The effects of the luminances of the surface and the surround on the activities of 26 of these neurons were in the same direction (either increased or decreased), while the effects on the remaining 25 neurons were in opposite directions. The activities of the latter group of neurons seemed to parallel the perceived brightness of the surface, whereas the former seemed to encode the level of illumination. There were differences across different types of neurons with regard to the layer distribution. These findings indicate that global luminance information significantly modulates the activity of surface-responsive V1 neurons and that not only physical luminance, but also perceived brightness, of a homogeneous surface is represented in V1.

INTRODUCTION

A variety of factors contributes to the perception of surface brightness. Light intensity is the primary one; however, perceived brightness is also affected by stimuli remote from the local surface or by the global configuration of the scene.

Notable examples of such phenomena include brightness induction (Hering 1964; Horeman 1963; Torii and Uemura 1965; Woodworth and Schlosberg 1954), the Craik-O'Brien-Cornsweet illusion (Cornsweet 1970; O'Brien 1958), and alteration of perceived brightness due to the three-dimensional interpretation of the scene (Adelson 1993; Gilchrist 1977; Lotto et al. 1999). Thus critically involved in the process of surface brightness perception is not only interpretation of local information, namely surface luminance, but also interpretation of global information, namely stimuli surrounding the surface. These characteristics of brightness perception provide an excellent opportunity to study the neural processes involved in the interactions between local and global information during visual perception.

The activities of neurons in the early visual areas, which have retinotopic organization, are affected not only by stimuli within their receptive fields (RFs), but also by stimuli outside the RF (Kapadia et al. 1995; Knierim and van Essen 1992; Lamme 1995; Zipser et al. 1996). It was recently reported that there are neurons in the primary visual cortex (V1) of anesthetized cats whose activity is modulated by temporal modulation of the luminance of a region outside of the RF (Rossi and Paradiso 1999; Rossi et al. 1996), and that the manner of the response modulation was consistent with changes in the perceived brightness of the surface covering the RF. These results suggest that the interaction between local and global information in brightness perception may be accounted for in terms of contextual modulation of the activities of luminance-sensitive neurons in the early visual area.

To better understand the neural representations of the brightness of a surface, we need to understand at least two things. First, it is necessary to know how the local luminance is represented in terms of neural activity. This can be tested by recording the neuronal responses to the stimuli covering the RF with various luminances while holding the luminance of the surround constant. Second, it is necessary to know how the global luminance information affects neural activity. This can be tested by recording neuronal responses while varying the luminance of the region surrounding and remote from the RF while holding the luminance in the RF constant.

It has been reported that there are neurons in monkey V1 whose activity vary depending on the luminance of a uniform stimulus that covers the RF, some with a dynamic range of

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over 3 log units (Bartlett and Doty 1974; Kayama et al. 1979; Maguire and Baizer 1982). But these studies did not address the effect of the luminance remote from the RF. To date, only Paradiso and his colleagues (Rossi and Paradiso 1999; Rossi et al. 1996) have studied the effects of both local and global luminance information on the same neurons within V1 of the cat. However, these authors were mainly concerned with the properties of V1 neurons whose activity appeared to encode perception in brightness induction. Our aim in the present study was to systematically investigate the effect of both local and global luminance on the activity of V1 neurons. Our findings support the idea that integration of both local and global information related to surface brightness takes place within V1. Brief reports of these experiments have appeared elsewhere (Kinoshita and Komatsu 1998).

METHODS

Behavioral task

Two macaque monkeys (*Macaca fuscata*) were used for the experiments. During the experiments, the monkeys sat in a primate chair and faced the screen of a cathode ray tube (CRT) monitor. Each monkey was trained to perform a fixation task (Wurtz 1969). A trial started when a small stationary spot (fixation spot) appeared on the screen. The monkey was required to foveate the fixation spot within 500 ms after it appeared and to maintain its gaze on the fixation spot for the rest of the trial. After the monkey had maintained its fixation for 500–1,200 ms, another visual stimulus was presented to study the response characteristics of a neuron. This stimulus was presented for 500–2,000 ms; typically presentations of 1,000 ms were employed to study the effect of the luminance of the stimulus; 500-ms presentations were used for other tests (e.g., RF mapping or testing for orientation selectivity). At the end of a successful trial, a drop of water was delivered to the monkey as a reward, the fixation spot was turned off, and an intertrial interval of more than 1 s started. Eye position was monitored using the magnetic search-coil technique (Robinson 1963). If the monkey's eye deviated from the fixation point more than 0.3–0.5° (typically 0.4°) during a trial, the trial was automatically terminated without reward and an intertrial interval started. After daily experiments, the monkeys were returned to their home cage, where food was available ad libitum. During experiments, the monkeys were deprived of water for about 20 h before each daily experimental session, which was terminated when behavioral signs of satiety were observed.

Surgical procedures and recording

Under pentobarbital sodium anesthesia, a stainless steel recording chamber and a socket for connecting the monkey's head to the primate chair were fixed to the skull using standard sterile surgical techniques. A search coil was also surgically placed under the conjunctiva of one eye using the method of Judge et al. (1980) and connected to a plug on top of the skull. The recording chamber, socket, and eye coil plug were all embedded in dental cement that covered the top of the skull and connected to the skull by implanted bolts. After the surgery, the monkeys were administered antibiotics and allowed to recover for at least 1 wk before starting the experiments. All procedures for animal care and experimentation were in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals (1996) and approved by the Animal Experiment Committee of the Okazaki National Research Institutes.

A glass-coated tungsten microelectrode (0.7–2.0 M Ω at 1 kHz) was advanced through the dura using a hydraulic microdrive (Narishige MO-951) for recording the activities of single and multiple units within V1. Neural signals were amplified and discriminated based on

spike amplitude and converted to pulses (BAK DDIS-1). The unit pulses were fed to a computer with a time resolution of 1 ms, displayed on-line and stored for off-line analysis. Eye position was also continually displayed.

Visual stimuli

Visual stimuli were generated on a frame buffer (FORCE GP-1122N) housed in a computer (NEC PC9821) and displayed on a CRT monitor (SONY GDM-2000TC). The display area of the monitor was 1,024 pixels (horizontal) by 768 pixels (vertical), and subtended visual angles of 34° horizontally and 26° vertically. The monitor was placed 61.7 cm from monkeys' eyes. The vertical refresh rate of the display was 60 Hz. During the intertrial interval (ITI), the display was painted as uniform gray (typically 3 cd/m²); during trials stimuli were presented against a background of the same gray. All stimuli and backgrounds used in this experiment were achromatic ($x = 0.31$ and $y = 0.32$ in the CIE-xy coordinates). Throughout the course of the experiments, the luminance and chromaticity of the stimuli and background were frequently calibrated using a colorimeter (MINOLTA CS-100) or a spectrophotometer (PHOTO RESEARCH PR-650). The fixation spot was white (or pinkish white when the fixation spot overlapped the visual stimulus) and subtended a visual angle of 4' or 8'.

To map the classical RFs of the recorded neurons, a small spot stimulus (10' to 40' in visual angle) was displayed at various locations on the display. The RF was defined as the region in the visual field where a neuron responded to this stimulus. To examine the effect of local surface luminance information on the activities of V1 neurons, a visual stimulus consisting of a uniform square at least three times larger at the edge than the diameter of the RF (surface stimulus; typically subtended 10°) was presented, and the relationships between the luminance of the surface and the evoked neuronal activity were evaluated (surface-luminance test; e.g., Figs. 1 and 2). To study the effect of global luminance information, we presented the surface stimulus together with a surrounding figure (surround stimulus) and examined the effects of the luminance of the surround on neuronal activity while holding the luminance of the surface constant (surround-luminance test; e.g., Fig. 7). The surround stimulus was typically two or three times as large as the surface stimulus. The size of the surface stimulus in the surround-luminance test was the same as that used in the surface-luminance test for each neuron. The surround stimulus was placed just outside of the surface stimulus without a gap, and both stimuli were presented simultaneously. The luminance of the surface stimulus in the surround-luminance test was determined based on the results of the surface-luminance tests, as described in detail in RESULTS. In both tests, the luminance of the stimulus was varied from 0.1 to 100 cd/m² in seven equal steps along a logarithmic scale (e.g., Figs. 2 and 7).

Orientation selectivity was tested using a bar stimulus (10' \times 30') presented in eight orientations separated by equal steps. To quantify the strength of orientation selectivity, orientation selectivity index was computed as $1 - (\text{minimum response})/(\text{maximum response})$. Stimulus size selectivity was tested using seven uniform, square stimuli, subtending from 0.25 to 16° on the edge, and separated by equal steps. A high contrast dark stimulus (0.1 cd/m²) or a bright stimulus (50 or 100 cd/m²) was used for RF mapping and for assessing orientation and size selectivity. In a given test, recordings were repeated at least four times (typically 7–11 times) per stimulus condition, and the various stimuli were presented in pseudo-random order.

Data analysis

The activities before stimulus presentation (–500 to 0 ms) and those during stimulus presentation (20 ms to 520 or 1,020 ms after stimulus onset) were compared to assess whether or not a given neuron responded to a surface stimulus. If the neuronal activities

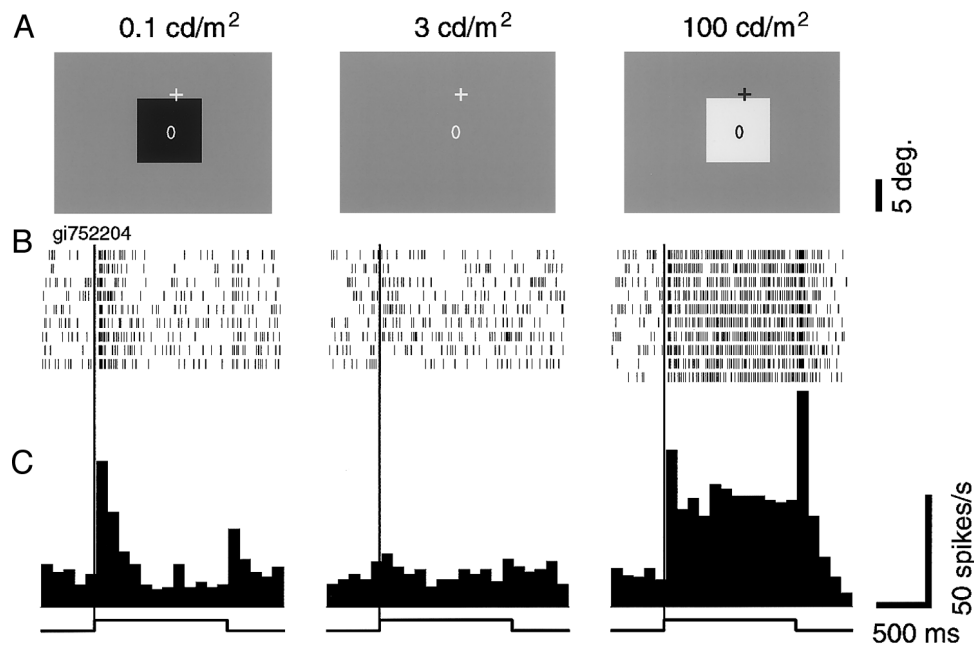


FIG. 1. A representative example of neurons whose activity varied in response to the luminance of a large uniform surface (surface stimulus). A: schematic drawings of the entire display (width, 34° ; height, 26°) as it appears during the stimulus presentation period. The middle square is the surface stimulus, which completely covers the receptive field (RF). The size and location of the RF of the recorded neuron is indicated by an ellipse, which was not actually presented on the display. In this and the following figures, except Fig. 9, all items, including the outline of the display, the stimuli, and the RFs are drawn proportionally. The luminances of the surface stimuli are indicated; background luminance was 3 cd/m^2 under each condition. In the middle panel, the stimulus had the same luminance as the background and was thus invisible. A cross indicates the location of the fixation point. B: rastergram of spike activities around the stimulus presentation period. Short vertical lines indicate the timing of spike discharge. Each row corresponds to a different trial. Long vertical lines indicate the onset of the stimulus presentation. C: peristimulus time histogram (PSTH) of spike activity; binwidth is 100 ms. The upward deflection of the line at the bottom of each panel indicates the stimulus presentation period. Each histogram begins at -480 ms from stimulus onset. During the early part of the response, there was no clear difference between the responses elicited by dark and bright stimuli, whereas later the responses differed markedly. Only activities of single neurons are exemplified in this and the following figures.

during these two periods were significantly different ($P < 0.05$ in Wilcoxon signed-rank test), we classified the neuron as “surface-responsive.” For the neurons tested only in four or five repetitions, the sign test was applied instead of the Wilcoxon test because the latter requires at least six paired data samples. To analyze the results of surface-luminance and surround-luminance tests, we used firing rates recorded during stimulus presentation without subtracting activity recorded before stimulus presentation. This was because prestimulus activity varied substantially, depending on the background luminance of the display in many neurons. Hereafter, we will refer to the activity during fixation but before stimulus presentation as “ongoing activity.” As will be shown in Figs. 3 and 8, the effects of surface luminance and surround luminance gradually developed within 500 ms or so and was then stabilized. So the effects of surface luminance and surround luminance were analyzed in detail in the period commencing at 520 ms after stimulus onset to the end of stimulus presentation. For a small number of neurons with shorter stimulus presentation, the analysis was commenced earlier depending on the period of stimulus presentation.

Recording site

Neuron activities were recorded from the dorsolateral surface of the occipital cortex. Judging from the sizes of the RFs and from the retinotopic map generated by a series of penetrations, the recording sites were identified as being within V1. With regard to the recording layer, we considered the region with high ongoing activity to be layer IV, which was located at an intermediate depth, between the cortical surface and the white matter (Poggio et al. 1977; Snodderly and Gur 1995). In this region, neurons exhibited smaller RF sizes and narrower

spikes than those in other regions. We considered the region shallower than layer IV to be layers II and III (layer II/III) and the region deeper than layer IV to be layers V and VI (layer V/VI).

RESULTS

Surface-responsive neurons in V1

We recorded 105 single and 80 multiple units from V1, and as their luminance sensitivities were similar (cf. Tables 1 and 3), we combined the results obtained from both groups. The eccentricities of the RF centers of the recorded neurons ranged from 0.9 to 8.0° of arc. Figure 1 shows the activity of a representative neuron that responded to the surface stimulus (surface-responsive neuron; see the right and left panels in Fig. 1A); the RF is shown as an ellipse. Of the 185 neurons examined, 137 (77 single, 60 multi) were classified as surface-responsive on the basis of the statistical criteria described in METHODS, although because we concentrated on recording from surface-responsive neurons, our samples must overestimate the proportion of neurons that are surface-responsive. The diameter of the RFs we recorded ranged from 0.3 to 4.6° of arc. Mean RF size of surface-responsive neurons (1.63° for single neurons, 1.50° for all neurons) was not statistically different from that of surface-nonresponsive neurons (1.58° for single neurons, 1.66° for all neurons; $P > 0.05$, Mann-Whitney U test). Orientation selectivity was examined in 123 neurons (70 single, 53 multi). Mean orientation selectivity index of surface-

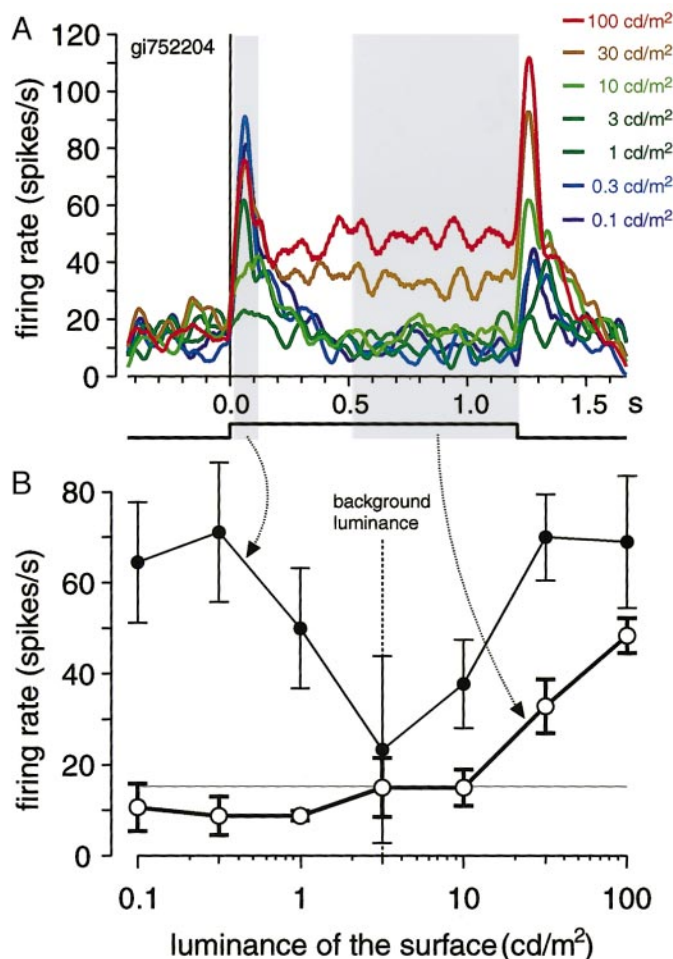


FIG. 2. Time courses of the responses to surface stimuli with various luminances. *A*: activities of the neuron shown in Fig. 1 are depicted as spike density plots smoothed with a gaussian filter ($\sigma = 50$ ms). The abscissa denotes the time aligned at the stimulus onset, the ordinate spike density. Different colors represent the surface luminances indicated in the inset. *B*: discharge rates (means \pm SD) early on (20–120 ms after stimulus onset, thin line) and later (520–1,220 ms after stimulus onset, thick line) during stimulus presentation. These periods are marked as gray in *A*. The abscissa is the luminance of the surface stimulus. The thin, horizontal line indicates the strength of the ongoing activity (0–500 ms before stimulus presentation). The vertical broken line indicates the luminance of the background. In this particular neuron, the response profile was V-shaped early on, with a valley at the same luminance as the background; later, activity increased monotonically with luminance.

responsive neurons (0.58 for single neurons, 0.56 for all neurons) was not statistically different from that of surface-nonresponsive neurons (0.64 for single neurons, 0.56 for all neurons; $P > 0.05$, Mann-Whitney U test). Thus we found no clear difference between surface-responsive neurons and others with regard to RF diameter or to orientation selectivity.

Dependence of neuronal responses on surface luminance

We found that a large majority of surface-responsive neurons was sensitive to the luminance of the surface stimulus that covered the entire RF. The minimum distance between the RF boundary and the edge of the surface stimulus was on average 3.3° , and the distance was always more than twice as big as the eye position window. This means that the RF was stimulated

only by the homogeneous region of the surface stimulus and not by the edge of it. The sensitivity of surface-responsive neurons to changes in surface luminance was particularly clear in the later part of the response period. With respect to the cell depicted in Figs. 1 and 2, for example, both dark and bright stimuli elicited activity early in the response period, but only bright stimuli elicited a response later in the period (Figs. 1C and 2A). Comparison of the effects of surface luminance on the mean discharge rates early (20–120 ms after stimulus onset; Fig. 2B, ●) and late (520–1,220 ms after stimulus onset; Fig. 2B, ○) in the response period revealed a marked difference in the respective profiles of the luminance-response relations. As in the example shown, early responses frequently had a V-shaped profile, with the valley occurring at a luminance equal to the background. On the other hand, the later response tended to monotonically increase as a function of increasing luminance. Figure 3 shows the percentage of different response profiles across the entire population of recorded neurons in every 100-ms time windows during stimulus presentation. Responses were classified as V-shaped or monotonic profiles using objective criteria as will be described later. Proportion of neurons exhibiting V-shaped response profiles rapidly declined from about 40% immediately after stimulus onset to only about 5% at 500 ms or later. At the offset of the stimulus, proportion of neurons exhibiting V-shaped profile increased again to a level comparable with that of the early ON-response.

The responses comprising the V-shaped profile were likely determined by the absolute value of the luminance contrast between the surface and the background. Consequently, there is ambiguity with regard to the sign of the contrast. In the monotonic profile, however, the response is uniquely determined by surface luminance, which thus seems to be more clearly represented in the later part of the response. In this study, therefore, we will analyze the way in which the later part of the response (ranging from at least 220 ms, typically 520 ms, after stimulus onset until the end of the stimulus) represents the luminance and brightness of the surface.

Quantitative classification of surface luminance-response relationships

We conducted surface-luminance tests with 115 (65 single, 50 multi) of the 137 surface-responsive neurons; Fig. 4 depicts two representative response profiles. The activity of the neuron in Fig. 4A increased monotonically with increasing luminance. A large majority of the surface-responsive neurons showed such a monotonic profile, although the activity of some was inversely related to the luminance (e.g., Fig. 5Ba). The neuron depicted in Fig. 4B shows a V-shaped response profile that was less common in the later part of the response. In this case, neuronal activity decreased with increasing luminance if the surface was darker than the background and then increased with brighter stimuli. To discriminate different response profiles quantitatively, we first divided the responses into two parts: one included responses to stimuli darker than the background, the other responses to the brighter stimuli (e.g., the left and right halves of Fig. 4, A and B, respectively). We then calculated the slopes of the linear regression lines in each half of the response profile (cf. Fig. 4C).

Figure 5A shows the relationships between the pairs of slopes for 115 surface-responsive neurons. The abscissa de-

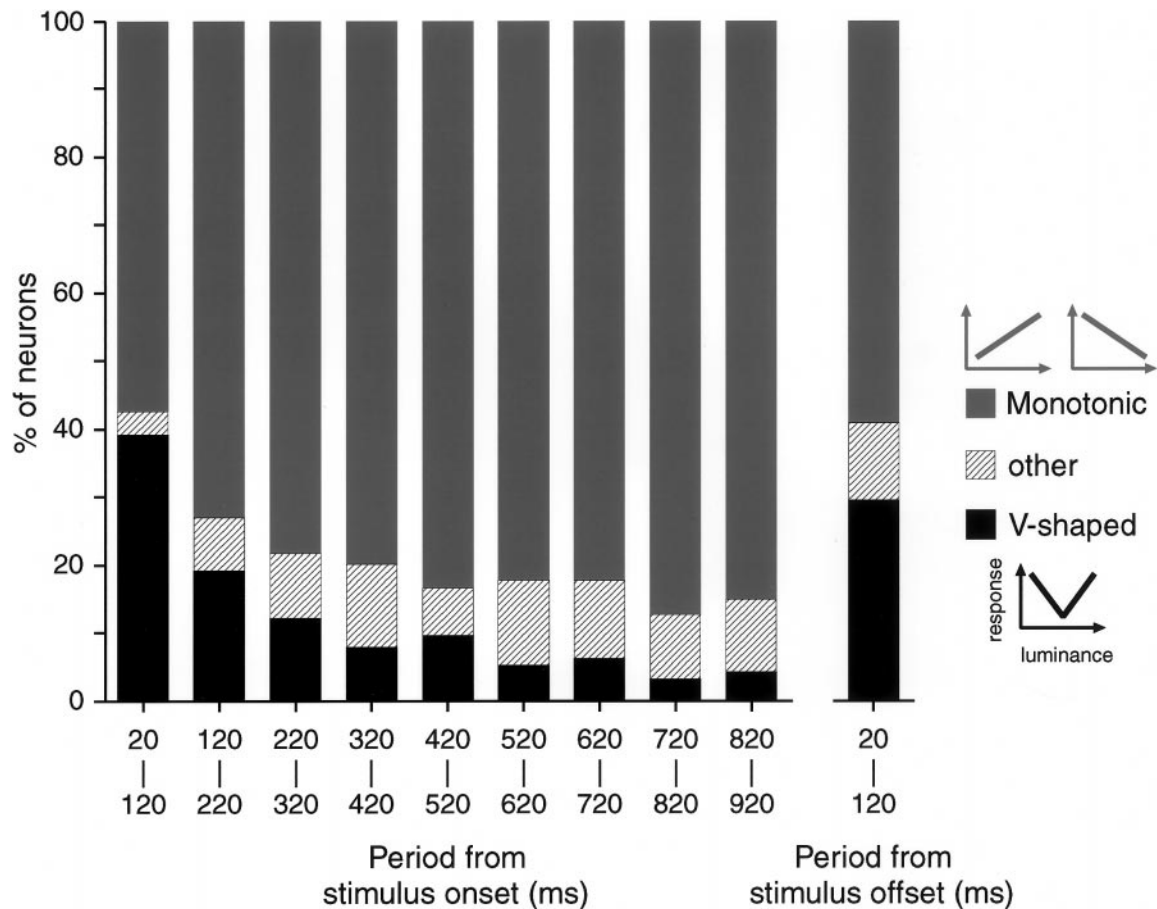


FIG. 3. Percentage of different response profiles across the entire population of 115 neurons tested in the surface luminance test in every 100 ms time windows during stimulus presentation and at the offset of the stimulus. Solid, gray and hatched parts represent V-shaped, monotonic and other profiles, respectively.

notes the slope for the dark stimuli (a in Fig. 4C), the ordinate the slope for the bright stimuli (b in Fig. 4C). The activity of neurons plotted in the *top right area* in Fig. 5A increased monotonically in response to increases in surface luminance (e.g., the neuron in Fig. 4A, which is marked as d in Fig. 5A). Because these neurons exhibited stronger responses to bright stimuli, we will refer to them as “bright-type” neurons. The activity of neurons plotted in the *bottom left area* in Fig. 5A declined monotonically with increasing surface luminance. Because these neurons exhibited more activity in response to darker stimuli, we will refer to them as “dark-type.” There were neurons exhibiting response patterns that were different from either bright-type or dark-type neurons (*top left area* in Fig. 5A). These neurons showed V-shaped response profiles. These three types of neurons did not constitute discrete classes as can be seen in Fig. 5A. Nonetheless, we classified each

TABLE 1. Layer distribution of surface-responsive neurons

	Bright-Type	Dark-Type	V-Shaped Type	Total
Layer II/III	13 (7)	6 (4)	0	19 (11)
Layer IV	51 (23)	5 (3)	8 (2)	64 (28)
Layer V/VI	11 (9)	17 (15)	1 (0)	29 (24)
Not identified	2 (2)	1 (0)	0	3 (2)
Total	77 (41)	29 (22)	9 (2)	115 (65)

Numbers in parentheses indicate single neurons.

neuron into one of three types according to the dominant response profile. A neuron was classified as bright-type if one of the following three criteria was satisfied: 1) the slopes to both the bright and dark stimuli were positive (e.g., Fig. 4A); 2) one of the two slopes was positive and the other was not statistically different from zero ($P \geq 0.05$, Spearman's rank correlation test; e.g., Fig. 5Bb); or 3) one of the slopes was positive and the other negative, but the absolute value of the positive slope was more than three times that of the negative slope (e.g., Fig. 5Bc). We included the third criterion so as to classify a neuron as bright-type that exhibited an overall tendency to become more active in response to increasing surface luminance. The diamonds in Fig. 5 represent bright-type neurons; those classified according to the second criterion are marked by open symbols. Neurons were classified as dark-type in a way analogous to classification of bright-type cells and are represented by squares in Fig. 5A. The remaining neurons were classified as “V-shaped” and are marked by filled circles (e.g., Fig. 4B corresponds to e in Fig. 5A).

Of the 115 neurons tested, 77 were classified as bright-type, 29 as dark-type, and 9 as V-shaped. Note that bright-type neurons are clustered around the vertical axis in Fig. 5A and are seldom seen around the horizontal axis. This means that the activity of this neuron type changes predominantly in response to bright stimuli (e.g., Fig. 5, Bb and Bc) and suggests that they encode mainly the luminance of surfaces brighter than the

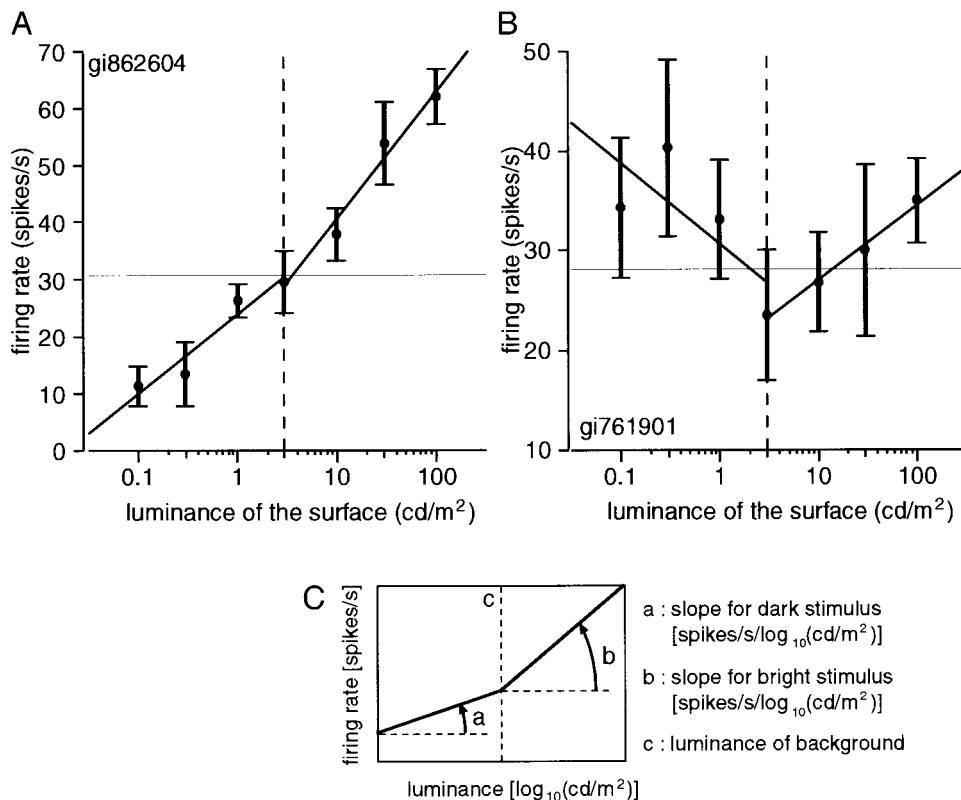


FIG. 4. Two representative response profiles in the later period obtained from surface-luminance tests. In A and B, the abscissa indicates the luminance of the surface stimulus, the ordinate the firing rate (means \pm SD). Straight lines in each graph are the linear regression lines calculated from the responses; the left half of each plot was obtained using stimuli darker than the background, the right half using stimuli brighter than the background. Responses to the stimulus having the same luminance as the background were included in the linear regression for both the darker and brighter sides. The vertical broken line indicates the luminance of the background. The thin, horizontal line indicates the ongoing activity before the stimulus presentation. A: neuron showing monotonic increases in activity with increasing surface luminance. B: neuron showing a V-shaped response profile; again note that the valley is at the same luminance as the background. C: schematic illustration of a set of slopes in the response profile that will be used to classify neurons, as shown in Fig. 5. a and b represent slopes of the regression lines for the dark and bright stimuli, respectively.

background. The dark-type neurons responded in opposite fashion, although less clearly so, and likely encode mainly the luminance of surfaces darker than the background.

Table 1 shows that about 80% (51/64) of the neurons recorded from layer IV were bright-type. Dark-type neurons accounted for only 8% of the neurons in layer IV (5/64), and neurons with V-shaped response profiles accounted for 12% of the neurons in layer IV (8/64), although this cell type was mainly found there (8/9).

Effect of the luminance of the surround

In some cases, the sensitivity of neurons to surface-luminance was tested at two different background luminances. Under these conditions, some neurons exhibited clear shifts in their response profile with a change in background luminance, even though the same set of surface luminances was used under both conditions (Fig. 6). Thus in some surface-responsive neurons, the luminance of the surround could modulate the responses to surface stimuli. We therefore tested the effect of varying the luminance of the surround, while keeping the luminance of the surface stimulus covering the RF (surround-luminance test) constant. For this test, we were careful to select a surface luminance that was within the dynamic range of the response profile, so that any modification by the surround stimulus (either excitatory or inhibitory) would be detected.

We conducted surround-luminance tests in 81 (50 single, 31 multi) of the 106 bright- and dark-type neurons. Figure 7 shows the stimuli presented and the responses of a representative cell in a surround-luminance test. All stimuli elicited similar levels of activity in the early part of the response. In the later part, however, the response changed dramatically with the luminance of the surround, although the luminance of the

surface that completely covered the RF was kept constant. Stimuli with dark surrounds elicited phasic responses, but the activity faded away within about 400 ms of the stimulus onset (Fig. 7B). Stimuli with bright surrounds, by contrast, elicited increases in neuronal activity that was sustained throughout the stimulus presentation. Thus while changes in the luminance of the surround elicited no systematic changes in activity during the early part of the response, activity during the later part of the response varied monotonically (Fig. 7C). Similarly, in many neurons tested, it was found that the change in the response due to the surround luminance was more obvious in the later part of the response than in the early part. Figure 8 shows the percentage of different effects due to the surround luminance across the entire population of recorded neurons in every 100 ms time windows during stimulus presentation. Response profiles were classified as constant ($P \geq 0.05$, Spearman's rank correlation test) or monotonic change (same criteria as used in Fig. 3). The proportion of neurons exhibiting constant response profiles rapidly declined from about 60% immediately after stimulus onset to about 40% within 500 ms. Figure 8 also shows that, at the offset of the stimulus, the proportion of neurons exhibiting constant response profile increased again to a level comparable with that of the ON-response immediately after stimulus presentation. In the following analysis, neuronal activity recorded only during the later part of the stimulus presentation period was included.

Classification of the effect of the surround

To better understand the relationship between the effects of the luminances of the surface and surround stimuli, we compared the results of the surface-luminance and surround-luminance tests for each neuron. Our analyses of three representa-

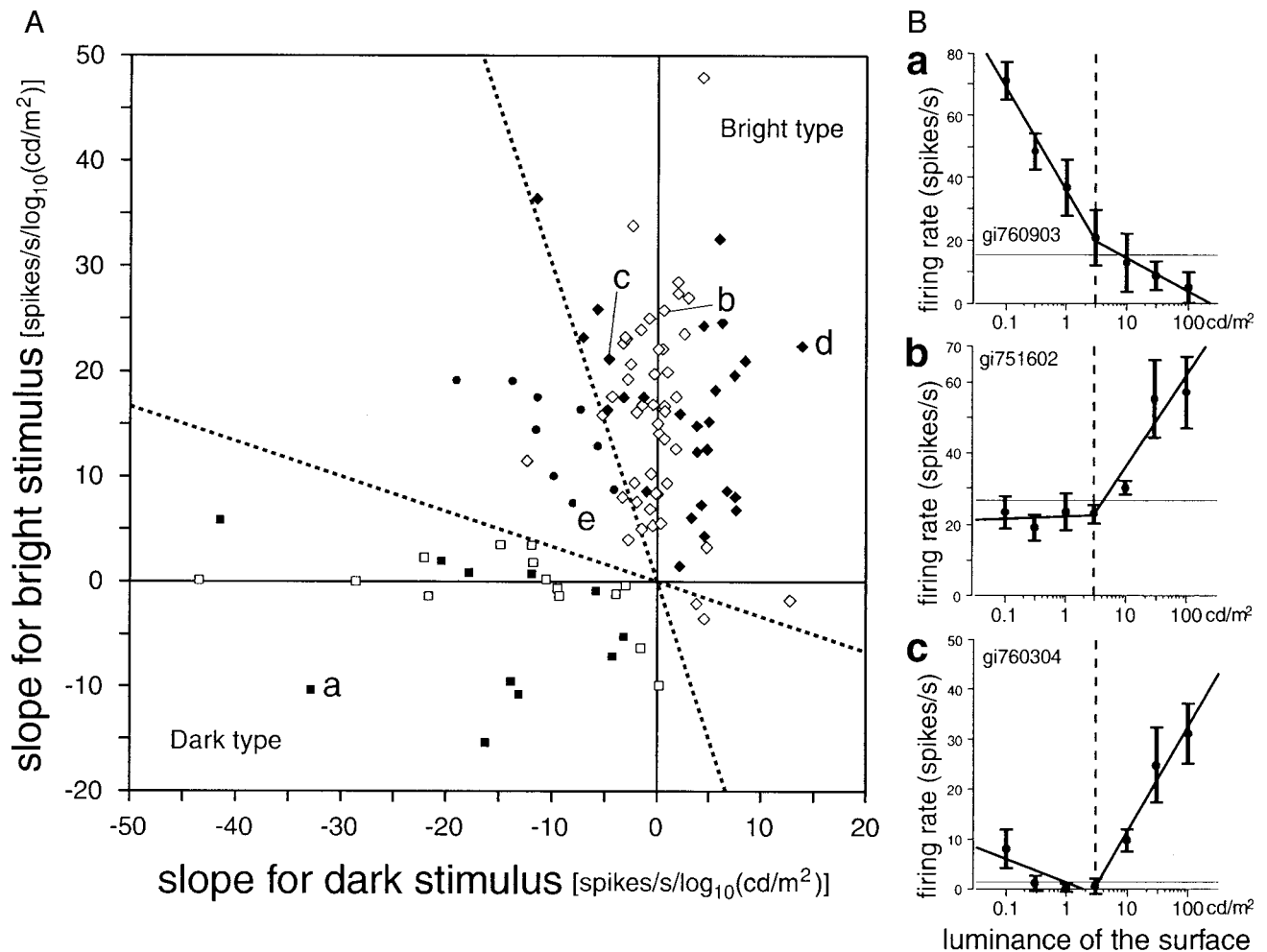


FIG. 5. Distribution of the slopes of the response profiles calculated as in Fig. 4C. A: the relationship between the slopes of the response profiles generated using dark stimuli (abscissa, cf. a in Fig. 4C) and those generated using bright stimuli (ordinate, cf. b in Fig. 4C). Based on the pairs of slope values, neurons were classified into 3 groups: square symbols represent neurons classified as dark-type, diamonds bright-type, and circles those with V-shaped responses. Open and filled symbols distinguish different criteria used to classify neurons (see text for details). Neurons marked with a, b, or c in A correspond to a, b, and c in B, respectively. Neurons marked with d or e correspond to those shown in Fig. 4, A and B, respectively. B: response profiles of 3 neurons, formatted as in Fig. 4, A and B.

tive neurons are shown in Fig. 9. The *top row* shows the results of the surface-luminance tests, formatted as in Figs. 4 and 5, while the *bottom row* shows the results of the surround-luminance tests, formatted the same way. Although all three neurons exhibited monotonic increases in activity in the surface-luminance test (bright-type neurons), the response profiles in the surround-luminance tests were markedly different.

The activity of *cell A* remained rather constant as the luminance of the surround was increased ($P \geq 0.05$, Spearman's rank correlation test, *bottom row* of *cell A*). This lack of sensitivity cannot be ascribed to saturation of the visual response: first, the luminance of the surface stimulus in the surround-luminance test was 50 cd/m², well within the dynamic range of this neuron as determined in the surface luminance test; and second, the firing rate during the surround-luminance test was about 25 spikes/s, an intermediate rate within the range obtained in the surface-luminance test. Indeed, we were able to predict the firing rates of this neuron in the surround-luminance test based on the results in the surface-luminance test (cf. *top row* of *cell A*). Thus the firing rates of this neuron seemed to be solely determined by the luminance of

the surface covering its RF in both tests and was unaffected by the luminance of the surround. We classified this type of neuron as type I, which showed monotonic changes in activity in response to changes in surface-luminance, but no systematic changes in response to changes in surround-luminance. Type I neurons may encode the luminance of the surface covering the RF.

Cell B showed a monotonic decline in activity in response to increasing luminance of the surround; consequently, the overall slopes of the response profiles for the two tests had the opposite sign. We classified this type of neurons as type II. When the luminance of the surround is changed while the surface luminance is kept constant, a change in perceived surface brightness is induced (brightness induction). Changes in the activity of type II neurons seemed to be correlated with changes in the perceived brightness of the surface stimulus. In surface-luminance and surround-luminance tests, bright-type neurons classified as type II exhibited stronger responses when the surface covering the RF was perceived as brighter. On the other hand, dark-type neurons classified as type II exhibited stronger responses when the surface was perceived as darker.

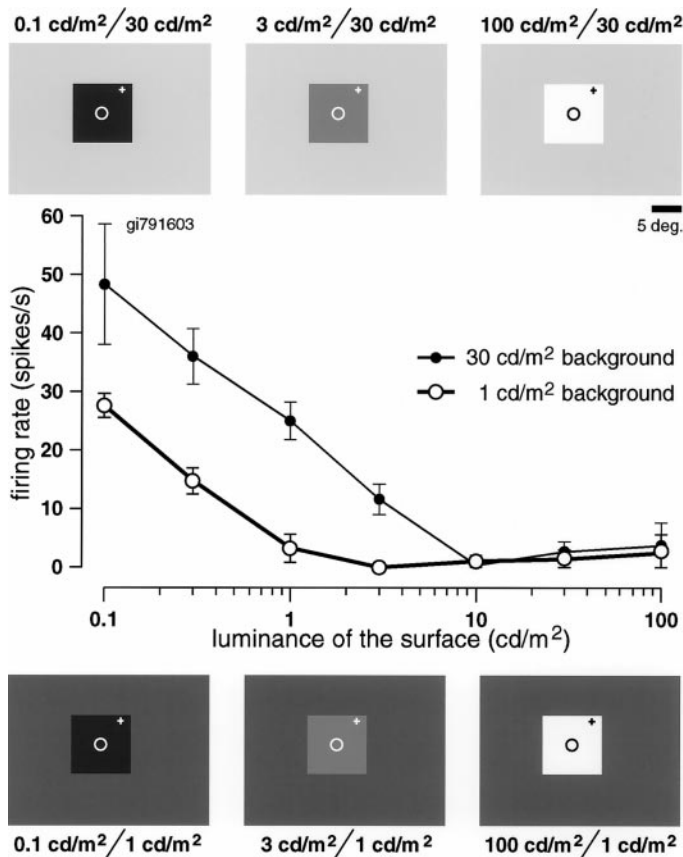


FIG. 6. Results of surface-luminance tests conducted using 2 different background luminances. *Top* and *bottom*: schematic drawings of the entire display during stimulus presentation. The figure format is the same as in Fig. 1A. The *top* row depicts the bright background condition (30 cd/m²); the *bottom* row the dark background condition (1 cd/m²). *Middle*: response profiles in the later period generated using the indicated backgrounds. The abscissa is the luminance of the surface stimulus, the ordinate the discharge rate. In this example, increasing background luminance caused the responses to be shifted toward the right.

For example, the cell depicted in Fig. 6 showed stronger responses to darker surfaces, and the magnitude of those responses increased when the background luminance increased, as if the same surface had become darker.

The activity of *cell C* also changed during the surround-luminance test, but in a way markedly different from *cell B*. The activity of this neuron increased monotonically with increasing luminance of the surround; consequently, the overall profile had the same sign in both tests. We classified this type of neuron as type III, which showed monotonic increases (or decreases) in activity in response to increases in the luminance of either the surface or the surround. This type of neurons may encode the mean luminance of wide area encompassing both the surface and the surround.

Figure 10 shows the relationships between the slopes of the response profiles obtained in the surround-luminance test for bright-type (A) and dark-type (B) neurons. The abscissa denotes the slope for the dark surround, the ordinate the slope for the bright surround. Quantitative classification of neurons was carried out using the same set of criteria used for classification of neurons into bright-type and dark-type in surface-luminance test (Fig. 5A). More specifically, bright-type neurons were classified as type II and type III according to the same set of

criteria used for the classification of neurons into dark-type and bright-type, respectively, in the surface-luminance test. Reverse combinations of criteria were employed for classification of dark-type neurons into type II and type III. Cells in the *bottom left* region in A and *top right* region in B delimited by broken lines are type II; those in the *top right* region in A and *bottom left* region in B are type III. Type I neurons are not shown in this graph. Of 81 neurons subjected to both the surface-luminance and surround-luminance tests, 25 were classified as type I, 25 as type II, and 26 as type III. The remaining

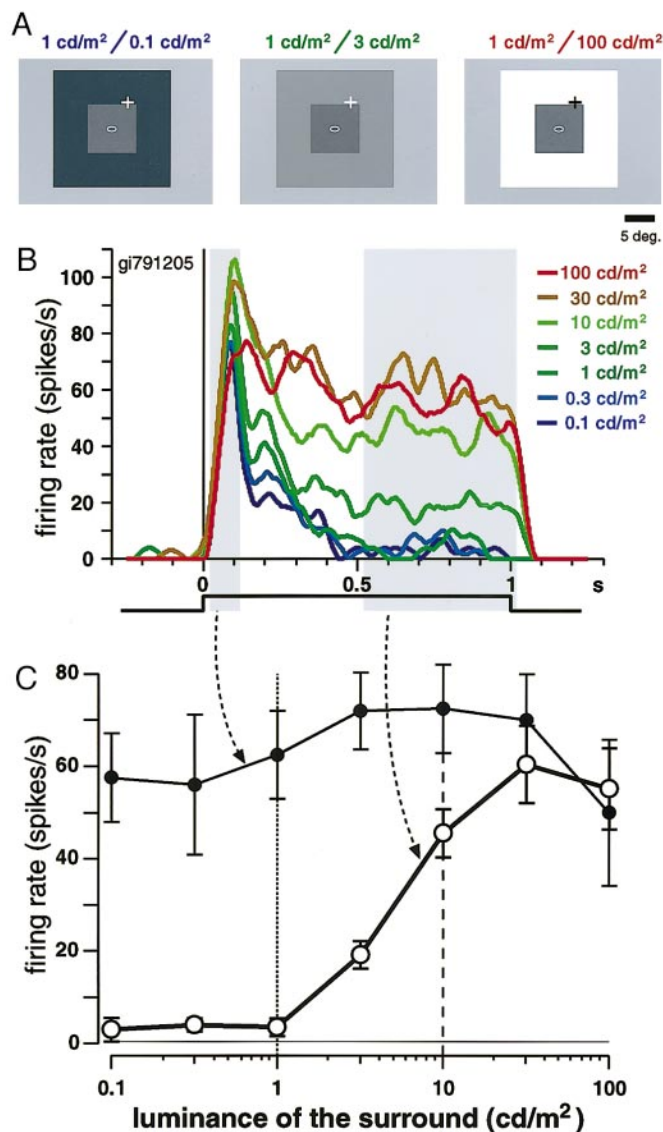


FIG. 7. Stimuli and responses of a representative neuron recorded during a surround-luminance test. A: schematic drawing of the display during stimulus presentation. The cell's RF is superimposed as an ellipse. The square surrounding the RF is the surface stimulus. The frame around the surface stimulus is the surround stimulus. The luminance of the surround stimulus was varied, while that of the surface stimulus was kept constant. B: spike density plots of the responses. Different colors represent the surround luminances indicated in the *inset*. Other formats are the same as in Fig. 2A. C: early (●) and late (○) response profiles. The vertical dotted line indicates the luminance of the surface stimulus (1 cd/m²). The vertical broken line indicates the luminance of the background (10 cd/m² in this case). Other formats are the same as in Fig. 2B. In this example, late neuronal activity increased monotonically with increasing surround luminance. In contrast, the early response profile is rather flat.

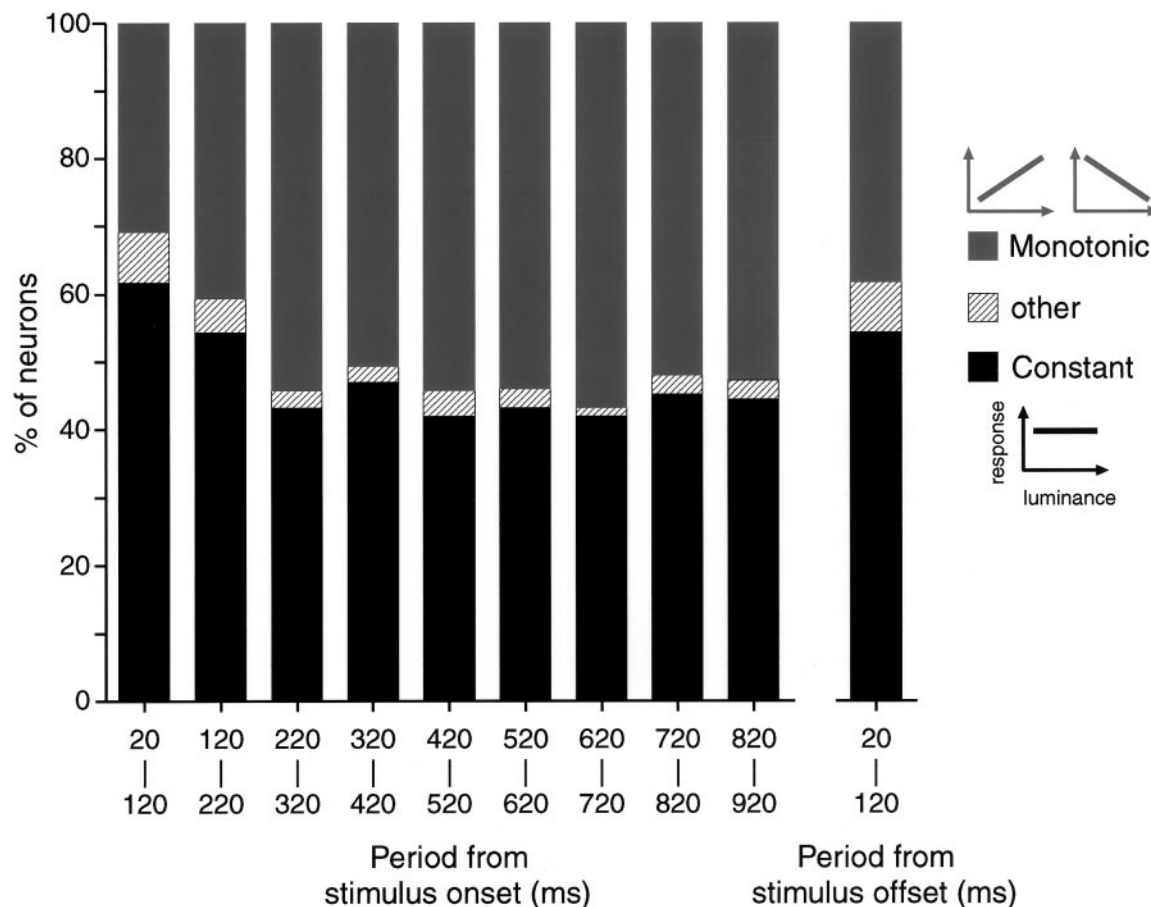


FIG. 8. Percentage of different types of effects from the surround across the entire population of 81 neurons tested in the surround-luminance test in every 100-ms time window during stimulus presentation and at the offset of the stimulus. Solid, gray, and hatched parts represent constant, monotonic, and other profiles, respectively.

five neurons showed V-shaped profiles in the surround luminance test and were not classified.

We found that there are differences in the response properties and layer distributions across type I, II, and III neurons. Table 2 shows that type I and III neurons were predominantly bright-type (80 and 85%, respectively), whereas there was little bias among type II neurons (56% bright-type and 44% dark-type). With regard to the layer distribution, type I neurons were mainly recorded from layer IV (21/25), but type II and III neurons distributed more evenly across the different layers (Table 3).

We also examined spatial summation properties in 68 of 76 type I, II, and III neurons using uniform square stimuli ranging from 0.25 to 16° in size. The luminance of the stimuli was 50 or 100 cd/m² for the bright-type neurons and 0.1 cd/m² or lower for the dark-type neurons. We found no clear relationships between the pattern of size-response curve and the type of neurons (I, II, and III). Furthermore, the curve was generally flat over the range of stimulus sizes used for the test of the effect of surface- or surround luminance. Therefore the effects of the surround are unlikely explained by the spatial summation property of neurons beyond the classical RF.

DISCUSSION

In the present study, we evaluated the effects of both local luminance information on the classical RF and global lumi-

nance information from the surround on the activity of V1 neurons in awake macaques. The activity of most surface-responsive neurons varied monotonically with surface luminance, and some were also affected by the luminance of the surround. Among these, the activity of type II neurons correlated with the perceived brightness of the surface, which is consistent with earlier reports suggesting that perceived surface brightness is represented in V1 (Rossi and Paradiso 1999; Rossi et al. 1996). On the other hand, the activity of type III neurons more likely represents luminance over a wide area in and around the classical RF, and the activity of type I neurons is unaffected by the luminance of the surround. There were differences in layer distribution across different types of neurons. These results should provide a firm basis for the understanding of the representation of luminance and brightness in the visual cortex.

Representation of surface luminance

Earlier studies reported that the activity of some V1 neurons that responded to a uniform surface varied with the luminance of the surface. Doty and colleagues (Bartlett and Doty 1974; Kayama et al. 1979) reported that many V1 neurons responded to diffuse steady illumination, and that their activity varied monotonically with light intensity over a range of 4 log units. They called such neurons “luminance units” (or “luxotonic units”). Maguire and Baizer (1982) studied the responses of V1

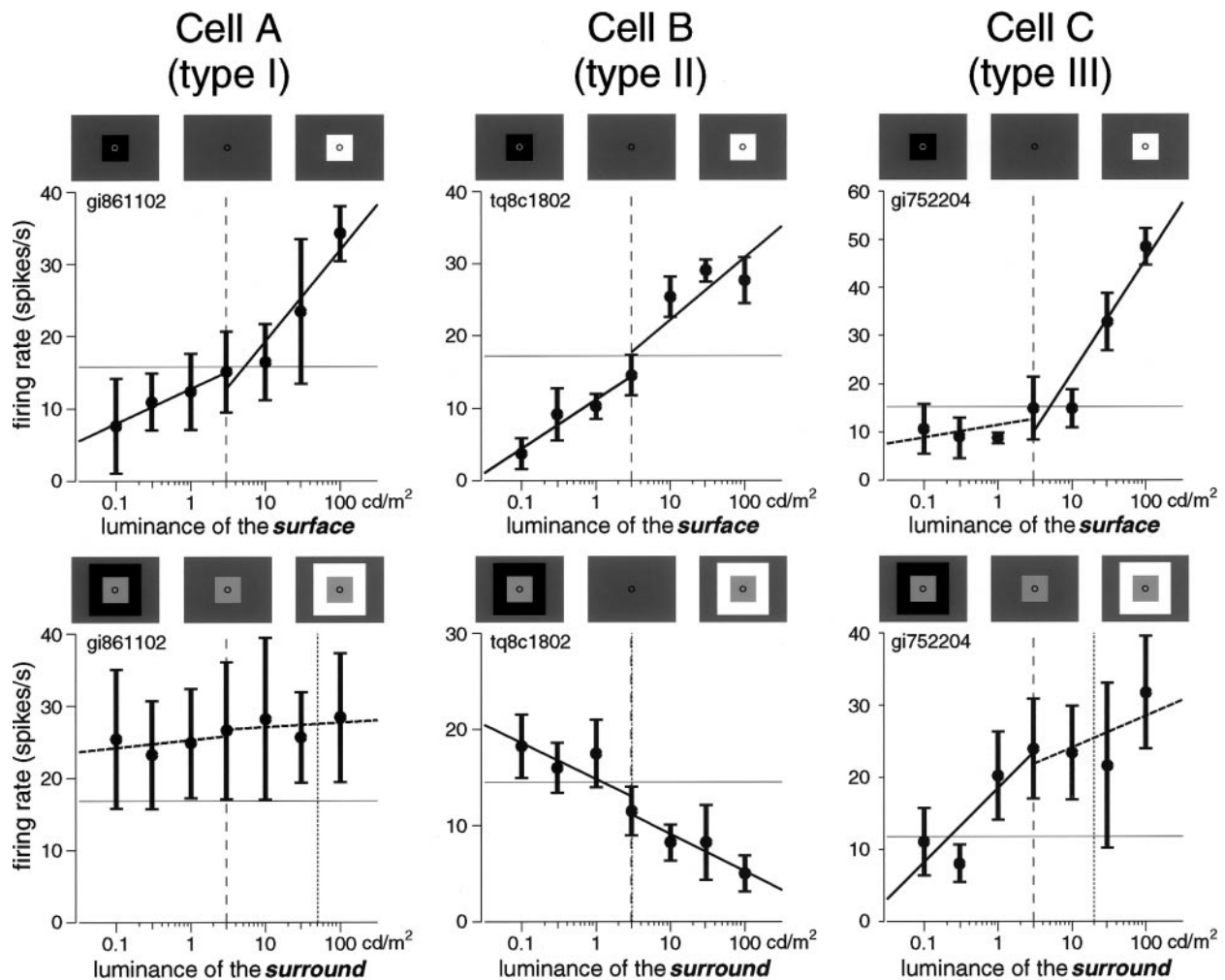


FIG. 9. Three representative neurons exhibiting similar responses to surface-luminance tests, but differing responses to surround-luminance tests. *Top row*: response profiles generated in response to surface-luminance tests (formatted as in Fig. 4, A and B). *Bottom row*: response profiles generated in response to surround-luminance tests (formatted as in Fig. 7C). The thin horizontal line indicates mean ongoing activity. The vertical broken line indicates luminance of the background. The vertical dotted line indicates luminance of the surface stimulus. Solid regression lines indicate significant correlations ($P < 0.05$, Spearman's rank correlation), and dashed regression lines indicate nonsignificant correlations ($P \geq 0.05$). All three neurons exhibited stronger responses to higher luminances in the surface-luminance test (bright-type). However, the activity of cell A was essentially unchanged during the surround-luminance test; the activity of cell B declined with increasing surround luminance; and the activity of cell C increased with increasing surround luminance. Using the criterion described in the text, these cells were respectively classified as type I, type II, and type III.

neurons to light spots larger than the RF with various luminances, ranging of 1.8 log units, in macaques while the monkeys performed a fixation task. In the present study, we employed preparations and stimuli similar to those used by Maguire and Baizer, except that our stimuli were either brighter or darker than the background, whereas theirs were always brighter than the background. Using surface luminances spanning a 3-log unit range (0.1–100 cd/m^2), we confirmed that the activity of surface-responsive neurons varied systematically with luminance level. The dynamic range of some of the neurons was broad enough that their activity varied monotonically over the entire range of luminances tested (e.g., Fig. 4A), while the activity of others only changed in response to stimuli brighter (bright-type) or darker (dark-type) than the background. It has generally been thought that mainly information about contrast is conveyed from the retina to V1. In fact, early ON-response as well as OFF-response frequently

showed V-shaped response profile that likely conveyed contrast information. However, the results of the present study and the earlier studies cited above suggest that information about the luminance of uniform surfaces is also conveyed to V1.

We found that the response profiles were often time dependent; monotonic variation in firing rate as a function of surface luminance was seen mainly during the later period (Fig. 3). A similar tendency was found in the results of the surround-luminance test (Fig. 8). For that reason, we focused our analysis on the later period of the response.

Effect of the luminance of the surround

The earlier studies of V1 neurons cited above described neural responses to surface luminance, but not the effect of the luminance of the surround, which can dramatically alter perceived brightness of a surface, even when the luminance of that

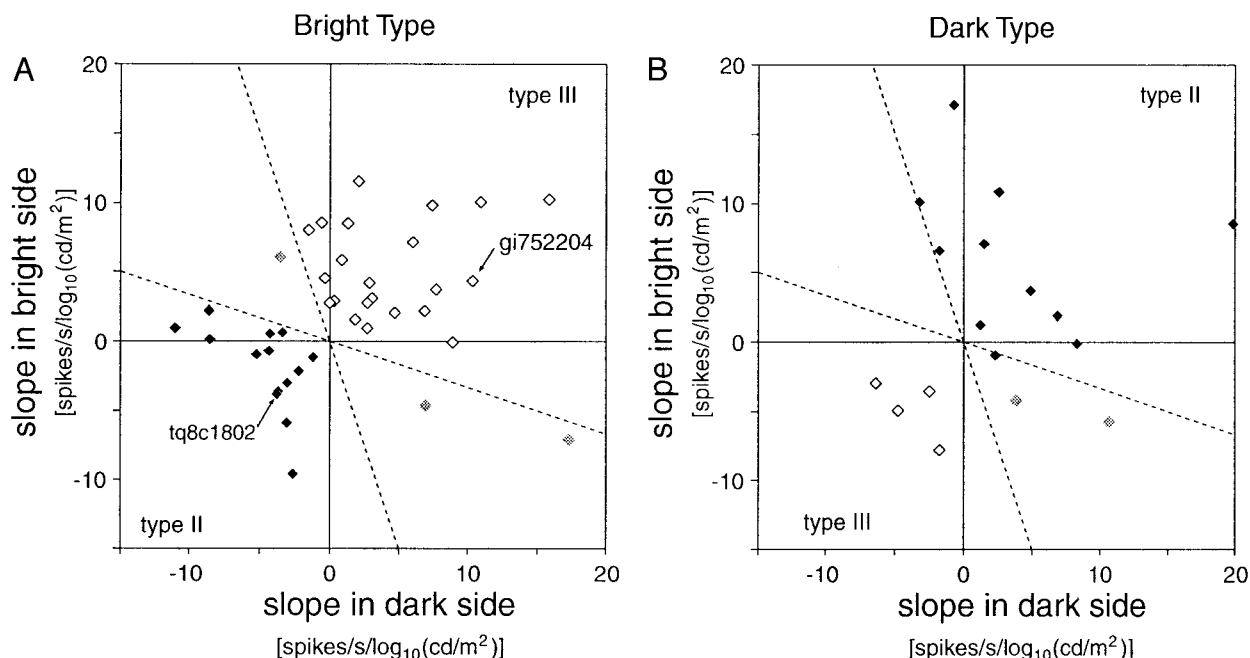


FIG. 10. Distributions of the slopes of the response profiles generated by surround-luminance tests. *A*: the activity of bright-type neurons. *B*: the activity of dark-type neurons (determined in the surface-luminance test). In each graph, the abscissa indicates the slope obtained using stimuli darker than the background, the ordinate stimuli brighter than the background. The graph format is the same as in Fig. 5A. Each symbol represents a cell. Cells in the bottom left region in *A* and top right region in *B* delimited by broken lines are classified as type II; those in the top right region in *A* and bottom left region in *B* as type III. Type I neurons are not shown. Five gray diamonds in the top left and bottom right regions represent cells unclassified as either type. See text for the details of the classification.

surface remains unchanged. Paradiso and colleagues recently studied the effect of the luminance of the surround on the activity of V1 neurons in anesthetized cats (Rossi and Paradiso 1999; Rossi et al. 1996). They found that, by temporally modulating the luminance of the surround while keeping the luminance of the surface constant, they could modulate the activity of V1 neurons. In some of these neurons, the modulation of the stimulus and the response was out-of-phase, and the change in activity was consistent with the perception of brightness induction. Interestingly, this modulation vanished when the frequency of the surround luminance modulation was over 4 Hz. This cutoff frequency matches well the cutoff frequency for human perception of brightness induction (De Valois et al. 1986; Rossi and Paradiso 1996). They also found neurons whose activities were modulated in-phase with modulation of the surround, although the properties of these neurons were not described in detail.

Despite differences in the experimental procedures and animal preparations, our findings on the integration of local and global luminance were consistent with those of the aforementioned reports. The activity of our type II neurons qualitatively parallels surface brightness perception. The activity of type II

neurons appears to correspond to the responses of neurons described by Paradiso and colleagues as exhibiting 180° phase differences. Indeed, we confirmed this by testing some type II neurons with a dynamic version of the brightness induction stimulus (data not shown). Our type III neurons, whose response profiles had the same sign between surface-luminance and surround-luminance tests (e.g., Fig. 9C), probably correspond to the neurons with 0° phase difference.

We found that the effect of the surround developed gradually in about 100–200 ms after the onset of the stimulus (e.g., Figs. 7B and 8). Such slow rise times appear to correspond to the low cutoff frequency of perception and V1 neuron activity during temporal modulation of a brightness induction stimulus (De Valois et al. 1986; Rossi and Paradiso 1996).

The dynamic version of brightness induction stimuli is advantageous for testing the correspondence between neuronal activity and perception. On the other hand, static stimuli, as employed in the present study, are advantageous for developing a quantitative description of the relationship between luminance, perceived surface brightness, and neural activity. We believe such quantitative data will provide a reference when

TABLE 2. Proportion of bright- and dark-type neurons among type I, II, and III neurons

	Type I	Type II	Type III
Bright-type	20 (9)	14 (10)	22 (13)
Dark-type	5 (4)	11 (8)	4 (2)
Total	25 (13)	25 (18)	26 (15)

Numbers in parentheses indicate single neurons.

TABLE 3. Layer distribution of type I, II, and III neurons

	Type I	Type II	Type III	Unclassified
Layer II/III	1 (1)	6 (3)	6 (3)	0
Layer IV	21 (9)	9 (7)	11 (6)	2 (1)
Layer V/VI	3 (3)	9 (7)	7 (5)	3 (3)
Not identified	0	1 (1)	2 (1)	0
Total	25 (13)	25 (18)	26 (15)	5 (4)

Numbers in parentheses indicate single neurons.

studying other global effects related to brightness perception, including perceptual filling-in (Gerrits and Timmerman 1969; Komatsu and Murakami 1994; Komatsu et al. 2000; Murakami et al. 1997; Ramachandran 1992; Ramachandran and Gregory 1991; Yarbus 1967), the Claik-O'Brien-Cornsweet illusion (Cornsweet 1970; O'Brien 1958), and the effect of the three-dimensional configuration of stimuli on brightness and/or color perception (Adelson 1993; Gilchrist 1977).

Transformation from physical luminance to perceived brightness

Neurons whose activities correlate with the perceived brightness of a uniform surface are seldom found in the lateral geniculate nucleus (De Valois and Pease 1971; Rossi and Paradiso 1999), and it is suggested that this property is formed in the visual cortex. Our finding that about half of the neurons recorded from layer IV were type I neurons is also consistent with this idea. If so, how is the luminance information transformed to the brightness information in V1? There are several possibilities. One is that the luminance contrast at the border between the surface and surround is detected by contrast-sensitive neurons having RFs located at the border, after which the signals from these neurons is transmitted to type II neurons via horizontal connections within V1 (Gilbert and Wiesel 1983). Alternatively, the activity of type II neurons may be explained by a combination of signals from different types of luminance-sensitive neurons in V1 by subtracting global information conveyed by type III neurons from local information conveyed by type I neurons. Finally, there is the possibility that global luminance information is detected in the extrastriate cortex and modulates the activity of V1 neurons through feedback connections. Further investigation is clearly necessary to determine how the transformation of luminance-related information takes place in V1.

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