Integration of surface information in primary visual cortex

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Ample evidence suggests that primary visual cortex is involved in the perception of form, and there is increasing evidence that it may also be important in the perception of surfaces. Perceptual qualities of surfaces, such as brightness, are based on extensive integration of information throughout the visual field. In primary visual cortex, we found that the responses of neurons to surfaces were also influenced by the intensity and organization of light in large portions of the visual field. Interactions with surrounding stimuli typically extended 10 to 20 degrees beyond a cell's receptive field, the same spatial scale as perceptual interactions. Moreover, there were both facilitatory and inhibitory influences, just as there are additive and subtractive perceptual interactions. Surprisingly, influences from outside the receptive field obtained with surface stimuli did not reliably correlate with influences recorded with gratings. These properties suggest that the underlying neuronal interactions may serve as the fundamental building blocks of surface perception.

Many previous studies of primary visual cortex (V1) indicate that this area of the brain is involved in the perception of visual contours. Recent work suggests that V1 may also be important for the representation of surfaces[1–6]. A range of visual effects illustrate that the perception of surfaces is powerfully affected by both additive and subtractive influences from throughout the visual field[7–10]. For example, in simultaneous contrast, the brightness of one region can be influenced by a neighboring area at a distance of 10 degrees or more[11,12]. Studies of lightness and color constancy suggest that the properties perceived in an area result from the integration of surface information across the entire visual field[10,13]. Because the spatial scale of the perceptual interactions can be much larger than the size of receptive fields in V1, it is not clear how activity within V1 could underlie the perceptual effects. To examine this point, we recorded from V1 and quantified the extent to which surface information beyond the receptive fields of the neurons modulates the response to stimuli within the receptive field. We explored situations in which there was one large surface extending outside the receptive field and also situations with one surface covering the receptive field and a second at some distance.

In addition to assessing the range and luminance sensitivity of spatial interactions, we determined whether they were facilitatory or inhibitory. We would expect to find both signs of effects because psychophysical studies of brightness show that both additive and subtractive perceptual interactions occur depending on spatial variables. In simultaneous contrast, a gray patch appears darker if it is surrounded by a lighter area[9]. However, in assimilation[7] and White's effect[8], the reverse is true–the surrounding light area makes the gray patch look lighter. Clearly, changes in configuration can dramatically change the sign and strength of contextual interactions, and it has been argued that opposing forces are always at work[4]. Evidently, the brightness an area is perceived to have is based on an interplay between the organization of surface areas and their intensities.

Results

Single-cell recordings were made from the central representation of primary visual cortex of 15 adult cats under barbiturate anesthesia. To be consistent with previous studies, minimum response fields were plotted and size determinations made using moving and flashed bars of light projected onto a tangent screen. All reported results were derived from monocular stimulation of the dominant eye. Computer-controlled study characterized the cells as simple or complex and quantified selectivity for orientation, spatial frequency and the spatial properties described below.

The first questions we investigated were whether neurons respond to light in the receptive field in the absence of contrast, and whether areas of light outside the receptive field modulate the cell's response to light in the receptive field. Although nearly all previous experiments have stimulated visual neurons with luminance or chromatic contrast, we found that this is frequently not necessary to evoke a response. The majority of striate cells that we studied was excited when a large uniformly luminous disk was positioned such that its edges were outside the receptive field, and of 119 cells studied with uniform disks, 86 (72%) had responses that significantly changed with disk size (t-test, $p < 0.05$). Both simple and complex cells showed this trait. The most common effect of increasing the size of a uniformly luminous disk was to increasingly inhibit the response until at some size this inhibition saturated (Fig. 1a). In almost all cases, the area associated with response inhibition exceeded the size of the receptive field, often to a considerable extent. Some cells exhibited a facilitatory region beyond the inhibitory area (Fig. 1b), whereas others showed inhibition that continued to increase to very large stimulus sizes (Fig. 1c). Other response curves indicated facilitation that saturated with distance (Fig. 1d), a facilitatory area surrounded by a larger inhibitory region (Fig. 1e) or facilitation that continued to increase to the largest size tested (Fig. 1f). In some cases (such as Fig. 1d and f), there was little or no response when a uniform area just covered the receptive field, but the response significantly increased when the area was made considerably larger than the receptive field.

Several aspects of these results are somewhat surprising. First, the responses were usually reliable and often strong without contrast within the receptive field. This is not at odds with previous studies, but virtually all previous quantitative studies used bars of light or gratings as stimuli. Second, the size of the area that modulated the response was often enormous compared to the receptive field. Third, the character of the modulatory areas was sometimes surprising, showing reversals between facilitation and inhibition, or progressively increasing facilitation (open bars in Fig. 2). The results suggest that small V1 receptive fields are surrounded by much larger areas, often extending 10–20 degrees, in which light can modulate the response to a central stimulus, even when there is no contrast in the receptive field. The extent of these spatial interactions, observed in single neurons, is roughly the same as that observed psychophysically in brightness and color perception[11,13].

The responses of V1 neurons to a bar of light or patch of grating in the receptive field are often modulated by extending the grating beyond the receptive field or by introducing a second peripheral bar (for example, side- and end-inhibition)[14–20]. We were interested in whether the zones outside the receptive field implied by these more conventional protocols would be the same as those implied by our surface stimuli. We studied 96 cells using sinusoidal luminance gratings that ranged in size from just covering to much larger than the receptive field (always at the optimal orientation and spatial frequency). Dependence on size was categorized in the same manner as for the uniform disks. The distribution of different types of size dependence (dark bars in Fig. 2) was rather different from that found with uniform disks. Gratings were less likely than disks to produce inhibition that saturated with distance, and more likely to give facilitation that saturated with distance and facilitation followed by inhibition.

The overlap in the distributions for gratings and disks could have been based on a systematic correlation in the extra-receptive-field effects of gratings and disks, or by chance. To investigate this point, we examined the responses of 21 cells that were fully studied with both stimulus types. In this population of neurons, about half (10/21) showed a dependence on size for one stimulus type but not the other. For the other half of the cells, there was considerable heterogeneity; in some cases the response varied with size in the same manner for both stimulus types (Fig. 3a), and in other cases there were striking differences (Fig. 3b). In general, the response to gratings was not a reliable predictor of the response to uniform surfaces (and vice versa). In other words, the structure of the extra-receptive-field area that would be inferred from the experiments with uniform stimuli and gratings were not reliably the same. Using the example in Fig. 3b, the grating results suggest that there was a facilitatory area surrounded by an inhibitory area beyond the receptive field.

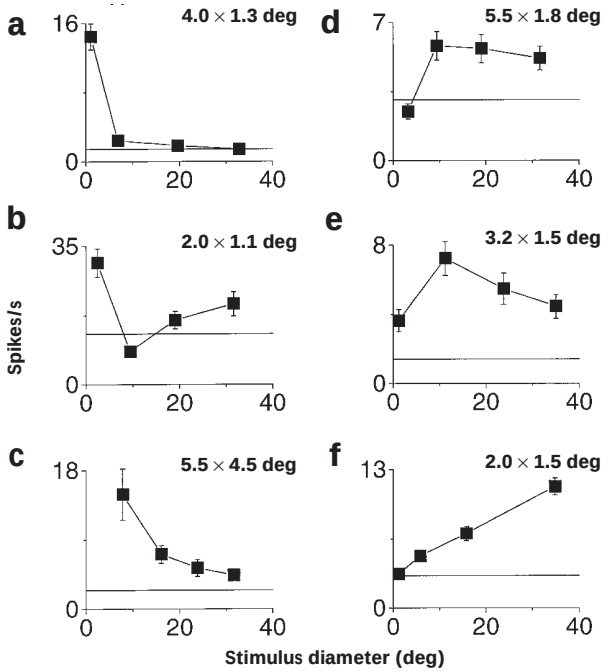

Fig. 1. Effect of uniform disk size on firing rate of six cells. The size of each neuron's receptive field is shown in the upper right corner of the graph. The significance of trends and inflections in the curves was assessed with *t*-tests ($p < 0.05$). Based on these tests, response curves were categorized as showing inhibition that saturated with increasing size **(a)**, inhibition followed by facilitation **(b)**, increasing inhibition with size **(c)**, facilitation that saturated **(d)**, facilitation followed by inhibition **(e)**, or increasing facilitation with size **(f)**. In this and subsequent figures, firing rate was taken as the average spikes/s during the 1.5-second stimulus presentation. The horizontal lines indicate the spontaneous firing rate of each neuron, and the error bars represent standard errors.

However, the disk results imply that the surround area was purely facilitatory. Presumably the different curves obtained with different stimuli result from the sensitivity of cortical neurons to both luminance and contrast.

To further assess the contribution of areas beyond the receptive field, we examined whether annuli of light at a range of distances outside the receptive field modulate the response to a uniform disk just covering the receptive field. One can view this as a highly simplified version of the 'Mondrian' stimuli commonly used in investigations of color and brightness constancy[21]. Of the 111

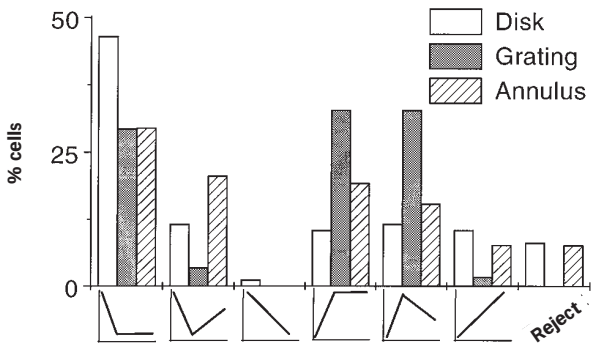

Fig. 2. Distribution of neurons into the six response categories illustrated in Fig. 1. From left to right, graphical icons along the abscissa correspond to inhibition that saturated with increasing size, inhibition followed by facilitation, increasing inhibition with size, facilitation that saturated, facilitation followed by inhibition, increasing facilitation with size and a final column for cells that did not fit any of the categories. The open white bars represent conditions in which the size of a solid uniform disk was increased beyond the receptive field. Solid bars represent tests with a grating patch that increased in size. Hatched bars show results when a disk of uniform light just covered the receptive field and a uniform annulus was placed at different distances from the receptive field.

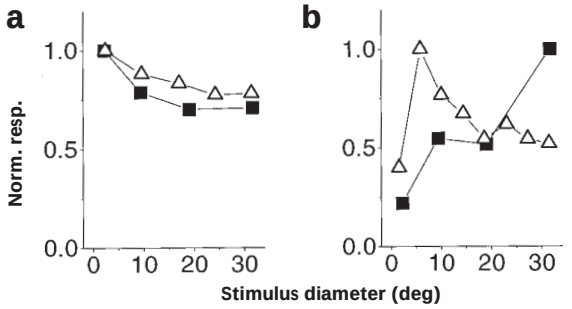

Fig. 3. Response of two cells to gratings (△) and uniform disks (■) as size increased beyond the receptive field. For the cell in **(a)**, the effect of extending the stimulus beyond the receptive field was similarly mild inhibition that saturated with size for both disks and gratings. For the cell in **(b)**, the response changed quite differently with the two stimulus types. As grating size increased, this neuron showed facilitation followed by inhibition. As uniform disk size increased, the same neuron showed only facilitation. More often than not, the effects of increasing stimuli past the receptive field were different for uniform disks and gratings. Receptive field size in (a) was 1.1 x 1.3 degrees and in (b) was 3.0 x 1.3 degrees. For clarity, error bars are omitted, but the average standard errors were as follows: left frame filled squares, 0.055; left frame open triangles, 0.037; right frame filled squares, 0.19; right frame open triangles, 0.065.

cells studied with such stimuli, 78 (70%) were significantly modulated by annulus distance outside the receptive field (*t*-test, $p < 0.05$). Considerable heterogeneity was found in the response curves (hatched bars in Fig. 2), with significant numbers of cells showing facilitation or inhibition with an annulus outside the receptive field and interactions that either saturated or reversed as the annulus was moved farther from the receptive field. On a cell-by-cell basis, we compared the response of 106 neurons as the edge distance of an annulus was varied to the response as the outer edge of a uniform disk was varied (Fig. 4). Many more cells showed facilitatory interactions with annuli than with the uniform disks. We found that for most cells, the response as a function of edge distance was not the same for annuli as for disks. Taken together with the disk/grating comparison above, these results suggest that there are modulatory effects of both luminance and contrast beyond the receptive field, and great caution must be exercised in attempts to define the structure of the extra-receptive-field area from responses to a single stimulus type.

As a final measure of the influence of light within and beyond the receptive field, we recorded responses of V1 neurons as the light level covering the receptive field or in a surrounding annulus was varied. Of 35 cells studied, 17 had responses significantly modulated by light level within the receptive field; 3 were facilitated (Fig. 5a) and 14 were inhibited (Fig. 5b) by increasing the light level. The responses of a smaller percentage of cells were inhibited (Fig. 5c) or facilitated (Fig. 5d) by increasing light level within an annular area outside the receptive field, when a uniform disk covered the receptive field. Over the luminance range we studied, responses of 18 of 60 cells were significantly modulated by light level in an annular surround; 12 were inhibited and 6 were facilitated by increasing the light level. Clearly, light intensity within and beyond the receptive field affects the response of some cells in primary visual cortex, in addition to the effects of the distribution of light and contrast.

Discussion

Our results show that many neurons in striate cortex have areas beyond their receptive field from which light can modulate the response to a surface covering the receptive field. Surprisingly, we found that most of the V1 neurons we studied gave significantly different responses to surfaces of different sizes, even though there was never any luminance contrast in the receptive field. Also, the response to a small surface covering the receptive field was usually modulated by the presence of a second surface (annulus) outside the receptive field and by the distance of this second surface. The spatial areas that modulated the response of a neuron were often quite large, extending 10–20 degrees beyond the receptive field. Our results suggest that a significant percentage of V1 neurons carry information about surfaces in addition to form. This is consistent with results of several other recent studies of brightness[1,4] and texture segmentation[2,3,6]. The scale of the spatial interactions we observed is intriguing because it is comparable to the interaction ranges reported in perceptual studies of brightness contrast[11,12] and constancy[13]. Moreover, we found both facilitatory and inhibitory interactions, which may be related to the additive and subtractive perceptual interactions that have been observed in simultaneous contrast, assimilation and White's effect. The interactions we observed between an annular surface outside the receptive field and a small surface covering the receptive field are also reminiscent of the widespread interactions found perceptually between patches in the Mondrian stimuli commonly used in color constancy experiments. Finally, the present results suggest a basis for the finding that many cells have responses correlated with simultaneous brightness contrast when light level is changed far outside the receptive field[1].

A few previous studies relate to the questions of surface representation and integration that we investigated. For example, some cells in macaque striate cortex were found to give a differ-

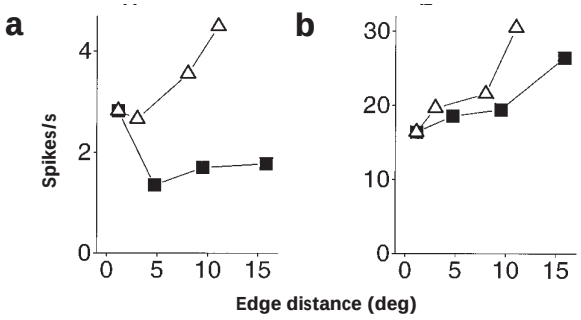

Fig. 4. Response of two cells with increasing distance from the center of the receptive field to the edge of a uniform disk (■) or to the inner edge of an annulus three degrees thick (△). For the cell in **(a)**, the effect of increasing uniform disk size was inhibition that saturated with distance. Adding an annulus just outside the receptive field (second data point from left) had little effect on the response to a disk alone covering the receptive field (left-most data point). However, as the annulus was moved further away from the receptive field, the response was increasingly facilitated. Thus, the disk and annulus tests led to quite different inferences about the contribution of the area outside the receptive field to the neuron's response. Conversely, for the cell in **(b)**, adding light beyond the receptive field seemed to have the same effect whether it was part of a uniform disk or an annulus. Receptive field size in (a) was 1.3 x 1.0 degrees and in (b) was 2.0 x 3.5 degrees. For clarity, error bars are omitted, but the average standard errors were as follows: left frame filled squares, 0.51; left frame open triangles, 0.78; right frame filled squares, 1.63; right frame open triangles, 1.22.

ential response to white and black ganzfelds (full field stimuli)[25,26]. Although these studies did not assess whether the source of the response modulation was from within or beyond the receptive field, they did establish that some striate cells are luminance sensitive, a point that we confirmed in more detail by using multiple luminance levels. For reasons we do not understand, in cat striate cortex, few cells gave a differential response to black and white ganzfelds[27]. In addition to a sensitivity to diffuse illumination, some cells in macaque V1 were reported to be sensitive to the size of a uniform disk extending beyond the receptive field[5]. In our experiments, a range of different sensitivities to size were observed, a finding that affects the interpretation of numerous earlier studies. We found that some cells only respond to stimuli roughly the same size as the receptive field and are inhibited by larger stimuli. Conversely, some cells only respond to surfaces much larger than the receptive field. Previous studies that found cortical neurons unresponsive to stimuli without contrast in the receptive field generally did not vary stimulus size, which would lead to an underestimate of the number of cells that would respond to some surface configurations.

There have been a large number of studies of extra-receptive-field influences using bars of light and gratings[14–19], and one wonders whether the results could have predicted our findings. We believe this is unlikely. Although there was sometimes agreement between the nature of the extra-receptive-field influences obtained with gratings and surfaces, more often they disagreed. A complicating factor comes from recent reports that the nature of extra-receptive-field influences obtained with gratings and Gabor patches depends on the stimulus contrast within the receptive field[19,20]. Is it possible that our results obtained with surface stimuli would agree with results obtained with gratings, if the proper contrasts were used? In one sense, this is an impossible comparison; by definition, our surface stimuli had no contrast within the receptive field, and the grating stimuli had suprathreshold contrast (50%). An alternative question is whether a grating at any suprathreshold contrast would show the same interactions with the extra-receptive-field area as our surface stimuli. This is conceivable, though the exhaustive comparisons between gratings and surfaces that might be needed to establish this point have never been done. In any event, such a comparison would not alter our basic point, which is that our results with surfaces clearly could not be predicted by the many experiments with fixed contrast gratings that have examined extra-receptive-field influences. Similarly, the single-surface stimuli (uniform disks) did not reliably imply the same contribution of the extra-receptive-field area as the two-surface stimuli (disk plus annulus). Presumably, the different results obtained with different stimuli resulted from a sensitivity to both luminance and luminance contrast outside the receptive field. The technical implication of this hypothesis is that a single stimulus type cannot be used to reliably and fully characterize the contribution of the area outside receptive fields. Conceptually, the implication is that the extra-receptive-field area provides a rich pattern of modulatory influences on the receptive field that might serve a variety of functional roles from texture segmentation to perceptual constancies.

The widespread neuronal interactions observed in V1 may provide an answer to a longstanding dilemma in visual neuroscience–how can important and necessary spatial interactions occur without interfering with high-acuity vision? If brightness perception were based solely on the integration of information within large extrastriate receptive fields, this could account for the long-range spatial interactions perceptually

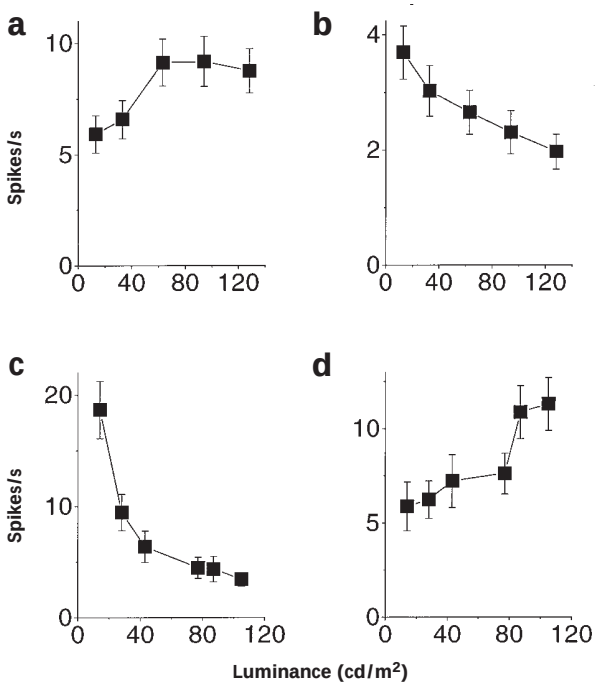

Fig. 5. Effect of light level on neural response. Increasing luminance of a uniform disk covering the receptive field had either a facilitatory **(a)** or inhibitory **(b)** effect. Likewise, increasing luminance in a surrounding annulus had either an inhibitory **(c)** or facilitatory **(d)** effect when the cell was excited by a constant disk in the receptive field. In (c), the receptive field was 2 x 3.2 degrees, the central stimulus was 2 degrees in diameter, and a 3-degree-thick annulus had an inner diameter of 19 degrees. In (d), the receptive field was 1.4 x 2 degrees, the central stimulus was 4.8 degrees in diameter, and a 3-degree-thick annulus had an inner diameter of 4.8 degrees. In all cases, error bars represent standard errors. Significance of trends was confirmed with one-way ANOVA ($p < 0.05$).

observed, but it would not clearly explain the fundamentally finer spatial scale of brightness perception. An alternative is that the resolution of brightness perception is limited by the small V1 receptive fields, but the scale of the spatial interactions is determined by either lateral connections within V1 (refs 28, 29) or feedback from extrastriate areas with larger receptive fields.

A challenge in understanding the relationship between our results and brightness perception is the considerable degree of heterogeneity in the integrative properties of the cortical neurons. Responses of individual V1 neurons sometimes correlate with perceived brightness to an impressive degree[1], but the heterogeneity of the population indicates that each cell cannot do so in all stimulus conditions. Nonetheless, perceptual effects such as assimilation[7] and induction[11] make it clear that both additive and subtractive perceptual interactions occur, and, consistent with the physiology, it has been argued that they are simultaneously present[30]. It seems that visual stimuli elicit a complex barrage of additive and subtractive neural interactions responsible for the final percept. One can speculate that the wider range of conditions that elicit subtractive (induction) rather than additive (assimilation) perceptual interactions may be related to our observation that inhibitory effects from outside the receptive field are more common. Ultimately, one must

know the net effect of interactions on the population of V1 neurons to assess how the neural representation in V1 correlates with perception. For the present, the important point that has been established is that the required signs and ranges of neural interactions are observable in V1. These interactions may serve as the fundamental building blocks for the perceptual interactions underlying surface perception.

Methods

PHYSIOLOGICAL PREPARATION. Experiments were performed on 13 female and 2 male adult cats, weighing between 2 and 4 kilograms. All procedures were conducted in accordance with NIH guidelines and were approved by Brown University's Institutional Animal Care and Use Committee. After placement of an IV cannula, cats were anesthetized with an IV injection of pentothal (thiopental sodium) at 10–20 mg/kg. Depth of anesthesia was maintained by making adjustments to the rate of continuous pentothal infusion as indicated by electro-encephalogram (EEG) and electrocardiogram (ECG), which were continuously monitored. After placement in a stereotaxic apparatus, animals were paralyzed by continuous infusion of atracurium besylate (1–2 mg/kg/hr) and artificially respired through a cannula inserted through a tracheotomy. End-tidal CO_2 and rectal temperature were monitored and maintained at 3.5% and 37.5°C, respectively. Nictitating membranes were retracted with a 10% ophthalmic solution of phenylephrine, and pupils dilated with 1% ophthalmic atropine sulfate. The eyes were refracted, and contact lenses of appropriate correction were fit to focus the eyes on a tangent screen and computer monitor at a distance of 57 cm.

A craniotomy was centered at Horsley-Clarke coordinates P3.0, L2.0, providing access to neurons representing the central visual field in area 17. Recordings were made with insulated tungsten electrodes, and the cortex was stabilized by filling the craniotomy with agar. At several depths along each electrode tract, electrolytic lesions were made for later reconstruction of the tract. At the end of the experiment, the animal was given an overdose of pentothal, and brain tissue was fixed with 10% Formalin. Frozen brain sections were cut at 40 µm and stained with cresyl violet to confirm that recording was in striate cortex and to reconstruct electrode tracts.

RECORDING PROCEDURES. After amplification, action potentials of individual neurons were isolated by a window discriminator on the basis of spike amplitude and timing. Receptive field properties were initially determined with a manually controlled bar of light projected on a tangent screen. Preliminary estimates were made of ocular dominance, orientation selectivity, direction selectivity, presence of on or off subregions and side or end inhibition. The receptive field was defined as the area on the screen that could be stimulated by hand with either drifting or flashing bars of light to elicit a response from the neuron. After preliminary studies with a hand-held stimulator, the non-dominant eye was occluded by an opaque patch, and the response of the neuron to stimulation of the dominant eye was explored with computer-controlled stimuli. Stimuli were presented on a 27-inch RGB monitor with 640 x 480 pixel resolution driven by a Number Nine graphics board. Except for the later experiments in which luminance was a controlled variable, the luminance of the uniform stimuli was 100 cd/m^2, and the background luminance was 1.5 cd/m^2, yielding an edge contrast of 0.97. The mean luminance of the gratings was 30 cd/m^2, and their contrast was 0.5. The stimuli were turned on in the blanking interval between successive video frames on the monitor. Stimuli were randomized within each block of trials, and there were 15–75 presentations of each stimulus. The response rates we report are the average for a 4-second (gratings) or 1.5-second (all other stimuli) interval beginning at stimulus onset and ending before stimulus offset.

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