Neural Responses in the Macaque V1 to Bar Stimuli With Various Lengths
Presented on the Blind Spot

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Submitted 9 August 2004; accepted in final form 31 December 2004

Matsumoto, Masayuki and Hidehiko Komatsu. Neural responses in the macaque V1 to bar stimuli with various lengths presented on the blind spot. J Neurophysiol 93: 2374–2387, 2005. First published January 5, 2005; doi:10.1152/jn.00811.2004. Although there is no retinal input within the blind spot, it is filled with the same visual attributes as its surround. Earlier studies showed that neural responses are evoked at the retinotopic representation of the blind spot in the primary visual cortex (V1) when perceptual filling-in of a surface or completion of a bar occurs. To determine whether these neural responses correlate with perception, we recorded from V1 neurons whose receptive fields overlapped the blind spot. Bar stimuli of various lengths were presented at the blind spots of monkeys while they performed a fixation task. One end of the bar was fixed at a position outside the blind spot, and the position of the other end was varied. Perceived bar length was measured using a similar set of bar stimuli in human subjects. As long as one end of the bar was inside the blind spot, the perceived bar length remained constant, and when the bar exceeded the blind spot, perceptual completion occurred, and the perceived bar length increased substantially. Some V1 neurons of the monkey exhibited a significant increase in their activity when the bar exceeded the blind spot, even though the amount of the retinal stimulation increased only slightly. This response increase coincided with perceptual completion observed in human subjects and were much larger than would be expected from simple spatial summation and could not be explained by contextual modulation. We conclude that the completed bar appearing on the part of the receptive field embedded within the blind spot gave rise to the observed increase in neuronal activity.

INTRODUCTION

Although there is no retinal input, the blind spot seems to be filled with the same visual attributes as its surround (Ramachandran 1992). This is called perceptual filling-in or completion at the blind spot and is not unique to humans (Komatsu and Murakami 1994). Filling-in also occurs in a variety of situations in the normal visual field (De Weerd et al. 1998; Kapadia et al. 1994; Ramachandran and Gregory 1991), which suggests that its underlying mechanism may play an essential role in normal visual information processing. It has been reported that when perceptual filling-in of a surface or completion of a bar occurs at the blind spot, neural responses are generated in the retinotopic representation of the blind spot in the primary visual cortex (V1) (Fiorani et al. 1992; Komatsu et al. 1996, 2000). In an earlier study, we found that most V1 neurons responsive to a surface stimulus that covered the blind spot and induced filling-in had receptive fields that extended out of the blind spot (Komatsu et al. 2000). We suggested that these neurons play an important role in filling-in by importing visual information from the surround to the inside of the retinotopic representation of the blind spot. However, this property raises a question when we consider the relationship between the neural responses and the percept. A visual stimulus causing filling-in or completion necessarily stimulates a part of the receptive field of the affected neurons that lies outside the blind spot and may generate a neural response. Consequently, we needed to dissociate responses correlating with a percept completed inside the blind spot from those correlating with retinal input stimulating the receptive field.

In this study, we attempted to dissociate these two sources and to determine whether or not responses of V1 neurons reflect the percepts of bars completed inside the blind spot. To do this, we first examined the perceived length of bars presented across the blind spot in humans and then examined, in monkeys, the length-tuning of V1 neurons whose receptive field overlapped the blind spot (Fig. 1). When one end of a bar was fixed at a position outside the blind spot and the bar was gradually elongated toward it (Fig. 1A), the retinal input received by the neuron and the perceived bar length both changed (Fig. 1, B and C). Once the end of the bar entered the blind spot, the retinal input and perceived bar length both remained constant. When the end emerged, perceptual completion occurred, and the perceived bar length increased substantially because the bar segment was perceptually completed inside the blind spot. However, because the completed bar segment lay mainly on the part of the receptive field inside the blind spot, the retinal input remained more or less constant. If the elicited neuronal response reflects only the retinal input, it should remain largely constant. On the other hand, if the response of the neuron reflects the percept of the completed bar segment, the response will exhibit a significant change when perceptual completion occurs. By measuring the length-tuning of V1 neurons to a set of bar stimuli presented on the blind spot, we were able to rigorously examine whether V1 neurons exhibit a response change when the perceptually completed bar segment appears on the receptive field. Our analysis of length-tuning showed that the activity of some V1 neurons significantly changed at the length where the bar stimulus would be perceptually completed inside the

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2374 0022-3077/05 $8.00 Copyright © 2005 The American Physiological Society www.jn.org

First published January 5, 2005; doi:10.1152/jn.00811.2004.
blind spot. Furthermore, this response change could not be explained by contextual modulation by a stimulus outside the receptive field. These results indicate that there are neurons in V1 whose responses correlate with the perceptual completion of a bar at the blind spot. A brief report of this experiment appeared in abstract form elsewhere (Matsumoto and Komatsu 2003).

METHODS

Human psychophysics

We quantified the perceived lengths of bars presented on the blind spot in four human subjects. The subjects sat facing a computer display (DEC VRX1-W3; 800 × 600 pixels; subtending 40 × 30°; 55 cm from the subjects’ eyes; 142 frames/s). Before the start of the experiment, each subject’s blind spot was mapped onto the computer display under monocular viewing conditions. A small spot [size, 0.25 × 0.25°; color, black (0.3 cd/m²); background, gray (9.5 cd/m²)] was randomly presented at positions that were expected to be in or around the blind spot such that each position was tested three times. Positions for which the small spot was not seen on two or more of the three trials were regarded as within the blind spot.

To measure perceived bar length, a visual stimulus consisting of a test bar and a reference bar (white, 71.8 cd/m²) was monocularly presented on a gray background (9.5 cd/m²) during fixation. A schematic illustration of these bar stimuli can be seen in Fig. 2A. The test bars were very similar to the bars used for the length-tuning test of V1 neurons. The reference bars were presented outside the blind spot and were parallel to the test bars. The subjects reported whether the test bar appeared longer or shorter than the reference bar by pressing keys. The orientations of the bars were either vertical, horizontal, or diagonal. We used six different test bar lengths for each subject, ranging from 3 to 3.5° for the shortest bars and from 13 to 17° for the longest bars. For each test bar length, the reference bar length varied between ±2° of the test bar length, and the test and reference bar lengths were varied randomly from one trial to the next. The position of the reference bar was randomly jittered (±1.25°) along its axis on each trial, so that the subjects’ judgment would be based on length and not on position. A red-filled ellipse that was 2.5–3.5° smaller than the size of the blind spot was presented inside the blind spot (Fig. 2A, black ellipse). When the subjects properly maintained

FIG. 1. Schematic illustration of the bar stimulus set used for the length-tuning experiment, resultant retinal input, and percept. A: examples of bar stimuli. Gray ellipse and dashed circle indicate the blind spot (BS) and receptive field (RF), respectively. One end of the bar was always fixed at the same position outside the BS, and bar length was varied by changing the position of the opposite end of the bar. B: retinal input of each bar stimulus when it was observed during BS eye (BE)-viewing. There was no retinal input within the BS. C: percept of each bar stimulus when it was observed during BE-viewing. In b and c, the bar appears to be truncated at the boundary of the BS, whereas in d, the bar is perceptually complete.

FIG. 2. Perceived lengths of bars presented on the BS in a human subject. A: schematic illustration of stimulus. Orientations of the test and reference bars were diagonal in this case. Distance between the upper border of the BS and the fixed end of the test bar was 5°. Gray ellipse represents the BS. Black ellipse represents a filled red ellipse presented within the BS to detect the occurrence of eye movement. B: percentage of trials in which the reference bar was seen as longer than the test bar during BE- (top) and non-BS eye (NE)-viewing (bottom) is plotted against the reference bar length. Each symbol represents the length of the test bar shown at the bottom of this figure. Smooth curves are cumulative normal fits of the data. C: perceived test bar length during BE- (top) and NE-viewing (bottom) is plotted against actual test bar length. Gray box in the top row and dashed box in the bottom row indicate extent of the BS during BE-viewing and region corresponding to the BS during NE-viewing. Diagonal line indicates where perceived and actual lengths are the same.
fixation, the red ellipse disappeared. If the red ellipse was visible, the trial was terminated.

Normal cumulative distribution functions (sigmoidal curves) were fit to human psychophysical data (Fig. 2B) using a nonlinear fitting function in MATLAB (Mathworks).

Electrophysiological experiments in the monkey

BEHAVIORAL TASK. Two macaque monkeys (Macaca fuscata) were used for 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 and were approved by the animal experiment committee of the Okazaki National Research Institutes.

A simple visual fixation task was employed throughout this study. During the experiments, the monkeys sat in a primate chair and faced a computer display (Sony GDM-F500R; 800 × 600 pixels; subtending 40 ° × 30 °; 56 cm from the monkeys’ eyes; 142 frames/s). Each monkey was trained to perform a fixation task either monocularly or binocularly. A trial started when a small fixation spot appeared on the screen (gray background, 9.4 cd/m²). The monkeys were required to look at the fixation spot within 500 ms and to maintain fixation within an electronic window (monkey KM, ±0.75 ° × 0.75 ° to ±0.9 ° × 0.9 °; monkey KS, ±0.6 ° × 0.6 °) around the fixation spot for the remainder of the trial. During fixation, a visual stimulus was presented for 500 or 1,000 ms. The task was controlled by a computer, and visual stimuli were generated using a graphics board (VSG2/3, Cambridge Research) in the same computer. Eye position was monitored using the magnetic search coil technique (Robinson 1963). If the monkey kept its gaze within the electronic window until the end of the trial, it was given a drop of water as a reward; otherwise the trial was terminated without reward. Trials were separated by 2–5 intertrial intervals.

SURGERY AND RECORDING. A stainless steel recording chamber and a head holder were fixed to the skull of each monkey under general anesthesia and sterile surgical conditions. Two search coils were also surgically placed under the conjunctiva of each eye and were connected to plugs on the top of the skull. The recording chamber, the head holder, and the eye coil plugs were all embedded in acrylic that covered the top of the skull and was connected to the skull by implanted bolts.

After surgery, the monkeys were allowed to recover for at least 1 wk, and then the location of the blind spot of each eye was determined using a monocular visual saccade task as described in previous reports (Komatsu and Murakami 1994; Komatsu et al. 2000). The locations and extents of the blind spots were similar in the two monkeys; they were located approximately along the horizontal meridian about 17 ° from the fixation spot and extended about 5 ° horizontally and 7 ° vertically.

The recording chamber was placed over the occipital cortex. A glass-coated Elgiloy microelectrode or varnish-coated stainless microelectrode (Frederick Haer) was advanced using a hydraulic microdrive (Narishige). Extracellular action potentials were amplified, and the waveforms were recorded on a computer at a sampling rate of 25 kHz. During the recording, the action potential was monitored using an oscilloscope and audio monitor. Single spikes were discriminated by off-line analysis.

Single neurons were recorded from within and around the retinotopic representation of the blind spot in V1 of three hemispheres of two monkeys. We identified this region by systematic receptive field mapping. Because receptive field positions change in a regular manner along the cortex, we were able to precisely determine the retinotopic representation of the blind spot within V1 (Komatsu et al. 2000). With regard to the recording layer, we considered the region with high ongoing activity to be layer 4, the region shallower than layer 4 to be layer 2/3, and the region deeper than layer 4 to be layer 5/6 (Poggio et al. 1977; Snodderly and Gur 1995).

When only the eye contralateral to the recorded hemisphere was open, the blind spot formed in the examined visual hemifield because the optic disk is located within the nasal hemiretina of each eye. For simplicity, the contralateral eye will be referred to as the blind-spot eye (BE), and the ipsilateral eye will be referred to as the non–blind-spot eye (NE). The viewing condition in which only the BE is open will be called BE-viewing. When the NE is open, no blind spot is formed in the examined visual hemifield, and the retinotopic representation of the blind spot in V1 can receive retinal input. This viewing condition will be called NE-viewing. To test neural responses during monocular viewing, one of the eyes was randomly occluded by an opaque mask driven by air pressure.

Visual stimuli

STIMULI FOR RECEPTIVE FIELD MAPPING. Once the spike of a neuron was isolated, the receptive field was mapped using a small stationary spot or bar stimulus with optimal orientation [size, 0.25–2.5 deg²; color, usually black (0.2 cd/m²) or white (72.1 cd/m²)], but occasionally with the preferred color of a given color-selective neuron (9.2–45.5 cd/m²²) presented at various locations during binocular viewing. The boundary of the receptive field was determined as the location where no response was detected by the on-line peristimulus time histogram (PSTH) and audio monitor.

STIMULI FOR THE LENGTH-TUNING TEST. The length-tuning test was the main experiment carried out in this study. In this test, we measured the length-tuning of V1 neurons during BE- and NE-viewing using sets of bar stimuli of various length. A schematic illustration of the bar stimulus can be seen in Fig. 1A together with a typical example of the spatial relationships between the receptive field, blind spot, and bar stimuli. For each stimulus, one end of the bar was fixed at a position outside the blind spot, and the position of the other end was varied. Thus short bars were situated entirely outside the blind spot but partially stimulated the receptive field (Fig. 1Aa); middle-sized bars had one end located within the blind spot (Fig. 1A, b and c); and long bars had ends located on opposite sides of the blind spot, with the bar crossing over the blind spot (Fig. 1Ad). We tested 8–11 different bar lengths with each neuron. Bar length was varied randomly from one trial to the next.

Figure 1B shows the retinal input of each bar stimulus shown in Fig. 1A when the stimuli are observed during BE-viewing. As the bar was gradually elongated, the retinal input and the amount of the stimulation of the receptive field gradually increased for as long as both ends of the bar were outside the blind spot (Fig. 1Ba). However, when the bar was elongated to the point that one end entered the blind spot, the retinal input was truncated at the boundary of the blind spot, and the amount of the stimulation of the receptive field no longer increased, even though the receptive field extended within the blind spot (Fig. 1B, b and c). This situation lasted for as long as the end remained within the blind spot. Finally, when the bar was elongated enough that the end emerged slightly on the other side of the blind spot, it generated a small amount of additional retinal input at the opposite side of the blind spot (Fig. 1Bd). For neurons that had receptive fields extending out from only one side of the blind spot (like the one in Fig. 1A), this additional retinal input was generated outside the receptive field and should not drive the neuron’s activity.

Figure 1C shows the percept of each bar stimulus shown in Fig. 1A when the stimuli were observed by human subjects during BE-viewing. When one end of the bar was inside the blind spot, the bar appeared to be truncated at the boundary of the blind spot, and a similar bar length was perceived even though the actual bar length increased (Fig. 1C, b and c). When the end emerged on the other side of the blind spot, the complete bar was perceived as a result of the perceptual completion, and the perceived bar length suddenly increased (Fig. 1Cd).
In the length-tuning test, we mainly focused on the comparison between the responses to bar stimuli whose far end was inside the blind spot (Fig. 1A, b and c) and those to bar stimuli whose far end emerged slightly out of the blind spot (Fig. 1A,d). Between these two conditions, physical stimulation (i.e., retinal input) of the receptive field by the bar stimuli remained the same or increased only slightly, but the perceived bar length appearing on the receptive field increased dramatically. Therefore if the neural responses changed significantly between these two conditions, we can presume that the response change was due to the change in the perceived bar length.

The bar stimuli were either solid [usually black (0.2 cd/m²) or white (72.1 cd/m²), occasionally with a preferred color (9.2–45.5 cd/m²)] or filled with a sine-wave grating moving in a direction perpendicular to the long axis of the bar [usually an achromatic grating (mean luminance = 36.2 cd/m², contrast = 99%); occasionally a grating with the preferred color with luminance modulation (mean luminance = 4.7–9.8 cd/m², contrast = 96–98%); spatial frequency, 0.5–1.0 cycles/°; temporal frequency, 2.15 cycles/s]. The orientation of the bar was determined so that the bar passed through the blind spot as well as the center of the receptive field; this differed from one neuron to another. At the chosen orientation, the bar stimulus evoked clear responses, although the orientation did not necessarily coincide with the optimal orientation of the recorded neurons.

STIMULI TO TEST FOR CONTEXTUAL MODULATION OF NEURAL RESPONSE. A third class of stimulus was used to control for the possible effects of contextual modulation. With long bars that induce perceptual completion (Figs. 1A,d and 6A,a), different parts of the bar stimulate separate parts of the visual field on opposite sides of the blind spot. As schematically shown in Fig. 6B, bar segment b is presented on the receptive field, whereas bar segment c is presented remote from segment b and outside the receptive field. This stimulus configuration is similar to one in which contextual modulation of neural responses occurs in V1 (Kapadia et al. 1995). To test whether response changes accompanying the perceptual completion in length-tuning tests can be explained by contextual modulation, we recorded neural responses using another set of four stimuli. In two of these, a single bar segment was presented either on the receptive field (Fig. 6Bb) or on the opposite side of the blind spot (c). In the third stimulus, the two segments were presented simultaneously. The remaining fourth stimulus was a complete bar presented across the blind spot. We examined the responses elicited by this stimulus set during both NE- and BE-viewing (Fig. 6, C and D, bottom, insets b, c, bc, and a). The interiors and orientations of the bar segments were the same as those used for the length-tuning test. The length of all bar segments sticking out of the blind spot was 3° during BE-viewing. Those inside the blind spot were 1.25° in length to make sure that one end of each bar segment was kept inside the blind spot despite small fluctuations in eye position during fixation. During NE-viewing, the length of each bar segment was 3°, and one end was positioned at the boundary of the region corresponding to the blind spot. It should be noted that, for either stimulus type, the extent of the retinal stimulation was the same during BE- and NE-viewing.

Data analysis

The visual response to a stimulus was defined as the discharge rate during stimulus presentation minus the background discharge rate recorded before the stimulus onset (300-0 ms).

In the length-tuning test, we examined whether the neural response changed at the length where the bar extended beyond the boundary of the blind spot and perceptual completion should occur. To do this, we compared the response to the shortest bar that exceeded the boundary of the blind spot (Fig. 1A,d) and the responses to bars that had one end inside the blind spot (Fig. 1A, b and c). We tested the statistical significance of any response change using Wilcoxon test. In addition, to examine whether the response change at the length where perceptual completion should occur could potentially be explained by stimulation of a classical receptive field (CRF) that extended to the opposite side of the blind spot, we examined the response to a bar presented alone at the opposite side of the blind spot (Fig. 3D) and evaluated the statistical significance of the difference between the linear prediction and the actual response. The linear prediction was computed as the sum of the response to the bar presented at the opposite side of the blind spot and the mean of the responses to the bars that had one end inside the blind spot (Fig. 3C, a). The actual response was computed as the height of the regression line calculated from the responses to the bars that extended beyond the boundary of the blind spot (Fig. 3C, thick dashed line) and at the corresponding length.

We tested the statistical significance of the difference between the linear prediction and the actual response using a bootstrap analysis (Efron and Tibshirani 1993). For each neuron, trials from each bar length were randomly resampled with replacements to form new bootstrap samples. This was repeated to produce a total of 1,000 bootstrap samples, each of which had the same number of trials as the original data set. For each bootstrap sample, the linear prediction of the summed response and the height of the regression line were calculated and compared. If the linear prediction was smaller than the height of the regression line in >950 bootstrap samples, it was deemed that the linear prediction of the summed response was significantly smaller than the actual response.

For each neuron, we calculated a suppression index and an ocular dominance index from responses to the stimuli in the length-tuning test and calculated an orientation index from responses to a set of bar stimuli with eight orientations during binocular viewing. The suppression index was defined as (R_MAX − R_MIN)/R_MAX, where R_MAX was the maximum response during NE-viewing, and R_MIN was the response to the longest bar during NE-viewing. The ocular dominance index was defined as (R_NE − R_BE)/(R_NE + R_BE), where R_NE was the response to the longest bar during NE-viewing, and R_BE was the response to the longest bar during BE-viewing. The orientation index was defined as (R_MAX − R_MIN)/(R_MAX + R_MIN), where R_MAX was the maximum response to the set of orientations, and R_MIN was the minimum response.

RESULTS

Perceived lengths of bars presented on the blind spot in human subjects

Figure 2 shows the result obtained from one subject when we examined the perceived lengths of bars presented on the blind spot during human psychophysical experiments. The subject compared the length of a test bar with that of a reference bar (Fig. 2A) during BE- and NE-viewing. The percentage of trials in which the reference bar was seen to be longer than the test bar is plotted against the length of the reference bar in Fig. 2B. Each symbol represents a different test bar length. The smooth curves are cumulative normal fits of the data. The perceived length of a given test bar was determined as the reference bar length at which the curve crossed fifty percent. Figure 2C shows the relationship between the perceived length of the test bar and its actual length. During BE-viewing (top), when one end of the test bar entered the blind spot (test bar length = 6.5, 8.6, and 10.6°), the perceived length remained constant at around 5°, as if the bar was truncated at the border of the blind spot, until the end emerged on the other side. When the end emerged (13.6°), perceptual completion occurred, and the perceived length suddenly increased substantially, even though the amount of retinal stimulation increased only slightly. During NE-viewing (bottom),
in contrast, the perceived length paralleled the actual length at all times, so that it gradually increased without abrupt changes.

The results were very similar in the three other subjects and were essentially the same across the vertical, horizontal, and diagonal test bar orientations.

**Neural responses to the long bar across the blind spot**

We recorded from 426 single neurons (layer 2/3, 78; layer 4, 14; layer 5/6, 321; unknown, 13) around the retinotopic representation of the blind spot in V1 of three hemispheres of two monkeys. Of the neurons recorded, 396 (layer 2/3, 74; layer 4, 9; layer 5/6, 300; unknown, 13) had receptive fields that partially or entirely overlapped the blind spot. Of these, 115 (layer 2/3, 15; layer 4, 0; layer 5/6, 98; unknown, 2) were driven by a bar across the blind spot during both BE- and NE-viewing. A neuron was regarded as responsive to the bar if the activity during stimulus presentation was significantly different from the background discharge (t-test, \( P < 0.05 \)) and if at least one of the following two criteria were met: the magnitude of the visual response computed from the mean discharge rate during stimulus presentation was >10 spikes/s or the magnitude of the peak response was >50 spikes/s. The proportion of cells responsive to a long bar across the blind spot was significantly larger among cells recorded from deep layers (98/300 = 32.7%) than among those recorded from superficial layers (15/74 = 20.3%; \( \chi^2 \) test, \( P < 0.05 \)), which is consistent with the results of our earlier study (Komatsu et al. 2000).

We were able to complete length-tuning tests with both eyes in 52 (layer 2/3, 5; layer 4, 0; layer 5/6, 46; unknown, 1) of the 115 neurons, and these 52 neurons comprised the sample used for this analysis. On average, the responses of these neurons to a long bar across the blind spot were significantly larger during NE-viewing [49.9 ± 40.6 (SD) spikes/s] than those during BE-viewing [28.9 ± 20.6 spikes/s; Wilcoxon test, \( P < 0.01 \)]. This should reflect the fact that the retinotopic representation of the blind spot in V1 is basically a monocular region receiving retinal input predominantly from the NE. The stronger response during NE-viewing is consistent with the results of our earlier study examining the responses to a large surface stimulus covering the blind spot (Komatsu et al. 2000).

All 52 neurons had receptive fields that extended out of the blind spot, which is also consistent with the results of our earlier study. The eccentricity of the receptive field center ranged between 13.0 and 19.0° horizontally and between −4.0 and 4.0° vertically. The size of the receptive fields (average of the horizontal and vertical extents) ranged from 1.3 to 12.0° (mean, 5.6°).

**FIG. 3.** Responses of a representative neuron (neuron 1) in the length-tuning test. A: positions of the BS of the left eye of monkey KM (gray ellipse), receptive field of neuron 1 (dashed circle), and a representative bar stimulus. Right end of the bar was always fixed at the same position; left end was elongated in the direction of the arrow. Receptive field was determined under binocular viewing conditions. B: responses to bar stimuli of various length during BE- (top) and NE-viewing (bottom) are shown as peristimulus time histograms (PSTHs), which are aligned at the onset of stimulus. Bar lengths are indicated below the PSTHs. Periods of stimulus presentation (500 ms) are indicated by thick horizontal lines below the PSTHs. PSTHs inside the gray and open boxes represent responses to bars that had 1 end inside the BS (BE-viewing) or the corresponding region (NE-viewing). PSTHs to the right and outside the gray box represent responses to bars that extended beyond the boundary of the BS and induced perceptual completion. C: length-tuning for responses shown in B; abscissa indicates bar length, and ordinate indicates response magnitude. •, responses obtained during BE-viewing; ○, during NE-viewing. Error bars indicate SD. Gray and dashed boxes indicate extents of the BS and receptive field, respectively. Thick horizontal line inside the BS is the mean of responses to 4 bars that had 1 end inside the BS during BE-viewing. Thick dashed line is the linear regression line calculated from responses to the 3 bars that extended beyond the boundary of the BS during BE-viewing. A, sum of the mean of responses to 4 bars that had 1 end inside the blind spot during BE-viewing and response shown in C. D: response to a bar segment presented at the opposite side of the BS during BE-viewing. Downward arrows indicate data points used to classify neurons into different groups described later. D: response to a bar segment presented at the opposite side of the BS during BE-viewing. Length of the bar segment extending out from the BS was 3°; that inside the blind spot was 1.25°. This bar segment was a part of a longer bar (dotted-line bar) used in the length-tuning test. There was no significant response to the bar segment (t-test, \( P > 0.10 \)).
Length-tuning at the retinotopic representation of the blind spot in V1

We recorded the responses to the stimulus set and analyzed the length-tuning during BE- and NE-viewing to determine whether V1 neurons would show a change in response at the stimulus length where perceptual completion should occur. Figure 3 shows an example of a single neuron (neuron 1) that exhibited such a change in response. The receptive field of this neuron is shown in Fig. 3A. For this neuron, one end of each bar stimulus was fixed 3° from the receptive field, and the position of the other end was varied among 10 different positions. The response to each bar length recorded during BE-viewing is shown as a PSTH in the top row of Fig. 3B, and length-tuning is shown as solid circles on a black line in Fig. 3C. As the bar was elongated, the response began to increase when the bar entered the receptive field (Fig. 3C, broken-line box). The response stayed roughly constant as long as one end of the bar was inside the blind spot (Fig. 3C, gray box). When the end of the bar emerged on the other side of the blind spot, however, the response suddenly increased and stayed roughly constant thereafter.

We examined the statistical significance of this change in neuronal activity by comparing the response to the shortest bar that exceeded the boundary of the blind spot (bar length = 10°) and the responses to the four other bars (5.0–8.0°) that had one end inside the blind spot. The mean of the responses to these four bars is represented by a thick solid horizontal line inside the blind spot in Fig. 3C; it should be noted that the retinal inputs of these four bars were the same. The first bar, which exceeded the boundary of the blind spot, should cause completion, but the other four bars should not. We found that the response to the first bar was significantly larger than to any of the latter four bars, as well as to the mean response to the four bars (Wilcoxon test, \( P < 0.01 \)), indicating that there was a substantial change in the response of neuron 1 when perceptual completion should have occurred.

We next examined whether the observed increase in neuronal activity was caused by stimulation of a large CRF that might extend to the opposite side of the blind spot. To test this possibility, the response to a bar presented alone at the opposite side of the blind spot (Fig. 3D, solid bar) was examined. With this stimulus, the length of the bar segment outside the blind spot was 3°; that inside the blind spot was 1.25°. This bar was the segment of the long bars that induced perceptual completion (Fig. 3D, dotted-line bar). As can be seen in the PSTH, no significant response was generated by this bar segment (\( t \)-test, \( P > 0.10 \)). The filled triangle in Fig. 3C represents the sum of the response to the bar segment and the mean of the responses to the four bars that had one end inside the blind spot. The triangle is plotted at the horizontal position that corresponds to the position of the end of the bar segment relative to the boundary of the blind spot. That the height of the triangle is significantly lower than the height of the regression line (Fig. 3C, thick dashed line), calculated from the responses to three bars that extended beyond the boundary of the blind spot and induced perceptual completion (bootstrap analysis, \( P < 0.01 \)), means that the increase in the response to the bar that induces completion was much larger than would be expected from the response to the bar shown in Fig. 3D. Thus the increase in neuronal activity seen at the length where perceptual completion should occur cannot be explained simply by the stimulation of a CRF extending to the opposite side of the blind spot.

During NE-viewing (PSTHs in the bottom row of Fig. 3B and ○ in Fig. 3C), the response of neuron 1 increased as the bar was elongated. However, at the length where completion should occur during BE-viewing, there was no increase in activity; indeed the response even declined slightly. The response to the shortest bar (10.0°) that exceeded the region in the visual field corresponding to the blind spot was not significantly different from the response to the longest bar (8.0°) that did not exceed that region (Wilcoxon test, \( P > 0.10 \)). Thus there was no specific structure in the receptive field that would cause the large increase in the response to a bar at the region corresponding to the boundary of the blind spot.

To evaluate the changes in neuronal activity elicited at the bar length where completion should occur, we calculated the difference between the neuronal responses to the shortest bar that exceeded the boundary of the blind spot and the mean of the responses to bars that had one end inside the blind spot during BE-viewing. Of the 52 neurons studied, 14 exhibited significant increases in activity (Wilcoxon test, \( P < 0.05 \)), and 1 exhibited a significant decrease. All of the 15 neurons that exhibited a significant change in activity were located in layer 5/6. In the following, we will analyze the nature of the observed response change in detail and determine whether they are related to perceptual completion.

Comparison between BE-viewing and NE-viewing

As mentioned above, we analyzed only neurons whose receptive field overlapped the blind spot. Thirty-four of these neurons had receptive fields that did not extend to the opposite side of the blind spot. We confirmed this by receptive field mapping (see METHODS) as well as the lack of a response to a bar segment presented at the opposite side of the blind spot (like the one in Fig. 3D). The remaining 18 neurons had receptive fields that extended to the opposite side of the blind spot. Among the aforementioned 34 neurons, 7 showed a significant difference between their response to the shortest bar that exceeded the boundary of the blind spot and the mean of the responses to bars that had one end inside the blind spot during BE-viewing. Of the 52 neurons studied, 14 exhibited significant increases in activity (Wilcoxon test, \( P < 0.05 \)), and 1 exhibited a significant decrease. All of the 15 neurons that exhibited a significant change in activity were located in layer 5/6. In the following, we will describe our analysis of the 34 neurons for which we can neglect the effect of receptive field stimulation on the response change at the length where completion should occur. We will then consider the responses of the remaining 18 neurons.

The results described so far indicate that there are neurons in V1 that exhibit a significant increase in activity when a bar appears to extend across the blind spot during BE-viewing. We first examined the changes in neuronal activity that occur during NE-viewing, in which perceived bar length parallels the physical bar length and compared the responses obtained during BE- and NE-viewing. In NE-viewing, we determined the response change as the difference between the response to the shortest bar that exceeded the region corresponding to the blind spot (Fig. 3C, solid arrow) and the response at the boundary of this region within the receptive field (open arrow), which was calculated by linearly interpolating a pair of responses sandwiching the boundary. These two bar lengths were
chosen so that the change in the perceived bar length between these two lengths during NE-viewing would be comparable to that during BE-viewing, in which the response change at the occurrence of completion was measured.

We classified the 34 neurons into three groups according to the above-mentioned comparison in NE-viewing: One group of neurons exhibited a significant increase in activity (Wilcoxon test, \(P < 0.05\)) after the bar stimulus crossed the region corresponding to the blind spot (e.g., neuron 1); these neurons will be referred to as the “increase group.” The second group exhibited no significant changes in activity (Wilcoxon test, \(P > 0.05\)); these neurons will be referred to as the “constant group.” The third group exhibited a significant reduction in activity (Wilcoxon test, \(P < 0.05\)); these neurons will be referred to as the “decrease group.” We can summarize the relationship between the stimulus and the response during NE-viewing as follows: increase (decrease) group neurons exhibited a response increase (decrease) when the bar appeared on the part of the receptive field within the region corresponding to the blind spot, whereas the constant group neurons exhibited no significant response change. Figure 4 shows the responses of three representative neurons that were respectively classified into each group. Neuron 2 (Fig. 4A) was classified into the increase group, neuron 3 (Fig. 4B) into the constant group, and neuron 4 (Fig. 4C) into the decrease group. In all, 16 neurons were classified into the increase group, 6 into the constant group, and 12 into the decrease group.

As mentioned above, during BE-viewing, 7 of the 34 neurons exhibited a significant response increase when we calculated the change in activity at the length where completion should occur. When we examined how these seven neurons responded during NE-viewing and determined which of the three groups they belonged to, we found there to be a clear tendency: of the seven neurons, six were classified into the increase group and one into the constant group, which indicates that most neurons exhibiting a response increase at the length where completion should occur during BE-viewing also exhibited a response increase when the bar appeared on the region corresponding to the blind spot during NE-viewing. Thus these increase group neurons exhibited a response change that was consistent with respect to BE- and NE-viewing when the bar appeared to extend across the visual field corresponding to the blind spot.

To further compare the response changes observed during BE- and NE-viewing, we summarized the response changes obtained during BE-viewing for each of the increase, constant, and decrease group, which were defined based on the response during NE-viewing (Table 1). Of the 16 increase group neurons, 6 exhibited a significant response increase (e.g., neurons 1 and 2), but the remaining 10 did not exhibit a significant response change. Of the six constant group neurons, five did not exhibit a significant response change (e.g., neuron 3), but one exhibited a significant response increase. And none of the 12 decrease group neurons exhibited a significant response change (e.g., neuron 4). The top row of histograms in Fig. 5 shows the distribution of the response changes normalized by the maximum responses of each neuron. The filled bars represent neurons that showed a significant change in response (Wilcoxon test, \(P < 0.05\)). In the increase group (Fig. 5A), the mean of the distribution (inverted triangle) was 0.20, which was a significant deviation from zero in the positive direction (Wilcoxon test, \(P < 0.01\)). In the constant group (Fig. 5B), the mean was −0.04, which was not significantly different from zero (Wilcoxon test, \(P > 0.10\)). In the decrease group (Fig. 5C), the mean was −0.01, which was also not significantly different from zero (Wilcoxon test, \(P > 0.10\)). These results suggest that, as a population, only increase group neurons exhibited an increase in activity at the length where completion should occur during BE-viewing.

The results summarized above indicate that, during BE-viewing, when the perceived bar length jumps at the occur-
TABLE 1. Numbers of neurons with receptive fields that extend to only one side of the blind spot classified according to the pattern of their responses at the bar length where completion should occur during BE-viewing for each group

<table>
<thead>
<tr>
<th>Response Change</th>
<th>Increase</th>
<th>Decrease</th>
<th>No Change</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Increase group</td>
<td>6</td>
<td>0</td>
<td>10</td>
<td>16</td>
</tr>
<tr>
<td>Constant group</td>
<td>1</td>
<td>0</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>Decrease group</td>
<td>0</td>
<td>1</td>
<td>12</td>
<td>12</td>
</tr>
</tbody>
</table>

Shown are the numbers of neurons exhibiting a significant increase, significant decrease, or no significant change in activity at the bar length where completion should occur during BE-viewing (Wilcoxon test, P < 0.05). These neurons had receptive fields extending to only 1 side of the blind spot. The response changes are based on a comparison of the responses to the shortest bar that exceeded the boundary of the blind spot and those to bars that had 1 end inside the blind spot. BE, blind-spot eye.

ence of completion, the population response of the increase group neurons significantly increases. During NE-viewing, in contrast, the perceived bar length parallels the actual bar length and only gradually increases at the length where completion should occur during BE-viewing. We therefore examined whether or not the population responses of neurons exhibit a significant change at this length during NE-viewing. To test this, for the same neurons shown in the top row of Fig. 5, we calculated the difference between the response to the shortest bar that exceeded the boundary of the region corresponding to the blind spot and that to the longest bar still having one end inside this region during NE-viewing. The bottom row of histograms in Fig. 5 shows the distribution of the changes normalized by the maximum responses of each neuron. None of the three groups showed a significant shift from zero (Wilcoxon test, P > 0.10), which suggests that, during NE-viewing, the population responses of each group did not exhibit a change at the length where completion should occur during BE-viewing.

Tests for contextual modulation in increase group neurons

A number of studies have shown contextual modulation within V1. Moreover, in some of those studies (Kapadia et al. 1995; Polat et al. 1998), a bar segment presented outside the CRF was shown to enhance the response to a bar stimulus presented on the CRF. We therefore considered the possibility that the increase in neural activity described above may be explained by a similar scenario. For instance, when bar stimulus a (Fig. 6A) was presented across the blind spot during BE-viewing, retinal stimulation was actually as in Fig. 6B. Bar segment b was presented on the CRF (dashed line in B), and segment c remote from b was presented outside the CRF. Consequently, the presence of a bar segment c on the opposite side of the blind spot may have caused contextual modulation that enhanced the response to bar segment b in a manner unrelated to the occurrence of perceptual completion. If this was the case, increased neuronal activity resulting from contextual modulation should be observed not only during BE-viewing, but also during NE-viewing, in which perceptual completion does not occur.

To test this possibility, we recorded the responses of nine increase group neurons to another set of four stimuli (a, b, c, and bc in Fig. 6, C and D; see METHODS for details). The responses of these increase group neurons to each of the four stimuli, as well as the sum of the responses to stimuli b and c obtained during NE- (Fig. 6C) and BE-viewing (Fig. 6D), were compared. The insets at the bottom of each figure depict the stimuli, and the normalized responses to each stimulus are shown as the bars above each stimulus. During NE-viewing (Fig. 6C), the complete bar a generated the largest response. Bar segment b presented on the receptive field also generated a clear response, albeit a weak one, but bar segment c presented on the opposite side of the region corresponding to the blind spot did not generate a significant response (Wilcoxon test, P > 0.10). When the segments were presented simultaneously (bc), the response was not significantly different from the sum of the responses to each segment (b + c; Wilcoxon test, P >

FIG. 5. Distributions of normalized response changes at the length where completion should occur during BE-viewing (top) and at the corresponding length during NE-viewing (bottom) for each of the 3 groups (A and D, increase group, n = 16; B and E, constant group, n = 6; C and F, decrease group, n = 12). Ordinate indicates number of neurons. In the top row, abscissa indicates difference between the normalized response to the shortest bar that exceeded the boundary of the BS and the mean of the normalized responses to bars that had 1 end inside the BS. In the bottom row, abscissa is difference between the normalized response to the shortest bar that exceeded the boundary of the region corresponding to the BS and the normalized response to the longest bar that still had 1 end inside that region. Filled bars represent neurons that showed a significant change (Wilcoxon test, P < 0.05). Inverted triangles indicate mean of each distribution.
Thus the presence of c did not cause contextual modulation of the response to b. On the other hand, during BE-viewing (Fig. 6D), the response to bc was significantly larger than b + c (Wilcoxon test, \( P < 0.01 \)). The presence of bar segment c together with b caused perceptual completion during BE-viewing, but not during NE-viewing. Therefore the difference between BE- and NE-viewing seems to be determined by whether or not the bar is completed across the blind spot. To summarize, these results indicate that the response increase observed during BE-viewing is accompanied by the perceptual completion of the bar, and this response increase cannot be simply explained by contextual modulation due to the presence of the bar segment at the opposite side of the blind spot.

**Effect of stimulation of the receptive field on the response increase**

To eliminate the effect of stimulating the receptive field on the response increase in the analysis described above, only the 34 neurons whose receptive field extended to only one side of the blind spot were studied. However, because the other 18 neurons, whose receptive fields extended to both sides of the blind spot, may also be involved with perceptual completion, we examined their length-tunings.

Figure 7 shows a length-tuning for a representative neuron (neuron 5) with a receptive field extending to both sides of the blind spot (broken-line box). Like neurons 1 and 2, neuron 5, which was classified into the increase group, exhibited a significant response increase at the length where completion should occur during BE-viewing. In contrast with neurons 1 and 2, however, this neuron showed a small response when a bar segment similar to the one shown in Fig. 3D was presented at the opposite side of the blind spot during BE-viewing. So, as was done for neuron 1, we calculated the sum of the responses to this bar segment and the mean of the responses to the four bars that had one end inside the blind spot (△). That the height of the triangle was significantly lower than the dashed regression line calculated from the responses to the bars exceeding the blind spot (bootstrap analysis, \( P < 0.01 \)) indicates that stimulation of the receptive field extending out from the opposite side of the blind spot is not sufficient to explain the magnitude of the response increase at the length where completion should occur; in other words, the response increase is not predictable from a simple summation of responses over the receptive field.

Of the 18 neurons used in this analysis, 11 were classified into the increase group, 2 into the constant group, and 5 into the decrease group. The changes in the responses of these neurons at the length where completion should occur are summarized in Table 2. During BE-viewing, 6 of the 11 increase group neurons exhibited a significant response increase at the length where completion should occur, but the remaining 5 did not exhibit a significant change. For five of the six neurons that did show an increase, as with neuron 5, the heights of the triangles indicating the effect of stimulation of the receptive field were significantly lower than the regression lines calculated from the responses to bars inducing perceptual completion (bootstrap analysis, \( P < 0.05 \)). With regard to the other neuron groups, the two constant group neurons did not exhibit a significant response change, whereas two of the five decrease group neurons did exhibit a significant change, but there was no clear tendency: one exhibited a decrease, whereas one exhibited an increase. These results are essentially the same as those obtained from neurons having receptive fields that extended to...
were averaged in Fig. 8. During BE-viewing (Fig. 8 the 17 increase group neurons obtained using the above bar set responses were averaged across neurons. The length-tunings of to the maximum response for that neuron, after which the response of each neuron to each bar length was normalized such that the lengths at the shortest bars and from 13.8 to 24.7° for the longest bars. 5.5, 6.5, 7.5, 8.5, 9.5, 10.75, 13.25, 14.5, and 16.5, which was used. This enabled us to average responses across neurons; whose lengths were normalized according to a common rule group neurons studied. For these 17 neurons, a set of 10 bars increase group neurons, which is a subset of the 27 increase population, we computed the population length-tuning for 17 neurons. To examine this, we calculated a suppression index (METHODS) for each neuron and compared these indices among the groups. We found that the mean suppression index for the increase group (0.13 ± 0.12) was significantly smaller than that for either the constant group (0.24 ± 0.15; Wilcoxon test, $P < 0.05$) or the decrease group (0.52 ± 0.21; Wilcoxon test, $P < 0.01$). This indicates that, as a population, increase group neurons responded more strongly to longer bars than the neurons in the other groups. We also examined whether several other response properties also differ across the three groups; we examined the orientation index, the receptive field size, and the difference between the optimal orientations of the recorded neurons and the orientation of the bar stimuli used for length-tuning test. None of these properties significantly differed across the three groups, however. With regard to the simple/complex cell classes, we were able to classify 18 of the 52 neurons tested using drifting grating stimuli. According to the conventional criterion (F1/F0 ratio $>1$ or $<1$) (De Valois et al. 1982), all 18 neurons were classified as complex cells. This contradicts the idea that the distinction among the three groups in the present study corresponds in some way to simple/complex cell classes. To summarize, these results suggest that our classification of the neurons reflects their length-tuning properties but none of the other response properties that we examined, and that the neurons more sensitive to long bars exhibited a response change at the length where completion should occur. Among the increase group neurons, 12 exhibited a significant response increase at the length where completion should occur during BE-viewing.

Population length-tuning of the increase group neurons

To understand how increase group neurons behave as a population, we computed the population length-tuning for 17 increase group neurons, which is a subset of the 27 increase group neurons studied. For these 17 neurons, a set of 10 bars whose lengths were normalized according to a common rule was used. This enabled us to average responses across neurons; the length of each bar was normalized such that the lengths at the boundaries on either side of the blind spot became 7 and 12, respectively. Applying this rule, the lengths of the bars were 4, 5.5, 6.5, 7.5, 8.5, 9.5, 10.75, 13.25, 14.5, and 16.5, which corresponded to actual bar lengths ranging from 3.4 to 6.0° for the shortest bars and from 13.8 to 24.7° for the longest bars. The response of each neuron to each bar length was normalized to the maximum response for that neuron, after which the responses were averaged across neurons. The length-tunings of the 17 increase group neurons obtained using the above bar set were averaged in Fig. 8. During BE-viewing (Fig. 8A), the population responses showed an increase at the length where completion should occur, and this increase was significant according to the same criteria used for individual neurons. Although a small response was elicited by bars presented at the opposite side of the blind spot, simple spatial summation cannot explain the magnitude of the response increase, as can be seen from the position of the triangle, which was significantly lower than the dashed regression line calculated from the responses to bars inducing perceptual completion (Wilcoxon test, $P < 0.01$). That this regression line had a positive slope indicates that, as a population, length summation occurred at the opposite side of the blind spot, and that the longer bar stimuli generated stronger responses.

During NE-viewing (Fig. 8B), in contrast, there was no summation of the response at the length where completion should occur during BE-viewing.

Response properties of recorded neurons

That only increase group neurons exhibited a response change (increase) at the length where completion should occur during BE-viewing. During NE-viewing (Fig. 8A), the population responses showed an increase at the length where completion should occur, and this increase was significant according to the same criteria used for individual neurons. Although a small response was elicited by bars presented at the opposite side of the blind spot, simple spatial summation cannot explain the magnitude of the response increase, as can be seen from the position of the triangle, which was significantly lower than the dashed regression line calculated from the responses to bars inducing perceptual completion (Wilcoxon test, $P < 0.01$). That this regression line had a positive slope indicates that, as a population, length summation occurred at the opposite side of the blind spot, and that the longer bar stimuli generated stronger responses.

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Response properties of recorded neurons

That only increase group neurons exhibited a response change (increase) at the length where completion should occur during BE-viewing. During NE-viewing (Fig. 8A), the population responses showed an increase at the length where completion should occur, and this increase was significant according to the same criteria used for individual neurons. Although a small response was elicited by bars presented at the opposite side of the blind spot, simple spatial summation cannot explain the magnitude of the response increase, as can be seen from the position of the triangle, which was significantly lower than the dashed regression line calculated from the responses to bars inducing perceptual completion (Wilcoxon test, $P < 0.01$). That this regression line had a positive slope indicates that, as a population, length summation occurred at the opposite side of the blind spot, and that the longer bar stimuli generated stronger responses.

During NE-viewing (Fig. 8B), in contrast, there was no summation of the response at the length where completion should occur during BE-viewing.

### Table 2. Numbers of neurons with receptive fields that extend to both sides of the blind spot classified according to the patterns of their responses at the bar length where completion should occur during BE-viewing for each group

<table>
<thead>
<tr>
<th>Response Change</th>
<th>Increase</th>
<th>Decrease</th>
<th>No Change</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Increase group</td>
<td>6</td>
<td>0</td>
<td>5</td>
<td>11</td>
</tr>
<tr>
<td>Constant group</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Decrease group</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>5</td>
</tr>
</tbody>
</table>

Shown are the numbers of neurons exhibiting a significant increase, significant decrease, or no significant change in activity at the bar length where completion should occur during BE-viewing (Wilcoxon test, $P < 0.05$). These neurons had receptive fields extending to both sides of the blind spot. Conventions are the same as in Table 1.

Only one side of the blind spot (Fig. 5, top). That is, as a population, only increase group neurons exhibited increased activity at the stimulus length where completion should occur during BE-viewing.

FIG. 8. Population length-tuning for 17 increase group neurons during BE- (A) and NE-viewing (B). Ordinate indicates normalized response; abscissa indicates normalized length. Gray box in A and open box in B indicate extent of the BS during BE-viewing and the region corresponding to the BS during NE-viewing, respectively. Error bars indicate SE. Filled triangle in A indicates sum of the mean response to 4 bars that had 1 end inside the BS and response to a bar segment outside the blind spot.

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occurred, but the remaining 15 did not. To determine whether particular response properties could be used to distinguish the former from the latter, we examined whether there is a correlation between the magnitudes of the response changes at the length where completion should occur and the suppression index, the ocular dominance index, the orientation index, the receptive field size, and the difference between the optimal orientation of the recorded neuron and the orientation of the bar stimulus used for length-tuning test. However, we found no significant correlations ($P > 0.05$) with any of these response properties. As mentioned above, with regard to the simple/complex cell classes, all increased group neurons were classified as complex cells regardless of whether or not they exhibited a significant response change at the length where completion should occur.

Another possible cause we may need to consider is saturation of the neural response. If the neural response to bars that had one end inside the blind spot was already saturated, the response could no longer increase at the length where completion should occur. To test this possibility, we examined whether there is a correlation among the increase group neurons between the magnitudes of the response increase at the length where completion should occur and the mean responses to bars that had one end inside the blind spot. When all 27 increase group neurons were considered, there was a significant negative correlation ($r = -0.407, P = 0.035$). When only the 16 increase group neurons whose receptive field did not extend to the opposite side of the blind spot were considered, there was also a weak negative correlation, although it was not significant ($r = -0.232, P = 0.39$). These results indicate that the larger the responses to bars that had one end inside the blind spot, the smaller the magnitudes of the response increases at the length where completion should occur. This suggests that one possible cause for the difference in the response change at the length where completion should occur among increase group neurons is the strength of the activation relative to the saturation level before the bar crossed the blind spot.

**Response latency**

Whereas visual signals are generated only at the retinal region surrounding the optic disk during BE-viewing, they are generated throughout the retinal image of the stimulus during NE-viewing. When visual signals are conveyed to V1 neurons whose receptive fields are mainly contained within the blind spot, extra steps may be required for BE-viewing, and this might cause the response latency during BE-viewing to be longer than during NE-viewing. To test this, we computed the latency of the response to the longest bar stimulus in 10 of the 12 increase group neurons that exhibited significant response increases at the length where completion should occur in the length-tuning experiment and compared the latency between BE- and NE-viewing; the remaining two neurons were excluded from the analysis because they exhibited anomalous response fluctuations around the first peak, which made determination of latency unreliable. To compute the latency, we first plotted the spike density profile ($\sigma = 10$ ms) for each neuron; the latency was defined as the time required for the resultant spike density profile to reach a set threshold (2 SD above the background discharge rate or 1 spike/s in the case of SD = 0). The latencies obtained during BE- and NE-viewing are plotted in Fig. 9A. On average, the latency was significantly longer during BE-viewing (mean latency, 48.0 ± 10.8 ms) than NE-viewing (mean latency, 36.1 ± 9.5 ms; Wilcoxon test, $P < 0.01$).

One possible cause of the longer latency during BE-viewing may be the comparatively weak driving force of the visual stimulation in BE-viewing; a weaker response tends to have a longer response latency. To control for this possibility, we compared the latencies of cells whose responses did not differ significantly between the two viewing conditions. In Fig. 9A, the filled circles indicate four neurons whose peak discharge rates were not significantly different under the two viewing conditions (Wilcoxon test, $P > 0.05$). However, the latencies...
of these neurons tended to be longer during BE-viewing (mean latency, 44.8 ± 7.5 ms) than NE-viewing (mean latency, 34.5 ± 5.1 ms). Figure 9B shows the average of the normalized spike density profiles of these four neurons during BE- (solid curve) and NE-viewing (dashed curve). We also found that the difference in the peak discharge rate between NE- and BE-viewing did not correlate with the difference in the response latency (r = 0.0454, P = 0.901). These results indicate that the longer latency during BE-viewing is not due to a weaker driving force of visual stimulation in BE-viewing. This result is consistent with our earlier study (Komatsu et al. 2000), in which the latency of the response to a surface stimulus covering the blind spot was longer during BE-viewing than during NE-viewing, and supports the idea that visual signals take a more indirect pathway during BE-viewing.

We then examined the time course of the response increase at the length where completion should occur during BE-viewing to determine whether the neural processes that generate the response increases require extra time. We compared the latency of the response to the longest bar that induces completion with that to shorter bars that had one end inside the blind spot and therefore do not induce completion. When response latency was computed for the same 10 increase-group neurons using the same procedures described above, we found that, on average, there was no significant difference in response latency between the longest bars (mean latency, 48.0 ± 10.8 ms) and the shorter bars (mean latency, 49.0 ± 10.7 ms; Wilcoxon test, P = 1.00). Figure 9C shows the average of the normalized spike density profiles of the 10 neurons elicited by the longest (solid curve) and shortest bars (dotted curve). The difference between the solid and dotted curve begins just after the onset of the visual response, indicating the early onset of the response increase at the length where completion should occur.

DISCUSSION

In this study, we used a bar stimulus set (Fig. 1A) to assess the length-tuning of V1 neurons to examine whether or not their activities correlate with percepts completed inside the blind spot. We found that during BE-viewing, some increase group neurons exhibited an increase in activity at the length where completion should occur. These response increases were consistent with those observed during NE-viewing; increase group neurons exhibited increased activity when, during NE-viewing, a bar appeared on a part of the receptive field within the region corresponding to the blind spot. In contrast, constant group and decrease group neurons exhibited neither increases nor decreases in activity at the length where completion should occur during BE-viewing. Increase group neurons also responded more strongly to longer bars than the other two groups of neurons. Because bars needed to be of a certain length to induce perceptual completion, neurons preferring longer bars may mainly correlate with completion. This could explain why only increase-group neurons exhibited response changes (increases) at the length where completion should occur during BE-viewing.

Controls

Several factors other than completion could explain the increased activity of increase group neurons at the length where completion should occur during BE-viewing. First, a CRF that extends to the opposite side of the blind spot could cause an increase in activity. However, in our analysis of neurons whose CRF did not extend to the opposite side of the blind spot, some increase group neurons nonetheless exhibited the increase in response. Furthermore, when we considered increase group neurons as a population, the response increases elicited by bars inducing completion were significantly larger than those attributable to the CRF. Thus the increase in activity cannot be simply explained by the stimulation of a CRF extending to the opposite side of the blind spot.

Second, the response increase could be caused by contextual modulation due to the presence of a collinear bar segment that is unrelated to completion. However, the control experiment summarized in Fig. 6 showed that the response enhancement did not occur during NE-viewing. These findings indicate that there is a tight link between the response increase seen in increase group neurons and the occurrence of perceptual completion.

Comparison with earlier studies

Our group previously reported that neurons in the retinotopic representation of the blind spot in V1 of awake monkeys were activated when the blind spot was covered by a surface stimulus (Komatsu et al. 2000). In that study, most of the neurons activated by a surface that induced filling-in had large receptive fields that extended out of the blind spot and were located within a deeper layer, which is consistent with the findings of this study. An important difference between this study and the earlier one is the stimulus used. By using a bar stimulus, we were able to more finely control the stimuli that did or did not induce perceptual completion. This enabled us to analyze the neural responses in relation to the percept caused by the stimulus in more detail.

Fiorani et al. (1992) previously reported that V1 neurons of Cebus monkeys whose receptive fields were wholly covered by the blind spot were activated by a bar across the blind spot. We did not find any such neurons; all neurons activated by a bar across the blind spot had receptive fields that extended beyond the blind spot. However, the result of the analysis summarized in Fig. 6D is similar to that of Fiorani et al., although they did not analyze responses elicited during NE-viewing. By examining length-tuning or contextual modulation during NE-viewing, when the perceived bar length parallels the physical bar length, we were able to make a more elaborate comparison between the neural response and the percept caused by perceptual completion. Our manipulation of the bar length showed that a small change in length can cause a large change in neuronal activity that is closely related to whether or not the stimulus caused perceptual completion. Fiorani et al. used long bars and large masks and emphasized the presence of a large integration field at the surround of the receptive fields of V1 neurons. In contrast, these results suggest that local mechanisms surrounding the blind spot are essential for producing a correlation between neural responses and percept.

Involvement of higher cortical areas in perceptual completion

In this study, we found that some increase group neurons in V1 exhibited a response increase at the length where comple-
tion should occur, but that their responses may not fully correspond to perception. For example, in Fig. 6, when we compared the population response of the increase group neurons to a complete bar (a) with the sum of population responses to b and c (b + c), the response increment during BE-viewing was smaller than during NE-viewing, indicating that the correlation between neural responses and perceptual completion is not totally achieved at the level of V1. This suggests that, in addition to V1, higher visual areas are also involved in perceptual completion. Furthermore, we used simple bar stimuli in this study, and perceptual completion or filling-in of more complex patterns also occurs at the blind spot (Kawabata 1983; Ramachandran 1992). Because such complex patterns are encoded at higher visual areas, it would be expected that they require greater involvement of higher visual areas for perceptual completion.

**Pathways of the signals for perceptual completion**

We will speculate on the possible neural mechanisms of perceptual completion based on the differences in the latencies of the visual responses across different conditions (Fig. 9), because they may provide a clue as to the underlying neural mechanisms. Figure 10 contains a simplified diagram of the neural circuits related to this study. A solid circle represents a neuron that exhibits increased activity at the length where completion should occur. This neuron receives retinal signals directly via the geniculostriate pathway (Fig. 10B, thick vertical arrow) during NE-viewing, but through some indirect pathway (Fig. 10A) during BE-viewing. The latencies of the responses to long bar stimuli were, on average, 11.9 ms longer during BE- than during NE-viewing. When we estimated the cortical distance between the location of the recorded neurons and the border of the V1 region representing the blind spot based on the center position of the receptive field of each neuron and the reported magnification factor of V1 (Van Essen et al. 1984), we obtained an average cortical distance of 0.69 mm. This means that to explain the 11.9-ms increase in the latency during BE-viewing, the extra pathway employed ought to have a very slow conduction velocity: 58 mm/s. Interestingly, this value is slower than, but not far from, estimates of the conduction velocity obtained in psychophysical experiments of brightness filling-in (Paradiso and Nakayama 1991) and Craik-O’Brien illusion (Davey et al. 1998).

On the other hand, when we compared the responses to long and short bars during BE-viewing, the modulatory signal that was the difference among these responses started to occur just after the onset of the visual response (Fig. 9C). This apparently contradicts the idea that cortical distances between the recorded cell and the boundaries on opposite sides of the blind spot differ; the distance is shorter for the receptive field side (mean = 0.69 mm) than the opposite side (mean = 1.55 mm). The signal-inducing response modulation is generated at the opposite side. If the modulatory signal is transmitted by a pathway similar to that inducing visual responses, the longer cortical distance from the opposite side to the recorded neuron, which was 0.86 mm (1.55 -0.69 mm), should cause considerable delay (>11.9 ms) in the occurrence of the response modulation compared with the onset of the visual response. This suggests that the modulatory signal from the more distant side takes a faster pathway than the above-mentioned visual signal.

The estimated velocity of the visual signal (58 mm/s) is within the range reported for intracortical horizontal propagation of activities within V1 (Tanifuji et al. 1994). On the other hand, both feedforward and feedback connections between visual cortical areas are very fast, on the order of 2–3 m/s (Girard et al. 2001). To reconcile our observation and the reported conduction velocities of signals in and around V1, we propose the following model. During BE-viewing, 1) visual signals from the bar segment presented on the receptive field are transmitted via slow horizontal connections within V1 (Fig. 10A, hn). It has been shown that such visual signals from a peripheral part of receptive field are transmitted via horizontal connections within V1 (Bolz and Gilbert 1989). 2) Modulatory signals from the opposite side of the blind spot are transmitted via fast feedforward (ff) and then feedback connections (fb) between V1 and V2. Modulatory signals from the opposite side may also be transmitted via horizontal connections (hf), but they will reach the recorded neuron later. The use of feedforward and feedback connections may serve not only fast propagation of modulatory signals but also completion of complex patterns. Although higher visual areas may play substantial roles in the perceptual completion of complex patterns, the use of feedback connections may involve V1 in the perceptual completion of such patterns. Presumably, signals about the global pattern fed back from higher visual areas to V1 can modulate local completion mechanisms in V1 by providing contextual information, and this may facilitate to achieve elaborate perceptual completion of complex patterns.

**ACKNOWLEDGMENTS**

We thank M. Ito, T. Ogawa, and N. Goda for comments on the manuscript, K. Koida for valuable discussion, and M. Togawa and N. Takahashi for technical assistance.

![Diagram of neural circuits related to this study](http://jn.physiology.org/)

**FIG. 10.** Simplified diagram of neural circuits related to this study. A: information flow during BE-viewing. Bottom: positions of the BS (gray ellipse), the receptive field (RF; line ellipse) of the recorded neuron, and the retinal image of the bar crossing the BS. Center of the RF is within the BS. Middle: primary visual cortex (V1), within which 3 neurons are shown as circles. ○, recorded neuron exhibiting an increase in activity at the length where completion should occur. Line box is the RF. ◯, V1 neurons located outside the retinotopic representation of the BS. Top: secondary visual cortex (V2) neuron. Thick arrows represent signals that can drive the activity of the postneuron. Thin arrows represent signals that cannot drive but can modulate the activity of the postneuron. hn and hf, horizontal connections within V1 that have a slow conduction velocity; ff and fb, feedforward and feedback connections between V1 and V2 that have a fast conduction velocity. B: information flow during NE-viewing. During NE-viewing, the recorded neuron can be activated directly via the geniculostriate pathway. hn, horizontal connection from near side; hf, horizontal connection from far side; ff, feedforward connection; fb, feedback connection.
GRANTS

This work is supported by “Biological Information Technology Grant for Top Priority Research and Development to be focused” from the Ministry of Public Management, Home Affairs, Posts and Telecommunications.

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