Receptive field focus of visual area V4 neurons determines responses to illusory surfaces

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Illusory figures demonstrate the visual system's ability to infer surfaces under conditions of fragmented sensory input. To investigate the role of midlevel visual area V4 in visual surface completion, we used multielectrode arrays to measure spiking responses to two types of visual stimuli: Kanizsa patterns that induce the perception of an illusory surface and physically similar control stimuli that do not. Neurons in V4 exhibited stronger and sometimes rhythmic spiking responses for the illusion-promoting configurations compared with controls. Moreover, this elevated response depended on the precise alignment of the neuron's peak visual field sensitivity (receptive field focus) with the illusory surface itself. Neurons whose receptive field focus was over adjacent inducing elements, less than 1.5° away, did not show response enhancement to the illusion. Neither receptive field sizes nor fixational eye movements could account for this effect, which was present in both single-unit signals and multiunit activity. These results suggest that the active perceptual completion of surfaces and shapes, which is a fundamental problem in natural visual experience, draws upon the selective enhancement of activity within a distinct subpopulation of neurons in cortical area V4.

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isual illusions are valuable stimuli for studying the neural basis of visual processing because they reveal the brain's internal mechanisms for interpreting sensory input. Illusory figures, for example, exploit the visual system's capacity to construct contours, shapes, and surfaces despite the lack of a continuous physical border (1, 2). Illusory figures are perceived by a range of phylogenetically diverse species, including monkeys, cats, owls, and bees, pointing to perceptual completion as a fundamental aspect of natural vision (3).

Neural correlates of illusory figures have been found in a wide range of brain areas. Recordings in monkeys revealed that illusory figures evoke spiking responses from neurons in visual areas as early as V1 and V2 and as late as the inferotemporal cortex (4-9). Neuroimaging studies in humans similarly found responses to illusory figures throughout visual cortex (10–13).

Several theoretical models postulate mechanisms of illusory figure perception (14–19). A common feature of these models is spatial integration of the inducing elements combined with an active interpolation to complete the surface. These processes are frequently assigned to neurons in midlevel areas, whose receptive fields are large enough to cover separate elements yet sensitive enough to distinguish between local features such as orientation, curvature, and colinearity (20, 21). A range of evidence suggests that visual area V4 in particular may play an active role in surface completion. First, the receptive fields of V4 neurons are large by comparison with V1 and V2 receptive fields and are therefore able to integrate information across spatially separated stimulus components (22). Second, psychophysical studies demonstrate that the perception of certain similar illusory figures varies over visual space in a manner consistent with the retinotopy of V4 (23, 24). Third, both human (10-13) and nonhuman primate (25) functional imaging studies reveal responses to illusory contours and surfaces in area V4. Fourth, ablation of area V4 in the macaque selectively impairs performance on discrimination tasks that involve illusory contours (26).

Here we investigate the neural representation of illusory surfaces in macaque area V4 using Kanizsa patterns known to give rise to the perception of illusory surfaces. Illusion-promoting patterns elicited electrophysiological responses that were often rhythmic and were significantly enhanced in their firing rate compared with physically similar control patterns that did not promote the illusion. This enhancement depended critically on the spatial alignment of the illusory surface with the point of peak V4 receptive field sensitivity, or "RF focus." Only neurons with receptive fields focused on the illusory surface showed elevated responses to the illusory surface, whereas those with receptive fields focused on the inducing elements did not. This effect was observed for neurons whose receptive fields, as defined by conventional mapping techniques, were several degrees in size and overlapped with both the illusory surface and the inducer elements. These observations suggest that V4 neurons play an active role in the representation of illusory surfaces and are sensitive to stimulus details much finer than would be predicted based on receptive field size alone.

Results

The central goal of this study was to assess the neuronal representation of illusory surfaces in visual area V4. We recorded

Significance

Visual information is often fragmented, such as when objects block each other from view, and our brain must actively deduce missing parts of an image to perceive key features of the world. This study asks whether neurons in cortical area V4 can infer the presence of an object's surface when visual clues are limited. Indeed, our experiments reveal that certain V4 neurons enhance their responses to an array of stimuli only when they are configured to give rise to an illusory surface. Intriguingly, this effect exhibited unexpected spatial precision relative to the inducing components of the illusion. These findings provide important clues about how the brain overcomes a fundamental challenge of vision.

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spiking activity in V4 using chronically implanted microelectrode arrays in two fixating adult macaques over 16 sessions (5 in monkey F). Square electrode arrays had a linear dimension of 3.6 mm and contained 64 active microelectrodes tips. In both animals, the arrays were implanted on the left hemisphere's prelunate gyrus, just dorsal to the rostral margin of the inferior occipital sulcus and caudal to the superior temporal sulcus (Fig. 1A). Spikes were sorted offline using cluster-based sorting techniques. As is typical for chronic multichannel recording techniques, the quality of spike waveform isolation varied considerably across electrodes and sessions. Evaluating the waveform data using a broad isolation criterion (Methods) yielded 705 clustered units, representing signals from both single neurons and multiunit activity. In addition, a stricter isolation criterion was applied to extract single neuron spiking (n = 328). Units across both datasets demonstrated similar effects and spatial specificity for our experiment.

In each recording session, we first estimated the position and extent of receptive fields using an automated mapping procedure in which a sequence of small stimuli was presented randomly across the visual field. This mapping provided a 2D response field matrix (RFM) of stimulus sensitivity with a 1° spatial resolution (Fig. 1B). Across the array, there was a moderate range of scatter in the receptive field positions and extents, providing coverage of the parafoveal region of the lower right quadrant (Fig. S1).

Following receptive field mapping, we presented the monkeys with test and control stimuli that were centered approximately on the point of maximal receptive field overlap. Two of these stimuli, IF1 and IF2, consisted of four solid white circles with 90-degree wedge cutouts ("inducers") configured to elicit an illusory

surface (Fig. 1 *C* and *D*). The remaining three stimuli (CF1, CF2, and CF3) did not give rise to the illusion and served as controls. Although we did not collect any behavioral responses, previous studies have demonstrated that similar stimuli give rise to the perception of illusory surfaces in both humans (27) and macaques (28). The fixed stimulus position, combined with the scatter of receptive field positions across the neural population, allowed us to investigate the importance of receptive field position relative to the stimulus (Fig. 1*E*).

Response Enhancement to Illusory Surfaces. In the main task, test and control stimuli were each presented for 1 s. We began by comparing neural responses elicited by illusory figure IF1 and those elicited by control figure CF1. Across the population, a large fraction of V4 units tested (299/705, 42%) showed significantly enhanced responses to IF1 compared with CF1 (t test, P < 0.05; Fig. 2 and Fig. S1). Although some units showed significantly diminished responses for the illusory stimulus, this was much less common (58/705, 8.2%).

A conspicuous feature of the observed response enhancement was the presence of low-frequency (~3–5 Hz) oscillations in the spiking response, which can be seen in Figs. 2–4. This rhythmic modulation, which was commonly observed in monkey B but only occasionally present in monkey F, is visible in both the raster plots and spike density functions and appears to be time-locked to the onset of the stimulus. Analysis of fixational eye movements demonstrated that such oscillations did not derive from the frequency or timing of microsaccades (Fig. S2). The observed oscillations are in some ways reminiscent of previous findings of oscillatory activity in this frequency range in area V4 (29) and the inferotemporal cortex (30, 31).

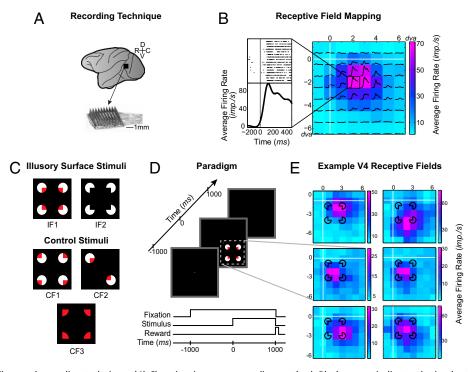


Fig. 1. Stimulus paradigm and recording technique. (A) Chronic microarray recording method. Black square indicates the implanted array location in macaque left cortical hemisphere. Sketch of the implanted microelectrode array shown below. (B) Receptive field mapping. (Upper Left) Raster plot showing the response of an example V4 unit to the repeated presentation of a circular random dot field centered at (2, -2 dva). Individual dots represent spikes as a function of time, and each row represents an individual trial. (Lower Left) Trial-averaged spike density function for the raster plot shown at Upper Left (convolved for display purposes). (Right) RFM for the same example unit. Spike density functions for each tested location of visual space are shown in black. The color axis represents the average spike rate over the 500-ms stimulus duration. White lines indicate horizontal and vertical meridians. (C) Illusory figures (IF1 and IF2) and control stimuli (CF1-3) used in the study. (D) Schematic of main task. Monkeys were required to fixate on a central fixation spot while an illusory figure or control stimulus appeared on the monitor for 1000 ms. (E) RFMs for six example units. Each grid location represents visual responses to stimuli at a given position of visual space. Color tables are normalized to each unit's maximum firing rate. Superimposed black outlines indicate the location and size of stimulus arrays used in the main task.

Response Enhancement Depends on Precise Alignment of RF Focus.

The inherent scatter of receptive field positions across the neural population allowed us to evaluate whether neural modulation depended on receptive field substructure. To investigate the importance of receptive field alignment with the Kanizsa stimulus, we first computed the location of peak retinotopic sensitivity, a singular position in retinotopic space that we termed the RF focus. The distribution of RF foci across our sample of combined multiunit and single-unit activity is shown for both monkeys in Fig. S3. Using this metric, we divided the neural population (n = 705) into four groups, with the RF focus situated either over the center of the illusory surface (n = 72), over one of the four inducer locations (n = 188), over one of the four illusory contours between adjacent inducers (n = 209), or elsewhere (n =236). The last of these groups was excluded from the main analysis. Defining the receptive field area as the largest contiguous patch of significant responses within the RFM (t test, P < 0.05), we found that the receptive fields in our main sample had a linear dimension that was $5.5 \pm 1.6^{\circ}$ across on average, which was larger than the $3.2 \times 3.2^{\circ}$ -stimulus array (*Methods*). Furthermore, roughly half of the analyzed units showed significant responses at all four inducer locations (48%).

The analysis of RF focus and stimulus position revealed a surprisingly straightforward relationship: units whose RF focus was strictly aligned with the illusory surface generally exhibited enhancement in spiking to IF1 relative to CF1 whereas those whose RF focus was situated over one of the inducers generally did not (Fig. 2 and Fig. S4 A and B). In many cases, this response enhancement was large, exceeding a twofold change in firing rate that was statistically significant between conditions (t test, P < 0.001).

Having observed this phenomenon in a number of example units, we next evaluated the relationship between RF focus and

response enhancement at the population level. We approached this problem from two different perspectives. First, we examined the differential responses to IF1 and CF1 for all units focused on the center of the illusory surface. We compared this activity difference to that from units focused on an inducer. This analysis revealed a large and significant difference between the two populations, whose RF foci differed in position by less than 1.5°, with only the former group showing significant enhancement to the illusory figure (Fig. 3A, Left vs. Right, and Fig. S4 C vs. D). Units with RF foci over the illusory contour between adjacent inducers showed intermediate levels of enhancement (Fig. 3A, Center) that emerged slightly later (~20 ms) compared with the surface-focused population (Fig. S5). The same trend was observed when the data were analyzed for each monkey individually (Fig. S6), for each electrode across session (Fig. S7A), and within a single representative recording session (Fig. S7B). These analyses showed that RF focus position is a strong predictor of response enhancement to the illusion-producing stimulus.

Second, we took a converse approach by first dividing the neural population into two groups based on whether or not units showed significant response enhancement to the illusory figure and then comparing the distribution of RF foci of the two groups. In this analysis, we found that the RF focus of units showing enhancement was most frequently positioned on the center of the illusory surface, with the next most common position being on the illusory contour (Fig. 3B and Fig. S2B). Only a few such units had their RF focus over the inducer locations. By contrast, units that failed to show significant enhancement had a more uniform distribution of RF foci, with peaks at the inducer positions (Fig. 3C). Together, these analyses suggest that V4 spiking responses to IF1 depend on the precise spatial relationship between RF focus and the illusory stimulus.

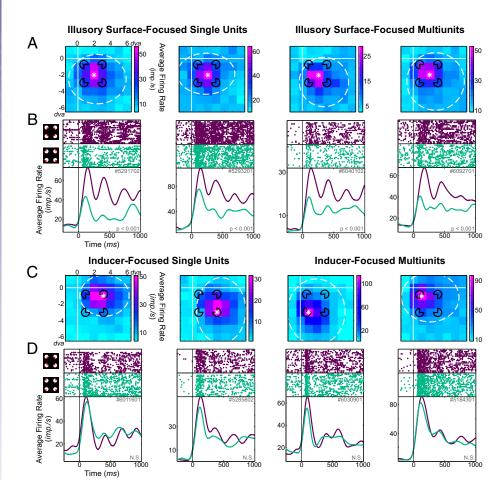


Fig. 2. V4 spiking responses to illusory figures. (A) Example RFMs. White asterisks indicate the location of peak retinotopic sensitivity, or RF focus. Dashed white lines indicate the interpolated boundary of significant visual responses (t test, P < 0.05) within the RFM. Solid white lines indicate the horizontal and vertical meridians. Location and size of main stimulus arrangement is indicated by black outlines superimposed on the RFM. (B) Raster plots and respective spike density functions showing responses to the main illusory figure (IF1, purple) and control figure (CF1, green) for the same units shown in A. Spike density functions were convolved with a 50-ms kernel for display purposes. The number of impulse discharges evoked by the main illusory figure was significantly greater than those evoked by the control figure over the displayed time course (t test, P < 0.001). (C) Units with peak retinotopic sensitivity over an isolated element of the stimulus array. All other conventions as in A. (D) Raster plots and spike density functions for the same units shown in C. Responses for the illusory figure and control condition were largely comparable (t test, $P \ge 0.05$).

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The mean response to the control stimuli was virtually identical for both the surface-focused and inducer-focused populations (Fig. 3A). This result is consistent with our observation that our recorded units had relatively large receptive fields. This finding also demonstrates that the spatial specificity of the RF focus position, although a strong predictor of enhancement to the illusion configuration, did not determine the overall response to the stimuli more generally. In other words, responses for the control stimuli behaved approximately as one might predict based on the receptive field size alone. It was only for the illusion-promoting stimulus that responses were highly dependent on the position of the RF focus.

Generalization to Other Stimuli. We next repeated the experiment above using additional illusory and control stimuli tested in prior psychophysical experiments (27). As acknowledged in previous studies, the inducing stimuli associated with illusory figures are difficult to manipulate without altering the perceptual effect, with alignment of the linear inducer contours being a crucial determinant (1). Here we settled on an alternative version of the illusory square stimulus (IF2) and compared it to an additional set of control stimuli (CF2-3) that varied in several critical stimulus attributes and did not induce the impression of an illusory surface (Fig. 1C). The rationale was to determine whether the response enhancement observed with IF1 would also be observed with other, related stimuli that either did (IF2) or did not (CF2) and CF3) give rise to an illusory surface.

In line with the results presented above, we found that, as for IF1, units showed spike rate enhancement to IF2 relative to the controls, consistent with the illusory surface itself being the important factor (Fig. S8). Moreover, the position of the RF focus was again critical, as the enhancement relative to controls was observed most strongly when the focus was over the center of the stimulus (Fig. 4 A vs. B).

Finally, we examined whether individual units showed the same response enhancement for different combinations of illusory and control stimuli. To do this, we computed a t-statistic for two different test vs. control pairs. Positive t-values indicate a higher response to the illusory stimulus, and negative t-values indicate a higher response to the control. Plotting the responses across the population revealed that individual units showed similar response enhancement for the two illusory stimuli (Fig. 4C). This trend did not hold true when the RF focus was centered over the inducer rather than the surface (Fig. 4D). The respective Pearson correlation coefficients for the surface-focused and inducer-focused populations were 0.438 (P < 0.001) and -0.074 (P = 0.54).

Discussion

Our data demonstrate that neurons in macaque area V4 exhibit enhanced spiking responses to stimuli known to elicit the perception of illusory surfaces. This finding is consistent with the results of previous studies linking V4 activity with subjective perception in other paradigms (32, 33). Our study also revealed that a crucial determinant of neural response enhancement was the precise spatial relationship between the peak retinotopic sensitivity and the details of the illusory stimulus. In the following sections, we attempt to understand these observations in the context of the spatial response characteristics of V4 neurons, we consider aspects of the illusion that might contribute to the response enhancement, and we discuss cortical area V4's role in midlevel vision more generally.

Multiple Spatial Modes of Visual Processing by V4 Neurons. V4 neurons do not sample visual space evenly, but instead harbor receptive "subfields" (34, 35). Our observed response enhancement cannot be ascribed to such nonuniform spatial sensitivity, because in the main stimulus contrast the spatial positions of the inducers were identical (IF1 vs. CF1). Instead, it appears that V4 neurons simultaneously exhibit two distinct spatial modes of visual processing. One aspect of their response, which might be described as having low spatial acuity, is the broad range of visual field positions for which a flashed stimulus elicits a response; V4 neurons have relatively large receptive fields. Another aspect of their response, and that featured in the present study, operates with a notably higher effective acuity. In this mode of operation, the same neurons are fastidious in their spatial requirements when it comes to response enhancement with illusory stimuli. Discovering how a given cell can simultaneously contribute to vision over two different spatial scales may be an important challenge for understanding enigmatic aspects of vision such as the establishment of positional and size tolerance (36), figure–ground organization (32), and biased stimulus competition (37).

On a physiological level, one might ask whether the observed enhancement results from factors other than the precise position of the RF focus. For example, enhancement of V4 neurons might depend upon a certain level of inclusion of all four inducing stimuli within the large receptive field. Although we cannot entirely eliminate such inclusion as being an important factor, our analysis suggests that it cannot be the primary determinant of

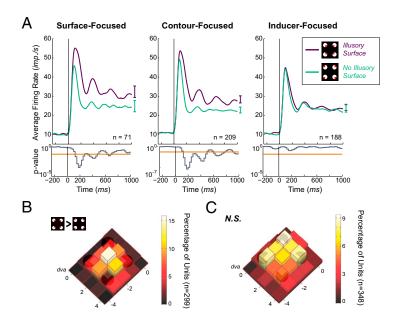


Fig. 3. Relationship between RF focus and response enhancement for illusory figures. (A, Upper) Population average of evoked responses to the main illusory figure (IF1, purple) and the control stimulus (CF1, green) for all (Left) surface-focused, (Center) contourfocused, and (Right) inducer-focused V4 units. The average time course was convolved with a 50-ms kernel for display purposes. Error bars indicate the SEM across units for the posttransient period (275 -1.000 ms). (A. Lower) P value as a function of time (t test for IF1 vs. CF1 across 25-ms nonoverlapping bins). Orange line demarcates $\alpha =$ 0.05. (B) Distribution of RF foci for both animals across the horizontal and vertical dimensions of visual space for all units with significantly greater responses to IF1 compared with CF1 (n = 299, t test, P < 0.05). The x and y axes are in visual degrees. Height and color temperature represent the proportion of recorded units with receptive field foci at each location of visual space. Black underlay indicates the location of the main stimulus arrangement (see Methods for exact scale and location). (C) Distribution of RF foci for the population of units without a significant (t test, $P \ge 0.05$) firing difference between IF1 and CF1 (n = 348). Image conventions as in B.

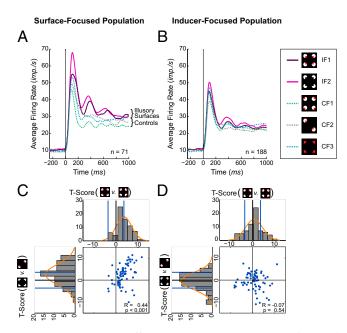


Fig. 4. V4 responses to different illusory and control stimuli. (A and B) Population response of surface-focused and inducer-focused units to all illusory and control stimuli used in the study. (C) Scatter plot of neural modulation to stimulus pair IF1-CF1 (abscissa) versus stimulus pair IF2-CF2 (ordinate) for the surface-focused population. Each dot represents one unit. The t-scores computed for the average activity within 80-500 ms following stimulus onset. Positive values represent greater spiking activity evoked by an illusory figure compared with a control stimulus. Note the significant correlation between stimulus pairs (R = 0.44, P < 0.001). Flanking histograms show the respective distribution of t-scores (horizontal orientation: IF1 vs. CF1; vertical orientation: IF2 vs. CF2). Blue lines indicate the median twotailed critical t-values at $\alpha = 0.001$ using trials as basis for the degrees of freedom (the exact number of trials varied with each monkey's performance). Orange lines represent a normal distribution fitted to t-score distributions (horizontal Gaussian: μ = 3.6, σ = 3.5; vertical Gaussian: μ = 2.6, σ = 4.6). (D) Neural modulation across stimulus pairs for the inducer-focused population. No significant correlation was found (R = -0.07, P = 0.54). All other conventions as in C (horizontal Gaussian: μ = 0.60, σ = 4.0; vertical Gaussian: $\mu = -0.42$, $\sigma = 3.8$).

enhancement. Roughly a quarter of our recording sites showing response enhancement did not show significant responses at all four inducer positions, whereas more than a third of units not showing response enhancement did show significant responses at all four inducer positions.

Another potential explanation of the observed response enhancement might stem from the spatially heterogeneous representation of stimulus features known to characterize area V4 (22). In other words, surface- and inducer-focused populations might differ in their illusion-related responses because they accidentally correspond to different functional modules with different stimulus selectivity. This possibility seems unlikely for two reasons. First, the enhancement associated with the illusory surface was present in both monkeys, which would require that in both cases the electrode arrays were placed in a module for which there was the same relationship between feature selectivity and eccentricity. Second, the enhancement effect was abolished for units with RF foci that were both more eccentric and less eccentric than the illusory surface in their position, and are thus unlikely to reflect the feature selectivity of a single patch of cortex.

Surface Completion as a Possible Basis for Neural Enhancement. Knowledge about perceptual illusions comes primarily from psychophysical studies in humans, which have shown that Kanizsatype stimuli give rise to the perception of subjective surfaces. Faced with such stimuli, the visual system subjectively "completes"

the surface, which is often perceived as having visible contours and being segregated in depth in front of the background. In the monkey, obtaining an in-depth description of a perceptual state is constrained by the lack of verbal communication. However, using objective psychophysical criteria, it has been shown that macaques can match illusory shapes to real shapes and are sensitive to parametric variations of the inducing stimuli in a manner that resembles human subjects (28).

In the present study, we did not have an explicit measure of the monkeys' perceptual experience. Thus, there is some uncertainty regarding the basis of the observed modulation. Neurons in area V4 are known to respond selectively to shaperelated features, such as curvature and convexity (38), and this alone could account for differences in firing between the illusionpromoting and control stimuli. However, there are several pieces of evidence suggesting that surface completion plays a role in the observed response enhancement. First, a larger percentage of neurons (42%) responded more to the illusion condition than to the control, but a much smaller fraction (8%) responded in the opposite manner. This asymmetry seems to reflect a sensitivity of V4 neurons to surface completion in addition to curvature. Second, response enhancement of individual units was robust for different illusion-promoting stimuli and controls (Fig. 4C), suggesting that the illusory surface, rather than the specific features of the inducers, was the critical factor in the enhancement. Third, our main finding that the RF focus must be aligned with the illusory surface or edge for enhancement to occur further points to the subjective component influencing the response. None of this evidence conclusively identifies surface completion as an explanation of our finding. However, it does suggest that if the observed responses were to be described in terms of stimulus selectivity, this selectivity would overlap with the specific features that are critical for surface completion in the Kanizsa illusion.

Role of V4 in Midlevel Vision. One interpretation of the observed enhancement is that it arises from areas involved in object vision, such as the inferotemporal cortex (9, 39). This hypothesis would be analogous to the speculation that feedback is responsible for some aspects of illusory figure perception in areas V1 and V2 (8, 15, 17). Feedback could also account for the relative insensitivity to the position of the inducers relative to the receptive field, reflecting the greater positional tolerance of higher cortical areas. However, our results show quite the opposite, and thus do not lend themselves easily to this interpretation. In our case, the positional requirements for illusory surface enhancement were much more stringent than for other types of responses. We interpret this finding as evidence that, despite having large receptive fields, V4 neurons are able to draw upon spatially specific input, and that the enhancement associated with surface completion may be computed before or within area V4.

Finally, our findings underscore the close connection between activity in area V4 and areas V1 and V2 in establishing the spatial details of visual boundaries, surfaces, and depth ordering. This relationship has been suggested in several previous studies. For example, electrophysiological recordings in monkeys concluded, based on latency information, that an explicit assignment of figure and ground is made in area V1 based upon signals coming from extrastriate areas (40–43). In another study, figure-ground modulation disappeared following surgical removal of V4 (44), which, when combined with a disrupted ability to perceive illusory contours following V4 lesions (26), suggests that the interplay between early visual areas is central to the visual completion of illusory figures. Very recent figure-ground experiments in the awake monkey further suggest, based on the earlier V1 responses to a figure's contour rather than to the figure's surface, that the neural processes underlying perceptual surface completion originate in area V4 (32). A more direct way of testing the causal direction of influences between V4 and early visual cortex could be gained from simultaneous recordings in these areas (45), possibly with the appropriate laminar resolution to dissociate feedback (extragranular) from feedforward (layer 4) activity.

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Methods

Subjects. Two healthy adult female rhesus monkeys (Macaca mulatta, B and F) were used in the study. The Animal Care and Use Committee of the National Institute of Mental Health approved all procedures.

Behavioral Task and Visual Stimulation. All training and data collection sessions began with a brief calibration procedure, during which the monkeys were presented with a small [0.2° of visual angle (dva)] fixation spot at one of nine positions on the screen (46). Each monkey was trained on both the receptive field mapping task and the illusory figure task (see Results and SI Methods for additional details). For both tasks, the animal was required to fixate on a central spot on the screen within a 1- to 1.5-dva window for at least 2 s to receive an apple juice reward.

Neurophysiological Procedures. Extracellular spiking activity was collected over 16 sessions (5 in monkey F) with chronically implanted 10×10 arrays of microelectrodes (Blackrock Microsystems), covering the perifoveal visual field representation of area V4 in the left cerebral hemisphere. The impedance of these electrodes ranged between 150 $k\Omega$ and 1 $M\Omega$ at 1 kHz. In all cases, voltages were measured against a local reference that was located over the parietal cortex. Extracellular voltages were amplified, filtered between 0.1 Hz and 44 kHz, and digitized at 22 kHz using a 64-channel RZ2 recording system (Tucker Davis Technologies). Spikes were detected using cluster analysis (Offline Sorter, Plexon, Inc.). Offline spike detection is known to be highly variable across researchers and laboratories (47). For this reason, we used both broad and strict criteria to determine which spike-sorted units to include in our analyses. The strict criteria (n = 328) included all sorted units that were visibly separated without any cluster overlap and a clearly biphasic mean waveform (Fig. S4 A

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and B). The broader criterion included data from all separable PCA-space clusters that demonstrated a response to visual stimulation (n = 705).

Data Analysis. All neurophysiological data were processed and analyzed using custom-written code for MATLAB (The MathWorks, Inc.). The populations of cells used for the main contrast (surface-, contour-, and inducer-focused) were determined through an automated selection process (see SI Methods for details). To estimate each unit's receptive field, we collected responses to a small, circular random dot field that was presented for 500 ms at one of 64 locations (100 for two sessions in monkey F) of a virtual grid while the monkeys fixated. RFMs were constructed by averaging each unit's visual responses throughout the 500 ms period of stimulus presentation. The largest contiguous patch of significant responses within the RFM (t test, P < 0.05) constituted the receptive field area. For visualization purposes, an ellipse was fit to this area to delineate the receptive field boundary (Fig. 2 and Figs. S4 and S8). Receptive field size was defined as the average diameter of this ellipse. Each unit's receptive field focus was defined as the location of maximal response within the RFM.

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