

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

Michele A. Cox^{a,b}, Michael C. Schmid^{a,c}, Andrew J. Peters^{a,d}, Richard C. Saunders^{a,e}, David A. Leopold^{a,f,1}, and Alexander Maier^{a,b}

^aSection on Cognitive Neurophysiology and Imaging and ^eLaboratory of Neuropsychology, National Institute of Mental Health, National Institutes of Health, Department of Health and Human Services, Bethesda, MD 20892; ^bDepartment of Psychology, College of Arts and Science, Vanderbilt University, Nashville, TN 37203; ^cErnst Strüngmann Institute for Neuroscience in cooperation with the Max Planck Society, DE-60528 Frankfurt am Main, Germany; ^dNeuroscience Graduate Program, University of California, San Diego, La Jolla, CA 92093; and ^fNeurophysiology Imaging Facility, National Institute of Mental Health, National Institute of Neurological Disorder and Stroke, National Eye Institute, National Institutes of Health, Department of Health and Human Services, Bethesda, MD 20892

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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.

visual perception | illusory contours | modal completion | nonhuman primate | visual cortex

Visual 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 non-human 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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¹To whom correspondence should be addressed. E-mail: LeopoldD@mail.nih.gov.

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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. 4A 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

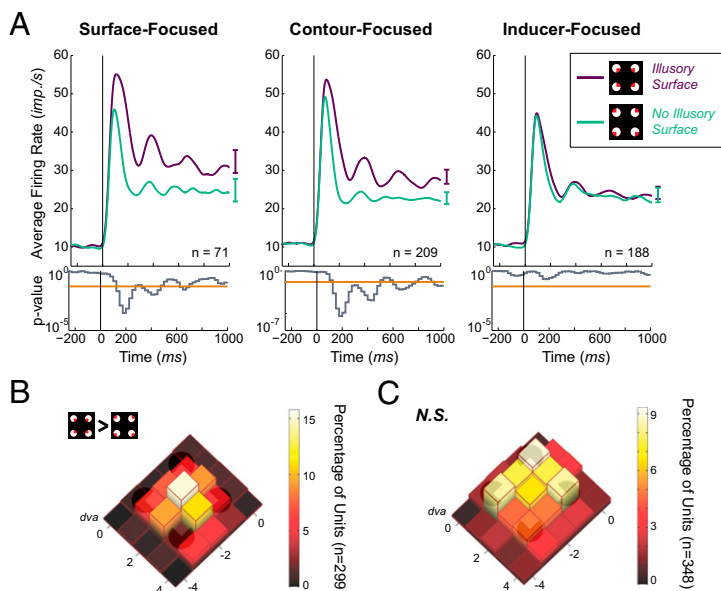


Fig. 3. Relationship between RF focus and response enhancement for illusory figures. (A, Upper) Population average of evoked responses to the main illusory figure (IF1, purple) and the control stimulus (CF1, green) for all (Left) surface-focused, (Center) contour-focused, and (Right) inducer-focused 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 overlay 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, $P \geq 0.05$) firing difference between IF1 and CF1 ($n = 348$). Image conventions as in B.

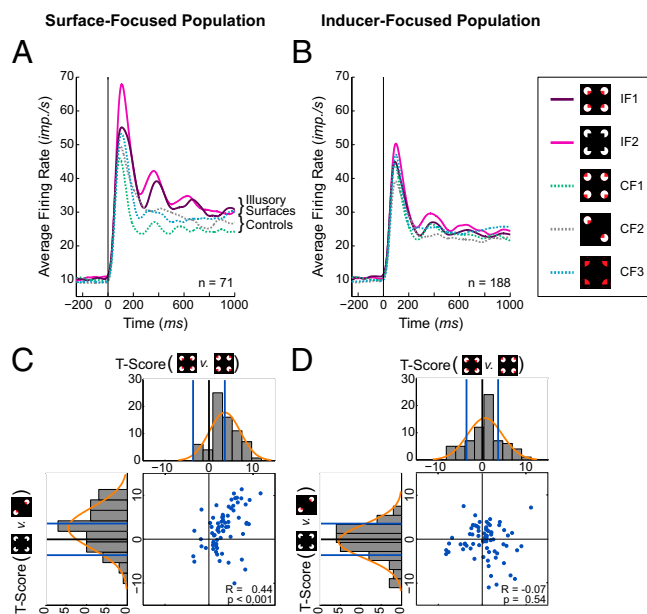


Fig. 4. V4 responses to different illusory and control stimuli. (A and B) Population response of surface-focused and inducer-focused units to all illusory and control stimuli used in the study. (C) Scatter plot of neural modulation to stimulus pair IF1–CF1 (abscissa) versus stimulus pair IF2–CF2 (ordinate) 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 two-tailed critical *t*-values at $\alpha = 0.001$ using trials as basis for each monkey's performance). Orange lines represent a normal distribution fitted to *t*-score distributions (horizontal Gaussian: $\mu = 3.6$, $\sigma = 3.5$; vertical Gaussian: $\mu = 2.6$, $\sigma = 4.6$). (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: $\mu = 0.60$, $\sigma = 4.0$; 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 Kanizsa-type 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 shape-related features, such as curvature and convexity (38), and this alone could account for differences in firing between the illusion-promoting 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.

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 micro-electrodes (Blackrock Microsystems), covering the perifoveal visual field representation of area V4 in the left cerebral hemisphere. The impedance of these electrodes ranged between 150 kΩ and 1 MΩ 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

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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