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V4 lesions in macaques affect both single- and multiple-viewpoint shape discriminations

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Abstract

The role of cortical area V4 in complex shape discriminations was studied by testing the effects of V4 lesions in macaques on the ability to visually discriminate between images of three-dimensional (3D) objects from different viewpoints. Stimuli were presented in pairs in the lower left or lower right visual field quadrants about 4 deg from the fovea, and the monkeys judged on each trial whether the two views were of the same or of different objects. Object similarity was varied to determine a threshold shape difference. V4 lesions caused profound, retinotopic, and apparently permanent disruptions of discrimination, regardless of whether the images represented single or multiple viewpoints. In V4 lesioned portions of the visual field, monkeys could discriminate objects only when they differed much more grossly in shape than was true in control locations. These effects of the lesion were virtually identical for discriminations that had been learned before lesions were placed and for those learned afterwards. As in previous studies, V4 lesions elevated contrast thresholds by approximately a factor of two, but control observations showed that this was not the basis of the disruption of shape discrimination. Manipulation of cues to shape showed that in control locations, monkeys maintained excellent shape discrimination despite a variety of stimulus alterations, whereas in V4 lesioned areas their performance was easily disrupted. This finding suggests that V4 may support visual shape discriminations by facilitating the use of multiple visual cues. However, the fact that single-viewpoint and multiple-viewpoint discriminations were similarly affected indicates that the disruption was not specific to 3D shape discrimination, but may apply to a variety of subtle discriminations.

Keywords: Shape discrimination, Three-dimensional shape, Viewpoint, Area V4, Macaque

Introduction

Several lines of evidence suggest that cortical area V4 plays an important role in the discrimination of two-dimensional (2D) shapes. V4 receives a large part of its input from the thin stripes and interstripes of area V2 (Felleman et al., 1997), a cortical area identified by a previous lesion study (Merigan et al., 1993) with shape perception. Physiological studies of area V4 suggest moderately specific trigger features for its cells, with specificities intermediate between those of areas V2 and TEO (Kobatake & Tanaka, 1994). The most consistent effect of lesions of area V4 in previous studies is a disruption of shape discrimination (Walsh et al., 1992; Merigan, 1996), especially complex discriminations that require comparison of information from different parts of the visual field. Finally, V4 is a major source of input to area TEO of the inferotemporal cortex (Distler et al., 1993), an area implicated in shape perception by lesion studies (DeWeerd, 1996) and by the physiological finding that its cells have highly specific trigger features (Gross, 1973).

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While the discrimination of three-dimensional (3D) shapes probably involves visual processing that is qualitatively different from that of 2D shape perception (Liu et al., 1995), recent theoretical work suggests that memory for 3D objects may involve storage of multiple 2D views (Vetter et al., 1995). The present study compared the effects of localized V4 lesions on thresholds for the discrimination of shape for two conditions: single viewpoint (2D only) and multiple viewpoints (2D plus 3D). The severe loss we observed for both conditions suggests that area V4 is important for a type of visual processing common to both discriminations, possibly detailed analysis of 2D images.

Methods

Subjects

Subjects were two adult, female monkeys (*Macaca nemestrina*) of approximately 5 kg body weight. They had free access to monkey chow, supplemented regularly with fresh fruit, and their water was withheld for approximately 20 h before threshold testing 5 days each week. All testing was done binocularly using controlled fixation, and neither monkey had more than 0.5 D of refractive error in either eye.

Monitoring fixation location

Fixation locus was monitored with a noninvasive infrared corneal reflection technique. Each monkey's head was held firmly during testing with a strap over the nose that held the head rigidly on an acrylic dental impression. In addition, a shaped and padded form pressed against the back of the head and prevented vertical, lateral, and posterior movements of the head. The position of the eye was monitored by tracking the corneal reflex of a focussed infrared LED through a CCTV camera with a 250-mm lens. An ISCAN pupillometry system, modified to detect the corneal reflex, provided horizontal and vertical eye position signals to the computer that controlled the experiments. On each trial, stimuli were presented and remained present only when fixation was within a ± 1 deg window.

Placement of lesions

In an aseptic procedure, the portion of area V4 from 1 mm above the dorsal tip of the inferior occipital sulcus (IOS) to about 10 mm dorsal to this locus and between the lunate and superior temporal sulci (LS and STS) was exposed with a craniotomy and durotomy. A dense grid of ibotenic acid injections (2 μl, 10 μg/μl) was made throughout this region with 2 mm center-to-center spacing, at a depth of about 0.7 mm below the cortical surface. An additional row of injections was placed below those along the border of the LS and STS at a depth of about 2.7 mm. The total number of injections and hemispheres for the two monkeys were as follows: monkey 238—93 injections in the left hemisphere, and monkey 257—67 injections in the right hemisphere.

Apparatus and procedures

The seated monkey faced a high resolution (1024×768) 17-inch Nanao display driven by a Macintosh computer at a distance of 114 cm. For each condition a two-alternative forced-choice procedure was used and the monkey chose by pressing on a right or left pushbutton on the panel in front of it. Correct choices were followed by a brief delivery of fruit juice, and incorrect choices by a buzzing tone. Daily sessions consisted of approximately 200

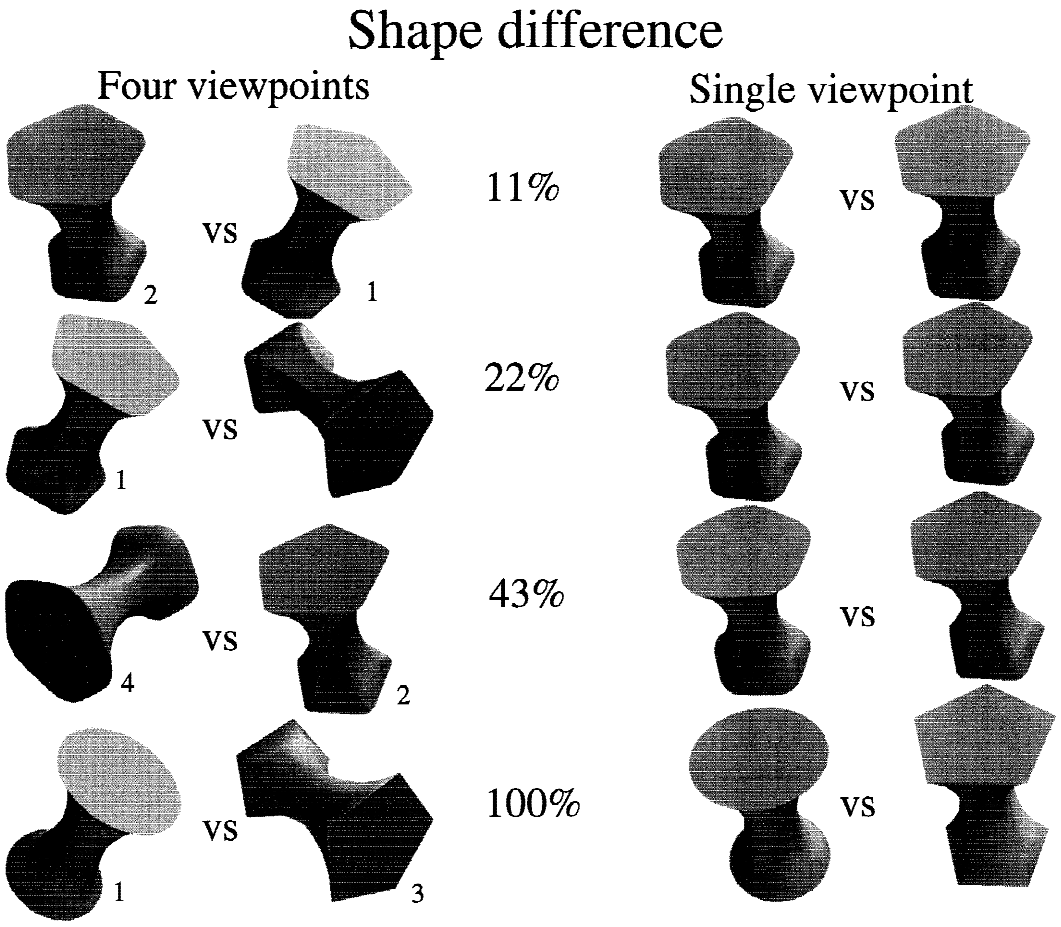

Fig. 1. Examples of stimulus pairs that differed in cross-sectional shape. Testing consisted of showing images of two objects and the subject reported whether they were the same or different. All stimuli were at the midpoint of the constriction dimension used in the other part of the experiment. The left and right portions of the figure represent the two conditions of testing; one in which each stimulus represented one of four viewpoints (left), and another in which all stimuli were shown from a single viewpoint. The particular viewpoints illustrated in the multiple-viewpoint portion of this illustration are indicated by the small number (1 to 4) beside the stimulus. The actual stimulus set for testing in the four-viewpoint condition consisted of 24 stimuli (12 same and 12 different) with mixed combinations of the four viewpoints. As can be seen here, multiple-viewpoint stimuli often differed markedly in lighting, but this difference was not relevant to the discrimination.

trials and the daily duration of a session was approximately 35 min.

Acuity and contrast sensitivity

These were measured by having the monkey report the vertical or horizontal orientation of a Gabor patch of grating (multiplication of vertical and horizontal spatial Gaussian envelopes times a vertically or horizontally oriented sinewave grating) which were presented with smoothed onset and offset (one cycle of a raised cosine) and a sigma (space constant) of 0.6 or 1. A precision attenuator (Pelli & Zhang, 1991) was used to achieve the fine control of contrast needed to measure sensitivity, and in these tests only the green gun of the display was used. Contrast threshold was determined with a staircase procedure which decreased contrast with probability 0.33 after correct choices and increased it with probability 1.0 after incorrect choices. For acuity measures the peak contrast was 0.55, and the Gabor patch was stationary with a 0.3 sec onset time. Contrast sensitivity was measured under three spatio-temporal conditions. The *low velocity* was measured at 6 cycles/deg with stationary stimuli and 0.3-s onset, the *mid velocity* at 2 cycles/deg with 0.1-s onset, and the *high velocity* at 0.67 cycles/deg with counterphase modulation at 15 Hz.

Initial shape testing

Each monkey was trained on a same-different discrimination in which two views of either a single or of two 3D objects were presented simultaneously on each trial. Monkey 257 was first trained and tested on the cross-sectional shape discrimination (Fig. 1) and monkey 238 on the constriction of sides discrimination (Fig. 2). After the completion of this testing, the two monkeys were then trained and tested on the other discrimination. Transfer to the second discrimination was rapid for both monkeys, who each reached over 80% correct by the third session, compared to several weeks to learn the first discrimination. Stimuli were presented in either the lower left or lower right visual field, centered at 4-deg eccentricity from the fixation point, in the approximate arrangement shown in Figs. 6 and 8. The images were presented in grey level on a white background. A right button press indicated that the views were of the same object, and a left button press that they were of different objects. The monkeys were initially trained

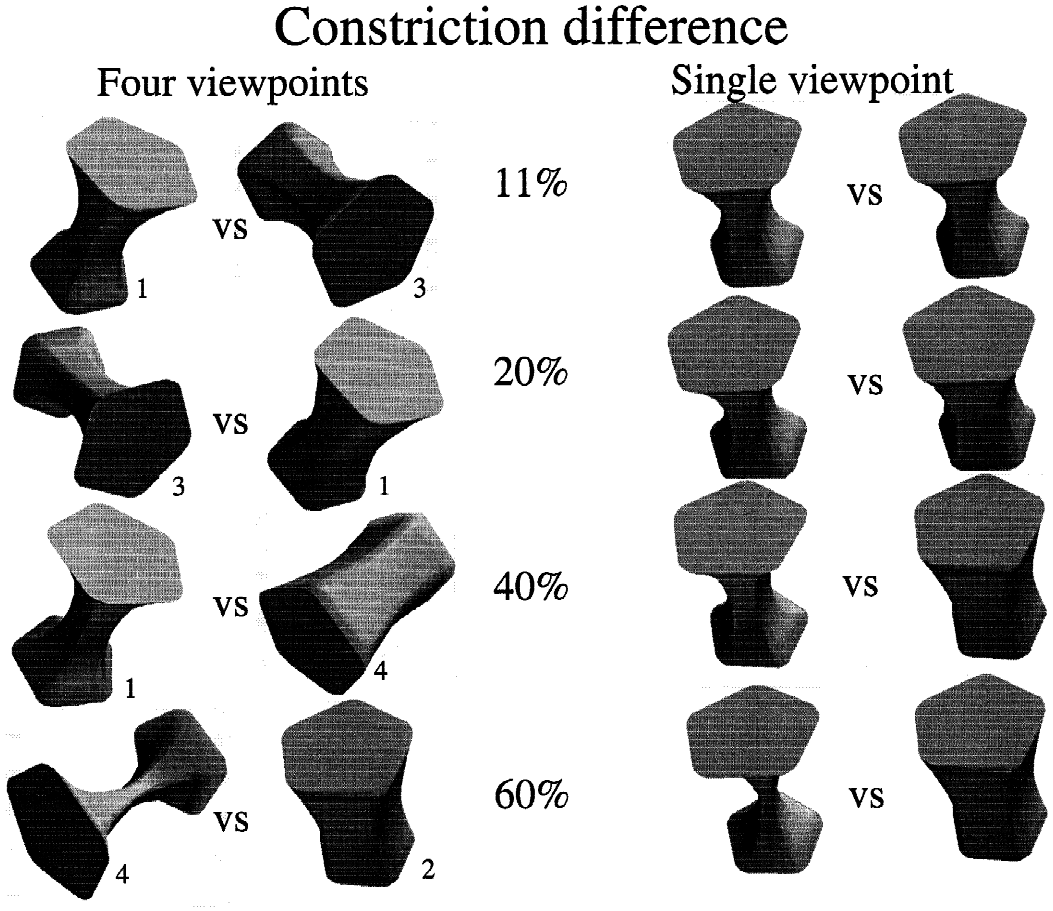

Fig. 2. Examples of stimulus pairs that differed in degree of constriction. Testing consisted of showing images of two objects and the subject reported whether they were the same or different. All stimuli were at the midpoint of the cross-sectional shape dimension used in the other part of the experiment. The left and right portions of the figure represent the two conditions of testing; one in which each stimulus represented one of four viewpoints (left), and another in which all stimuli were shown from a single viewpoint. The particular viewpoints illustrated in the multiple-viewpoint portion of this illustration are indicated by the small number (1 to 4) beside the stimulus. The actual stimulus set for testing in the four-viewpoint condition consisted of 24 stimuli (12 same and 12 different) with mixed combinations of viewpoints. As can be seen, multiple-viewpoint stimuli often differed markedly in lighting, but this difference was not relevant to the discrimination.

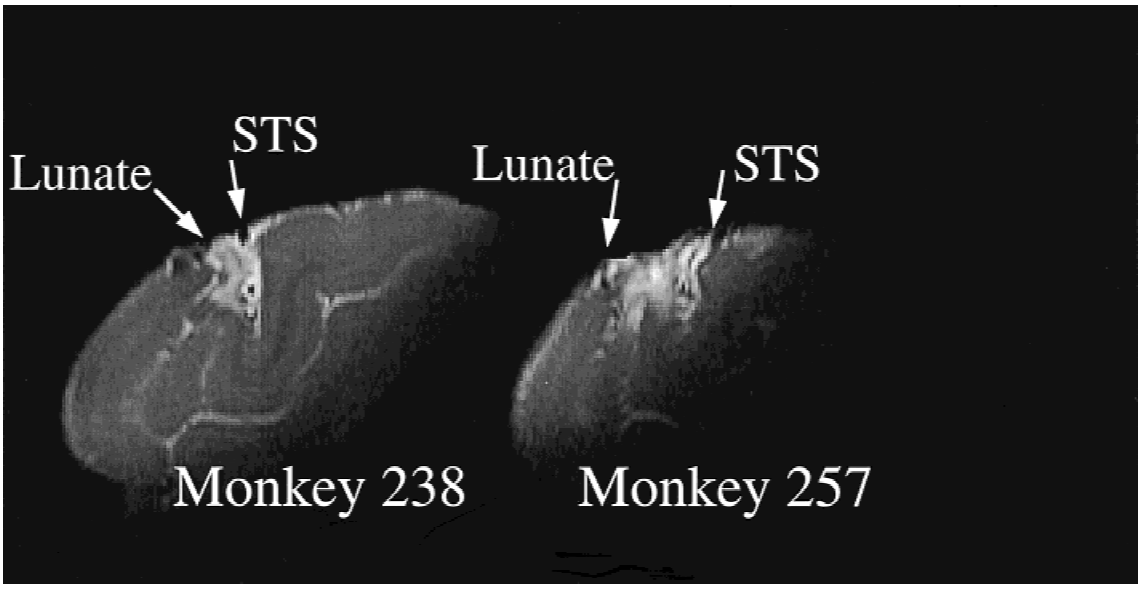

Fig. 3. MR images, in an axial plane, of the brains of the monkeys tested in this study, showing the location of the lesions. The location of the lunate sulcus (lunate) and superior temporal sulcus (STS) are shown by arrows. Reconstructions were made from the T2-weighted images shown here ($TR = 5000$, $TE = 90$, slice thickness 1 mm, $FOV = 10$ cm, 128 by 256 voxels). The lesion can be seen in these images as the lighter region between the lunate and superior temporal sulci.

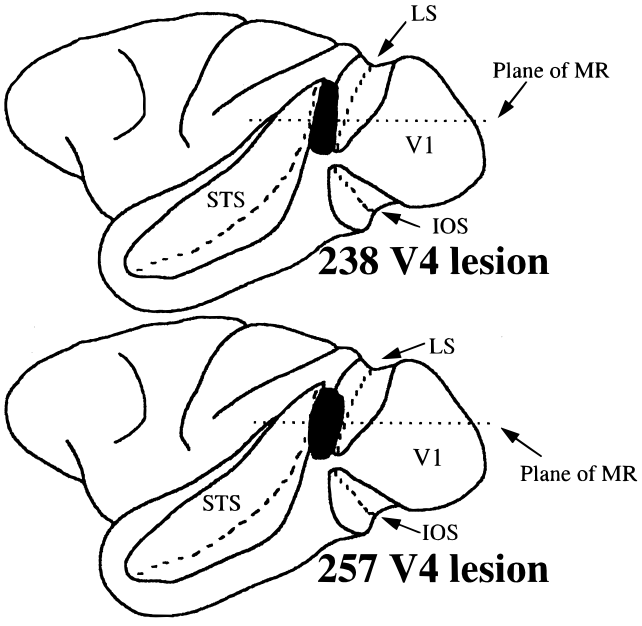

Fig. 4. Lesion reconstruction on a partially flattened lateral view of the monkey brain. The lesion was placed in the left hemisphere for monkey 238 and in the right hemisphere for monkey 257. The blackened region shows the area over which the full cortical thickness was lesioned. In both cases, the lesion appears to include the lower quadrant representation of area V4 from near the fovea to approximately 10-deg eccentricity. Areas bordering the lesion which could have been partially damaged include area V3 in the lunate sulcus and area V4t in the superior temporal sulcus. The dotted lines mark the approximate location of the MR images shown in Fig. 3. LS is the lunate sulcus and STS is the superior temporal sulcus.

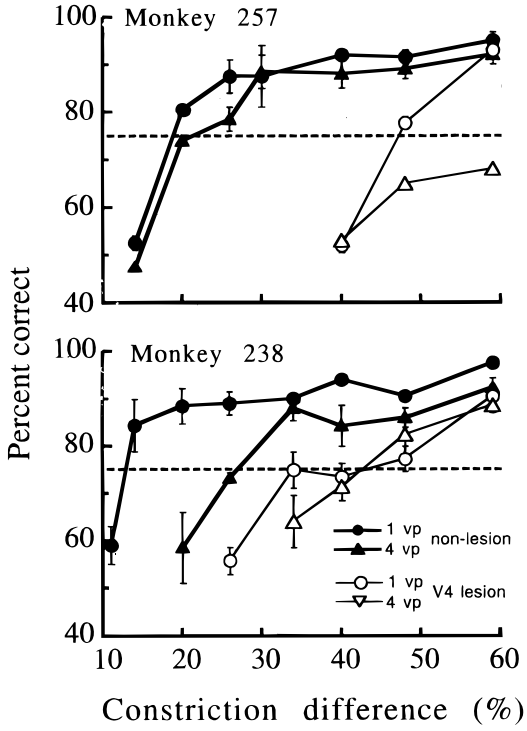

Fig. 5. Percent correct shape discrimination for the two monkeys as a function of the difference in degree of constriction of the stimuli. Filled symbols and heavier lines show results for the nonlesioned portion of the visual field, while round symbols show single-viewpoint (1 vp) results and triangles four-viewpoint (4 vp) results. Threshold shape discrimination was taken at 75% correct (dashed line). Error bars show ±S.E.M.

with pairs that were maximally different, and then tested on each successively more difficult discrimination (progression from bottom to top of Figs. 1 and 2) until performance stabilized. The two images presented on each trial were each chosen randomly from four 2D images of different 3D viewpoints of each object (four-viewpoint conditions) or from one viewpoint (single-viewpoint condition). Following placement of the lesions, the two monkeys were first retested on the discrimination they were initially trained on.

Switch of the shape dimension to be discriminated

The discriminated dimension for the two monkeys was switched following the completion of postlesion testing of the first dimension. After the switch, monkey 257 discriminated objects on the basis of the constriction of sides, and monkey 238 on the the basis of cross-sectional shape.

Alterations of stimuli at lesion and control locations

Subsequent to the testing described above, we examined the effect of stimulus alteration on discrimination performance. For monkey 238, we increased and decreased the contrast gradient within each image in the stimulus for those stimuli whose shape was just suprathreshold for the monkey at the two locations (arrows in Fig. 7). We tested more substantial stimulus alterations for monkey 257 at both control and lesion locations at the conclusion of the testing described above. These changes included removal of shading cues in upper or lower halves of each figure, blurring of edges, addition of high-contrast shadows, and replacement of the upper or lower half of the hexagonal figure by the corresponding part of the round figure. In a final test of the nature of the discrimination, monkey 257 was tested with one of the shapes replaced by a vertical line and the other by a horizontal line. Thus, the monkey had to judge on each trial whether the lines were of the same or different orientation. For all of the above testing, a complete set of stimuli was made up that included all possible pairings of the novel stimuli.

Reconstruction of lesions

Approximately 10 months after placement of the lesions, lesion location and extent were estimated from high-resolution magnetic resonance images of the right occipital area. The most useful details came from T2-weighted images made with $TR = 5000$ and $TE = 90$. Images were 128 by 256 voxels with a 10-cm field of view for an in plane voxel size of 780 $\times$ 390 microns. Slice thickness was 1 mm.

Results

Fig. 3 shows transverse magnetic resonance (MR) images of the lesion locations in the two monkeys. These are T2-weighted images and the location of the lesion can be seen as an area of increased signal between the lunate and superior temporal sulci. The lesion in both monkeys extended into the bordering sulci and was complete from the end of the inferior occipital sulcus to about 10 mm dorsal and medial to this location.

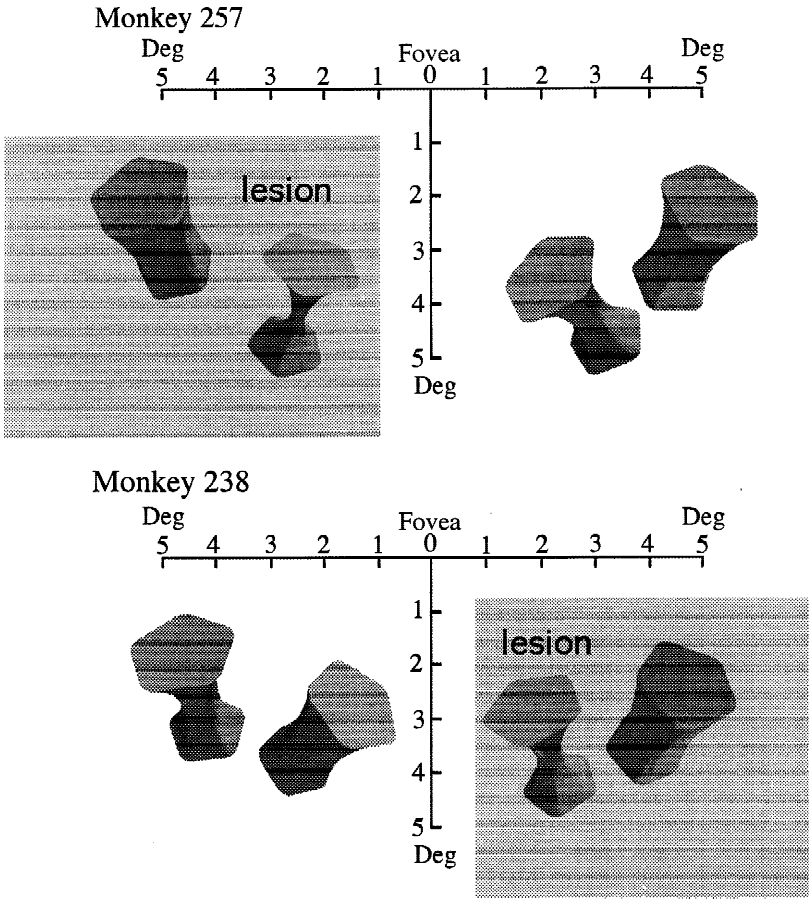

Fig. 6. Visual field locations at which the monkeys showed normal (white) and severely degraded (grey) constriction difference thresholds. Insets in the white and grey regions show examples of approximately threshold discriminations for each of the regions.

Fig. 4 illustrates a reconstruction of the lesions in the two monkeys on a lateral view of the monkey brain with sulci partially opened (Maunsell & Newsome, 1987). In both cases, the lesion extended from just above the dorsal tip of the inferior occipital sulcus (IOS) dorsally for about 10 mm along the prelunate gyrus. It also extended about 1.5 mm into both the lunate sulcus and superior temporal sulcus (STS). On the basis of the lesion reconstructions, we expected that the affected portions of the visual field would be the lower quadrant opposite the lesion, extending from approximately 1 to 10 or more degrees eccentricity.

Fig. 5 shows performance of the two monkeys on the constriction difference discrimination. Both monkeys showed excellent performance in the nonlesioned portion of the visual field, with single view thresholds of 20% or less. Monkey 257 had a similar threshold for four-viewpoint stimuli, but monkey 238 could not discriminate constriction differences with four viewpoints much below 30%. Shape sensitivity was substantially worse in the V4 lesioned portion of the visual field, with thresholds of 45–50% for monkey 238 for the two tasks and 50% for monkey 257 for the single viewpoint task. Monkey 257 was completely unable to perform the discrimination with four viewpoints. These effects appeared stable over the extended postlesion period (3 weeks to 28 months for previously trained discriminations) during which shape thresholds were measured.

Fig. 6 shows in grey the retinotopic locations where constriction discrimination thresholds were disrupted, as well as examples of the stimulus pairs that could just be discriminated in control and lesion locations. The borders of the regions of disrupted shape discrimination were determined by measuring constriction difference thresholds along a vertical profile 3 deg lateral to the fovea and along a horizontal profile 3 deg below the fovea.

Discrimination of cross-sectional shape is shown for the two monkeys in Fig. 7. Both monkeys could discriminate shape differences as small as 20% in the nonlesioned portion of the visual field, although monkey 238 could not discriminate four-viewpoint stimuli much below 40%. Performance in the V4 lesioned locations was greatly inferior, reaching threshold for both stimulus types between 70 and 80% for monkey 238 and near 80% for the single viewpoint for monkey 257. Monkey 257 could not perform the four-viewpoint discrimination even at the largest shape difference.

The visual field locations at which V4 lesions disrupted performance, and examples of threshold object pairs are shown in Fig. 8. Reliable disruptions of performance were found 1 to 2 deg from the vertical and horizontal meridia of the visual field. The location of the defects in the visual field were similar for the constriction (Fig. 6) and cross-sectional shape (Fig. 8) measures.

Acuity and contrast sensitivity measures for control and V4 lesioned locations are illustrated in Fig. 9. For both locations, acuity was decreased about 20% and contrast sensitivity was reduced by slightly less than a factor of 2. In control experiments (described below), the effect of the reduced contrast sensitivity was evaluated by testing shape discrimination in control visual field locations with stimuli that were reduced in contrast. This manipulation had no effect on shape difference thresholds.

Finally, we measured the effects of a variety of stimulus changes on discrimination performance in lesion and nonlesion locations. Fig. 10 shows the effect of modifying, for monkey 238, the contrast of stimuli which were just suprathreshold for shape discrimination at lesion and nonlesion locations. Both increases and decreases of stimulus contrast at the lesion location (open circles) severely disrupted discrimination, while contrast changes in the

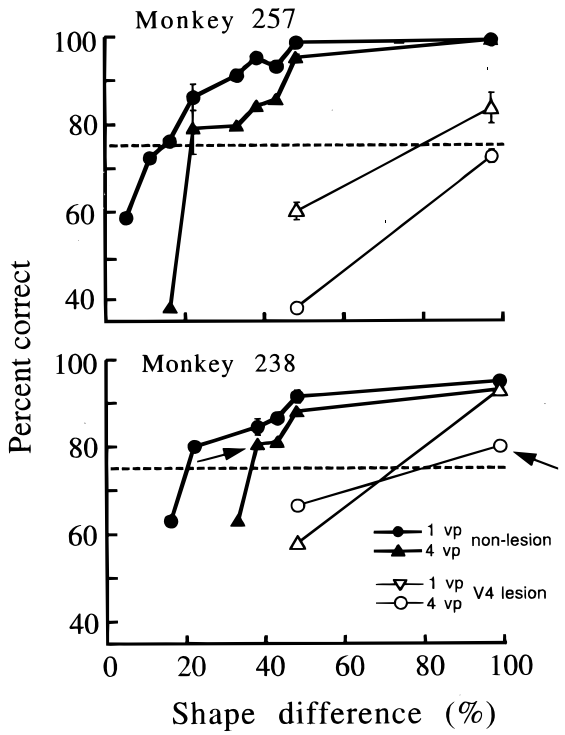

Fig. 7. Percent correct shape discrimination for the two monkeys as a function of the difference in cross-sectional shape of the stimuli. Conventions are the same as in Fig. 5. Threshold shape discrimination was taken at 75% correct (dotted line). Arrows show the performance further tested with manipulation of stimulus contrast (results shown in Fig. 10). Error bars show ±S.E.M.

nonlesioned location (filled triangles) had no effect on discrimination. Similarly, the very substantial stimulus alterations described in the Methods section for monkey 257 reduced discrimination performance at the lesioned location to below 75% threshold. However, performance at the nonlesioned location was unaffected by any of the changes, despite the fact that the monkey had never seen the altered stimuli before. The final stimulus alteration, in which shape stimuli were replaced by vertical *versus* horizontal lines, did not disrupt discrimination performance at either control or lesion locations.

Discussion

Localized quadrant lesions of cortical area V4 caused profound retinotopic deficits in both single- and multiple-viewpoint shape discrimination, that remained stable over several months of testing. Systematic manipulation of cues to shape, such as stimulus contrast, revealed that discrimination performance was robust in control portions of the visual field, but easily disrupted at locations with V4 lesions. Approximately equal effects were seen on discriminations learned before the lesion and those learned afterwards. The lesions also caused two-fold losses of spatial contrast sensitivity, but control experiments showed that this was not the basis of the shape discrimination deficits.

Implications for the role of V4 in shape perception

There is now compelling evidence from single-unit physiological studies that there is increasing form selectivity in the response of

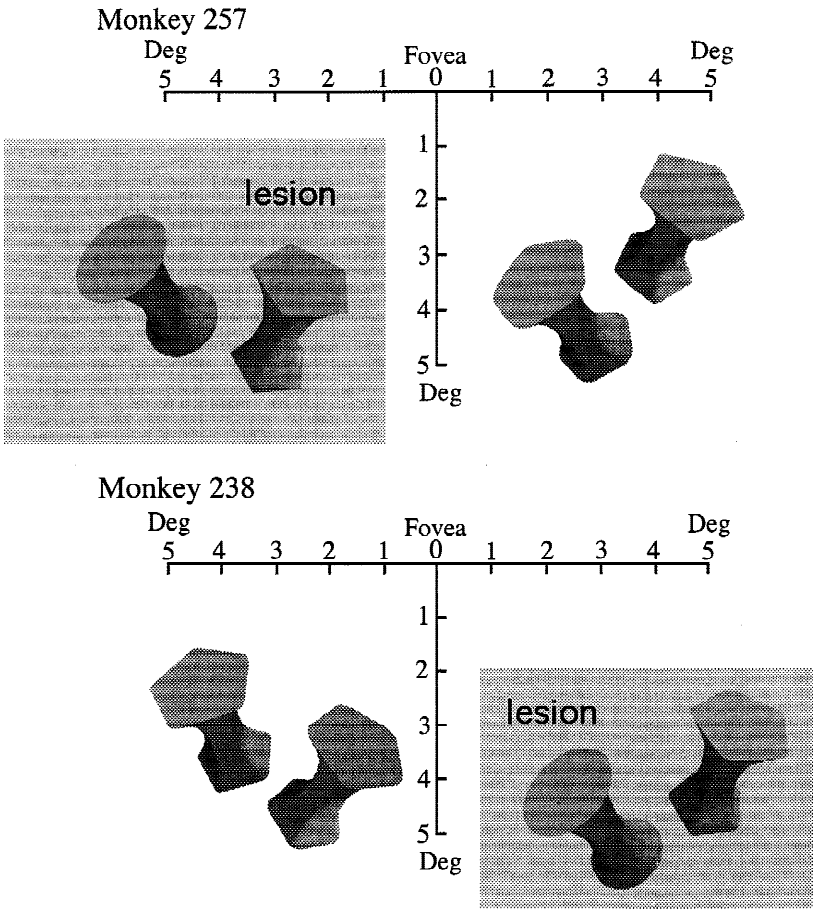

Fig. 8. Visual field locations at which the monkeys showed normal (white) and severely degraded (grey) shape discrimination thresholds. The location of the disrupted thresholds was determined by measuring thresholds along a horizontal contour 3 deg below fixation and along a vertical contour 3 deg to the right (238) or left (257) of fixation. Insets in the white and grey regions show examples of approximately threshold discriminations for each of the regions.

cells in progressively higher areas of the ventral visual pathway (Kobatake & Tanaka, 1994). This organization suggests the possibility that the selectivity of cells in higher cortical areas may be due to conjoint activation by features of lower level cells that converge upon them. Such a physiological result also suggests that lesions of higher visual areas might disrupt progressively more selective visual responses. Indeed, our earlier lesion results are at least roughly in accord with this expectation. While lesions of area V1 result in complete blindness, lesions of cortical area V2 cause disruptions of grouping performance, but relative sparing of acuity and orientation contrast sensitivity (Merigan et al., 1993). Lesions of area V4 disrupt thresholds for both single- and multiple-viewpoint shape discrimination (present study), as well as grouping (Merigan, 1996), but spare the discrimination of simple geometric shapes (Merigan, 1996), as well as single- and multiple-viewpoint shape discriminations that are far suprathreshold (present study). Preliminary results with lesions of inferotemporal cortex suggest sparing of most of the above discriminations, and disruptions of only very complex discriminations (Huxlin et al., 1996). One limitation of lesion analysis is the likelihood that lesions of a particular cortical area will disrupt discriminations that rely strongly on that area, as well as discriminations that rely on areas to which the lesioned area projects. Thus, the present finding that V4 lesions disrupt shape discrimination thresholds is consistent with the possibility that the processing critical for these shape discriminations involves either V4 or such areas as TEO or TE.

One striking result of the present study was the very similar effects of V4 lesions on both four-viewpoint and single-viewpoint shape discriminations. Multiple-viewpoint shape discriminations are generally considered qualitatively different from single-viewpoint discriminations, because the former involve either an explicit 3D representation of shape in memory or an interpolation process between 2D views that knows the rules by which 2D views are combined to match 3D shapes (Liu et al., 1995; Vetter et al., 1995). Thus, the present results suggest that the neuronal selectivity needed for 3D shape processing may be present only in cortical areas beyond V4. A recent study (Logothetis et al., 1994) showed that many neurons in macaque inferotemporal cortex each responded to a range of views of 3D objects, which before training had been unfamiliar to the monkeys. Only a few neurons responded in a view-invariant manner to these objects, suggesting a higher level of selectivity than that seen in neurons that were not view invariant. How V4 neurons would have responded to these objects is not clear, although it seems likely that V4 responses would not have been viewpoint invariant. Thus, V4 neurons may simply process and then transmit features of shape response from which inferotemporal cortex neurons derive 3D shape selectivity. According to this analysis, lesions of inferotemporal cortex should also disrupt 3D shape selectivity by damaging the neurons involved in the final computations.

Retinotopic and enduring nature of effects

The disruptions we found in shape discrimination were confined to single quadrants of the visual field. This pattern is entirely consistent with the cortical layout of receptive-field centers, which do

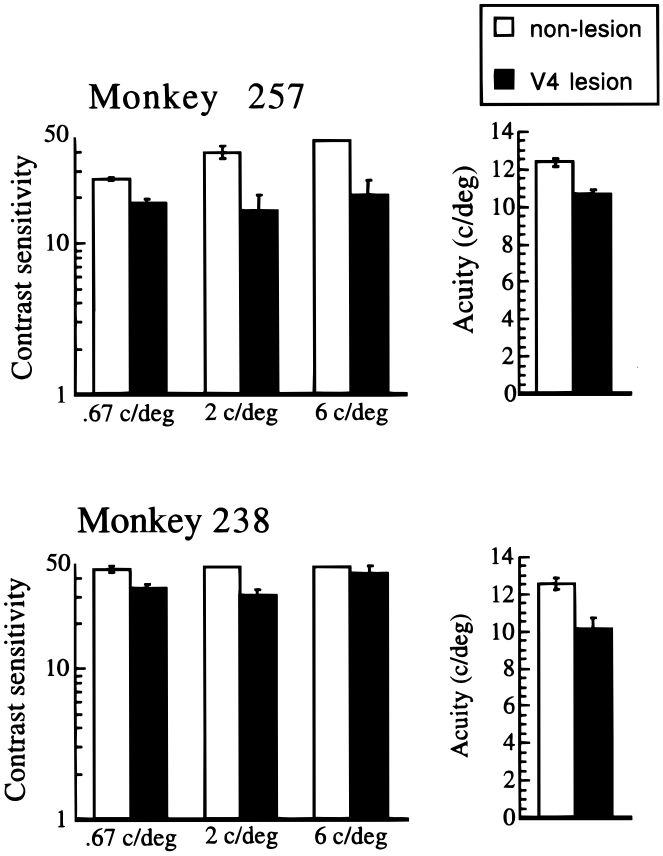

Fig. 9. Luminance contrast sensitivity and acuity of the two monkeys in lesion and control locations. Error bars are ±S.E.M.

not extend across the vertical and horizontal visual field meridia (Gatass et al., 1988). One might expect from the visual field layout of receptive-field centers that the loss of shape discrimination would have been precisely along the meridia, but the deviation we found is not surprising given that we were testing with extended stimuli. On the other hand, receptive-field surrounds of V4 cells extend well across both vertical and horizontal meridia (Desimone et al., 1993). If damage to these surrounds had affected the shape thresholds measured here, we would have found performance decrements extending well across the meridia. Thus, these results suggest that we are measuring deficits caused by damage to V4 receptive-field centers.

The disruptions we found were stable over the 3-week to 28-month duration of the study. While it is possible that we missed a transitory disruption of even greater magnitude, such an effect would be very hard to document. On the other hand, the enduring disruption of visual function we find here is similar to the stable deficits reported earlier after V2 (Merigan et al., 1993) and V4 (Merigan, 1996) lesions, and quite different from the largely transitory disruptions found previously after MT lesions (Newsome & Paré, 1988). This pattern may also be different from the transitory severe disruption, followed by enduring smaller disruption, found for eye movements and motion perception after MT/MST lesions (Yamasaki & Wurtz, 1991; Pasternak & Merigan, 1993). Further studies will be needed to determine if these apparent differences are related to the different cortical pathways studied or the nature of the visual tasks.

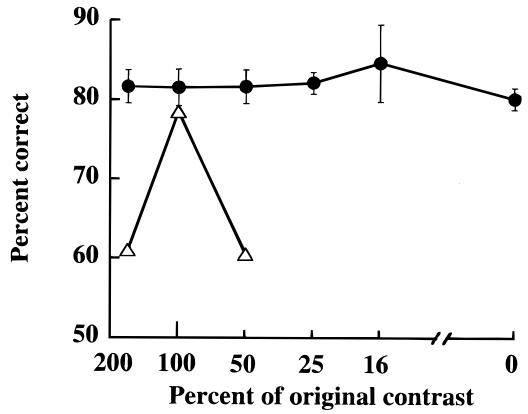

Fig. 10. Effect of increases or decreases in the contrast gradient (within the image) of shape stimuli on the discrimination performance of monkey 238. Open triangles show results for the 100% shape difference at the V4 lesion location, and filled circles show results for the 38% shape stimuli at the control location in the visual field.

Contrast sensitivity changes

As in a previous study (Merigan, 1996), V4 lesions caused a small elevation of contrast thresholds, an effect that may be due to increased internal noise resulting from the lesion (Pelli, 1985). Similar effects of V4 lesions were recently reported (Rudolph & Pasternak, 1996). We tested the possible effect of altered contrast thresholds on shape discrimination by reducing the contrast of the shape stimuli (see Fig. 10), and this did not alter shape discrimination.

What aspects of the shape stimuli were discriminated?

It is clear that the monkeys learned to perform a same-different discrimination, given that they switched immediately to near perfect performance with stimuli they had never seen before. This was true at both lesion and control locations for simple discriminations (e.g. oriented bar) and at the control location even for complex discriminations (e.g. upper part of stimuli made identical). Our results also suggest that the monkeys coded the multiple-viewpoint shape discriminations as different views of two 3D objects, given that their performance was well above chance after switching to new 3D stimulus pairs (see Figs. 1 and 2). Simple generalization could not have accomplished this result, since all new views of both objects were typically intermediate to those they had been exposed to in the previous testing. In addition, the large variation between stimuli in lighting would make this an extraordinarily difficult discrimination if the different examples were not tied together by their relation to the 3D object. The fact that removal of contrast cues to 3D shape, in the control experiment, did not seriously disrupt performance at the nonlesioned location shows that this discrimination could be performed without grey scale cues, although we do not know if the discriminations could have been learned without these cues.

Relation to previously reported effects of V4 lesions

The most consistently reported effects of V4 lesions are alterations of shape perception. Walsh and colleagues (Walsh et al., 1992) found severe disruptions of a variety of shape perception tasks,

most of which tested discriminations between slightly rotated letters. Schiller and colleagues (Schiller & Lee, 1994) have also reported difficulties with discriminations of simple geometric forms, although in a previous study (Merigan, 1996), we found that monkeys could perform such discriminations after V4 lesions. The present study suggests that simple shape discriminations may not be disrupted by V4 lesions, while complex ones are disrupted.

A second previously reported effect of V4 lesions was that they disrupt performance of some tasks (color matching to sample) only if the monkey had not been trained on that task at the lesion location before the lesion was made (Merigan, 1996). In the present study, we evaluated the effect of pretraining on one shape dimension followed by testing along two different shape dimensions after the lesion was placed. For monkey 257 the pretrained dimension was cross-sectional shape and for monkey 238 it was parallelism of sides. After the lesion, both monkeys were also tested on the previously unlearned discrimination, but we did not find greater disruption by the lesion. This suggests that the effect observed in the previous study may be confined to postlesion learning of a new task, not of new stimulus dimensions within a previously learned task.

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