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13. The thalamic origin of the sustaining activity is probably LGN subdivisions other than the A layers, all of which project to both V1 and V2, and possibly the pulvinar (*5*). We have determined that many cells in upper layers of V2 remain active during blockade of layer A (C. Lee, T. G. Weyand, J. G. Malpeli, unpublished data).
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23. We thank S. Adler, K. Akins, E. Dzhafarov, R. LaClair, D. Lee, T. Weyand, and two anonymous reviewers for advice and comments. Supported by NIH grant EY02695.

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The Role of the Primate Extrastriate Area V4 in Vision

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Area V4 is a part of the primate visual cortex. Its role in vision has been extensively debated. Inferences about the functions of this area have now been made by examination of a broad range of visual capacities after ablation of V4 in rhesus monkeys. The results obtained suggest that this area is involved in more complex aspects of visual information processing than had previously been suggested. Monkeys had particularly severe deficits in situations where the task was to select target stimuli that had a lower contrast, smaller size, or slower rate of motion than the array of comparison stimuli from which they had to be discriminated. Extensive training on each specific task resulted in improved performance. However, after V4 ablation, the monkeys could not generalize the specific task to new stimulus configurations and to new spatial locations.

TO UNDERSTAND HOW VISUAL INformation is analyzed by the brain, philosophers and psychologists have classified perception into such categories as color, brightness, form, motion, and depth (*1*). After the discovery of the numerous visual areas of the occipital, parietal, and temporal lobes (*2*), it was assumed that each area is involved in the analysis of one of these categories. This idea received strong impetus from work on the extrastriate area V4 of the monkey, which Zeki had proposed to be specialized for color vision (*3*). This inference was based on the claim that most single cells in V4 respond selectively to various colors. Subsequently it was demonstrated, however, that pattern and motion selectivities are also common among area V4 neurons (*4*) and, furthermore, that the responses of many of these neurons are affected by such factors as attention and stimulus relevance (*5*). Lesions of area V4 have resulted in a range of perceptual deficits, from virtually none to significant losses in color and in pattern perception (*6*).

To attempt to resolve the controversy about the function of area V4, we have examined the effects of its ablation on a broad range of visual capacities. Five monkeys were trained to do both visual detection and discrimination tasks that allowed us to confine stimuli to selected portions of the visual field and to test concurrently in regions that were intact and those that were affected by the V4 lesions (*7*). Each trial was initiated by the appearance of a small spot on a color monitor screen. After the animal had fixated this spot, as determined by eye-movement recordings (*8*), either a single stimulus or an array of stimuli appeared, and the animal had to shift his gaze to the appropriate visual stimulus by making a saccadic eye movement directly to it, to be rewarded with a drop of apple juice. Eye movements made to other locations were not rewarded and were recorded as errors. In the detection task a single target stimulus appeared somewhere on the monitor screen, whereas in the discrimination task several stimuli appeared simultaneously (4 to 64, but most commonly 8), one of which, the target, was different from the other identical stimuli (*7, 9*).

We examined brightness, size, shape, color, pattern, motion, and stereoscopic depth perception. Brightness discrimination was tested by the appearance of an array of identically shaped stimuli, one of which was of a different contrast from the other stimuli. The contrast difference between the target and comparison stimuli, as well as the location of the target within the array, was varied randomly by trial. To be rewarded the animal had to saccade to the odd stimulus (the target). There are two principal ways brightness discrimination can be tested with this task. In the first (Fig. 1A), the contrast of the target is higher than the comparison stimuli; in the second (Fig. 1B), the contrast of the target is lower. These two forms of testing revealed one of the new deficits we report here after V4 lesions. For size discrimination the targets and comparisons were similar to those shown (Fig. 1, C_1 and

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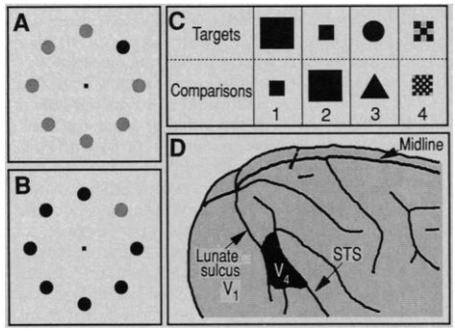

Fig. 1. (**A**) Brightness discrimination task as seen on the monitor screen; the contrast of the target relative to background is greater than the contrast of the comparison stimuli. (**B**) Stimulus parameters are the same as in (A), but the target is of a lower contrast than the comparison stimuli. (**C**) More examples of targets and comparisons that were used in arrays with similar arrangements to those in (A) and (B). In (C_1) the target is larger than the comparisons; in (C_2) the situation is reversed. (C_3) shows an example of a shape discrimination task and (C_4) a pattern discrimination task. (**D**) Example of a V4 lesion. Gray matter is removed on the cortical surface and to a depth of 3 to 5 mm down the anterior bank of the lunate sulcus and 2 to 3 mm within the posterior bank of the superior temporal sulcus (STS), resulting in removal of a large portion of the lower quadrant of the contralateral visual field representation of area V4 without impingement on neighboring areas.

C_2), also providing two principal ways of testing by having the target either bigger or smaller than the comparison stimuli. For color discrimination the target and comparison stimuli differed in wavelength composition and were set isoluminant, as determined in separate experiments with flicker photometry (*7*). The color values were varied systematically in steps along various color axes as represented in the Commission Internationale de l'Eclairage (CIE) chromaticity diagram (*7*). Examples of tests for shape and pattern perception are shown (Fig. 1, C_3 and C_4). We studied motion by presenting arrays of dots that moved coherently within small target regions. Depth perception was examined with stereoscopically viewed random dot stereograms.

After extensive training of the monkeys, area V4 was ablated by aspiration under general anesthesia (sodium pentobarbital) in all five. An example of a typical lesion appears in Fig. 1D. We aspirated on the average 1 cm^2 of surface area of V4 gray matter, which represented predominantly the lower quadrant of the visual field (*10*). The region of the visual field affected was mapped with testing procedures that were sensitive to the V4 lesion deficits. We then tested visual performance concurrently in the intact and the lesioned portions of the visual field at comparable eccentricities for several months by obtaining 1000 to 3000 trials daily from each animal. We measured both the percent correct performance and the saccadic response latency.

Results for color, pattern, brightness, and size discrimination obtained from one representative monkey are shown (Fig. 2). The animal had mild to moderate deficits in color and pattern discrimination, the magnitude of which increased as the difference between the targets and comparison stimuli was decreased (Fig. 2, A and B). Significant differences in response latencies were evident even with the easiest discrimination task (open arrows). For the brightness and size discrimination tasks (Fig. 2, C through F) a notable asymmetry is evident for the two modes of testing: there are only mild deficits when the target is brighter or larger than the comparison stimuli (Fig. 2, C and E), but there are dramatic deficits when the task is reversed so that the target is dimmer or smaller than the comparison stimuli (Fig. 2, D and F). The large difference in performance under these two sets of conditions is also reflected in response latency: with the targets brighter or larger (Fig. 2, C and E), response latencies were 15 to 20% longer at the lesion site, but with the targets dimmer or smaller (Fig. 2, D and F), they were 80 to 97% longer. As controls, we presented the targets used in Fig. 2, D and F, singly. The monkey's performance in this detection situation was close to 100% at both the normal and the V4 lesion sites, indicating that there was no difficulty in detecting the presence of the targets (*11*). Thus the sizable deficits seen with targets that had less contrast or were smaller than the comparison stimuli were not due to the animal's inability either to detect these stimuli or to perceive the differences between them and the comparison stimuli (Fig. 2, C and E). It appears that the crucial factor in the

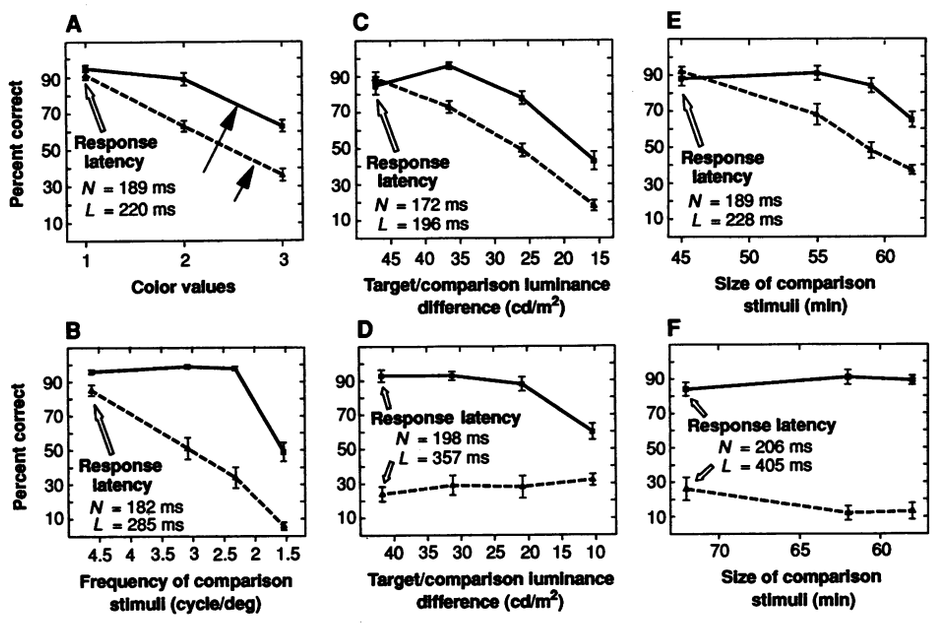

Fig. 2. Color, pattern, brightness, and size discrimination data obtained concurrently at normal and V4 lesion sites for one representative animal. (**A**) Color discrimination: The target stimulus was a yellow disk. The seven comparison stimuli appeared randomly on successive trials in three different colors selected along the red-green axis of the CIE chromaticity diagram from yellow toward red (1, reddish orange; 2, orangish yellow; 3, yellowish orange). The stimuli were isoluminant at 14 cd/m^2, and the background was white at 5.2 cd/m^2. Stimulus size was 65 min visual angle. (**B**) Pattern discrimination with checkerboard stimuli. The target frequency was constant at 1.15 cycles per degree, and comparison stimulus frequencies are shown on the abscissa. Luminance of the black and white checkerboards was 5.2 and 47 cd/m^2 and background was 5.2 cd/m^2. (**C** and **D**) Brightness discrimination task using eight stimuli with identical sizes (65 min visual angle) and shapes. The target in (C) was always brighter (57 cd/m^2) and in (D) was always dimmer (16 cd/m^2) than the comparison stimuli. Background luminance was 5.2 cd/m^2. (**E** and **F**) Size discrimination with target stimulus in (E) was always larger (65 min visual angle) and in (F) always smaller (32 min visual angle) than the comparison stimuli. Stimulus luminance was 52 cd/m^2 and background was 12.4 cd/m^2. Data points are based on a minimum of 100 trials each. Chance performance, as determined in control experiments using eight identical stimuli, was between 6 and 12%. The error bars represent ±1 SE. Response latency data are shown for the easiest discrimination in each graph (open arrows) (*N*, normal; *L*, V4 lesion data).

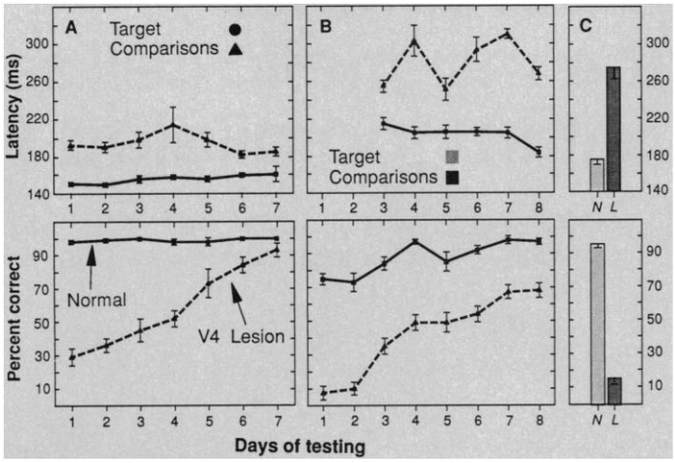

Fig. 3. Percent correct and saccadic response latencies over a period of several days for shape and brightness discriminations for one representative animal. (**A**) Shape discrimination tested for seven successive days with 60 to 100 trials per day per stimulus position. The error bars represent ±1 SE. (**B**) Brightness discrimination with target dimmer than comparison stimuli tested for eight successive days with 60 to 100 trials per day per stimulus position. (**C**) Same stimuli and task as in (B) but with stimulus array rotated 22.5°. (*N*, normal; *L*, V4 lesion data.)

failure to select the targets was that they were less intense or smaller than the comparison stimuli.

Similar results were also obtained when we used a discrimination task involving stationary and moving dot patterns. As long as the target was the moving stimulus, there was no discernible deficit at V4 lesion sites; when the situation was reversed, however, monkeys consistently failed to select the stationary target appearing in the midst of a group of moving comparison stimuli. In separate experiments we also established that there are only minimal or no deficits in the detection of singly presented targets when they are made visible from the background by virtue of only chrominance, motion, or stereoscopic depth information (*12*); however, when such targets appeared within an array of comparison stimuli, the same asymmetrical deficits arose as the ones observed with luminance cues (Fig. 2, E and F), indicating that the deficits pertain to the selection of "lesser" stimuli in arrays rather than to the processing of basic color, depth, or motion information. The tendency to react to and orient toward the most intense and largest stimuli in the environment is a basic, reflex-like disposition of living systems. To be able to select and attend to stimuli that have lesser physical characteristics (less intense, smaller, and so forth), sophisticated neural circuitry is necessary that apparently involves the color-opponent system of the primate retina and the areas to which it extensively projects: areas V1, V2, and V4 and the temporal lobe (*13*).

To determine the extent to which the animals could recover from the deficits we saw after V4 lesions, we tested them repeatedly on the same sets of tasks for thousands of trials. In doing so we uncovered a second major deficit after V4 lesions. For any given specific test there was a gradual improvement in performance with practice. An example of this appears for a shape discrimination task in Fig. 3A. The improvement was limited to percent correct performance; the response latencies did not change significantly. This improvement did not reflect a general recovery, however. Every time a new task was introduced, again a large deficit was observed that recovered with extensive practice. This is shown for a brightness discrimination task in Fig. 3B: initially poor performance was followed by a general improvement. When the same array that had yielded recovery over time was shifted to a new set of spatial locations, the animal's performance dropped again. In the example shown in Fig. 3C, the stimuli used for obtaining the results in Fig. 3B were all kept at the same eccentricity but were rotated 22.5 degrees; this relocation produced no difficulty in the intact portions of the visual field but devastated performance in the lesion area. We tested animals this way for several months on a variety of tasks with similar results: performance on each new task reached high levels rapidly in intact portions of the visual field and was not affected by shifting of the targets to new locations in the visual field, whereas performance at the V4 lesion sites always started at a low level and improved only gradually over time. On the basis of these observations it may be said that though normally what monkeys learn is readily applied to new stimuli and to new spatial locations, this is not the case in the V4 lesion area.

In summary, our results suggest that area V4, rather than being devoted only to specific, basic attributes of vision such as color and pattern, is part of neural systems that play a role in the selection of stimuli whose physical attributes render them less compelling than other stimuli that appear in arrays. The area is involved in visual learning and the translation of learned pattern relationships across the visual field. The persistent latency increase on all tasks suggests that area V4 also augments the speed with which visual analysis is performed. Our findings are consistent with current single cell recording studies in trained, alert animals that have shown that the responses of neurons in area V4 are modulated by attention, stimulus relevance, and perceptual context (*5*). In several respects the deficits we report here are similar to those that have been obtained by Mishkin, Gross, and others after lesions of the inferotemporal cortex (*14*).

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