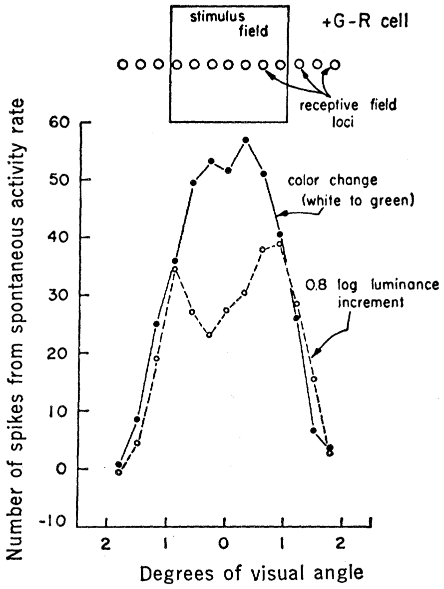

Fig. 2. Plot of the responses (spikes per second) of a +G—R cell to two different figures, each presented in different loci with respect to its receptive field. The relative locations of the receptive field and the figure for each data point are indicated in the drawing above the graph. The cell gave its maximum responses to the luminance figure when its receptive field was at the borders of the figure, whereas the largest responses to the color figure occurred when the figure was centered on the receptive field.

to black figures, and no border enhancement to colored figures.

Simultaneous brightness contrast is a very striking perceptual phenomenon: if a gray figure on a black background is compared to the same gray figure on a white background, it appears in the first case white and in the second black (the common textbook illustrations of this phenomenon give only a feeble indication of the strength of brightness contrast, because of the limited intensity range of the printed figures). This changed appearance of a figure depending on its background extends over the whole figure, not to just the border regions, and over retinal areas of many degrees of extent.

The same lateral inhibitory systems that are invoked to explain Mach bands have been assumed also to account for brightness contrast. A cell with an excitatory center and an inhibitory surround should indeed give a larger response to a gray figure on a black background than to the same gray figure on a white background (which would stimulate the inhibitory surround and thus diminish the response). But this response would hold only for figures that are roughly the size of the center of the cells' receptive fields. Although we find some variation in the size of the receptive field, such as that postulated by those who suggest the presence of different size-specific channels (*7*), none of the cells in this sample and none of the cells among many others we have examined in other experiments have receptive fields nearly large enough to account for brightness contrast over large areas. The cells receiving their inputs from the center of the eye have receptive fields whose centers are from about 1 to 30 minutes of arc, whereas brightness contrast operates over areas of 20° or more.

Despite the common assumption that a center-surround receptive field organization provides the mechanism for brightness contrast, there is no report in the literature of an examination of the responses of visual units under conditions in which the presence of contrast, as opposed to border enhancement, can be assessed. We did that with the cells in this study. In the experiment reported above we examined the responses to black and white squares on the same gray background; in this second experiment we recorded the responses to a gray square on either a white or a black background when the square was centered on the receptive field of the cell.

In no case did we find brightness contrast to be operating. A cell that fires to a white square, for instance, does not show a larger response to the gray square on a black background (which appears white by contrast) than to the gray square on a white background (which appears black). The responses to these two gray squares were always either the same or slightly different in the direction opposite to that expected from simultaneous contrast (as one would expect from stray light). Tests of spectrally opponent cells for color contrast (with a gray square on a red versus green background, for instance) also produced no evidence for contrast.

The center-surround organization of the cells' receptive fields should, we believe, be considered as a contour-enhancing mechanism. Except perhaps for very small visual objects, it does not produce brightness (or color) contrast. For that effect some other presumably cortical process must operate upon the border information.

RUSSELL L. DE VALOIS
PAUL L. PEASE

Primate Vision Laboratory,
Department of Psychology,
University of California,
Berkeley 94720

References and Notes

1. L. A. Riggs, F. Ratliff, J. C. Cornsweet, T. N. Cornsweet, *J. Opt. Soc. Amer.* **43**, 495 (1953).
2. Ernst Mach's papers on this topic have been translated and presented in F. Ratliff, *Mach Bands* (Holden-Day, San Francisco, 1965).
3. F. Ratliff and H. K. Hartline, *J. Gen. Physiol.* **42**, 1241 (1959).
4. G. Baumgartner, J. L. Brown, A. Schulz, *J. Neurophysiol.* **28**, 1 (1965).
5. A. M. Ercoles-Guzzoni and A. Fiorentini, *Atti Fond. Giorgio Ronchi Contrib. Ist. Naz. Ottica* **14**, 135 (1958); G. A. Fry, *Amer. J. Optom.* **25**, 162 (1948); G. J. C. van der Horst and M. A. Bouman, *J. Opt. Soc. Amer.* **59**, 1482 (1969).
6. R. L. De Valois, I. Abramov, G. H. Jacobs, *J. Opt. Soc. Amer.* **56**, 966 (1966); R. L. De Valois and R. T. Marrocco, in preparation.
7. A. Pantle and R. Sekuler, *Science* **162**, 1146 (1968); C. Blakemore and F. W. Campbell, *J. Physiol.* **203**, 237 (1969).
8. Research supported by PHS grant 5 R01 EY 00014 and by a PHS postdoctoral fellowship, 6 F02 MH 45700, to one of us (P.L.P.).

28 September 1970

■

Visual Attention in the Tree Shrew: An Ablation Study of the Striate and Extrastriate Visual Cortex

Abstract. *Removal of the striate area in tree shrews results in increased distractibility, which prevents the animals from learning to discriminate form when hue is an irrelevant and distracting cue. Removal of the extrastriate visual cortex results in the reciprocal deficit: an increase in perseveration manifested by an inability to shift attention when irrelevant dimensions are made relevant.*

The tree shrew (*Tupaia glis*) possesses two visual projections to the cortex: in the first, the lateral geniculate nucleus relays optic tract impulses to the striate area; in the second, the pulvinar nucleus relays superior colliculus impulses to the temporal area (*1*). Inasmuch as neither cortical area is the *sole* link in the chain connecting visual impulses to the other, the two systems are anatomically independent. We have obtained evidence (*2*) for some functional independence of the extrastriate visual area and the striate area as well. Without temporal cortex, tree shrews are severely retarded in learning to discriminate pattern and are unable to develop a reversal learning set. Without striate cortex, tree shrews can learn visual pattern discrimination at a normal rate and can develop a reveral learning set with visual discriminations. Indeed, the chief symptom so far uncovered by removal of striate is relatively mild—an increased susceptibility to camouflage; the animals are more easily misled or distracted by nonrelevant patterns adjacent to the relevant cues (*2*). This combination of factors—the relative independence of the two systems and the surprising degree of visual capacity preserved after removal of the striate system—provides an unusual opportunity for further ablation study. The symptoms produced by destruction of striate cortex not only provide clues about the normal function of striate cortex but may reflect the activity of the temporal system unbalanced by its partner. Similarly, symptoms resulting from ablation of temporal cortex can be regarded as reflecting the presence of the remaining striate cortex as well as the loss of the temporal area.

Our experiment was based on nine tree shrews: three normal animals, three with complete removal of the striate cortex, and three with large lesions of the temporal area. (It is not necessary to remove the entire pulvinar target in order to produce the syndrome just described.) Cortex was removed by suction, and aseptic precautions were strictly observed. As a behavioral measure we decided to use a test called a "nonreversal shift" (*3*). We trained the nine tree shrews (six of which had already suffered cortical ablation) to discriminate between horizontal and vertical stripes by rewarding the animals for choosing the horizontal orientation. The card bearing horizontal stripes (made from black and white construction paper) was sometimes in the left door and sometimes in the right door of a conventional two-choice apparatus [see (*2*) for details].

In addition, and this is the critical aspect of the experiment, on one-half of the trials the light transilluminating the horizonal stripes was red, and on the other half the light was blue; thus, the animal perceived red and black stripes or blue and black stripes. In the room where the animals were trained, the only sources of light were two Leitz projectors, one behind each door. To achieve a red or blue hue, Bausch and Lomb filters (either 450 or 630 nm) were placed in a holder between the projector and the door (*4*). Whichever color illuminated the card with horizontal stripes, the alternative color illuminated the card bearing vertical stripes.

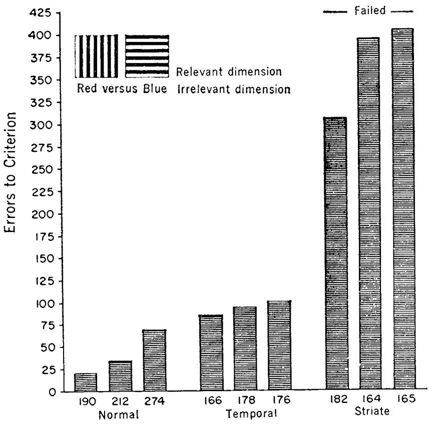

Fig. 1. Errors to criterion or until training was discontinued. The three animals with striate lesions failed to reach criterion in 35 sessions.

The animal then faced four kinds of trials: (i) left horizontal blue versus right vertical red, (ii) left horizontal red versus right vertical blue, (iii) left vertical blue versus right horizontal red, and (iv) left vertical red versus right horizontal blue. Each of these four combinations was presented five times every two sessions, and sessions (consisting of ten trials) continued daily until the animal reached a criterion of 100 percent correct. To achieve this learning criterion, the tree shrew had to attend to orientation but ignore color and position for the purpose of choosing between doors. When the animals had reached the original criterion, the sign of the correct door was changed from orientation of stripes to the hue of the light illuminating the stripes. At this stage of the training, the animal faced the new task of shifting attention from orientation to hue. The adjective "nonreversal" is used to describe this shift in order to distinguish it from one in which the dimension remains the same but the positive and negative values are reversed (*3*).

The results on the initial learning of the discrimination task are illustrated in Fig. 1. The chief point conveyed by the comparison of errors is the difference between the three groups. The animals with striate lesions gave by far the poorest performance; indeed, none of the three achieved the learning criterion without special remedial training, which consisted of reducing the distraction created by changing hues. When it was clear that the three animals with striate lesions were making no progress, we changed the procedure in an effort to simplify the task. Instead of giving four kinds of trials every session, only two combinations of color, position, and orientation were presented in a session: for example, left horizontal blue versus right vertical red, and left vertical blue versus right horizontal red. In two consecutive sessions, however, all four combinations were presented; if blue was on the left one day, red would be on the left on the next day. This procedural change was sufficient to permit two of the three animals with striate lesions to learn to select horizontal stripes.

Remedial training in these two cases carried over to the original problem, for when the position of the color again varied from trial to trial the tree shrews succeeded in ignoring the variation. Therefore eight out of nine animals eventually learned to discriminate orientation in the face of a nonrelevant or distracting cue, but the two successful tree shrews with striate cortex removed succeeded only after receiving remedial training. The third animal with a striate lesion never learned to discriminate orientation until color differences were entirely eliminated and both stimuli were given the same hue. Training was then terminated, since this animal could contribute nothing to the next question under investigation.

In the next step of the experiment the eight animals were presented with the same four combinations, but this time with hue as the relevant dimension and with blue as the positive cue. The plan was to shift back again to orientation after the animals had learned to choose on the basis of hue and to continue to alternate between hue and orientation until eight shifts had been completed. The results of this phase of the experiment are illustrated in Fig. 2 by individual learning records selected from each group. With respect to the shift from dimension to dimension, Fig. 2 shows that the animals with striate lesions now resembled the normal animals. The representative normal animal (tree shrew 274) took less and less time to learn with each successive shift and showed continued improvement on the first day after a shift. A similar improvement was shown by tree shrew 182 with a striate lesion, and the sixth and seventh shifts were accomplished without a single error, indicating the formation of a learning set. (The first trial is not included in the score since the animal must have a chance to learn the rules for any session.) In contrast, the animals with temporal lesions, illustrated by Tupaia 176, returned to a chance level with each shift. The two animals whose performance records are not illustrated also returned to chance level, but they were not so retarded in learning as was Tupaia 176.

Chance level, of course, is with respect to the stimulus dimension upon which the current shift is based. More significant than the failure of the animals to respond to the new dimension is their perseveration in responding to the previous cue dimension. For example, on the ninth day following the first shift, Tupaia 176's score was only 50 percent, or chance, when based on blue as the correct choice, but on that same day the animal's score for selection of horizontal stripes was 100 percent; even on the 21st session the proportion of trials in which horizontal was chosen was greater than the proportion in which blue was chosen (80 percent as compared with 60 percent). Similarly, after the second shift the animal perseverated in responding to blue, so that on the seventh and eighth sessions its performance was chance with respect to the correct orientation, but was 100 percent with respect to the previously correct hue.

Histological analysis of the lesions had not been completed in time for this report, but inspection of the cortical surfaces after the brains were removed suggests that the ablations were similar to those described in an earlier report (*2*).

These results can be explained if the two visual cortical systems concurrently mediate reciprocal aspects of selective visual attention. The striate region appears to participate in a mechanism that enables the tree shrew to concentrate his attention or to focus upon relevant cues in the presence of distracting stimuli. By contrast, the temporal region seems to contribute to a mechanism that induces the shift of attention from one cue dimension to other dimensions of greater relevance.

Since the tree shrew may represent an early stage of primate development (*5*), these results have significance for interpreting primate brain evolution. In particular, comparisons between the temporal cortex of tree shrew and that of monkey might prove fruitful. Indeed there is good evidence that the inferotemporal area of the monkey

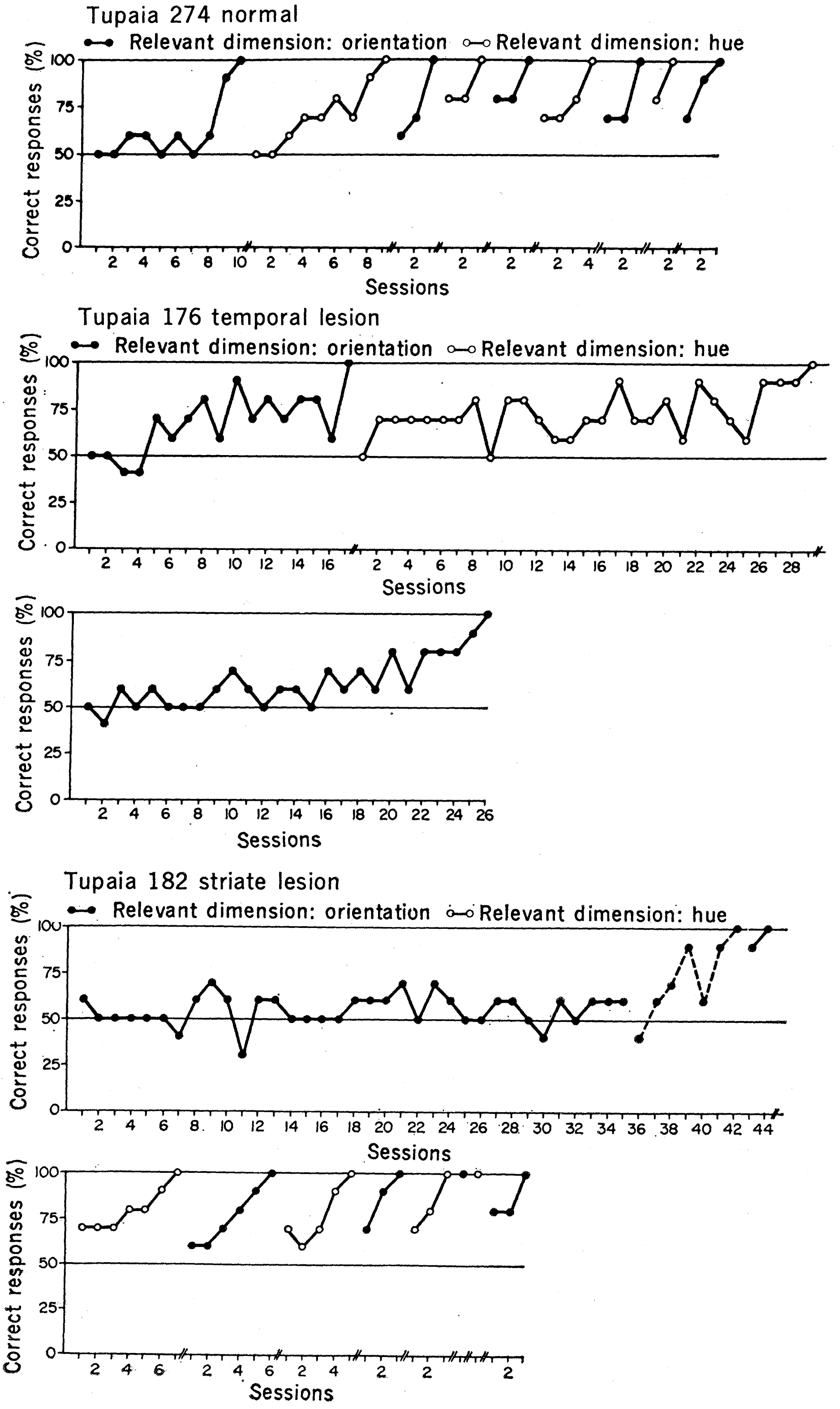

Fig. 2. Individual performance records for three tree shrews, one normal, one with removal of temporal cortex, and one with removal of striate cortex. After 35 sessions, tree shrew 182 received special training in which the position of the hues was held constant for each session; this training is depicted by a broken line.

plays a role in attention, and two symptoms have been described that bear on our results. The first symptom is a restriction in attention to only the most salient features of a stimulus (*6*); the second symptom is a difficulty in learning a less salient dimension when a more salient dimension is present and irrelevant (*7*). When viewed in terms of the salience of the stimulus dimensions, both symptoms seem to reflect a single deficit; but, when looked at in terms of our distinction between perseveration and distractibility, a different conclusion is suggested. The first symptom fits our picture of a tree shrew deprived of temporal cortex inasmuch as we would expect such a preparation to produce failure to notice less salient dimensions. But the second symptom could well apply to our animals with striate lesions, since their difficulty might be described as a failure to attend to a less salient dimension (pattern) when distracted by a more salient dimension (hue). Since we now know that the inferotemporal area of the monkey contains two functional subdivisions, we cannot help wondering whether the lesions in the two experiments cited differed in their rostral-caudal extent; the first symptom might be related to the rostral sector and the second symptom to the caudal sector (*8*). But if the visual cortex has undergone further differentiation between the evolutionary stages represented by tree shrew and monkey with the result that *three* main centers have replaced two, is there any good reason to assume that the subdivision of psychological functions present in the earlier stages will be preserved in the later stages? For example, we may ask whether the functional distinction between striate and temporal areas found in the tree shrew corresponds to separate centers throughout vertebrate history. The answer is almost certainly No, since there must have been a time in vertebrate history when the visual system had only one mechanism of control and integration, probably the optic tectum (*9*). As vertebrates evolved, the single system differentiated; two new centers developed at the targets of two separate pathways, the tectopulvinar path and the geniculostriate path.

Raising these questions points to the main significance of the present line of inquiry: the prospect of determining how psychological functions become further specialized as the anatomical substrate differentiates and, eventually, of understanding the evolution of higher intellectual faculties.

H. KILLACKEY
I. T. DIAMOND
Department of Psychology, Duke University, Durham, North Carolina

References and Notes

1. P. Abplanalp and W. Nauta, personal communication; ———, paper presented at the Conference on Subcortical Vision, Massachusetts Institute of Technology, Cambridge, June 1969 (*Brain Behav. Evolut.*, in press); I. T. Diamond, in *Contributions to Sensory Physiology*, W. D. Neff, Ed. (Academic Press, New York, 1967), vol. 2; ———, M. Snyder, H. Killackey, J. Jane, W. C. Hall, *J. Comp. Neurol.* **139**, 273 (1970); M. Snyder, W. C. Hall, I. T. Diamond, *Psychonom. Sci.* **6**, 243 (1966); M. Snyder and I. T. Diamond, *Brain Behav. Evolut.* **1**, 244 (1968).
2. H. Killackey, M. Snyder, I. T. Diamond, *J. Comp. Physiol. Psychol.*, in press.
3. N. J. MacKintosh, in *Animal Discrimination Learning*, R. M. Gilbert and N. S. Sutherland, Eds. (Academic Press, London, 1969), chap. 7, part 2.
4. For a detailed description of the characteristics of these filters, see M. Snyder, H. Killackey, I. T. Diamond, *J. Neurophysiol.* **32**, 554 (1969).
5. G. G. Simpson, *Bull. Amer. Mus. Natur. Hist.* **85**, 1 (1945); W. E. Le Gros Clark, *The Antecedents of Man* (Edinburgh Univ. Press, Edinburgh, 1959); J. A. Jane, C. B. G. Campbell, D. Yashon, *Science* **147**, 153 (1965); M. C. McKenna, *Folia Primatol.* **4**, 1 (1966); L. Van Valen, *Evolution* **19**, 137 (1965); A. S. Romer, *Science* **158**, 1629 (1967).
6. C. M. Butter, M. Mishkin, H. E. Rosvold, in *Stimulus Generalization*, D. I. Mostotsky, Ed. (Stanford Univ. Press, Stanford, 1965).
7. L. A. Rothblat and W. A. Wilson, Jr., *Psychonom. Sci.* **17**, 149 (1969).
8. E. Iwai and M. Mishkin, *Exp. Neurol.* **25**, 585 (1969); M. Mishkin, in *The Brain and Human Behavior*, A. G. Karczmar, Ed. (Springer-Verlag, New York, in press).
9. I. T. Diamond and W. C. Hall, *Science* **164**, 251 (1969).
10. Supported by National Institute of Mental Health grant 4849.

8 September 1970 ■

Taste of Water in the Cat: Effects on Sucrose Preference

Abstract. *Electrophysiological recordings show that water is not tasteless to cats. Also, unlike most mammals, cats appear indifferent to sucrose, but this may be because the taste of the sucrose is masked by the taste of the water in which it is dissolved. When the water taste is suppressed by the addition of small amounts of sodium chloride, cats take sucrose avidly.*

Cross-species investigations led Zotterman and his co-workers to conclude that cats, dogs, monkeys, and pigs have taste fibers responsive to water, but rats and men do not (*1, 2*). This conclusion was later revised on the discovery that responses to water in squirrel monkeys, cats, rats, and hamsters (*3, 4*) are contingent on the preceding adapting stimulus: fibers respond to water-after-NaCl, or water-after-sucrose, or the like, but not to water per se. Responses to water occur in every species tested, although the optimal contingencies differ from species to species. In man, water tastes sweet after quinine hydrochloride (QHCl) and citric acid, salty after urea, and bitter after sucrose and NaCl. The saliva of some individuals contains enough NaCl in itself to make water taste bitter (*5*). The experiment reported here demonstrates an unusual effect of the taste of water: water can prevent a preference for sucrose, presumably through its ability to mask the taste of sucrose in the cat.

To the student of taste, sucrose is of special interest because it is accepted by so many animals including man, insects, pigeons, chickens, rats, rabbits, hamsters, cattle, and monkeys (*6, 7*). Are cats an exception to the general rule? Carpenter (*7*) found that they fail to discriminate between water and sucrose at any concentration up to 1.0*M*. In addition, in early electrophysiological studies no sucrose-sensitive fibers were found (*8*). Nevertheless Frings (*9*) observed that cats find sucrose (0.5*M*) highly acceptable when dissolved in milk rather than water. The study reported here resolves this apparent discrepancy. Cats do have some fibers sensitive to sucrose (*3, 10*), but they also have water sensitive fibers that under normal salivary conditions may mask the sucrose responses and thereby interfere with taste discrimination. It is possible, however, to suppress the water responses and thereby render sucrose highly acceptable.

The idea that the water response is suppressible grew out of a study of neural responses from 26 single fibers obtained from 12 cats. The animal was anesthetized with sodium pentobarbital, and the chorda tympani taste nerve was surgically exposed and cut centrally. Action potentials from small groups of fibers separated from the whole nerve were recorded with a silver–silver chloride wick electrode,