

of ribonuclease; (c) observation of a hole or channel at the center of short rods of X-protein, which contains no nucleic acid.

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NONVISUAL FUNCTIONING OF OCCIPITAL CORTEX IN THE MONKEY*

BY J. ORBACH[†]

YERKES LABORATORIES OF PRIMATE BIOLOGY, INC., ORANGE PARK, FLORIDA

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In neurological theory the cerebral cortex has come to be regarded as a mosaic of specialized anatomico-functional regions. Recent work on the behavioral effects of cortical lesions in the monkey has, in general, supported this view.¹ Striate cortex is the example par excellence of a region highly differentiated in a structural and functional sense.² Its boundaries can be determined with the unaided eye, and its participation in vision is unquestioned.

It has been proposed a number of times that regions of the cortex participate in more general nonspecific functions as well. Over a century ago Flourens proposed an *action commune* in addition to the *action propre* of each part of the brain.³ Since then, Goltz⁴ and Lashley⁵ especially have propounded similar notions. Lashley demonstrated experimentally the nonspecialized functioning of virtually every sensorimotor zone in the cortex of the rat.⁶ Maze performance of cortically blinded rats, for example, was extremely inefficient as compared with normals or with *peripherally blinded rats*. The same effect was demonstrated in rats enucleated just after birth to rule out the possibility that learned imaginal processes were disrupted by the cortical lesions.⁷ Clearly, occipital tissue was involved in the nonvisual solution of the maze problem and in the maintenance of efficient performance. Lashley argued that the principle of localization be re-examined and proposed the theory of mass action to account for data such as these.

Recently the present writer launched an experimental program to compare the effects of brain lesions in the monkey with those reported by Lashley and others in the rat.⁸ Homologies in cortical regions of the two species are often difficult to draw, but striate cortex is exceptional in this respect and was chosen for initial study. The immediate aim was to demonstrate that striate cortex participates in nonspecific, nonvisual problem-solving and retention in the monkey. Tasks, too, are difficult to "homologize." Initially, a large battery of nonvisual tests was constructed, including simple discriminations (somesthetic and auditory), tests of generalization and transfer (in somesthesia), and tests of ability to respond differentially according to context (delayed response, alternation, and conditional reaction). A stylus maze, duplicating the pattern of the locomotor maze used by Lashley (maze 3),⁶ was also included in the battery. Four rhesus monkeys learned these tasks in total darkness to insure that response would be controlled by non-visual cues. Observation was possible with the use of a snooperscope, a device which converts infrared light to visible light seen by the experimenter only. Pre-operative retention scores were obtained and served as a base line to which post-operative retention scores were compared.

It is enormously difficult to remove striate cortex without damage to other structures in a fissurated brain like the macaque's, where a third or more is hidden in the depths of the calcarine fissure. In contrast to the case of the rat, however, there is no danger of damaging subcortical nuclei. In order to spare nonstriate cortex, partial striate cortex lesions were produced in two monkeys. In the remaining two, virtually all striate cortex was removed, with concomitant damage to peristriate cortex on the medial surface of the hemispheres. Thalamic studies of retrograde degeneration indicated that less than 1.3 per cent of the neurons remained in the lateral geniculate bodies. All operations were performed in one stage, using aseptic precautions. Tissue was removed by blunt dissection and aspiration.

The operation appeared to have no effect on the nonvisual behavior of any of the monkeys.⁸ The delayed-response performance suffered somewhat in one monkey but was unaffected in the remaining three. It is especially to be noted that the stylus maze habit was extremely well retained by all four. These monkeys were unquestionably efficient performers on all the tasks outlined above. Clearly, no support for Lashley's contention that striate cortex exerts a facilitative action on other regions of the brain was indicated.

In an attempt to rule out the remaining doubt in the writer's mind, a locomotor replica of Lashley's maze 3, suitable for monkeys, was constructed. Five naive rhesus monkeys and one sophisticated one were selected as subjects. The procedure followed Lashley's in every detail.⁹ The monkeys learned to traverse the maze errorlessly, after which they were peripherally blinded. They were enormously affected by the lack of vision but eventually reached the same pre-established level of accuracy. Following a two-week rest interval, retention for the habit was determined (again used as base line to which postoperative retention was contrasted). Large occipital lesions were produced, involving virtually all striate cortex and a sizable portion of peristriate cortex. A two-stage operation was performed on three monkeys, a one-stage operation in the remaining three. Testing commenced two weeks after operation in each case.

The unilateral lesions appeared to have no effect on the maze habit (one of these three monkeys succumbed to a severe attack of dysentery before the second operation). On the other hand, bilateral occipital lesions (produced in one or two stages) had a consistently adverse effect on maze performance. All monkeys made a larger number of errors and traversed the maze more slowly after both hemispheres were involved in the lesion. Total errors made in the first ten trials of testing are summarized in Table 1. Deficits were in no way as striking as those re-

TABLE 1
ERRORS MADE DURING THE FIRST TEN TRIALS OF TESTING IN TRAVERSING
AN EIGHT CUL-DE-SAC MAZE

	SUBJECTS					
	Styx	9	10	11	12	13
After two-week rest preoperatively	1	12	4	6
After unilateral lesion	2	11	6
After bilateral lesion	603	26	41	10	44	..

ported for the rat, but the maze performance, though mildly inefficient, was in marked contrast to the lack of effect on the host of nonvisual tasks and the stylus maze used previously. Additional confirmation of these facts was provided by one of the maze-deteriorated monkeys who learned and was tested on a number of the nonvisual discrimination tasks, none of which suffered as a result of the operation.

In summary, the data indicate the following: (1) Nonvisual discriminations of varying degrees of complexity and stylus maze performance are not affected by occipital lesions. (2) Locomotor maze performance suffers as a result of occipital lesions. The monkeys do not appear "demented," nor have they completely lost the habit,⁹ since some show large savings in relearning the maze. This result is to be contrasted, on the one hand, with the more deteriorated maze performance reported for the rat and, on the other, with the lack of effects on discrimination tasks of varying complexity in the monkey. Both one- and two-stage operations lead to the same effects. And problem-solving sophistication seems not to be a relevant factor. (3) The differential effects summarized in points 1 and 2 have been recorded in a single monkey.

No marked success has yet been achieved in an analysis of the differential requirements for the solution of locomotor and stylus maze problems.

There is no way of ruling out at present the possibility that the locomotor maze deficits are related to the large peristriate cortex lesions and not at all (or only partly) to the "primary visual" cortex. If this should eventually prove to be the case, it will provide additional evidence opposing the traditional view that peristriate cortex constitutes a visual "association" area in the monkey.

The principle of corticalization of function has received much support from comparative studies of the visual system. It is fitting, therefore, that striate cortex should provide evidence of lack of complete specificity of function. From a comparative point of view, the present data, together with Lashley's and Tsang's, suggest that increasing specificity proceeds in parallel with increasing corticalization as the phylogenetic scale is ascended. And, just as corticalization is incomplete in the monkey, so is specificity of cortical function.

* A detailed report of the data and anatomical verification of the lesions will appear elsewhere.

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DO FUCUS EGGS INTERACT THROUGH A CO₂-pH GRADIENT?

BY LIONEL JAFFE*

HOPKINS MARINE STATION, PACIFIC GROVE, CALIFORNIA

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In 1889 Rosenvinge¹ reported that the direction of the main morphological axis, or polarity, of the eggs of the Fucaceae could be determined by neighboring eggs. Developing in darkness, they were found to germinate proximally, i.e., to develop their rhizoids or basal poles toward their neighbors. This so-called "positive group effect" has been well confirmed,^{2, 3, 4} though a tendency toward proximal germination between the smallest of groups, a pair of eggs, was found to occur only below pH 7.6.^{5, 6}

An understanding of this mutual orientation would bear upon two broader problems: the origin of polarity and the mechanisms of morphogenetic interaction between cells. Rosenvinge¹ suggested an oxygen gradient to be responsible for the positive group effect; Olsen and du Buy,⁷ an auxin gradient; Whitaker,⁸ a CO₂-pH gradient. Whitaker supported his proposal by demonstrating that when *Fucus* eggs are exposed to a CO₂-pH gradient in darkness, where they respire, they do, in fact, germinate toward the high CO₂, high H⁺ pole (except at very low pH's, on the border line of growth inhibition).⁹ Moreover, so many other facts fit neatly into this picture that Whitaker's hypothesis has won wide acceptance: In a gradient of white light, rhizoids develop from the darker side; in a thermal gradient, from the warmer side; in a gradient of dinitrophenol (averaging 10⁻⁵ M at threshold) or of potassium indole acetate (averaging 10⁻³ M at threshold), from the side of higher concentration.^{8, 10}

However, the positive group effect has been reported to appear in illuminated, and hence presumably photosynthesizing, cultures.^{1, 2, 3} Although this suggests oriented development in a direction opposite that expected on the basis of Whitaker's hypothesis, the results are ambiguous. First, it cannot be inferred from the published data that the illuminated eggs maintained net photosynthesis. Second, the observed effects may in part have been due to mutual shading of the eggs, since in a gradient of white light rhizoids develop from the darker sides. For these