Vision in Monkeys after Removal of the Striate Cortex

by
N. K. HUMPHREY*
L. WEISKRANTZ*
Psychological Laboratory,
University of Cambridge

Monkeys deprived of their visual cortex (area 17) have been thought to be unable to discriminate much more than "total luminous energy". In particular, they have been considered incapable of localizing visual events in space. It has now been shown that they can be trained to detect and accurately reach out for objects of certain kinds presented visually.

TOTAL removal of the striate cortex in monkeys results in a loss of vision so severe that in their ordinary behaviour the animals seem blind. In formal testing situations, however, it has been possible to demonstrate a certain degree of visual capacity: pupil responses to light are still present; opto-kinetic nystagmus elicited by a large field of moving stripes is present, at least some months after surgery[1,2]; in addition, performance may be good on certain kinds of visual discrimination. Kluver, in a series of classic papers[3], analysed the visual discrimination capacity of the de-striate monkey as an ability to discriminate "total luminous energy". More recently Weiskrantz[4] has shown that some discriminations are possible even when the discriminanda are matched for luminous flux and has suggested that there is an ability to discriminate "total retinal activity"—contour length, movement and flicker contributing besides luminous flux. There has been general agreement, however, that spatial information is no longer available: the lesion eliminates "visual space with its dimensions"[3]. We wish to report here new observations on two de-striate monkeys which show that they can not only detect but accurately locate certain objects by vision.

The subjects were two adolescent rhesus monkeys. Bilateral total removal of striate cortex was carried out under 'Nembutal' anaesthesia by occipital lobectomy followed by aspiration of the striate tissue remaining on the lateral surface and in the depths of the calcarine fissure. Histological verification of the lesions has not yet been made because the animals are still alive awaiting the completion of subsequent experiments.

The observations were made about 19 months and 5 months, respectively, after surgery. During the previous months both monkeys had been tested on various kinds of visual discrimination[4] and had reached a good level of performance on some of the problems. These discriminations included brightness problems, for example, black versus white, and elementary pattern problems, for example, black and white stripes versus homogeneous grey (matched for total luminous flux), but the visual capacity revealed could be interpreted in terms of discrimination of total retinal activity and required no supposition of spatial discrimination. In addition, the monkeys had been tested in a nystagmus drum and showed clear opto-kinetic nystagmus; they also showed good pupil responses. Apart from this evidence they had given almost no sign of visually guided behaviour.

A surprising fact had, however, been noticed: the monkeys occasionally turned their heads or eyes in the direction of a moving object. We were inclined at first to attribute this to an acute sound sense or an ability to detect movements of air. Further observation convinced us, however, that the response was genuinely based on vision and we were led to examine it more carefully. Within a few days we were able to demonstrate a quite unexpected visual capacity.

Both monkeys showed similar development of visually guided performance and a case history of one (monkey Hln, 19 months post-surgery) can serve to describe the testing method and results. Testing was carried out

* Present address: Institute of Experimental Psychology, University of Oxford.

in the home living cage, fitted with a 2 ft. × 2·5 ft. front of 2·5-in. wire mesh. The first stage was to train the monkey to reach through the mesh to find a morsel of food (a nut or piece of fruit) which was held out to him by the experimenter. The requirement was that he should search the field by reaching from one place to another until he made contact with the experimenter's hand holding the food. This training was accomplished by a simple process of shaping in which at first the experimenter deliberately moved his hand to whatever position the monkey happened to reach and then progressively required him to reach closer and closer to his hand before rewarding him. Within a short time the monkey learned to find the experimenter's hand in any part of the field by a series of exploratory reaches. The next stage was to try to help him in his search by visual cues.

It was soon clear that when the experimenter held his hand stationary the monkey had no idea where it was and reached at random. If, however, the hand was moved, by waving it gently or wagging a finger, he did have some idea of its location and reached at once in roughly the right direction. It seemed at first that his ability to localize was very poor, but with practice he got better and better. Eventually he could reach for the hand promptly and accurately as soon as it moved; but while it was stationary he still appeared quite blind. To ensure that his ability to locate movement was not based on non-visual cues, he was tested in darkness, whereon his performance dropped to a chance level.

A man's hand at monkey's arm's length is a rather big target and the accuracy of reaching had not yet been tested to its limit; moreover, the effective stimuli had not been well defined. Further testing was therefore undertaken more systematically. Observation so far had shown that the response of reaching to touch a perceived object was a simple and seemingly natural response for the "blind" monkey; it had the advantage also that it was self-correcting because success or error in locating the object was immediately signalled by touch. This response was therefore retained as the index of vision. Instead of the experimenter's hand, the objects to be detected were 1-in. square wooden blocks held by the experimenter on the ends of wire sticks. Different visual stimuli could be attached to or painted on these blocks and they could be held stationary or moved. The monkey was required to reach out and grasp the block. Success was rewarded by a morsel of food put directly into his hand which he held out expectantly after letting go of the block. With this procedure, the following visual ability has been demonstrated.

Detection of a moving object. The monkey is extremely sensitive to moving objects of all kinds. In a typical case, he will reach out to grasp with a sure hand a 1-in. black cube which is waved very slightly at arm's length from him. His sensitivity is so acute that it is hard to hold objects still enough to prevent him detecting their tremor. Speed of movement, over a wide range, seems not to matter. All sizes and shapes of objects from a 0·25 in. cube to a long straight bar are detectable, although with large objects he tends to reach for one edge. The objects can be lighter or darker than the background. The absolute level of illumination may be varied over the

whole range over which a human observer can easily see; he has, for instance, performed well both in a very dimly lit room and under very bright illumination while a film was being made.

For most routine testing the stimulus object has been a 1 in. cube painted with black and white stripes. In order to avoid ambiguity concerning where the monkey should reach to, the movement given to it is rotation about its centre rather than change in position. When the monkey sees the object he usually shows an obvious expression of recognition (an "aha!" reaction) and turns his eyes towards it before reaching. He is best at detecting the object if it is presented near the centre of his visual field and will often miss it in the peripheral field; rough observation suggests that he gets very inefficient about 40° out from the centre. He is equally good in all quadrants of the field. He does not appear to be able to discriminate distance and if the object is presented nearer or farther away than the standard arm's length he over- or under-reaches; he will, for instance, reach forlornly for a moving object 6 ft. away. It is not necessary for movement of the object to be kept up until he reaches for it or even until he has had time to fixate it; he can detect and locate a sudden sharp movement. He can remember the location of an object after it has stopped moving and if, for instance, he has his hands full of food or is otherwise occupied when the object is moved he may defer reaching for several seconds but then reach accurately. If translational movement is used rather than simple rotation, he can often reach accurately for an object which has moved and come to a stop, although he may sometimes reach to a point along the object's path rather than its terminal position. He does not, however, seem to be able to track a moving object and is unlikely to reach accurately for it while it is still moving along; this inability is paralleled by his apparent failure to follow a moving object with his eyes.

Detection of a stationary object. The monkey never detects a stationary black or white painted cube. This is so even though he may search actively with his eyes and thus cause the image of the object to move over his retina. He cannot reliably detect a stationary neon light in ordinary room illumination, although occasionally he does reach for it with surprising accuracy. If the background illumination is reduced, however, he does become able to detect the light, and in darkness can locate it well. With a light of 1·5 log foot lamberts his performance becomes good below about 2·7 log foot lamberts background illumination. No systematic observations have been made on eye movements or the relative efficiency of different parts of his visual field here because it is difficult for the experimenter to see.

Detection of light flashes. The monkey can detect and locate a flashing neon light in either room illumination or darkness. He is very sensitive to flash rates of about 10 per sec (flash duration 5 msec). As the flash rate is increased he remains good until about 45 per sec, but is unable to detect rates beyond 55 per sec. This threshold corresponds very closely to the critical flicker fusion frequency for a human observer. If the flash rate is initially high, say 100 per sec, so that the light appears stable, and is then progressively lowered, he detects the light at about the point where it begins to flicker for a human observer. He can detect slow flash rates down to single isolated flashes, although he does have more trouble in locating the latter. With slow rates of about 1 flash per 4 sec he does not reach after the first flash but turns his eyes towards it and waits for the next flash to occur in nearly central vision before reaching. With single isolated flashes where he can get no further information by waiting he tends to reach rather tentatively, although often quite accurately, unless the flash happens to occur close to where he is already looking, in which case he is more confident. As with detection of movement, he is much less efficient in the peripheral than in the central field.

Detection of two objects presented together. To test further the monkey's ability to localize objects in space, an attempt was made to train him to respond to two objects presented simultaneously in different positions. The objects were held out as before and he was required to grasp one and then the other in sequence to get a reward. Pairs of rotating 1-in. cubes or flashing neon lights were used. They were presented in random spatial relationship to each other.

The monkey very quickly caught on to the procedure. He can perform well with both kinds of stimuli. He is best when the objects are fairly widely spaced, about 10 in. apart, but can also do well with them closer together; when they are less than about 3 in. apart, however, he sometimes reaches for the same object twice or occasionally reaches between them. The relative spatial orientation of the two objects does not matter and he is just as good at locating two objects one above the other as two objects side by side. This capacity provides him with the basis for simple spatial pattern discrimination: for instance, he clearly discriminates a horizontal from a vertical relationship when he responds appropriately to objects presented in the two ways. He nearly always fixates each object before reaching for it, although he does not have to. With moving objects, the movement does not have to be kept up until he reaches and he can accurately locate two objects which are given only a sudden rotational jerk; he has not, however, shown much ability to locate two single light flashes.

Two general features of the monkey's performance are of interest. One is that he performs well only when he attends to what he is doing. If he is over-excited or distracted by some commotion outside his cage his performance breaks down and he tends to reach wildly. Although this may seem obvious, it would not in fact be typical of a normal monkey performing the same task. The other feature is that he sometimes shows "false positive" responses, reaching apparently purposively to an empty part of the field. Together, these observations suggest that he is working not far beyond the threshold of his capacity and that he may mistake internal "noise" for an external stimulus.

The other monkey in the group (monkey Hmr, 5 months post-surgery) has showed a similar ability to detect both moving objects and stable and flashing lights. His performance at best is as good as that of the monkey just described. He has, however, developed a bad habit of swiping for the object instead of reaching straight to it. He also shows rather more false positives than the other monkey. In general he appears less eager to be tested and tries less hard.

The most conservative explanation of these results would be that the striate cortex has not been removed completely in either monkey. The removal of the last vestige of striate tissue from the depths of the calcarine fissure is surgically difficult and the possibility of incomplete removal cannot be discounted until histological verification of the lesions is made. Allowing, however, that this may be so, there is good reason to doubt that it would be an adequate explanation of the results. First, any remaining striate tissue must lie in an area serving a small part of the far periphery of the visual field; but the monkeys are consistently better at locating objectsl near the centre of the field; they fixate objects with central vision, they can locate two objects at once in different parts, and they show no bias towards any quadrant of the field. Second, Cowey and Weiskrantz[5], using a method of perimetry with monkeys that accurately controls for eye movements, have shown that after striate lesions there is an ability to detect light flashes over the whole of the affected area of the field which certainly does not depend on remaining striate tissue. Although their study did not bear on the ability to localize flashes, the clear demonstration of the possibility of extra-striate vision makes it easier to accept the present results without special pleading.

The most striking feature of the present study is the evidence for spatial localization by the de-striate monkey. Similar findings have never been reported in detail, although Pasik, Pasik and Krieger[6] say that, some months after surgery, their de-striate monkeys "followed large white targets and grasped at a source of light". When compared with evidence for other species, however, the results may be thought less surprising. In lower mammals there are several reports of the existence of considerable visual capacity after removal of striate cortex, in particular an ability to discriminate moving from stationary objects (reviewed by Weiskrantz[7]). Especially notable is the recent study of the tree shrew[8] where striate ablation was found to have no obvious effect on visually guided behaviour. In the cat it has been reported that striate ablation soon after birth may have little effect on the subsequent development of vision[9]. But in man also there are reports in the clinical literature of cases of cortical "blindness" after damage to the striate area where residual vision existed in the affected fields. Riddoch[10] describes several cases showing ability to perceive movement within perimetrically blind fields. He says, "The patients have great difficulty in describing the nature of the movement they see: it is so vague and shadowy. But they are quite sure that neither shape nor colour can be attributed to it, and that it can be detected in a field which is entirely blind to stationary objects". Describing a similar case, Holmes[11] says, "only large white moving objects may be recognized . . . when they cease to move he sees them no longer; they disappear". Bender and Krieger[12] report cases showing an ability to perceive and localize movement and also an ability to see a flickering light or a stable light under conditions of otherwise total darkness. They mention that the perceptions were often unstable and that sometimes illusory movement was seen. Denny-Brown[13] reports a patient with complete hemianopia who could perceive small moving objects in the blind half of the field. He comments that self-induced head movements did not help the patient to see an object if it was stationary. In few of these clinical cases, however, has there been adequate post-mortem verification of the extent of damage to striate cortex. Perhaps for this reason, the possibility of extra-striate vision in man has received little acknowledgment.

The question remains as to what nervous structure may mediate the residual vision after striate lesions. The obvious candidate is the superior colliculus. We have recently made electrophysiological recordings from single units in the superior colliculus of monkeys and the response properties of these units are in fact well suited to underly the visual behaviour described in this study. It would, however, be disingenuous to press an analogy between single unit responses and behaviour when a direct method for testing the hypothesis is available. We hope, therefore, soon to study the effects of making collicular lesions in our two de-striate monkeys.

Note added in proof (July 4, 1967). Since this paper was submitted, further work with the same animals has revealed a degree of visual capacity beyond that described. With more extensive training there has plainly been a progressive change in the limits to what the animals can see. Monkey Hln has developed an ability to locate stationary lights at much lower contrast levels than those given above: he can now respond to even a dim pea-bulb in room illumination, although he remains apparently quite unable to detect objects darker than the background. The other monkey, Hmr, who has become more willing to be tested, has shown a still more surprising development: he can now respond reliably to almost any small stationary object in room illumination, whether lighter or darker than the background. Both monkeys still apparently find the task of detecting stationary objects relatively hard compared with, say, moving objects. The impression is that they have central tunnel vision for stationary objects. They look from one place to another until, as though by chance, the object falls near the central field and then they may stare fixedly at it before reaching; when they do reach, their accuracy is as good as with moving objects. In view of these new results we should say that we cannot be confident that we have even yet demonstrated the full potential for vision of these animals.

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Cutaneous Receptive Fields of Single Nerve Cells in the Thalamus of the Cat

by
G. GORDON
J. R. MANSON
Laboratory of Physiology,
University of Oxford

This article describes some new receptive properties of cells in the nucleus ventralis posterolateralis. It is shown that the nucleus contains mechanoceptive cells with excitatory or inhibitory thermoceptive influences on them, that the observation of surround inhibition in this nucleus depends in part on the type of anaesthesia used, and that some of the cells have directional sensitivity.

THE study of the receptive fields of single cells in the various nuclei of sensory systems has been valuable in understanding the transformations used by these nuclei in the analysis of sensory information. In the sensory systems of the skin, receptive field is usually defined as the area of skin from which natural stimuli, thermal or mechanical, cause excitation of the cell. In anaesthetized cats, we have investigated cells in that part of the thalamus (the main core of the nucleus ventralis posterolateralis) which receives the main output of the dorsal column nuclei, where analytical transformation defined in a semi-quantitative way by previous experiments[1] has already occurred. This region projects in turn to the cerebral cortex. The position of the tungsten recording electrodes was checked histologically, and the position of many cells marked by electrolytic lesions.