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## Vision in a monkey without striate cortex: a case study

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**Abstract.** A rhesus monkey, Helen, from whom the striate cortex was almost totally removed, was studied intensively over a period of 8 years. During this time she regained an effective, though limited, degree of visually guided behaviour. The evidence suggests that while Helen suffered a permanent loss of 'focal vision' she retained (initially unexpressed) the capacity for 'ambient vision'.

### 1 Introduction

In 1965 Weiskrantz removed the visual striate cortex from an adolescent rhesus monkey, Helen. In the 8 years between the operation and her death in 1973 this monkey slowly recovered the use of her eyes, emerging from virtual sightlessness to a state of visual competence where she was able to move deftly through a room full of obstacles and could reach out and catch a passing fly. Helen's history has been told in part in earlier papers (Humphrey and Weiskrantz, 1967; Humphrey, 1970; 1972; Weiskrantz, 1972). Now that she is dead and histological evidence of the extent of the brain lesion is available it is time to take stock. This paper provides an account of the histology, a résumé of the behavioural evidence, and a brief theoretical discussion.

### 2 Anatomy<sup>(1)</sup>

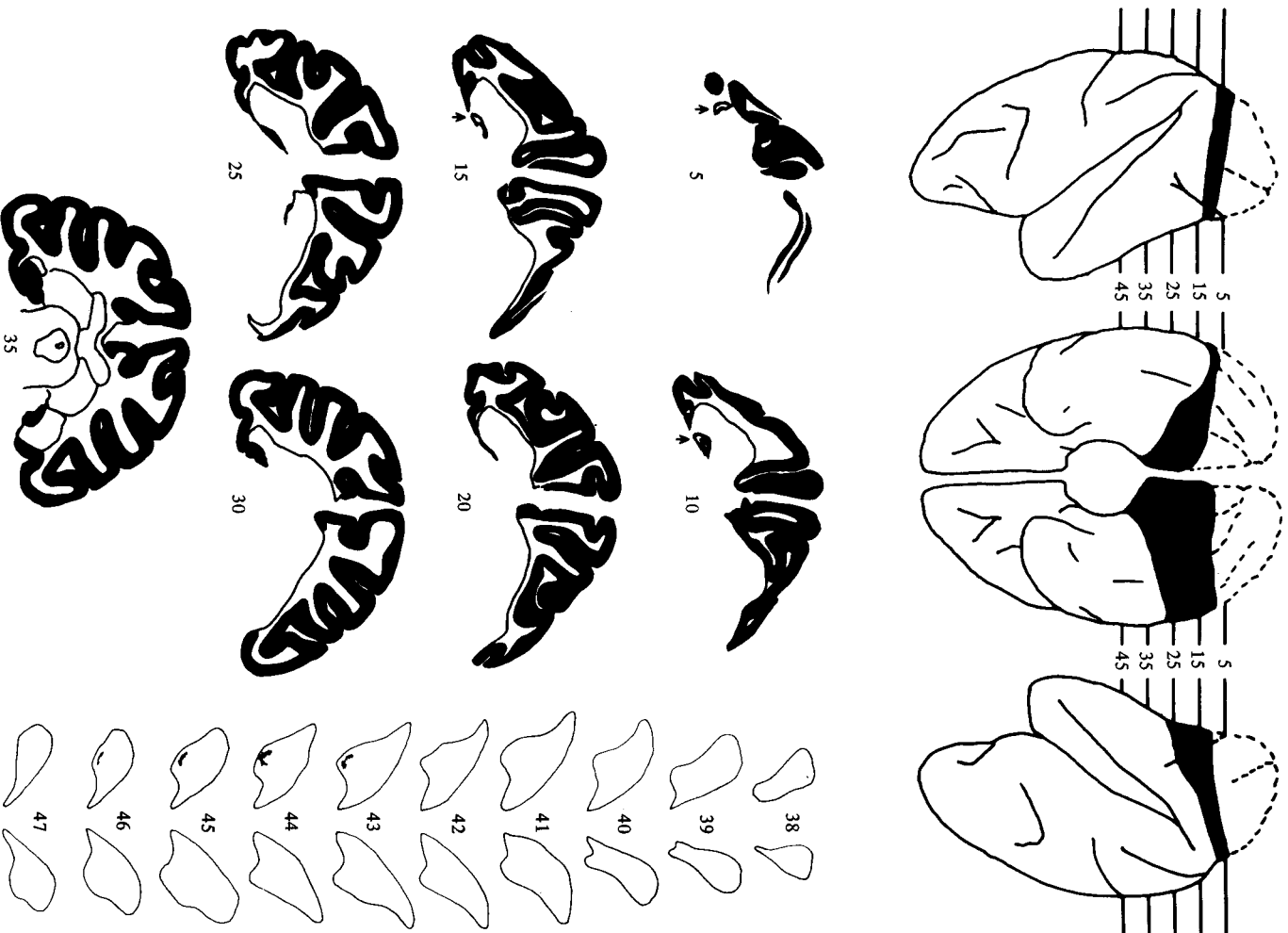
#### 2.1 Brain

The animal was tranquilised with an intramuscular injection of Sernylan, then deeply anaesthetised with Nembutal. After the eyes had been removed, the animal was killed with an overdose of Nembutal and was immediately perfused through the heart with 0.9% saline followed by formal-saline. The head was mounted in a stereotaxic instrument and the dorsolateral surface of the brain was exposed. A vertical coronal cut was made through the brain at stereotaxic coordinate A 25 mm. The entire brain was then removed from the head, photographed, and the posterior three-quarters embedded in L.V.N. Sections were cut at 50  $\mu$ m and every twentieth section was stained with thionin. An intermediate 1 in 20 series was stained with cresyl violet.

Figure 1 shows the surface extent of the lesion and cross sections through the cortex and lateral geniculate nuclei. In both hemispheres the lesion extended beyond the margins of area 17 to include areas of nonstriate cortex, especially on the ventral surface. On the left-hand side a small island of striate cortex was left apparently intact in the depths of the calcarine fissure. Corresponding to this area of spared cortex there was a small region of apparently normal cells in the anteroventral part of the dorsal lateral geniculate nucleus on the left side.

The lateral geniculate nucleus is probably a better indicator than the cortex of the extent to which the geniculostriate pathway was spared, since the island of cortex, which looked normal, may have been undercut. Unfortunately no accurate map is available of the projection of the retina onto the lateral geniculate nucleus, so that it is not possible to say with confidence how large an area of the visual field was not directly affected by the lesion. However, Polyak's (1957) drawings of the

<sup>(1)</sup> Dr Alan Cowey supervised the histology and made the examination of the eyes.



**Figure 1.** Reconstruction of Helen's brain. In the drawings of the surface of the brain black areas indicate absence of cortex, dotted lines show the boundaries of the occipital lobes before lobectomy. In the cross-sections through the whole brain black areas show intact nonstriate cortex; the fragment of intact striate cortex is shown by arrows. In the cross-sections through the lateral geniculate nucleus stippling indicates the presence of apparently normal cells. Numbers refer to every tenth section (sections were cut at 50  $\mu\text{m}$ ).

retinogeniculate projection, based on his own studies of retinal lesions in the rhesus monkey, provide a reasonable guide. From these it may be estimated that the normal cells in the lateral geniculate nucleus corresponded to an area in the visual field as shown in figure 2, lying in the upper right-hand quadrant, extending in from the periphery to about 60 degrees from the fovea.

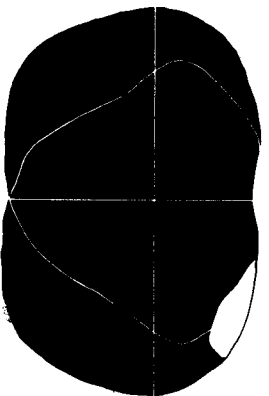


Figure 2. Helen's visual fields showing the probable extent of the cortical field defect.

## 2.2 Eyes

Histological examination of the retinae revealed a remarkable depletion of ganglion cells. The findings are described in detail by Cowey in the accompanying paper (Cowey, 1974). Whereas in a normal eye the ganglion cells are densely packed near the fovea and thin out rapidly towards the periphery, in Helen's eyes the ganglion cells were sparsely and almost evenly distributed right across the retinae. In terms of ganglion cell density the whole of her retina had come to look like the peripheral retina of a normal eye.

## 3 Behaviour

### 3.1 Spatial vision

For 19 months following the operation nothing was seen in Helen's behaviour to suggest any capacity for spatial vision. She was not unreactive to light, but such vision as she had could be accounted for in terms of an ability to discriminate 'total retinal activity' (Weiskrantz, 1963) and there was no reason to doubt Klüver's dictum that striate cortex lesions 'abolish visual space with its dimensions' (Klüver, 1942).

Perhaps because we were too much under Klüver's spell, we did not notice sooner a paradoxical aspect of Helen's behaviour, namely that she would occasionally turn her head or eyes towards a moving object in the visual field.

These directed eye movements were at first not easy to elicit. But by a simple shapling procedure, with food as a reward, it proved possible not only to increase the frequency with which she would 'look' at moving targets but also to induce her to reach out with her hand towards the object which caught her eye. In this way she was trained within a few weeks to reach out and grasp small moving objects held up in front of her on the end of wire sticks. At first her reaches were clumsy and ill-directed, but their accuracy rapidly improved and she was soon able to reach unhesitatingly towards a moving target presented in any part of the visual field. She seemed unable, however, to judge distance and always reached to her full arm's length even when the object was actually closer or further away.

At first she would look at and reach for objects only if they moved. This limitation did not last, and within a short time she became able to detect a flashing light source, then a stationary light source against a dark background, and finally a stationary black object against a light ground. As these abilities unfolded it was apparent that she initially found it easier to see objects near the centre of the visual field. Indeed in our first report (Humphrey and Weiskrantz, 1967) we were led to describe Helen

as having 'central tunnel vision' for stationary objects, although at the same time she could detect moving objects all over the visual field. Later, however, the ability to detect stationary objects spread to the whole field, and within a year she could reach immediately towards a stationary black dot in whatever part of the field it was presented. When two dots were presented she would still in general reach first for the more central one. Her 'acuity' for detection also progressively improved and, while at first she would reach only for objects ~1 cm across, she eventually had no trouble in locating a black dot no more than 2 mm wide.

Her reaches were always either preceded or accompanied by fixation eye movements. These eye movements appeared to be normal saccades, bringing the fixated object to the centre of the retinae. To fixate an object before reaching for it is natural to any foveate animal, but it is worth noting that Helen was never seen to do something which is certainly within the capacity of a normal monkey—namely to reach for an object which was neither presently nor just previously in the direct line of sight. While her eyes could locate an object in the peripheral field, her hand, it seemed, did no more than follow her eyes.

For the first 3 years Helen lived and was tested entirely within the confines of a small laboratory cage. During this time I concentrated primarily on formal tests of detection and discrimination, using a technique which required the monkey to reach through the widely spaced bars of the cage to a small knob protruding from a flat vertical board (see section 3.2). In this situation *depth* vision had no real relevance to her, since inside the cage there was little to do or see (and its layout was in any case thoroughly familiar), while outside almost all the significant visual events took place at a standard distance from her. If, as seems likely, she had no capacity for depth vision at the start of training, these impoverished conditions can have done nothing to aid her in acquiring it. It was hardly surprising therefore that when, on one occasion during this period, we let her out in the corridor of the animal laboratory she blundered about helplessly.

In 1970 Helen was moved to the Sub-Department of Animal Behaviour at Madingley, Cambridge. At Madingley there was at first no testing room available. But we had access to a wood and a large field, and so—at the instigation of Mirielle Bertrand—I put Helen on a leash and took her for walks in the open air (figure 3). In the context of this newfound freedom she began to exploit her vision in quite unexpected ways.

To begin with, as might have been predicted from her previous behaviour, these walks were fairly hazardous. She continually bumped into obstacles, she collided with my legs, and she several times fell into a pond. But then, day by day, there was an extraordinary change in her behaviour. On the one hand she began systematically to anticipate and skirt round obstacles in her path, while on the other she began actually to approach the trees in the field, turning towards them as we passed by, walking up and reaching out to grasp their trunks. There was an old elm tree which she specially liked to climb, and, with her perched in a hole in its trunk, I would hold up bits of fruit and nuts for her to reach for; and now she did something else she had not done before—she would reach out when the target was within arm's length but ignore it if it was too far away. It was clear that, given at least the experience of three-dimensional space, she was quickly developing a kind of three-dimensional spatial vision.

When a room became available an indoor arena was set up in which she could freely move around. The game was for her to pick up small bits of chocolate or currants from the white floor. She soon learned, for instance, to run straight to a tiny currant 2.5 m distant from her. Her vision was in fact so acute by this time that it was hard to keep the floor clean enough to prevent her trying to pick up

specks of dirt. When twenty-five currants were scattered at random over an area of 5 m<sup>2</sup> she took only 55 s on average (over four trials) to pick up every one. In the latter situation her search strategy was not as efficient as it might have been—she would for instance sometimes run past several currants on her way to a more distant one—but there was no evidence that she consistently ignored any part of the field.

Somewhat surprisingly, her preferred method for picking up the currants was to take them directly with her mouth rather than her hand. When, however, she was given live cockroaches to chase she very soon learned to grab them—and crush them—with her hand. If cockroaches and currants were both present in the arena simultaneously she then also took the currants with her hand. When she did reach with her hand she would now judge both the direction and the distance accurately, bring her hand down on top of the object (except on a few occasions when she reached behind a swiftly running cockroach). But in one respect her hand movements were clearly abnormal: she never used fine finger movements in the way characteristic of a normal monkey: but instead grasped the object with her open palm (cf Brinkman and Kuypers, 1973).

Having been led to expect food in the arena, she treated any small dark object as a potential titbit. Thus she would regularly be deceived by a 1.5 cm square of dark sticky tape stuck to the floor (even though it might be coloured red or green). With a 20 cm long strip of black tape she initially tried to pick up one end or the other, though in this case she fairly soon desisted. In general she showed a striking failure of 'object recognition'—a failure in line with her performance in the formal discrimination tests. The only evidence for visual selectivity was her tendency

(i) to ignore large objects, outside the size range of the usual food items—she would, for instance, make no attempt to pick up a 5 cm diameter circular black disc (although if she spotted it at a distance she would often take some steps towards it before dismissing it), and (ii) with small objects, to go for the most 'conspicuous'



Figure 3. At large in the wood at Madingley.

object in sight—thus she would take larger bits of chocolate before smaller ones and darker coloured Smarties before lighter coloured ones. The evidence of the discrimination tests suggests that if the size and brightness of the food items had been strictly standardised she would probably have learned to be rather better at rejecting ‘fakes’, but this control was not attempted.

When she picked up objects in the arena she herself was almost always on the move. On the basis of this evidence alone it could be argued that her ability to judge distance depended on the ‘dynamic’ visual information provided during active approach. In her previous outings in the field she had, however, shown signs of being able to judge the distance of an object whilst sitting in a tree. To confirm this potential for *static* depth perception it was necessary to return her to a cage.

A horizontal white table was set up in front of the cage and currants were scattered on it so that they fell at different distances. In this situation, while she sat relatively immobile at the front of the cage (her head pushed through the bars), she proceeded without further training to reach to just the right distance for each currant, bringing her hand down on top of it (Figure 4). If a currant happened to be out of reach she would look at it but generally make no attempt to get it: if she did attempt to get it she would do so with obvious preparation, turning her shoulder towards the currant

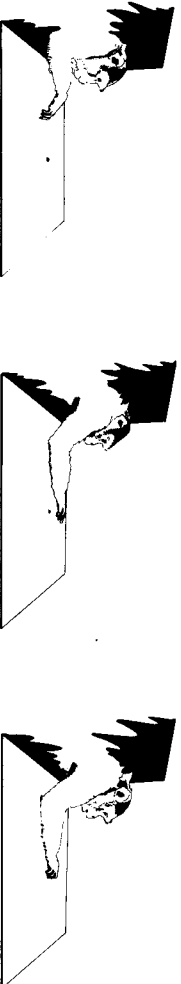


Figure 4. Helen reaches for a piece of chocolate on the table. Note the open spread of her fingers. (Drawings made from a cine film).

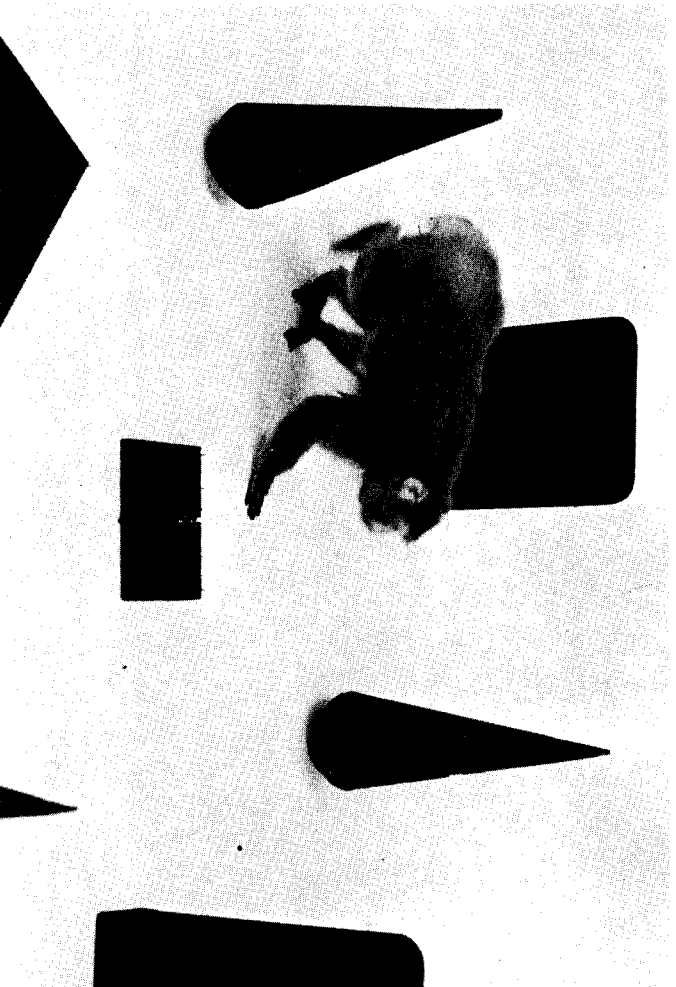


Figure 5. She runs for a currant in the arena.

and pushing her upper arm through the cage bars as far as she was able in order to maximise her stretch. When the surface of the table was moved up or down relative to the floor of the cage her performance was in no way disrupted (although when the table was raised to neck height she sometimes tried to reach to a currant from underneath it). It is unlikely, therefore, that she judged distance simply by the elevation of an object in the visual field.

Once she was familiar with searching for food in the open arena, I investigated her ability to avoid obstacles by sight. An assortment of solid black cones and upright baffles were placed in the arena. At first she sometimes bumped into them, but within a few days she began to move among these obstacles as deftly as if her sight was unimpaired. Next some bits of black board were placed flat on the floor. To start with she paid no attention to these boards and walked straight over them; but when the boards were given a prickly surface she quickly took to walking round them (figure 5). There was nothing fussy or exaggerated in the way she avoided either the boards or the upright obstacles—rather, she would simply steer a safe but economical course between them, passing within inches, but seldom so much as brushing up against them.

The obstacles did not have to be totally opaque to provide effective visual barriers. Equally effective were upright sheets of transparent perspex painted with black stripes 2 cm wide (vertical or horizontal) with 4 cm gaps between them; transparent Perspex covered with black checks would also do. When an area of the floor was laid out with a regular array of nine 1.5 cm square bits of black sticky tape arranged in a 3 × 3 matrix with 10 cm gaps between them, that too was treated as an obstacle to be walked round. Furthermore she avoided stepping on an outline square drawn on the floor with black tape 1.5 cm wide, provided the square was not much more than 4.5 cm wide. Interestingly, she never tried to pick up the bits of tape in the regular array and neither would she pick up a bit of tape (or a currant) *within* an outline square, although she did try to pick up an isolated bit of tape placed some distance away. When the floor was laid out as shown in figure 6, in a test lasting 3 min she made nineteen responses to the isolated bits of tape and none to the bits either in the matrix or the outline square.

Though her avoidance of obstacles placed flat on the floor was clearly based on vision, it could have been that she used reflected sounds to detect the upright obstacles. Accordingly, two control experiments were made: (i) she was tested in

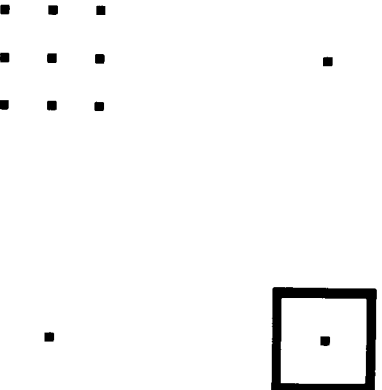


Figure 6. Pattern of tape on the floor (see text).

the presence of intense white noise—and it made no difference, (ii) a transparent barrier was placed in amongst opaque ones made of the same material—and she repeatedly bumped into it.

Most of the observations of her ability to avoid obstacles were made while she was searching out currants. She would wander around until she spotted one and then run over to it. While she ran she would usually keep her eyes fixed on the currant and it seemed clear that she used peripheral vision to guide her way round any intervening obstacle. Thus, in this context at least, she demonstrated that visual spatial information from the peripheral field was directly available to control movements of her limbs as well as her eyes. Nonetheless she would *reach* for a small object only if she had first fixated it.

All in all, Helen had made a remarkable recovery, yet no one who observed her for long would have been persuaded that even the grosser aspects of her spatial vision were in fact entirely normal. It was hard to pinpoint what was wrong. But my impression was that her visual space was a purely subjective, self-centred space in which she could place things in relation to her own body but could not place them in any more stable spatial framework. When, for instance, a small bit of black tape was stuck to the floor in the presence of surrounding obstacles she would return to try to pick it up again and again, never learning to ignore it on the basis of where it lay in relation to the stable objects round about it; every time she moved away and then caught sight of the tape again she appeared to treat it as a new discovery. By contrast, when a bit of tape was stuck to the table in front of her cage she would reach to it once or twice and then ignore it, while continuing to take currants from other parts of the table. In the latter case she did not move her body and consequently could keep track of the tape's position.

There was one other more obvious abnormality. Her performance regressed when she was in any way upset—to the extent that if she was severely scared the capacity for spatial vision seemed to desert her. A door slamming behind her or an unexpected pinch on her flank might be enough to make her quite oblivious of the obstacles in the arena. Despite the apparent effortlessness of her performance when she was relaxed, vision never became entirely 'second nature' to her.

### 3.2 *Detection and discrimination*

Helen would reach to an object which 'caught her eye'. What kind of visual stimuli did catch her eye? Could she distinguish one eye-catching stimulus from another? These questions were studied in an extensive series of more formal tests, involving in all about twenty-five thousand trials over a period of 4 years. To describe the results in detail would take considerable space and, in view of the fact that the lesion was not quite complete, there are grounds for supposing that this might not be justified (see the discussion in section 4). The following paragraphs give the bare bones of the story.

3.2.1 *Detection*. From the start it was evident that moving targets were more easily detected than stationary ones, and this remained true throughout the study: even at the end her attention could almost always be diverted from a stationary object by presentation of a moving one. But stationary objects were by no means all equally easy to detect.

The relative detectability—'salience'—of different stationary stimuli was investigated using a Fantz-type visual preference technique. A vertical board was set up in front of the cage, 30 cm distant, bearing two protruding knobs on which visual stimuli were mounted (figure 7). Helen was trained to reach out and touch one or other of these stimuli, choice of *either* being rewarded. The positions of the stimuli were changed from trial to trial by rotating the board. In this situation—the task being merely to



find a target—it may be presumed that she reached to the one which was most immediately detectable. Hence by counting the frequency with which she reached to one stimulus rather than the other it was possible to obtain a measure of their relative salience.

The results showed that salience was greatly influenced by the size and brightness contrast of the target stimuli. With black spots on a white background, salience increased with the diameter of the dot (up to  $\sim 12$  mm). With grey spots, 10 mm in diameter, salience increased with the brightness contrast against the background (up to  $\sim 1$  log foot lambert). Colour contrast, however, had no influence: a green spot on a red background was no more salient than a red spot on a red background when the green was approximately matched to the red in photopic brightness.

No significant effects of shape were found, except that in general a solid figure was more salient than a broken one. (Further details of the method and results are given in Humphrey, 1970.)

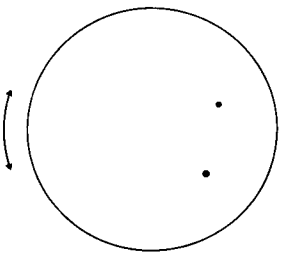


Figure 7. Testing board used in the preference tests.

**3.2.2 Discrimination.** In the 'preference' tests Helen was rewarded for reaching for either of the two stimuli, so that no premium was placed on discrimination. In subsequent tests she was selectively rewarded for reaching for one of the stimuli and not the other. The stimuli were now placed on diametrically opposite sides of the board and the tests were run in two ways.

- (i) 'Simultaneous discrimination' (figure 8a): both the positive and negative stimuli were presented, in new positions on each trial, and she was rewarded for reaching to the positive one.
- (ii) 'Successive discrimination' (figure 8b): the lower half of the board was hidden by a screen bearing a blank 'dummy' knob and either the positive or the negative stimulus was presented in the upper central position—when the positive stimulus appeared she was rewarded for reaching to it and when the negative stimulus was presented she was rewarded for reaching to the dummy.

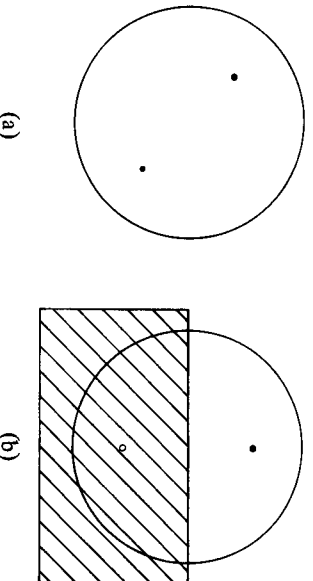


Figure 8. (a) Arrangement for simultaneous discrimination tests. (b) Arrangement for successive discrimination tests.

The results showed that Helen had no trouble in distinguishing stimuli which the earlier tests had indicated to have different salience for her. Thus she would readily discriminate between two spots differing either in size or brightness. She scored better than 75% in discriminating between two black circles, 10 mm and 8 mm in diameter, and between two 10 mm grey circles differing in brightness by 10%. She performed just as well when she was required to choose the least salient stimulus as she did when required to choose the more salient stimulus. Moreover, her performance on successive discrimination was almost up to that on simultaneous discrimination. On the successive task her ability for size and brightness discrimination was comparable to that of an (unpractised) member of the Oxford laboratory staff.

However, if two stimuli were *matched* in salience she was, in general, quite unable to discriminate them. When, for instance, a 10 mm red circle was paired with a 10 × 5 mm black rectangle—earlier tests having shown these to have equal salience—she scored no better than chance over one thousand trials. Correspondingly, it turned out that she could not discriminate either size or brightness as an *independent* dimension. Thus a 10 mm light grey circle on a white background was indistinguishable from a 5.5 mm darker grey circle. However, the 'equivalence point' was not the point at which the two stimuli were equal in total luminous flux but rather, in this particular instance, when the smaller circle had approximately  $\frac{2}{3}$  the flux of the larger one (*negative flux*, in fact, since the stimuli were darker than the background).

The one exception to the rule that stimuli of equal salience were indistinguishable was her ability to discriminate between a dark circle and a light circle on a mid-grey background. Earlier tests had indicated that the salience of these two stimuli would be approximately matched when they had the same absolute contrast with the background (independently of its sign), and I half expected that at this point her discrimination would break down. This proved not to be so. Indeed no manipulation of size or brightness would induce her to confuse positive contrast with negative contrast.

The results of a test of colour discrimination were somewhat at odds with the earlier findings. She was required to discriminate a 15 mm red circle from a 15 mm green circle on a white background. When the brightness of the green circle was systematically changed, while that of the red one was kept constant, there was indeed a point where her discrimination broke down—evidence, as before, that colour *per se* was not discriminable. But, in contrast to the results of the 'preference' tests, the two stimuli became indistinguishable when the green circle was considerably darker than the red one in terms of *photopic* brightness: the 'equivalence' point fell, in fact, closer to a scotopic than a photopic brightness match. Thus at first sight it looks as though Helen had two spectral sensitivity functions: photopic for detecting a green spot on a red background (the case in the preference test), and mesopic for comparing a red spot with a green spot on a white background (the case in the discrimination test). One possible resolution of this paradox is to suggest that red is in fact a more salient colour than green when seen against a white background: in that case the green circle would have needed 'extra' brightness contrast to be a match in salience to the red one. In *man Koffka* (1935) and others have noted that red figures are indeed better 'articulated' ( $\equiv$  salient?) than green ones.

An attempt to measure 'minimal separable acuity' was made by getting Helen to discriminate a 15 mm disc bearing a black-and-white checker pattern from a 15 mm grey disc of equivalent overall luminous flux (figure 9). When the size of the checks was progressively reduced from 4 mm to 1 mm her performance deteriorated. She scored 75% correct with 2 mm checks—which corresponds to an angular separation at the eye of  $\sim 23$  minutes of arc. One should be careful, however, in equating this with a conventional measure of acuity, since what she was almost certainly doing was simply

discriminating differential salience. Indeed it turned out that even with the larger checks her performance dropped to no better than chance if the brightness contrast of the grey disc was sufficiently increased, i.e. if the disc was made more salient.

Finally a study was made of shape discrimination. The stimuli were a black outline circle, 8 cm in diameter and 1 cm thick, and an outline triangle of equal perimeter. A black spot was placed at the centre of each figure for Helen to reach for (see figure 10). In one thousand trials she scored no better than chance. Since she was reaching for the centre of the figures it might have been that she simply did not notice the surrounding contours. Accordingly, as a control, she was tested for her ability to discriminate a spot surrounded by an 8 cm circle from a spot on its own (figure 11). Here she scored close on 100% and indeed continued to do so when the diameter of the circle was increased to 20 cm. So there can be no question of her ability to *detect* the figures in the shape discrimination test. In fact, rather than the central spot distracting her attention from the surrounding contour, further tests



Figure 9.

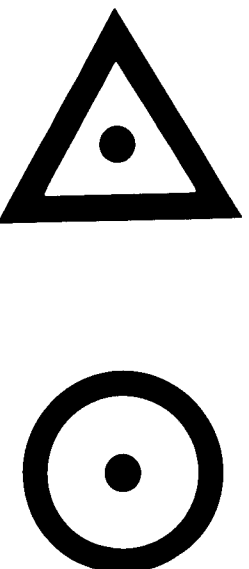


Figure 10.

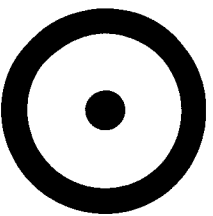


Figure 11.

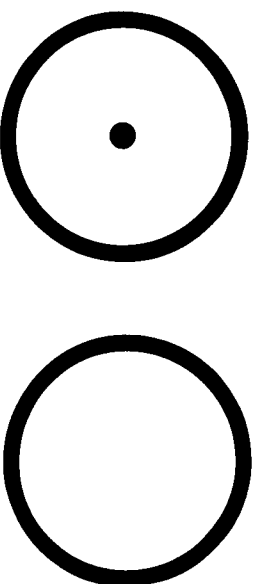


Figure 12.

indicated that the contrary was true. When she was required to discriminate a 15 cm diameter, 1 cm thick, circle containing a 1.5 cm spot from a similar circle *without* a spot (figure 12), she failed to do so in one thousand trials. Only when the thickness of the outer circle was reduced to 2.5 mm did this seemingly so-simple discrimination become possible for her.

The evidence of all these tests—that Helen could classify stimuli in terms of visual salience but of visual absence only—was fully born out in the rest of her behaviour. With the important exception of her spatial vision she appeared in fact to be totally agnostic. After years of experience she never showed any signs of recognising even those objects most familiar to her, whether the object was a carrot, another monkey, or myself.

### 3.3 *Eye movements*

In contrast to her early state of visual apathy, by the end of the study Helen spent much of her time apparently watching what went on around her—despite the fact that she could make so little sense of what she saw.

Shortly before Helen's death, Dr Colwyn Trevarthen made systematic recordings of her eye movements, using cine film and an oculographic recording method which allows head and eye movements to be monitored independently (Trevarthen and Tursky, 1969). Details of this study will be published separately, but in outline the findings were as follows.

The eyes moved with normal conjugation (synchronously and with equal angular displacement) and they were also coupled in an apparently normal way to head movements. Saccades were of normal velocity and shape. They were of varied extent and distributed in all directions, there being no evidence of a bias towards picking up signals from an 'intact' part of the peripheral field. Fixation was seldom maintained for long. Even at times of intent regard there was a tendency for the eyes to drift and a paucity of fine correction saccades. On several occasions when the head moved, the eyes overcompensated for the movement and then rolled back. Nystagmus was also occasionally present.

Thus in many ways the eye movements looked normal, the only obvious deficit being in the locking of gaze in fixation.

## 4 Discussion

### 4.1 *Significance of the spared striate cortex*

In the light of the histological evidence for the sparing of a small area of the peripheral visual field, it is essential to give an opinion about the part this played in the monkey's vision. The study would lose much of its significance if a plausible case could be made for supposing that Helen, rather than using extrastriate vision, was in effect looking out of the corner of her right eye with her intact visual field.

With regard to her capacity for spatial vision, there is no reason to entertain this possibility. All the relevant evidence is directly contrary to it. Throughout the study I and others who examined Helen were alert to the risk that an area of cortex had been spared and we watched carefully for any sign of an anisotropy in her visual fields. Apart from the unusual dependence in the initial stages on *central* vision, no such evidence emerged—neither in reaching for objects, nor in her behaviour in the arena, nor in Trevarthen's eye-movement recordings. Gardner (1966), in his expose of 'finger sight', has warned against the tricks that conjurers get up to, but it would have taken more than a magician to have done what Helen did by some clever kind of squinting.

But with the formal discrimination tests it is difficult to be so sure. She was, it must be said, highly motivated to do well and one must assume that she would have

adopted the most effective strategy open to her. To *detect* the stimuli she almost certainly used the whole visual field, but to *discriminate* between them it is just conceivable that she took quick glances with the intact peripheral field. I never caught her using such a devious strategy, but when the discriminations were difficult she did take time over each judgement, glancing from one stimulus to the other, and I cannot be wholly confident. With the simple 'preference' tests there is less cause to worry, since here she was under no pressure to do other than detect one of the stimuli. The reader will make up his own mind on this matter. For my part, I believe the balance of probability is that *none* of Helen's vision was mediated by the spared striate cortex.

#### 4.2 Evidence from other primate studies

4.2.1 *Spatial vision.* With the exception of a short note by Denny-Brown and Chambers (1955), the published reports of monkeys with striate cortex lesions give no evidence of any ability to locate objects in space, and much of the evidence would in fact go against it. But this negative evidence may be attributed at least in part to a failure to train the monkeys in an appropriate way. Recently, Weiskrantz *et al.* (1973) have made a deliberate attempt to confirm and extend the findings obtained with Helen and have succeeded in showing that other destriate monkeys can be taught to reach out and touch a small visual stimulus, even when the stimulus is a brief light flash presented randomly in the visual field. Meanwhile, in human subjects, Poppel *et al.* (1973) have obtained evidence that subjects with large striate cortex lesions can direct their eyes to a light flash presented in an area of the field which is cortically blind. More pertinent still, Sanders *et al.* (1974) have shown that a patient with an homonymous hemianopia can both fixate and point with remarkable accuracy to a small light spot presented in the hemianopic field. In both these studies the patients denied that they 'saw' the stimuli.

Helen's ability to avoid obstacles by sight is, however, unparalleled to date either in monkey or man. In the one published study which specifically relates to 'ambulatory spatial vision' Marks and Jane (1974) found with squirrel monkeys that the ability to run across an arena to a distinctively lighted doorway (to escape shock) was abolished by visual cortex lesions. But the lesions were considerably larger than Helen's, including areas 18 and 19 in addition to 17. Moreover, since the monkeys were under the threat of shock it is likely that they were rather scared—a condition in which Helen herself would have performed relatively poorly. There have been no comparable studies of people with cortical blindness. Closely relevant, however, and of great importance are Trevarthen's experiments on split-brain patients from which he has inferred that *ambient* spatial vision—perception of 'the space to be moved through'—is mediated by subcortical structures (Trevarthen and Sperry, 1973).

4.2.2 *Discrimination.* Although Helen was exceptionally acute in resolving small differences in size and brightness, her capacity for discrimination in the formal testing situation was generally similar in scope and limits to what almost all others, from Kliver onwards, have described (for a notable exception, see below). Weiskrantz's suggestion that the sole discriminable dimension for a destriate monkey is 'total ganglionic activity' makes a useful unifying hypothesis, provided it is assumed that the summation area is not the whole retina but the area defined by the focus of attention (and provided one remembers that, in Helen's case at least, the ganglion cells were not all there!). I prefer to talk about 'visual salience' rather than 'ganglionic activity', but if the assumption is made that the two are monotonically related then the issue is simply one of the level of description.

The exception comes from some of the latest work of the Pasiks (Schilder *et al.*, 1972). These authors have confounded all previous notions by demonstrating that

destriate monkeys can be trained, using a 'pull-in' technique, to discriminate both shape (*triangle versus circle*) and colour (*red versus green*). The controls they used make it very unlikely that their results can be explained in terms of differential salience of the test stimuli. That the stimuli were pulled in towards the monkey was probably a critical factor in the successful training; but the stimuli were stationary at the time of choice, so it cannot be argued that relative movement provided any necessary visual information.

#### 4.3 *An interpretation*

A single case study such as this one has obvious limitations. Helen was a special monkey with a special history and certain aspects of her behaviour may well have been untypical both of her species and of her pathological condition. For this reason, if none other, it would be wrong to put too much weight on every detail of the study. But one may try at least to draw the major threads together—and see what kind of yarn emerges.

I would characterise Helen's visual capacity under three headings.

(i) Figure-ground differentiation. Her ability to detect small objects and classify them according to their relative salience suggests that she possessed, almost unimpaired, a capacity to differentiate visual 'figures' from the background. The factors which Rubin and others (Koffka, 1935) identified in human subjects as important for 'good articulation' of a figure are closely similar to those which in Helen contributed to visual salience. Further, Helen's ability to discriminate on the basis of salience has a counterpart in the ability of trained human subjects to make subjective reports of the relative degree of articulation of different figures (a technique on which the Gestalt psychologists relied).

(ii) Location of 'figures' in space. Helen's visual capacity clearly extended to identifying the *locus* of each differentiated figure. But I would question whether she perceived objects as occupying positions in visual space in any ordinary sense of the term perceive. Since she invariably fixated an object when reaching for it, the evidence leaves open the possibility that information about a figure's spatial locus was directly available only to the oculomotor centres of the brain. In that case the information required to guide her hand movement could have been derived indirectly by monitoring the command signals to the eyes. This hypothesis is weakened by the fact that Helen was able to use not only directional but also distance information in reaching. Possibly, however, eye convergence may have provided the essential cue.

(iii) Ambient vision. Helen's ability to avoid obstacles involved, I believe, a qualitatively different kind of vision from that she used in reaching for small objects. Trevarthen has argued cogently for a distinction between 'focal' and 'ambient' vision (Trevarthen, 1968). When a subject looks attentively at an object, he brings focal vision into play, but when he moves unheedingly past obstacles he makes use of ambient vision: focal vision is for identifying what objects are, ambient vision for assessing how solid/empty space is momentarily structured around the subject's body. While Helen's capacity for focal vision was reduced to a rudiment (figure-ground differentiation and nothing more), it seems that her capacity for ambient vision was still operating quite effectively. It is important to note how much this means. In moving around the arena she could apparently appreciate not only the direction and distance but also the *shapes* of intervening obstacles (or the gaps between them); moreover, her body movements were here guided directly by the flow of information to the peripheral retinal field, without the need of eye movements as an intermediary.

This characterisation goes, admittedly, beyond the data. Weiskrantz (1972) has taken a more cautious line and suggested that Helen—and other destriate monkeys—may best be described as 'amblyopic', having something like normal peripheral vision

over the entire visual field. To the extent that 'peripheral vision' means 'ambient' as opposed to 'focal vision', this description has much to recommend it. Yet one should bear in mind that even in normal animals ambient vision is not restricted to the periphery but is probably just as well-developed in the central field: to that extent, normal animals also have 'peripheral vision over the entire visual field'. In the central field of normal animals, however, ambient vision is supplemented—and in some ways overshadowed—by the insistent presence of focal vision. Removal of the striate cortex scalped Helen's visual system of the capacity for focal vision.

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#### References

- Brinkman, J., Kuypers, H. G. J. M., 1973, "Cerebral control of contralateral and ipsilateral arm, hand and finger movements in the split-brain rhesus monkey", *Brain*, **96**, 653-674.
- Cowey, A., 1974, "Atrophy of retinal ganglion cells after removal of striate cortex in a rhesus monkey", *Perception*, **3**, this issue.
- Denny-Brown, D., Chambers, R. W., 1955, "Visuomotor functions in the cerebral cortex", *Journal of Nervous and Mental Disease*, **121**, 288-289.
- Gardner, M., 1966, "Dermo-optical perception: a peek down the nose", *Science*, **151**, 654-658.
- Humphrey, N. K., 1970, "What the frog's eye tells the monkey's brain", *Brain, Behavior and Evolution*, **3**, 324-337.
- Humphrey, N. K., 1972, "Seeing and nothingness", *New Scientist*, **53**, 682-684.
- Humphrey, N. K., Weiskrantz, L., 1967, "Vision in monkeys after removal of the striate cortex", *Nature*, **215**, 595-597.
- Klüver, H., 1942, "Functional significance of the geniculostriate system", *Biological Symposia*, **7**, 253-299.
- Koffka, K., 1935, *Principles of Gestalt Psychology* (Routledge and Kegan Paul, London).
- Marks, K. E., Jane, J. A., 1974, "Effects of visual cortical lesions upon ambulatory and static localisation of light in space", *Experimental Neurology*, **42**, 707-710.
- Polyak, S., 1957, *The Vertebrate Visual System* (University of Chicago Press, Chicago).
- Poppel, E., Held, R., Frost, D., 1973, "Residual visual function after brain wounds involving the central visual pathways in man", *Nature*, **243**, 295-296.
- Sanders, M. D., Warrington, E. K., Marshall, J., Weiskrantz, L., 1974, "'Blindsight': Vision in a field defect", *Lancet*, **707-708**.
- Schilder, P., Pask, P., Pask, T., 1972, "Extrageniculostriate vision in the monkey. III. Circle vs. triangle and 'red vs. green' discrimination", *Experimental Brain Research*, **14**, 436-448.
- Trevarthen, C. B., 1968, "Two mechanisms of vision in primates", *Psychologische Forschung*, **31**, 299-337.
- Trevarthen, C. B., Sperry, R. W., 1973, "Perceptual unity of the ambient visual field in human commissurotomy patients", *Brain*, **96**, 547-570.
- Trevarthen, C. B., Turky, B., 1969, "Recording horizontal rotations of head and eyes in spontaneous shifts of gaze", *Behavior Research Methods & Instrumentation*, **1**, 291-293.
- Weiskrantz, L., 1963, "Contour discrimination in a young monkey with striate cortex ablation", *Neuropsychologia*, **1**, 145-164.
- Weiskrantz, L., 1972, "Behavioural analysis of the monkey's visual nervous system", *Proceedings of the Royal Society (London), Series B*, **182**, 427-455.
- Weiskrantz, L., Cowey, A., Darlington, C., 1973, "Spatial responses by destriated monkeys to brief flashes of light", *Brain Research*, **66**, 360.