

Research Reports

VISUAL FIELD DEFECTS IN MONOCULARLY AND BINOCULARLY DEPRIVED CATS

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SUMMARY

(1) A perimetry test was used to measure the visual responsiveness of discrete regions in the visual field of 2 normal, 4 monocularly deprived (MD) and 2 binocularly deprived (BD) cats. One of the MD cats as an adult underwent a reverse suture operation which forced it to use its formerly deprived eye for a 9 month period. Except for this MD cat which was tested only with its formerly deprived eye, each cat was tested binocularly and monocularly with each eye.

(2) In agreement with previous results, normal cats responded binocularly to objects presented anywhere in the region bounded approximately from 100° right-lateral to 100° left-lateral. The monocular visual fields were measured to be approximately from 100° ipsilateral (to the open eye) to 45° contralateral. Thus the binocular segment of visual field includes the region bounded bilaterally by about 45°, and the monocular segment of each side is bounded approximately between 45° and 100°.

(3) Each of the 3 MD cats tested with both eyes showed a normal monocular visual field for the non-deprived eye. Each with the deprived eye, however, ignored objects presented in the binocular segment yet, after a period following eye-opening, responded fairly normally to objects presented in the monocular segment. Binocularly, the visual fields of these cats appeared fairly normal. This response pattern was evident during the first testing after opening of the deprived eye although the responses with this eye improved considerably in the ensuing days.

(4) The MD cat with reverse suture had a monocular visual field for its formerly deprived eye which closely matched the deprived eye fields of the other 3 MD cats.

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The reverse suture procedure resulted in no qualitative improvement for the formerly deprived eye.

(5) Each BD cat had a fairly normal binocular visual field. When tested monocularly, however, they consistently ignored stimuli presented in the hemifield contralateral to the open eye. Unlike the MD cats, no visual responses were seen in the BD cats for several days after eye-opening.

(6) The behavior of MD cats is suggested to be related to physiological deficits which are limited to the binocular segment of the geniculostriate system, and perhaps also to this segment of the superior colliculus. It is further suggested that the behavior of BD cats results from a cortex which is non-functional for visually guided behavior and a superior colliculus which controls this behavior but which receives functional visual afferents almost exclusively from the contralateral retina.

INTRODUCTION

Cats reared under conditions of monocular or binocular deprivation (MD cats or BD cats respectively) have deficient visual behavior^{2,5-7,14}. Studies of anatomical and physiological abnormalities in the visual systems of such cats^{5,8,9,12,18,19,25-30} offer a neurological correlate for this behavioral deficiency. However, two recent studies of the main laminae in the dorsal lateral geniculate nucleus (LGNd) have shown that in MD cats the neurological abnormalities associated with the deprived eye, the histological decrease of mean cell size⁹ and physiological loss of Y-cells¹⁸ are not uniform throughout the nucleus. Specifically, these abnormalities were apparent only in the medial, laminated segment of the nucleus where the central, binocularly viewed portion of the visual field is represented^{9,18}. The lateral unlaminated portion of the nucleus, where the peripheral, monocularly viewed crescent of the visual field is represented, appeared histologically normal⁹ and had the normal complement of Y-cells¹⁸. In BD cats a decrease of mean cell size (Guillery, personal communication; see also ref. 5) and Y-cells¹⁸ was found throughout the mediolateral extent of the LGNd, but both of these abnormalities were less severe than those in the deprived laminated portion of the LGNd in MD cats.

These data suggest that behavioral deficits may be unevenly distributed in the visual field of the deprived eye of an MD cat and uniformly distributed in the visual field of a BD cat. In the present study, a perimetry technique was used to assess the ability of normal, MD and BD cats to respond to objects presented in confined regions of their visual field. In this way, behavioral deficits were demonstrated which were not uniformly distributed throughout the visual field in either MD or BD cats.

METHODS

Subjects

Eight cats were used. Two were introduced into the laboratory as adults and

were considered to be normally reared controls (C1 and C2). The other 6 were taken from 6 separate litters which were born and reared in the laboratory. At the eighth postnatal day, 4 of these 6 had one eyelid closed and two had both eyelids closed by a previously described suturing technique²⁷. Of the monocularly deprived (MD) cats, two had their right eyelids closed and are referred to below as RMD1 and RMD2; the other two (LMD and LMDR) had their left eyelids closed. During its seventh postnatal month LMDR underwent an additional operation during which its left eye was opened and its right eye closed. LMDR was maintained for the remainder of the experiment, including the period of testing during the sixteenth postnatal month, in an environment which thus forced it to use the deprived eye. The two binocularly deprived (BD) cats are referred to as BD1 and BD2. The originally sutured lids of all cats were opened under ether anesthesia when the cats were 6–12 months old so that the period of deprivation included all of the ‘critical period’ defined by Hubel and Wiesel¹². Ophthalmoscopic observation revealed clear corneas, lenses, ocular media and normal fundi in the deprived eyes.

In all cats except LMDR, interocular alignment (of the visual axes) was assessed after eye-opening by a previously described technique which required observing in each eye the relationship between a corneal reflex of a strong light source and the constricted pupil¹⁶. LMDR has not been observed with both eyes open. LMD and RMD1 thus appeared to have a small (about 10°) convergent strabismus and BD1 appeared to have a small (about 10°) divergent strabismus. Although none was apparent in either RMD2 or BD2, each could have had a small strabismus due to the relative crudeness of the technique¹⁶.

Tests of visually guided behavior

General conditions during testing. All behavioral tests were conducted on or near a 66 cm × 90 cm white-topped table (see Fig. 1) in an evenly illuminated room under photopic conditions. Light gray curtains surrounded the table to provide a uniform background, and even illumination was produced by light reflected from the white ceiling and curtains. The cats were partially food deprived, and visual stimuli consisted of either small pieces of food (about 1 cm in diameter) held in long forceps or a red, 1 cm square painted onto the surface of a white ball (3 cm in diameter) attached to the end of a 50 cm long stiff wire. The latter was used frequently as a visual stimulus to ensure that the stimulus for the elicited behavior was visual and not olfactory.

Before opening their sutured eyelids, the MD cats were pretrained to all tests with their non-deprived eyes. This means that LMDR was pretested with its right eye before the reverse suture operation. The BD cats were brought into the testing room and taught to eat freely before their eyes were opened; they seemed relaxed and unafraid during this period. The final testing of LMDR was solely with its left eye owing to the reverse suture. The other 7 cats, after eye-opening in the MD and BD cats, were tested both binocularly and monocularly with each eye during every daily test session. Monocular testing in these cases was achieved by placing an opaque

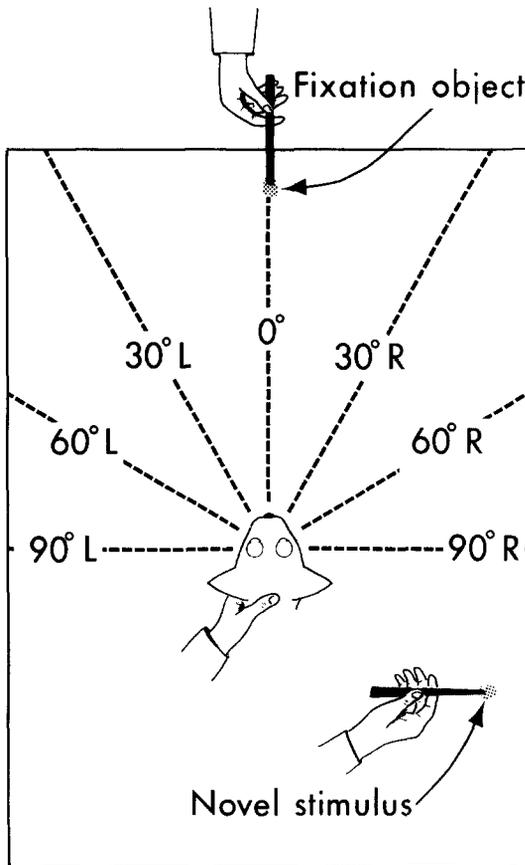


Fig. 1. Method for perimetry testing. The cat is restrained with its lateral canthi aligned along the 90° guidelines and its nose pointed along the 0° guideline to the *fixation object* (a piece of food in forceps). For tests of *specific visual responses* the *novel stimulus* (food in forceps or a painted ball at the end of a stiff wire) is introduced along one of the guidelines after which the cat is freed from restraint and its behavior noted. For control tests of *non-specific responses*, the novel stimulus either is not introduced or is introduced at approximately 120° lateral (out of the cat's visual field) before the cat is freed.

occluder, shaped and ground like a contact lens, over one cornea.

Non-perimetry tests. Three tests of visually guided behavior, used in many studies of feline vision^{2,7,20-22}, were applied repeatedly to each of the cats over a period of at least several weeks. These were visual placing, visual following of interesting moving objects (*i.e.* the visual stimuli described above) and the ability to reach with a forepaw to ensnare interesting objects. Visual placing was tested by lowering the cats towards the table top, and the other tests were carried out while the cats stood on the table.

Visual field perimetry method. The perimetry test was a slightly expanded version of that described by Sprague and Meikle²² (see also refs. 20, 21) and it made use of the cat's visually guided behavior. The white table top was divided with black guidelines

into six 30° sectors. The guidelines were designated 90° L, 60° L, 30° L, 0°, 30° R, 60° R and 90° R (see Fig. 1). Two people were required for this testing. With his left hand the experimenter restrained the cat's head and body so that the lateral canthi of the cat's eyes were aligned with 90° L and 90° R at a height of about 10–15 cm above the table top, and its nose was directed along 0°. A *fixation object*, consisting of a piece of food in forceps, was held by an assistant at 0° about 50 cm in front of the cat. The forceps were jiggled to enhance visual cues and tapped on the table to provide auditory cues. This tapping enabled a 'blind' cat (*i.e.* either an MD cat with an occluder in the non-deprived eye or a BD cat, both before eye-opening during pretraining) to 'attend' to the fixation object and to locate it readily when released.

While the cat attended to this fixation object, the experimenter with his right hand introduced a *novel stimulus* (forceps-held food or the painted ball on a wire) from above along one of the guidelines at a distance of about 20–40 cm from the cat's nose and within 5 cm of the horizontal plane through its nose. Approximately 1 sec after introduction of the novel stimulus the cat was freed from its restraint and its behavioral response was scored as follows. (1) If the cat immediately oriented head and body towards the novel stimulus *and* approached it to explore or eat it, this was recorded as a *positive* response for the guideline at which the novel stimulus was presented. (2) Failure to orient to and/or approach the stimulus was recorded as a *negative* response for that guideline. On negative responses the cat almost always rushed forward to take the food of the fixation object at 0°, but in certain cases MD cats oriented initially but transiently towards the novel stimulus and then moved toward the fixation object. This peculiar negative response is referred to below as a *transient orientation*. Very rarely, a cat scored a negative response by making an orienting movement appropriate for neither the fixation object nor the novel stimulus.

As a control for the above data, each cat was given a number of *blank* trials for which the novel stimulus either was not introduced or was introduced at approximately 120° right or left (outside the visual field of both normal cats^{20–22} and the visually deprived cats; see also Results), and the cat's behavior after release was scored as follows. (1) If it immediately rushed toward the fixation object, this was recorded as a *negative* response for the blank trial. (2) If it hesitated and/or turned head and body apparently searching for the absent novel stimulus, this was recorded as a *positive* response for the blank trial (even if the cat failed to locate the novel stimulus if presented at 120° lateral). Average blank trial responses were nearly equal whether the novel stimulus was introduced at 120° lateral or whether it was not introduced at all, and scores obtained in these two situations were pooled.

Each cat was visually tested several days per week and had 60 or more trials in a daily test session. Except for LMDR (see above) each session included several (usually 3–10) blank trials and trials for each guideline under the 3 conditions of right-monocular, left-monocular and binocular viewing. Also, the order of the viewing was randomly changed from one session to the next. In this manner a quantitative evaluation of a cat's responsiveness to novel stimuli in various parts of its visual field was determined after 10 or more daily tests sessions. These evaluations are shown in Figs. 2, 4, 5, and 7 as the *specific visual response levels* (for stimuli presented at one of

the guidelines) to be compared to the *non-specific response levels* (for blank trials).

Visual field perimetry: assumptions. This perimetry test requires two assumptions which should be considered before evaluating the data. (a) First, it is assumed that the cats during presentation of the novel stimulus are fixating on or near the fixation object at 0° (that is, their visual axes pass through or near the fixation object), and several observations support this assumption. All of the animals appeared to be fixating directly ahead, although in the cat an eccentric fixation of up to 15° would go undetected without special techniques¹⁶. The cats' pinnae were directed towards the acoustic cues of the fixation object, and the cats usually fought their restraint in an apparent attempt to advance to the food of the fixation object. Also, the fact that the results were reproducible for every cat with a precision of 5–10° implies that each cat held its visual axes with a consistent direction during testing. Although the small strabismus in the MD and BD cats raises the possibility that they could be fixating with an eccentricity of about 10°, this would not substantially affect the interpretation of the results presented below. (b) Second, it was assumed that the experimenter handling the cat did not unconsciously transmit to it certain cues regarding the location of the novel stimulus. As a control in a brief series of tests at the conclusion of the experiment, the perimetry of MD and BD cats was assessed by a separate method. Here the experimenter closed his eyes while restraining and releasing the cats on cue from an assistant who placed both the fixation object and novel stimulus. These tests provided the same assessment of visual perimetry as the tests described above. Thus the experimenter, not knowing the position of the novel stimulus, could not have unconsciously biased the cat's behavior.

RESULTS

Normal cats

The two control cats displayed practically identical visually guided responses which are in agreement with previous reports^{20–22}. Visual placing was consistently elicited with either normal cat, both monocularly and binocularly. That is, when slowly lowered towards the table top, they extended one or both forepaws to anticipate tactile contact. Both cats, monocularly and binocularly, actively followed stimuli moving in all directions, frequently and accurately striking with either forepaw to ensnare the object.

Fig. 2 shows in polar coordinates the extent of visual field from which orientation to the novel stimuli was elicited in these cats. In accordance with previous conventions^{9,18} the 0° and both 30° guidelines are within the *binocular segment* of each monocular visual field, while the 60° and 90° guidelines are within the *monocular segment* of the appropriate monocular visual field (see Figs. 2, 4, 5, 7). Although these behavioral perimetry results were based on many days' testing, the extent of visual field for each normal cat was apparent during the first test day.

It is against this background of normal behavior that the following description of behavior in visually deprived cats will be assessed.

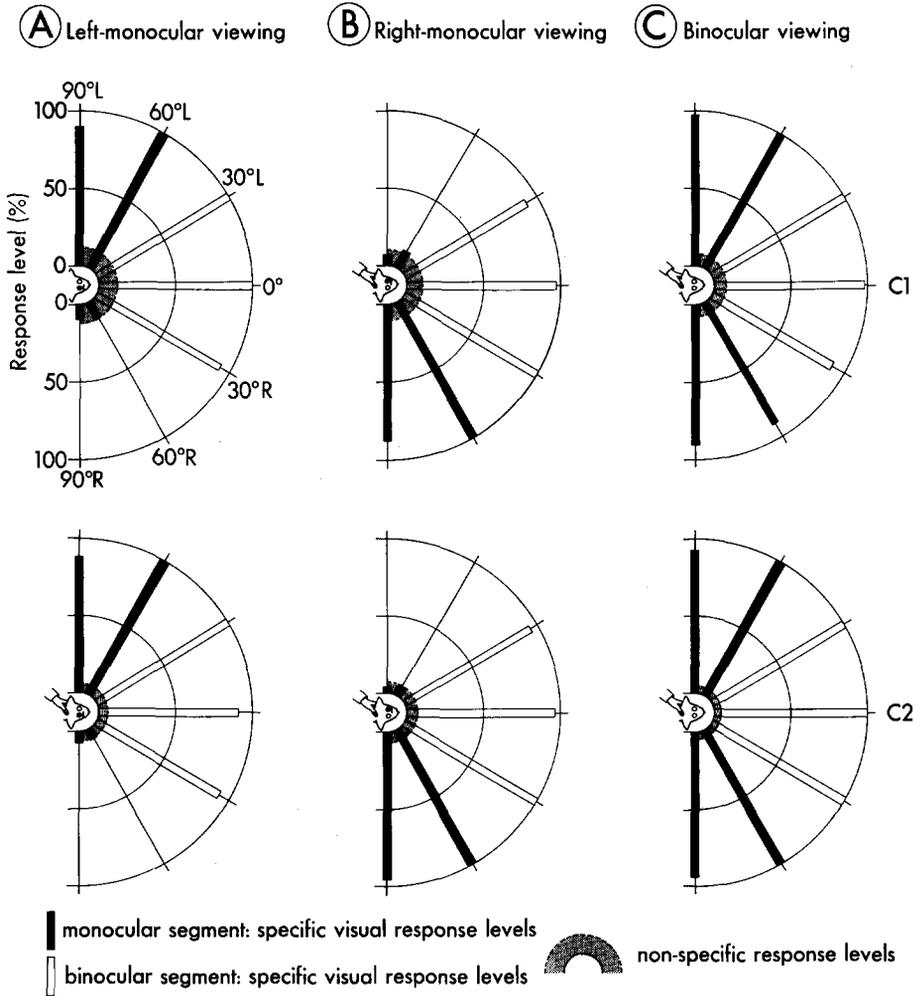


Fig. 2. Visual field perimetry of normal cats. Each graph in polar coordinates shows the specific visual response levels for stimuli presented at each of the guidelines. Levels for guidelines in the binocular segments (see legends for Fig. 8) are indicated by open bars; in the monocular segments these are indicated by filled bars. The levels for non-specific responses during blank trials (see Methods) are shown by the shaded region in each graph under the dashed semicircular baseline. Only bars above the baseline represent regions of the visual field to which the cat attended. The occluded eyes are indicated as filled in with a line covering the cornea. A, Perimetry for C1 and C2 during left-monocular viewing. B, Perimetry for C1 and C2 during right-monocular viewing. C, Perimetry for C1 and C2 during binocular viewing.

MD cats

Non-perimetry tests

Each of the MD cats displayed the normal behavior on tests for visually guided placing, following and paw-reaching using its non-deprived eye. This was true both during monocular testing of that eye before and after eye-opening and during binoc-

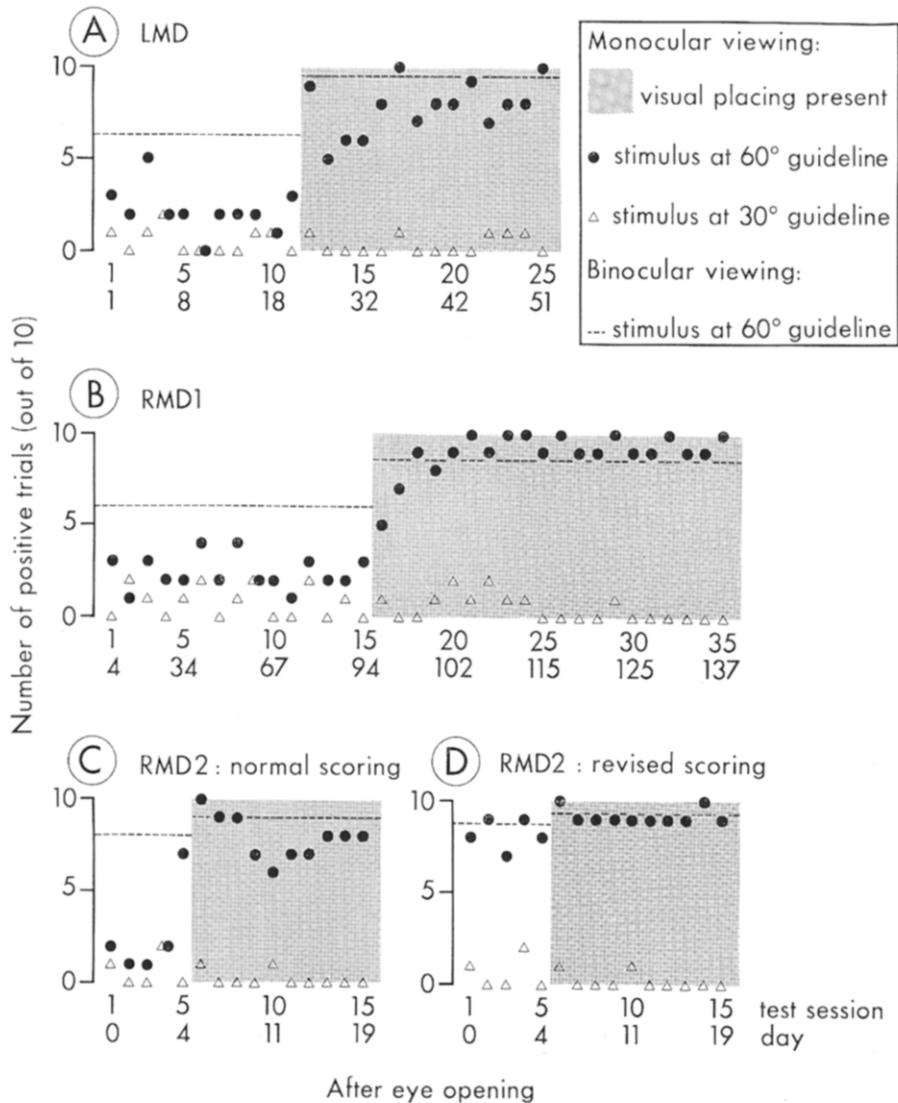


Fig. 3. Time-course of visually guided behavior after eye-opening in MD cats. Each graph shows the response levels (number out of 10) as a function of time both in days and number of test sessions. During monocular testing of the deprived eye, levels for stimuli presented at ipsilateral 30° are indicated by open triangles (Δ), and levels for stimuli presented at ipsilateral 60° are indicated by filled circles (\bullet). The dashed lines indicate the average response levels for stimuli presented at 60° ipsilateral to the deprived eye during binocular testing in the periods before and after the appearance of visual placing for the deprived eye. The former period is indicated by the unshaded portion of each graph and the latter, by the shaded portion. A, B and C, Time-courses for LMD, RMD1 and RMD2 respectively with *normal scoring* for which *transient orientations* (see text) are scored as negative trials. D, Time-course for RMD2 with *revised scoring* for which these transient orientations are scored as positive trials. As shown in C and D, RMD2 was first tested on the day of eye-opening.

ular testing after eye-opening. The following describes the visually guided behavior in these cats during monocular testing of the deprived eye.

Visual placing responses were not elicited for some time after eye-opening. They appeared with least delay in RMD2, appearing after 5 days during the sixth test session, and with greatest delay in RMD1, appearing after 95 days during the sixteenth test session (see also Fig. 3). Even once they appeared these responses were generally less clear and less consistent than those elicited when the non-deprived eye was open. Furthermore, extension of the paws was frequently elicited during testing of the deprived eye when the cat was still well away from any visible surface, and this inappropriate extension was never seen when the non-deprived eye was open, nor was it seen during testing of cats C1 and C2.

During monocular testing of the deprived eye, objects moving steadily from the ipsilateral visual periphery towards the midline and beyond never elicited orienting movements in these cats. However, objects moving from the midline into the ipsilateral periphery elicited ipsiversive following by their heads and bodies. For RMD1 and RMD2 this response was clearly apparent during the first test day after eye-opening, and for all 3 MD cats, this response appeared well before the appearance of visual placing guided by the deprived eye. However, these visual following responses became noticeably stronger in all 3 MD cats after they achieved visual placing with their deprived eyes. Before placing, they typically made a single, brief turning response to a moving stimulus in the periphery, but after placing they would often continue following the stimulus for several seconds and through more than 360° when it was kept moving in the periphery.

Visual stimuli such as the food in forceps never elicited paw-reaching in RMD1 and LMD during monocular testing of the deprived eye. On rare occasions RMD2 reached with a forepaw while following a stimulus moving in the ipsilateral visual periphery, but this reaching was always directed forward and well away from the stimulus.

Since LMDR was not tested for 9 months after the reverse suture operation, only its final, stable behavior was noted, and its behavior did not change appreciably during the course of testing. Basically, its behavior was identical to that of the other MD cats during monocular testing of their deprived eyes. It had poor but clear visual placing, it followed objects moving ipsiversive in the periphery ipsilateral to the deprived eye, and it never reached with a forepaw for such objects. Although the general appraisal of this visual behavior of LMDR was that it seemed slightly brisker than for any of the other MD cats, it was clear that the procedure which forced usage of the deprived eye resulted in no qualitative improvement in any of these tests.

Perimetry testing

Soon after eye-opening: LMD, RMD1 and RMD2. Monocular testing of the non-deprived eye in these MD cats, both before and after opening of the deprived eye, showed a normal visual field with responses elicited to stimuli from 90° ipsilateral to 30° contralateral (see Fig. 4A). During the first monocular testing of the deprived eye after its opening each MD cat showed both responsiveness to stimuli presented

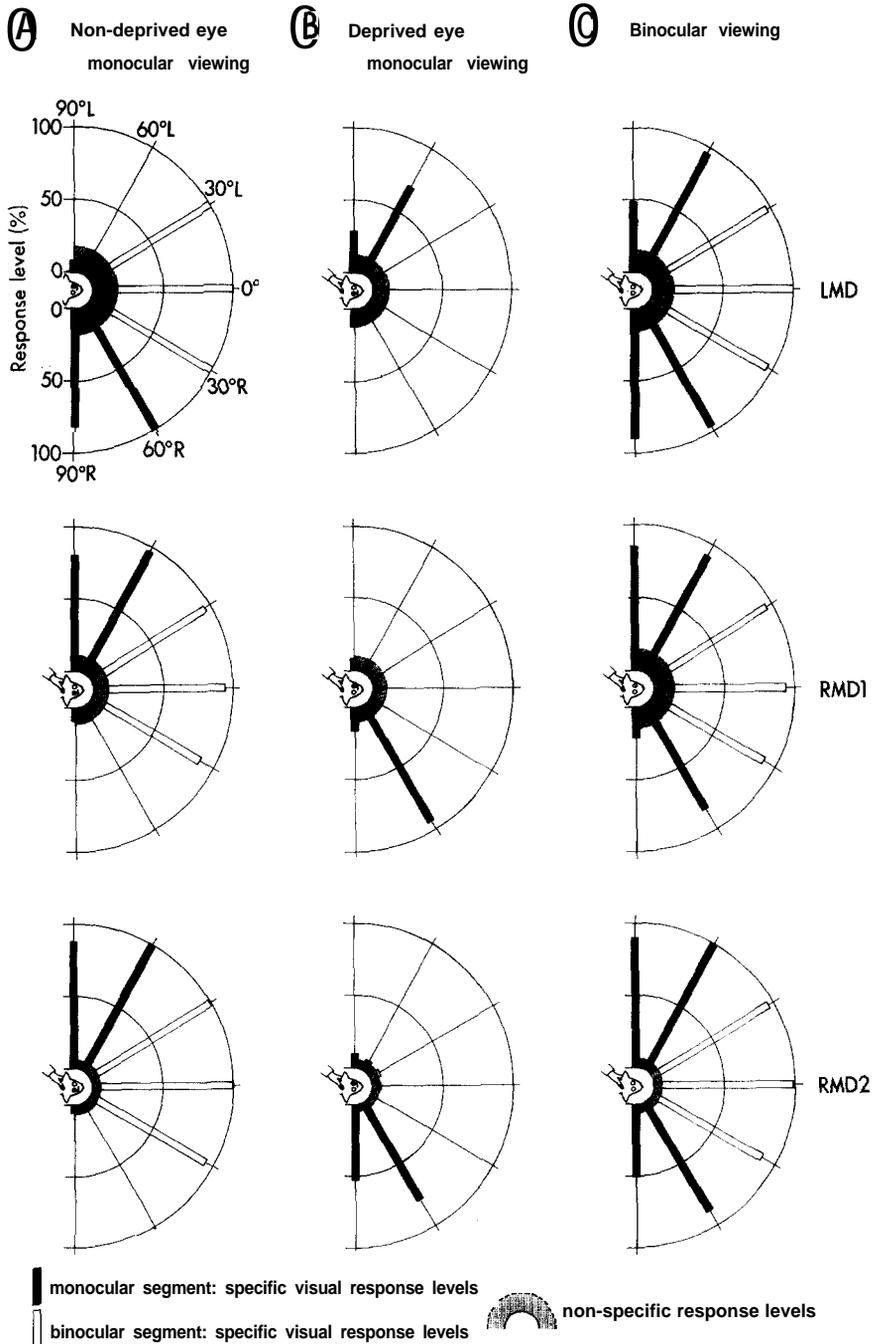


Fig. 4. Visual field perimetry of MD cats. The graphs in polar coordinates represent the specific visual response levels for the binocular and monocular segments and the non-specific response levels as in Fig. 2. A, Perimetry for LMD, RMD1 and RMD2 during non-deprived eye monocular viewing. This, of course, means right-monocular viewing for LMD and left-monocular viewing for RMD1 and RMD2 as indicated by the occluded, filled eyes. B, Perimetry for LMD, RMD1 and RMD2 during deprived eye monocular viewing. C, Perimetry for LMD, RMD1 and RMD2 during binocular viewing.

in the eye's monocular segment of visual field (*i.e.* along the ipsilateral 60° and 90° guidelines) and total neglect of stimuli presented in the eye's binocular segment of visual field (*i.e.* along the ipsilateral 30°, 0° and contralateral guidelines). For each day, in addition to several tests at all other guidelines during binocular and both monocular viewing conditions, the cats were monocularly tested with their deprived eyes 10 times each at the ipsilateral 30° and 60° guidelines. Fig. 3 illustrates that even before visual placing could be elicited with its deprived eye, each MD cat responded clearly, albeit poorly, with that eye to stimuli in the monocular segment of the visual field. During this period, each MD cat had significantly higher response levels for stimuli at the 60° guideline than for stimuli at the 30° guideline (on χ^2 tests, $P < 0.001$ for LMD and RMD1; $P < 0.02$ for RMD2); response levels for the stimuli at the 30° guideline were not different from the baseline non-specific response levels (see Methods). For the periods both before and after the appearance of visual placing, the dashed line in Fig. 3 also shows the average level of positive trials during binocular viewing for stimuli presented at 60° ipsilateral to the deprived eye.

During the initial period after eye-opening a stimulus presented at 60° or 90° ipsilateral to the deprived eye often elicited a response in which the cat transiently oriented its head and body towards the novel stimulus but then neglected this stimulus and approached the fixation object (see Methods). Except in Fig. 3D, these transient orientations were scored as negative. They were not seen for stimuli except those presented along the 90° and 60° guidelines ipsilateral to the deprived eye. They occurred relatively frequently during monocular deprived eye testing but rarely during binocular testing. Apparently during binocular testing, these transient orientations seen in monocular testing were replaced with unambiguously positive responses. For example, Figure 3A–C shows that in the time soon after eye-opening (*i.e.* before the appearance of placing guided by the deprived eye) the percentage of positive responses to stimuli at the 60° guideline ipsilateral to the deprived eye was higher in all 3 MD cats during binocular testing than during monocular testing of the deprived eye. This transient orientation was most marked in RMD2 and in this cat it was scored separately from the other negative responses. If these are counted instead as positive responses ('revised scoring' in Fig. 3D) the response levels to stimuli presented at the 60° guideline ipsilateral to the deprived eye were nearly equal both for the conditions of binocular and right-monocular viewing and for early and late periods after eye-opening.

Stable and final appearance for LMD, RMD1 and RMD2. After visual placing could be elicited with the deprived eye, each MD cat achieved a relatively stable level of response to stimuli in the monocular segment of the deprived eye's visual field (see Fig. 3). Fig. 4, as Fig. 2 for normal cats, presents the data pooled from the final 10–15 sessions of testing, all after visual placing was elicited with the deprived eye, and illustrates 3 points apparent in each cat. (1) The visual field of the non-deprived eye appeared to be normal (Fig. 4A). (2) Responses could be elicited only from the monocular segment of the deprived eye's visual field, and these response levels appeared nearly normal for ipsilateral 60° but reduced for ipsilateral 90° (Fig. 4B). The reduced level for ipsilateral 90° is consistent with the possibili-

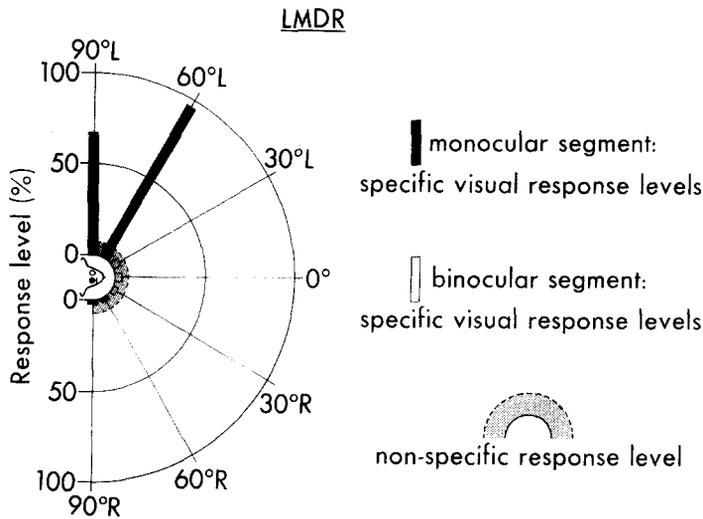


Fig. 5. Visual field perimetry of the deprived (left) eye of LMDR. The graph in polar coordinates represents the specific visual response levels for the binocular and monocular segments and the non-specific response level as in Fig. 2.

ty that the MD cats have slightly eccentric fixation due to a convergent strabismus. (3) The binocular visual field seems to be a composite of the monocular visual fields; that is, a normal binocular field except for a reduced response level for stimuli at 90° ipsilateral to the deprived eye (Fig. 4C). The last point indicates that MD cats during binocular viewing do not suppress visual regions associated with their deprived eyes.

Although these MD cats appeared responsive to novel stimuli in the monocular segment of the deprived eye's visual field, two observations lead to the conclusion that they do not fixate with the monocular segment of retina. First, each MD cat quickly oriented to novel stimuli in the monocular segment of its deprived eye's visual field by realigning the visual axis of that eye so as to bring the stimulus into the functionally blind, binocular segment. When, during monocular testing, the stimulus was kept stationary in the originally monocular segment after the MD cat made an orienting response, the cat readily located it; but when the stimulus was moved about 10° in any direction after this orientation, the cat would explore the original stimulus location and fail to relocate it. Second, the region of the deprived eye's visual field attended to by these cats remained stationary with respect to the table. If these cats during monocular deprived eye testing attempted to fixate eccentrically on the object at 0° with their peripheral, nasal retina, one would have expected the responsive region to shift with respect to the table toward 0° .

Perimetry in LMDR. Fig. 5 shows that the monocular visual field of LMDR's deprived eye appeared essentially identical to these fields in the other MD cats (see also Fig. 4B). This cat responded only to stimuli at the 60° and 90° guideline ipsilateral to the deprived eye, and this response pattern was evident during the first testing of the deprived eye. Transient orientations were not seen in LMDR, and like the other MD cats, it failed to relocate novel stimuli which were moved after an orientation response.

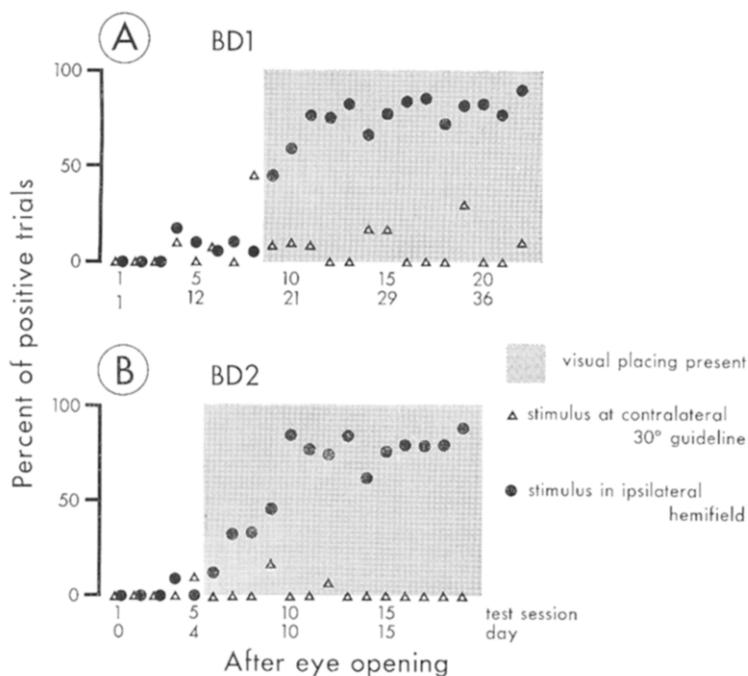


Fig. 6. Time-course for visually guided behavior after eye-opening in BD cats. Each graph shows the response levels in percent for monocular viewing as a function of time both in days and number of test sessions. The levels for stimuli presented at the contralateral 30° guidelines are indicated by open triangles (Δ) and levels for stimuli at the ipsilateral 30°, 60° and 90° guidelines are indicated by filled circles (\bullet). Responses to stimuli at 0° are not included. Each point includes the sum of both eyes' monocular testing, and represents 10–25 trials. The period before visual placing appeared is indicated by the unshaded portion of each graph; the period after it appeared is indicated by the shaded portion. A, Time-course for BD1. B, Time-course for BD2. Note that BD2 was first tested on the day of eye-opening.

As in the other tests, forced usage of the deprived eye resulted in no qualitative improvement in this eye's perimetry as compared to the perimetry of deprived eyes in the other MD cats.

BD cats

Non-perimetry tests

Both BD cats seemed totally blind for some time after eye-opening. Then visual placing, following of moving objects, and reaching with a forepaw for visual objects all appeared within the same day for each cat, after 17 days during the ninth test session for BD1, and after 5 days during the sixth test session for BD2 (see Fig. 6). All 3 responses, however, remained deficient. First, visual placing in the BD cats resembled the inaccurate placing elicited by the deprived eye in an MD cat (see above). Second, during binocular testing the BD cats followed moving objects in both horizontal directions with essentially normal skill, but during monocular testing only objects moving ipsiversive (to the open eye) in the ipsilateral hemifield were followed.

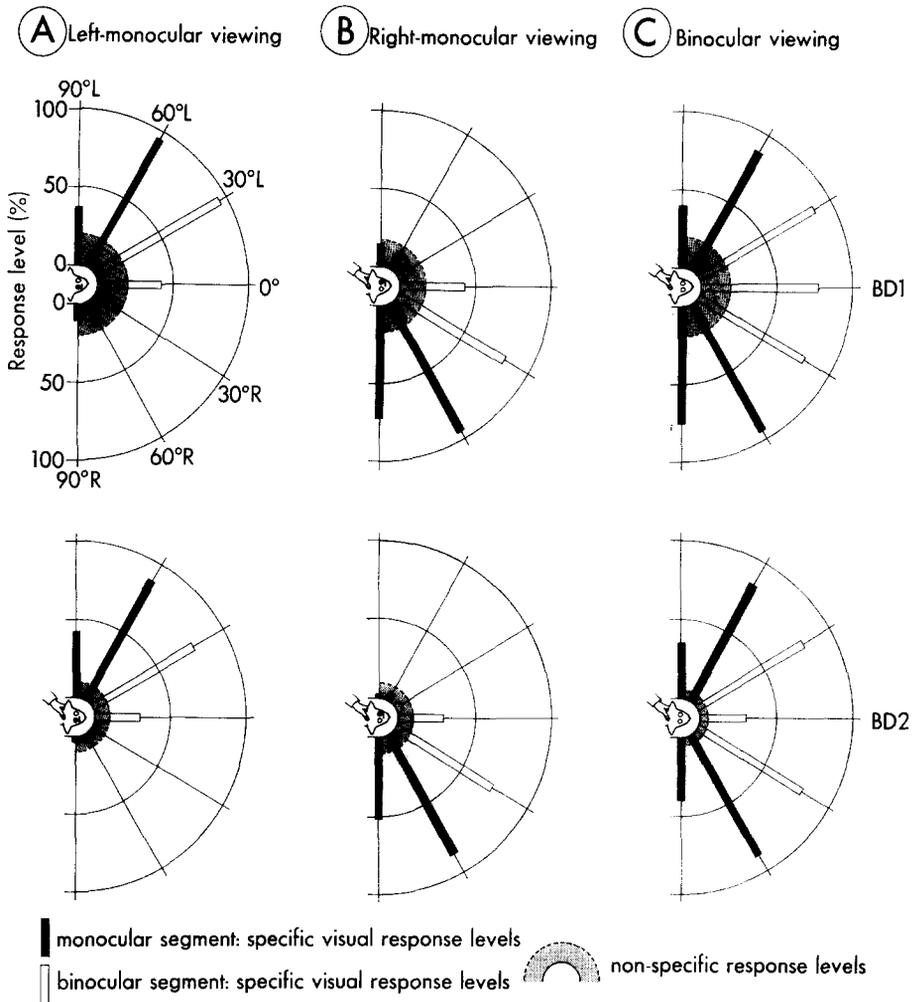


Fig. 7. Visual field perimetry of BD cats. The graphs in polar coordinates represent the specific visual response levels for the binocular and monocular segments and the non-specific response levels as in Fig. 2. A, Perimetry for BD1 and BD2 during left-monocular viewing. B, Perimetry for BD1 and BD2 during right-monocular viewing. C, Perimetry for BD1 and BD2 during binocular viewing.

Third, both monocularly and binocularly, the BD cats frequently attempted, with fair but less than normal accuracy, to ensnare visual objects in their forepaw; however, they often continued to paw at empty space long after the object had been removed, and this behavior was not seen in cats C1 or C2.

Perimetry testing

The BD cats made no consistent positive responses during either binocular or monocular testing for any of the guidelines until approximately the appearance of the visually guided behavior described above. Fig. 6 illustrates the time-course of the appearance of responses elicited during monocular testing, and this timing was

essentially the same for binocular testing. This figure shows that tested monocularly neither BD1 nor BD2 ever responded consistently to stimuli in the contralateral hemifield but did develop high response levels for stimuli in the ipsilateral hemifield soon after the appearance of visual placing.

Fig. 7C shows that, once stabilized, the binocular visual fields of both BD cats appeared fairly normal in extent, although the response levels were slightly less than those seen in normal cats (Fig. 2C). The major visual field defect of BD cats was found during monocular testing (see also Fig. 6). Each monocular visual field included only the ipsilateral hemifield (see Fig. 7A, B). Stimuli presented at the contralateral 30° guideline were neglected. In the normal cat (see Fig. 2A, B) such stimuli elicited high levels of response. Actually, many of the trials recorded for the contralateral 30° guideline were for stimuli presented between 5° and 30° in the contralateral hemifield, suggesting that the BD cats neglected all stimuli between 0° and contralateral 30°.

If, after a BD cat with one eye occluded made an orienting response to and approached the novel stimulus, the stimulus was then moved either rapidly or slowly about 15° ipsiversive to the occluded eye, the cat was unable to relocate it. If the stimulus was instead moved ipsiversive to the open eye, the cat readily relocated it. If such movements were made in either direction during binocular testing the cat also relocated the stimulus. This is consistent with both the perimetry and following responses of these BD cats.

DISCUSSION

The MD and BD cats of this study had deficits in their visually guided behavior. Yet by using stimuli limited to small regions of the visual field, it was shown that stimuli in certain regions elicited practically normal orienting responses whereas stimuli elsewhere were ignored.

Fig. 8 summarizes the 'idealized' visual field in normal, MD and BD cats which have both visual axes aligned on the fixation object. The absolute limits of the functional visual field have been placed 10 or 15° beyond the most peripheral guideline at which stimuli elicited specific visual responses. The binocular fields of normal, MD and BD cats are similar, being the sum of the monocular fields. Fig. 8A shows that in a normal cat each monocular field extends from about 100° ipsilateral (from the data of Sprague and Meikle²²) to about 45° contralateral. It also shows that the binocular segment of each monocular field is bounded bilaterally at about 45°, while the monocular segment on each side extends from about 45° to about 100°. This division into binocular and monocular segments is in good agreement with similar data based on LGNd physiology^{3,10,15,18}. Fig. 8B shows that the monocular field of the non-deprived (left) eye of an RMD cat is normal, but that the monocular field of the deprived (right) eye includes only the monocular segment for that eye. Fig. 8C shows that in the BD cat each monocular field encompasses only the ipsilateral hemifield. From this summary, there is thus no binocularly viewed visual field for either MD or BD cats.

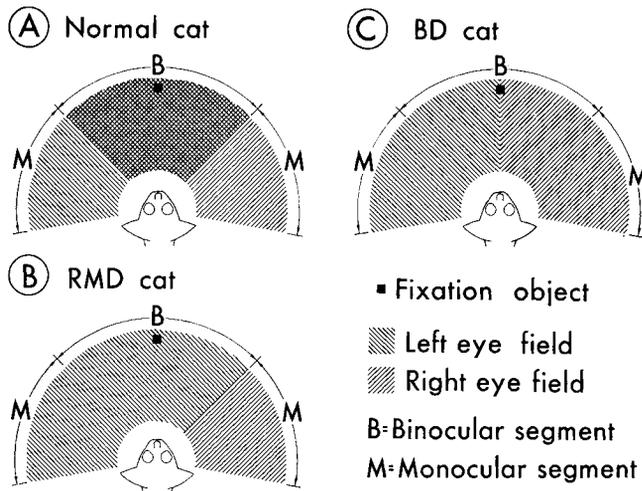


Fig. 8. Summary of idealized visual field perimetry testing of cats in this study, after correction for eccentric fixation (see text). This figure does not include response levels. It is assumed here that each cat has both visual axes aligned on the fixation object. A, *Normal cats*. The binocular field extends between about 100° on either side. The monocular fields each extend from about ipsilateral 100° to contralateral 45° which delineates the *binocular segment* of visual field as bounded bilaterally by about 45° on either side and the *monocular segment* on each side as extending from about 45° to about 100° . B, *MD cats*. The binocular field has a normal extent as in A. Also, the non-deprived eye monocular field is normal but the deprived eye monocular field includes only the monocular segment. C, *BD cats*. The binocular field has a normal extent as in A, but each monocular field includes only the ipsilateral hemifield.

Comparison with previous studies

Visually guided behavior

MD cats. Previous papers have reported that, when using their deprived eyes, MD cats were behaviorally blind soon after eye-opening and developed some visually guided behavior in the ensuing days or weeks^{5,7,28,29}. The MD cats in this study showed clear signs of visual behavior with their deprived eyes during the first test after eye-opening, which was held on the same day as eye-opening for RMD2 (see Fig. 3). This initial behavior was elicited only by stimuli in the monocular segment of the deprived eye's visual field, and thus could well have been missed in earlier reports^{5,7,28,29}. There was, nevertheless, considerable improvement on all tests during the period after eye-opening (see Fig. 3). Each MD cat behaved as if it were initially confused by a deprived eye field consisting only of the ipsilateral periphery. Specifically, with deprived eye monocular viewing the cat initially oriented to novel stimuli presented in the functional monocular segment of visual field but then ignored the stimulus, presumably because the reflex orientation of its visual axis brought the stimulus into the blind binocular segment. This is probably the basis of the transient orientation response seen in MD cats, especially in RMD2, during monocular deprived eye testing (see Fig. 3C, D). On the other hand, with binocular viewing a

stimulus in the monocular segment of the deprived eye's visual field would elicit an initial orienting response which would bring the stimulus into the normal visual field of the non-deprived eye. This would explain the higher positive response level of MD cats to such stimuli with binocular viewing than with monocular viewing and the consequent reduction in the aforementioned transient orientation for binocular viewing (see Fig. 3). Finally, as the cat learned to use the monocular segment of its deprived eye's visual field, it developed visual placing with that eye concurrently with improvements in orienting to and locating stimuli in the appropriate region of visual field.

It has been reported^{6,7} that a reverse suture operation in an MD cat results in better vision for its eye than for such an eye of an MD cat which never had its normal eye surgically closed. In the present study, tests of LMDR provided the same qualitative results as tests of deprived eyes in the other MD cats. The slightly brisker visual behavior of LMDR could simply result from the fact that its deprived eye was exposed to a normal environment for a longer period than the deprived eyes in the other MD cats and thus not be a direct consequence of forced usage of that eye. Of course, the testing used here differed from the testing in other experiments^{6,7} and may not have been as sensitive in revealing improvements in the deprived eye due to forced usage.

BD cats. Unlike the MD cats, neither BD1 nor BD2 showed signs of any visual behavior for a number of days after eye-opening. This is in agreement with other observations that BD cats seem blind immediately after eye-opening^{2,5,29}. It is possible that this difference between MD and BD cats is an artifact due to their different sensory experience before eye-opening which resulted in less confusion for MD cats than for BD cats after eye-opening: the environment of MD cats provided them with specific visual experience through their non-deprived eyes whereas the BD cats received only tactile, auditory and olfactory experience. Also, during pretraining before eye-opening, the MD cats became acquainted with the test through vision whereas the BD cats experienced these tests through alternative senses. On the other hand, it is possible that this behavioral difference represents a more basic neurological difference between MD and BD cats.

Visual discrimination learning

Earlier reports indicate that during monocular testing both MD cats using their deprived eyes^{5-7,14} and BD cats⁵ had considerable difficulty in making pattern discriminations. The results presented here suggest that while attempting to solve the discrimination problems, the cats could use only parts of their visual fields, and that they might have difficulty in keeping the stimulus within the functional portions of the visual field: thus BD cats might 'lose' the stimuli if their visual axes moved slightly ipsilaterally, and MD cats probably cannot fixate with their deprived eyes. This predicts that if a discrimination test were used which limited the stimuli to appropriate retinal regions, there would be less difference in learning among normal, MD and BD cats.

With the above suggestion in mind, an interpretation can be proposed for the

data of Rizzolatti and Tradardi¹⁴. They have reported that a MD cat, while using its deprived eye to learn a pattern discrimination, commonly made large 'scanning' movements of the stimuli with its head. Such movements were not seen when the cat used its non-deprived eye. Perhaps these scanning movements during testing of the deprived eye represent an attempt by the cat to bring the stimuli into the monocular segment of the visual field.

Neurological substrates for the visual deficits

Sprague²¹ has demonstrated that, in the cat, the visual cortex and superior colliculus interact to subserve the type of visual behavior studied in this experiment. It is interesting, therefore, to consider the behavioral deficits described here in the context of previously described functional deficits in the LGNd^{18,19,27}, striate cortex^{5,8,12,28-30} and superior colliculus^{25,26} of visually deprived cats.

MD cats. The visual fields of MD cats summarized in Fig. 8B correlate well with what is known of the physiological abnormalities in these cats. Considering cortical neurons with receptive fields in the binocular segment of the visual field, most neurons in normal cats are binocularly driven¹¹, but nearly all in MD cats are normally driven only by the non-deprived eye^{5,8,12,28,29}. Similarly, most superior collicular units are binocularly driven in normal cats²³ but are driven almost exclusively by the non-deprived eye in MD cats²⁵. The LGNd in a normal cat has a mixture of X-cells and Y-cells¹⁰ and the non-deprived eye of MD cats drives a normal proportion of X- and Y-cells in the LGNd¹⁸. The deprived eye almost exclusively drives X-cells in the binocular segment of the nucleus¹⁸; but in the monocular segment of the LGNd contralateral to it, the deprived eye drives the normal complement of X- and Y-cells¹⁸. Since the LGNd seems abnormal in its binocular segment but normal in its monocular segment, it seems possible that cortical neurons with receptive fields in the monocular segment of the deprived eye's visual field have normal properties. Furthermore, the analogous portion of the superior colliculus might remain normal since many functional properties of this structure in both normal²⁴ and MD cats²⁵ seem to be influenced by the corticotectal projection. This pattern of receptive field properties would provide a clear physiological basis for the behavior of MD cats.

BD cats. No correlate for the behavior of BD cats summarized in Fig. 8C is apparent from physiological studies of the BD geniculostriate system. Cortical abnormalities in these cats were reported to be less severe than in MD cats and to include a slight decrease in binocular interaction on single cells and an increase in the frequency with which both unresponsive cells and cells with poorly organized receptive fields were found^{5,29}. Their LGNds exhibit both a relatively moderate loss of Y-cells¹⁸, and a reduction of binocularly inhibited neurons¹⁹. One suggestion¹⁷ is that the visual cortex in BD cats has become non-functional for visually guided behavior although it might continue to function for other visual behavior such as discrimination learning (see for example ref. 1).

If this is the case, then the superior colliculus might alone control visually guided behavior. This follows because Sprague²¹ has shown that after unilateral cortical removal the ipsilateral superior colliculus maintains the cat's ability to

respond to visual stimuli throughout the contralateral hemifield. The BD superior colliculus appears abnormal in that its neurons are driven almost exclusively by the contralateral eye with reduced direction selectivity, and these deficits are similar to those in the superior colliculus of a decorticate cat^{24,26}. This evidence that the BD cat has a non-functional corticotectal pathway was the basis for the above suggestion that the visual cortex in this cat does not participate in visually guided behavior¹⁷. If each eye in the BD cat maintains functional connections for visually guided behavior nearly exclusively with the contralateral superior colliculus, one would expect this cat to respond during monocular testing only to stimuli in its ipsilateral hemifield. Furthermore, the ipsiversive following of moving stimuli during monocular testing in BD cats (see Results) could be a simple consequence of this visual field defect since stimuli moving in the reverse direction would soon enter the non-functional region of visual field and be lost.

This tentative correlation between BD behavior and physiology has two major assumptions which require further data for acceptance or rejection: (1) that the BD geniculostriate system is non-functional for visually guided behavior as studied here, and (2) that the BD superior colliculus controls this behavior by maintaining normal connections with the contralateral retina.

Difference between MD and BD cats

A good deal of evidence has been recently gathered which suggests that different mechanisms control visual development in MD and BD cats. This suggestion¹⁷ was based on certain qualitative differences in the development of interocular alignment¹⁶, in the LGNd anatomy (ref. 9 and Guillery, personal communication; see also Introduction) and physiology¹⁸, and in the superior collicular physiology^{25,26} which could not easily be explained by any single, common mechanism. Two differences in visual behavior seen in this study could be added to the above list. First, MD cats showed visual behavior with their deprived eyes when first tested after eye-opening whereas BD cats seemed blind for some time after eye-opening. Second, the final visually guided behavior and visual fields of MD cats were different from those of BD cats, and, as suggested above, each MD cat seemed to behave as if guided by normal development of the monocular segment of visual cortex (and perhaps also the superior colliculus) whereas each BD cat seemed to behave as if guided by normal development of only contralateral retinotectal pathways. These behavioral differences, therefore, are consistent with a previous suggestion that separate mechanisms guide visual development in MD and BD cats¹⁷.

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