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PERMANENCE OF VISUAL PERIMETRY DEFICITS IN MONOCULARLY AND BINOCULARLY DEPRIVED CATS

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SUMMARY

(1) Monocularly (MD) and binocularly deprived (BD) cats were tested to determine the permanence of previously described behavioral deficits on a visual perimetry test. Three group I MD cats and 2 group I BD cats had both eyes open as adults for up to 2 years before testing. At a similar time before testing, 2 group II MD cats had a reverse-suture operation (deprived eye open, non-deprived eye shut), and 2 group II BD cats had the right eye open.

(2) Group I cats showed no recovery from previously described deficits. The MD cats had a normal visual field for the non-deprived eye (from 45° contralateral to 90° ipsilateral), but with the deprived eye responded only to objects in the monocular segment (60°–90° ipsilateral) while ignoring objects throughout the binocular segment (45° contralateral–45° ipsilateral). The BD cats with each eye responded to objects only in the ipsilateral hemifield, ignoring the contralateral 45° field of view.

(3) Group II cats with the open, deprived eye had deficits identical to the above indicating that lack of usage of the non-deprived eye resulted in no improvement of visual field for the deprived eye. The group II BD cats, when monocularly tested 4 h after opening of the left eye, displayed visual behavior similar to that seen for the right eye.

(4) Given the techniques used in this experiment, it is concluded that MD and BD cats develop permanently reduced visual fields as a result of their early visual deprivation.

INTRODUCTION

Considerable behavioral, anatomical and neurophysiological data have been accumulated which show that early visual deprivation severely affects the developing mammalian visual system. Much of this work has been done on monocularly (MD) and binocularly deprived (BD) cats[10], and known effects include: (1) generally poor vision while using the deprived eyes[2,3,11,16]; (2) histologically smaller cells in the lateral geniculate nucleus (LGN) as a result of early deprivation[1,5,6,14,16]; and (3) inability of deprived eyes to effectively or normally drive many LGN and cortical cells via visual stimuli[1,4,12,15,16].

While there is general agreement with regard to the above, there exists considerable doubt regarding the permanence of many deprivation effects. In other words, how much recovery from these abnormalities is possible in an MD or BD cat? On the one hand, Wiesel and Hubel[17] report that for MD cats the aforementioned cortical and LGN abnormalities remain despite exposure to a normal visual environment for up to 5 years. On the other hand, Chow and Stewart[1] report post-deprivation LGN histological changes in MD and BD cats which underwent an extensive period of specific visual training. They also suggest slight recovery from cortical electrophysiological abnormalities in their cats[1].

Likewise, implicit contradictions concerning post-deprivation recovery exist in published behavioral data for MD and BD cats. Reports tend to agree that poor but asymptotic behavior is achieved by the deprived eyes within a few weeks after eye-opening, and further improvement has not been reported[2,3,11]. However, if in MD cats opening of the deprived eye coincides with closing of the non-deprived eye (a reverse-suture procedure) the asymptotic level reached by the deprived eye is higher than the level in such cats with both eyes open[2,3]. This then suggests that behavioral recovery in at least MD cats is partly a function of their adult visual environment. Finally, a recent, brief report points to substantial behavioral recovery in reverse-sutured MD cats[9].

In order to arrive at answers to the important question concerning the permanence of early deprivation effects, it is necessary to gather more data on the long-term effects, particularly with regard to a more recent appreciation of the effects of early visual deprivation[6,11,12]. This paper describes one such study of the permanence of previously described visual perimetry losses in MD and BD cats[11].

Normal cats respond to visual stimuli with each eye from approximately 45° contralateral to 90° ipsilateral[11,13]. MD cats respond with a normal field of view for the non-deprived eye, but orient with the deprived eye to stimuli only in the 'monocular segment' (*i.e.*, the ipsilateral 45°–90° normally seen only by one eye)[11]. BD cats respond with each eye only from the midline to 90° ipsilateral[11]. Thus in the first few weeks after eye-opening it was determined that MD cats, with their deprived eyes, have lost their entire binocular field of view (bounded bilaterally by 45°), whereas BD cats have lost their contralateral 45° of view with each eye. The purpose of the present experiment was to determine to what extent certain types of adult visual experience decrease these deficits in MD and BD cats.

MATERIALS AND METHODS

Subjects

Deprivation. Nine cats from 9 separate litters, all born and reared in the laboratory, were used in this experiment. After weaning and for the duration of the experiment, the cats were housed in individual cages. Five MD cats had one eye sutured shut from 8 days of age until 5–12 months of age; 4 BD cats had both eyes sutured for the same period. Six of the cats (LMD1, RMD1, RMD2, LMDR, BD1, and BD2) provided data for a previous visual perimetry experiment in the weeks after eye-opening[11].

Post-deprivation experience. All of the cats had 8–26 months of visual experience with previously deprived eyes before final testing. Fig. 1 gives the details of this experience for each of the 9 cats. In terms of post-deprivation experience, the cats were divided into two groups. Group I (LMD1, RMD1, RMD2, BD1, and BD2) simply had their deprived eyes opened for the entire period and thus had a binocular environment. Group II (LMDR, RMDL, BD7, BD9) had only one eye opened during this period: the MD cats had a reverse-suture operation whereby each deprived eye was opened while the non-deprived eye was closed; the BD cats each had only the right eye opened. It was felt that the closure of the non-deprived eye might potentially provide a competitive advantage for the deprived eye and thus enhance the chances of the deprived eye's functional recovery. Indications of this possibility are found in previous work[1–3,9].

Perimetry test

The perimetry test used in this experiment is a minor variant of one which has been fully described elsewhere[11], and it is briefly outlined below.* Food-deprived cats were tested on a table marked off into sixteen 15° sectors by intersecting guidelines designated 120 °L, 105 °L, . . . etc . . ., 0°, 15 °R, . . . etc . . ., 120 °R (see Figs. 2–5).

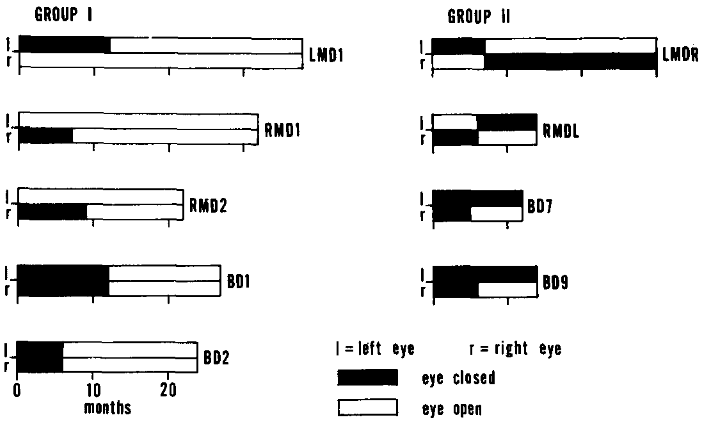

Fig. 1. Deprivation and post-deprivation history of cats before testing. For each cat, the final response levels of Figs. 2–5 were accumulated in the month following the histories indicated here. In addition, all group I cats plus LMDR were tested some months prior to this as indicated in Figs. 2–4 ('early response levels'). This prior testing in group I cats was immediately after eye-opening, and in LMDR was during its 16th postnatal month.

* The previous report[11] should be consulted for the assumptions underlying the test.

A cat was restrained so that its lateral canthi were aligned with the 90° guidelines and its nose pointed along 0°. It was pretrained to fixate to visual and/or auditory cues provided by a piece of dry cat food held in forceps and tapped on the table at 0° approximately 50 cm from the cat's nose; this was the *fixation object*. While the cat was thus fixating, a *novel stimulus* (food in forceps or a 1 cm diameter red cardboard circle at the end of a long, stiff wire) was presented vertically 20–40 cm from the cat's nose along one of the guidelines. The cat was then immediately released from restraint and its behavior noted.

If the cat immediately oriented to *and* moved toward the novel stimulus, this was scored as a *positive* trial for the guideline tested. Any other behavior was scored as a *negative* trial and almost always (> 95% of negative trials) consisted of the cat's ignoring the novel stimulus and immediately approaching the fixation object[11]. The cat ate regardless of its response, and thus there would appear to be little or no motivational pressure on the cat to respond positively. Since stimuli presented at 0° required no initially detectable orientation by the cat for a positive response, this guideline was scored differently: on positive trials the cat stopped short of the novel stimulus and would begin to explore it before making tactile contact; on negative trials the cat apparently took no notice of the novel stimulus until making tactile contact, at which time the cat gave a distinct startle response; the few (< 10%) responses that could not be clearly classified as above were scored separately and will not be further considered.

The assistant holding the fixation object observed the cat's eyes and ascertained that no detectable (*i.e.*, > 15°; see ref. 11) eye movements occurred except during orientations to the novel stimulus.

Group I cats were tested binocularly and monocularly (by means of an opaque occluder completely covering one cornea). LMDR and RMDL were monocularly tested only with their originally deprived eyes. BD7 and BD9 were first tested monocularly during many daily test sessions with their previously opened right eyes. Each of the group II BD cats was then anesthetized with halothane and had its left eyelid surgically parted. Monocular testing began 4 h later for a single test session with the right eye occluded. Immediately following this, each cat was again anesthetized and had its left eyelid resutured to allow further study with only about 5 h of adult experience with the left eye.

An important control consisted of many *blank trials* during which the cat was released with no presentation of the novel stimulus. If the cat then immediately came to the fixation object, this was scored as a negative blank trial. Any other behavior (almost always orienting movements as if the cat were searching for the absent novel stimulus) counted as a positive blank trial.

Each cat was repeatedly tested over a number of daily test sessions until each viewing condition (monocular and binocular) typically had 20 or more responses for each guideline plus 100 or more blank trial responses. During every session the order of trials was randomized. No day-to-day variability was detected. The results in Figs. 2–5 are the averages for all test sessions. Only visual regions where response levels were higher than blank response levels are considered to be regions in which the cat was visually responsive[11]. Thus the scoring for Figs. 2–5 is 'normalized' against the blank response levels which were considered as zero. That is, if the blank response level is B% and the raw score for a guideline is G%, then the 'normalized' score for that guideline becomes (G—B)/(100—B)% if G > B, and is zero if B > G. Blank trial response levels were typically 5–10% and never more than 20%.

In addition to this perimetry test, the cats were also tested for visual placing and visual following of moving objects (generally the novel stimulus) using routine methods previously described[11].

RESULTS

Group I cats

MD cats. LMD1, RMD1 and RMD2 responded on tests for visual placing and following much as they had previously[11]. With the non-deprived eye occluded, each had inconsistent visual placing that seemed 'coarser' than normal. That is, placing movements mostly involved the more proximal joints, while normal cats or the MD cats using the non-deprived eye could make fine adjustments using their distal joints. Perhaps this difference is equivalent to the dissociation of the visual placing response into elicited and guided components as suggested by Hein and Held[7]. During deprived-eye testing, each cat could follow moving objects only when these were kept in the ipsilateral periphery (monocular segment) of the visual field.

Fig. 2 summarizes the perimetry data for these cats. It is clear that during the extensive post-deprivation period in a normal visual environment (see Fig. 1) there had been no discernable expansion of the abnormally small visual field. The cats using their deprived eyes still responded only to stimuli in the monocular segment of visual field while ignoring stimuli throughout the binocular segment.

A final point is that these cats, as before[11], failed to use the monocular segments of their deprived eyes for fixation. This was seen in two ways. First, no MD cat was seen to adduct the deprived eye during fixation so as to bring the fixation object into the monocular segment of the visual field. In line with this is the fact that there was no tendency for the visual perimetry (see Fig. 2A) to shift towards 0° as might be expected if the cat began to adduct its eye during fixation. However, it could be argued that such a cat would be expected to maintain eccentric fixation by turning its head rather than its eyes, and that the head restraint employed in the experiment prevented the cat from doing so. Second, when, after an orientation to the novel stimulus in the monocular segment during deprived eye testing, the novel stimulus was moved about 10° in any direction, the cat headed towards the original position of the stimulus and did not follow the movement[11]. It should be noted that in this latter case the cat's head was 'movement' freed from restraint and could turn to achieve eccentric fixation, but the cat apparently did not do this.

BD cats. Like the MD cats, BD1 and BD2 appeared unchanged in their visual placing and following of moving objects. Their placing was indistinguishable from that described above for the deprived eye of MD cats, and monocularly they could follow objects only if moved ipsiversively into the ipsilateral hemifield[11].

Fig. 3 shows the perimetry data for BD1 and BD2 immediately after eye-opening

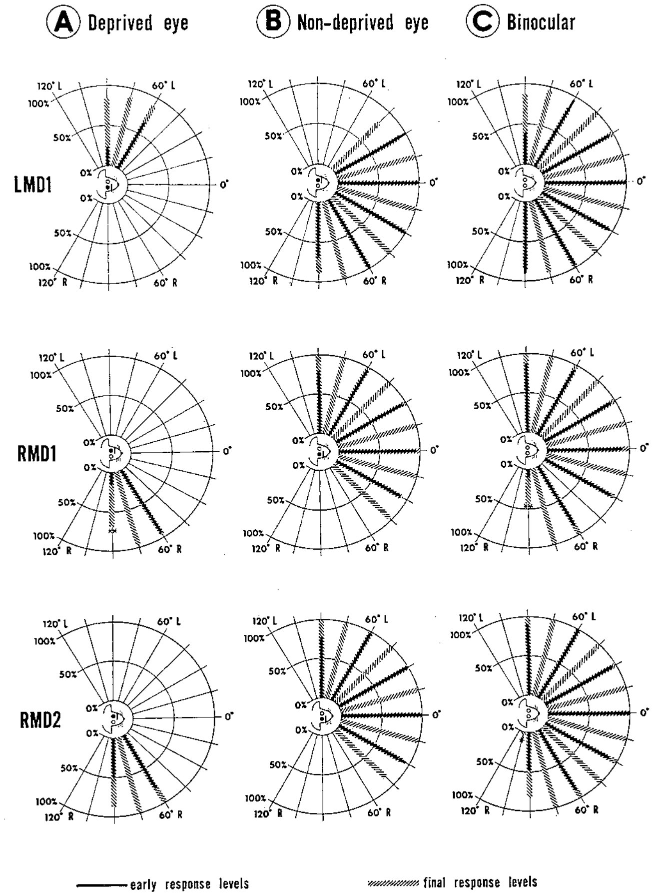

Fig. 2. Visual field perimetry in the Group I MD cats. Each graph in polar coordinates shows the positive response levels for each guideline against a baseline of 'blank positives' (see Methods) during the 3 conditions of viewing. The occluded eye is shown as filled in with a line covering the cornea. Data from the 'early response levels' were previously reported[11], and at the time only the 0°, 30°, 60°, 90°, and 120° guidelines were tested. All guidelines shown were tested in each graph, and the absence of an indicated response level simply means that this level was equal to or less than the blank positive level. Unless otherwise indicated by asterisks, all response levels shown are significantly greater than the blank positive level ($P < 0.001$ on a χ^2-test). A: perimetry for LMD1, RMD1, and RMD2 during monocular testing of the deprived eye. Note that this is the left eye for LMD1, but the right eye for RMD1 and RMD2. B: perimetry for LMD1, RMD1, and RMD2 during monocular testing of the non-deprived eye. C: perimetry for LMD1, RMD1, RMD2 during binocular testing. * Final response level (in C, for RMD2) not significantly greater than the blank positive response level. ** Early response levels (in A and C, for RMD1) greater than the blank positive response level but with marginal significance ($P < 0.05$); final response levels are significantly greater ($P < 0.001$).

and again after a 16 or 18 month period of a normal visual environment. As in the MD cats, there has been no recovery from the previously described deficits: with monocular testing these cats still could not respond to stimuli in the normally responsive contralateral 45° of visual field.

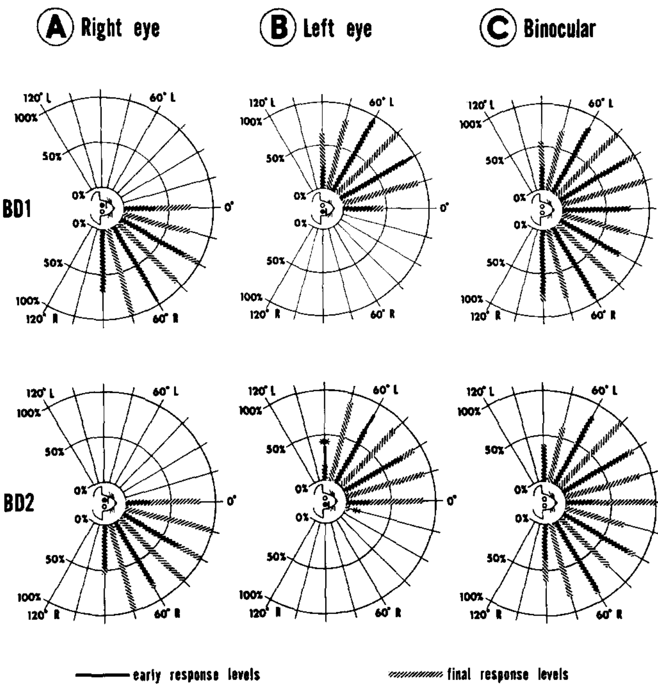

Fig. 3. Visual field perimetry in the group I BD cats. Each graph in polar coordinates shows the visual response levels for each guideline as in Fig. 2. A: perimetry for BD1 and BD2 during monocular testing of the right eye. B: perimetry for BD1 and BD2 during monocular testing of the left eye. C: perimetry for BD1 and BD2 during binocular testing. * Final response level (in B, for BD2) not significantly greater than the blank positive response level. ** Final response level (in B, for BD2) significantly greater than the blank positive response level at lower level of significance ($P < 0.02$); early response level significantly greater ($P < 0.001$).

Group II cats

MD cats. LMDR and RMDL behaved on all tests essentially the same as did LMD1, RMD1, and RMD2 when the group I cats had their non-deprived eyes occluded. The group II MD cats had the same deficits in visual perimetry (see Fig. 4).

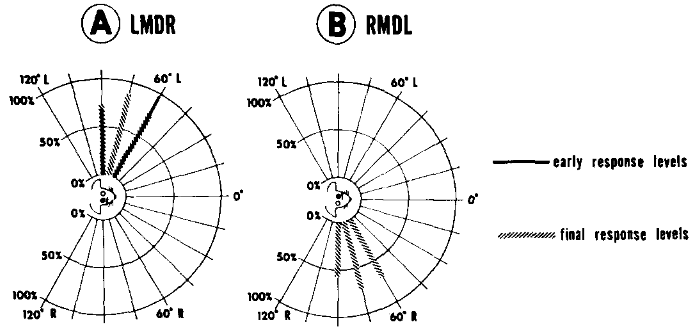

Fig. 4. Visual field perimetry in the group II MD cats. Each graph in polar coordinates shows the visual response levels for each guideline as in Fig. 2. A: perimetry for LMDR during monocular testing of the left (originally deprived) eye. B: perimetry for RMDL during monocular testing of the right (originally deprived) eye.

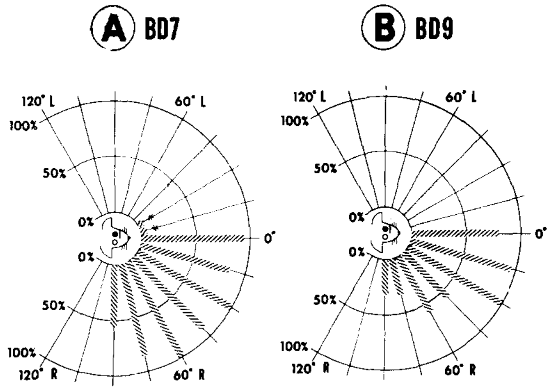

Fig. 5. Visual field perimetry in the group II BD cats. Each graph in polar coordinates shows the visual response levels for each guideline as in Fig. 2. A: perimetry for BD7 during monocular testing of the right eye. B: perimetry for BD9 during monocular testing of the right eye. * Response levels (in A) not significantly greater than the blank positive.

Thus, despite the 8 or 23 month period of lack of usage of the non-deprived eye, no functional recovery of lost visual field for the deprived eye was apparent in these cats. Like the group I cats, LMDR and RMDL did not appear to learn to fixate with their monocular segment (see above).

BD cats. As with the MD cats, BD7 and BD9 behaved indistinguishably from BD1 and BD2 when the latter were monocularly tested. This is evident mainly from the extensive right-eye testing of BD7 and BD9 which is indicated in Fig. 5. Because these cats were tested for only one day with the left eye, only a few responses for most guidelines were possible, and these qualitatively indicated a perimetry including only the ipsilateral hemifield. Normal cats which are monocularly tested demonstrate high response levels for both the 30° guideline ipsilateral and the 30° guideline contralateral to the open eye, whereas BD cats which are monocularly tested show high response levels for the 30° guideline ipsilateral to the open eye but apparently ignore objects presented at the 30° guideline contralateral to the open eye (see above and ref. 11). Thus during the single test session with the left eye for BD7 and BD9 attention was focused on both of the 30° guidelines (ipsilateral and contralateral), and each was tested 20 times. Table I presents these results and indicates a significant difference for both cats between response levels for the ipsilateral and contralateral 30° guidelines ($P < 0.001$ on a χ^2-test), and this strengthens the above suggestion that visual perimetry for the left eyes of BD7 and BD9 includes only the ipsilateral hemifield.

Finally, Table I demonstrates that these cats can orient using their previously sutured left eyes within hours of eye-opening. During this test session they also displayed clear though weak visual following, but not placing, responses. Thus, except for the extent of visual perimetry, these BD cats when tested immediately after eye-opening were very much like MD cats similarly tested[11].

DISCUSSION

Post-deprivation experience of up to 2 years failed to relieve the deficits in

TABLE I

RESPONSES FROM MONOCULARLY TESTING LEFT EYES OF BD7 AND BD9, 4 H AFTER EYE-OPENING

This compares the responses to stimuli placed in the ipsilateral hemifield both with those for stimuli placed in the contralateral hemifield and also with blank trials.

	BD7		*BD9*	
	Positive	*Negative*	*Positive*	*Negative*
30° Ipsilateral	15	5	12	8
30° Contralateral	2	18	0	20
Blank	2	13	1	16

visually guided behavior and visual perimetry as seen in the MD and BD cats of this study. These deficits remained fully apparent even in the group II cats which were prepared in such a way as to give a competitive advantage to their previously deprived eyes[1–3,9]. That is, MD cats with the deprived eye continued to ignore stimuli in the binocular segment of visual field and BD cats with each eye continued to ignore stimuli in the contralateral hemifield. There is in Figs. 2 and 3 some suggestion that MD and BD cats with their deprived eyes eventually improve their response levels within the attended regions of visual field. However, the final levels are not significantly higher than the early levels, and there is thus no data to support even this type of improvement.

On the surface, the above would seem to contradict results suggesting considerable behavioral recovery in reverse-sutured MD cats[2,3,9]. This contradiction may be more apparent than real for two reasons. First, subtle differences in the deprivation schedule, post-deprivation conditions, and testing procedures (especially motivational levels — see Methods) could be important variables in post-deprivation recovery. For one example, it may be that the visually deprived cats in this study never used their deprived eyes during the entire post-deprivation period except for the relatively brief test sessions. This is quite possible since there is no obvious need for vision in the cats' caged environment, and an environment which forces the cats to use their visually deprived eyes might allow for considerable recovery in the visual field perimetry deficits. Therefore the recovery could be highly dependent on post-deprivation conditions, as well as the other above-mentioned variables, and until more is known concerning this point, great care should be taken in comparing the conclusions based on this study with those of similar studies of visually guided behavior[3,9], and especially learning[1,2].

Second, even assuming that the above-mentioned variables do not play a major role in post-deprivation recovery, the conclusion that visually deprived cats show no post-deprivation recovery of their reduced visual fields is still consistent with reports that considerable behavioral recovery is possible in these cats. It may be, for instance, that MD and BD cats 'learn' to make the best of their limited visual capacity (*i.e.*, reduced visual field, acuity, etc.). In this context it is interesting to note that, with the motivational levels and techniques used here, none of the MD cats apparently learned to fixate with the monocular segment of the deprived eye (however, see Results for the group I MD cats). It is conceivable that during discrimination learning[2] MD cats could learn to use eccentric fixation involving the monocular segment, and this alone might significantly improve the cats' visuomotor abilities.

However, based on this study and a previous report[11], the present MD and BD cats showed no qualitative post-deprivation improvement in their visually guided behavior. Previously, it was shown that MD cats within hours of eye-opening already display their basic pattern of visually guided behavior with the deprived eye[11], and this has now been seen in several other MD cats (S. M. Sherman, unpublished observations). Previous reports suggesting that MD cats are totally blind for some period after eye-opening[2,3,14–16] could be due to the failure of earlier investigators to test the monocular segment.

BD cats presented a contrasting picture in that the same techniques failed to demonstrate any visually guided behavior for some weeks after eye-opening[11]. One suggestion then offered was that an MD cat, having been reared with visuomotor experience via the non-deprived eye, has immediate visuomotor abilities with the deprived eye, and that a BD cat, with no previous visual experience, did not at first have visuomotor abilities because of some sort of undefined 'confusion' with its novel sensory modality. The data from this experiment, *i.e.*, that a BD cat given visuomotor experience through the right eye will demonstrate visuomotor ability with the left eye within hours of opening that eye, are in agreement with this general view. Also, despite differences in methodology, it is interesting that this scheme supports the view put forth by Hein and Diamond[8] that in visually deprived cats the ability to respond with 'visually elicited' behavior is interocularly transferred from the experienced to the naive eye.

In summary, given the present techniques, especially the cats' post-deprivation environment and motivational level, there is no evidence for post-deprivation changes in the visually guided behavior of either MD or BD cats. This conclusion apparently runs counter to a recent report using slightly different techniques[9]. The interesting possibility that changes in methodology could substantially alter the above conclusion should certainly be tested. This general line of research is being continued to determine the permanence of various other deficits in MD and BD cats[1,5,6,11].

ACKNOWLEDGEMENTS

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