Recovery from the Effects of Monocular Deprivation in Kittens

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ABSTRACT   Significant recovery from the effects of early unilateral eye closure has been found following a period of reversed deprivation involving forced usage of the deprived eye. A simple period of binocular vision, however, has been reported to be ineffective. We have compared these two recovery conditions (reversed deprivation and binocular vision) in kittens initially deprived to the age of 45 or 60 days, and given seven to eight weeks of recovery. We estimated *behavioral recovery* by measuring visual acuity through the deprived eye. Kittens deprived to day 45 attained nearly normal grating resolution in their deprived eyes (5-6 cycles/degree), while those deprived to day 60 showed enduring partial acuity deficits (4-5 cycles/degree). Surprisingly, the deprived eye's acuity in kittens given binocular vision during recovery was nearly the same as that possessed by the deprived eyes of reverse-deprived kittens. We estimated *physiological recovery* from the visual response properties and eye dominance of 359 cortical neurons; all kittens showed shifts in eye dominance from the situation that obtains after a period of deprivation. Reverse-deprived kittens, in agreement with previous reports, showed more pronounced shifts of cortical eye dominance than did binocularly recovered kittens. Nevertheless, significant recovery of both the deprived eye's influence and of the selectivity of its receptive fields was seen in kittens given binocular vision. In no case was there significant recovery of cortical binocular interaction: most neurons were monocularly driven, and were aggregated into ocular dominance columns strongly dominated by one eye or the other. Since both behavioral and electrophysiological measurements suggest considerable recovery of function even in cases where kittens were merely given binocular vision during recovery, we conclude that the two eyes' effectiveness is not solely determined by competitive interaction—significant changes can occur when neither eye has a competitive advantage over the other.

The majority of neurons in the visual cortex of a young kitten may be influenced by visual stimuli delivered to either eye. Allowed normal correlated binocular visual experience throughout the first months of life, these neurons refine their binocular specificity, providing in the adult cat the substrate for binocular single vision and stereopsis (Hubel and Wiesel, '62, '63; Barlow et al., '67; Pettigrew et al., '68; Pettigrew, '74; Packwood and Gordon, '75). If, however, the normal pattern of input is disrupted by covering one eye, cortical neurons lose their functional connections with that eye, and may only be activated through the eye that was open (Wiesel and

Hubel, '63b, '65a). The changes in cortical binocularity are accompanied by a profound behavioral deficit: tested through its deprived eye, a monocularly deprived cat at first seems almost totally blind (Wiesel and Hubel, '63b, '65a; Dews and Wiesel, '70). Other disruptions of binocular visual experience, such as causing one eye to deviate (preventing simultaneous correlated binocular stimulation of corresponding points on the two retinae) result in an equally marked breakdown of cortical binocularity (Hubel and Wiesel, '65). Humans who have suffered similar anomalies of early binocular visual experience have long been known to lack binocular fusion and stereopsis,

and it is likely that they, like deprived kittens, lack the normal complement of binocularly driven cortical neurons (Movshon et al., '72; Mitchell and Ware, '74).

Functional changes in the visual pathway may only be produced by visual deprivation imposed within a certain "sensitive period" early in life. In kittens, this period extends from the third week to the fourth month of life (Hubel and Wiesel, '70). If a period of monocular deprivation extends through the end of the sensitive period, the functional changes that result seem largely permanent: Wiesel and Hubel ('65b) found little or no restoration of the influence of the deprived eye in the cortex following either extended periods of binocular vision, or even of forced usage of the deprived eye. The behavioral recovery in these animals is also very limited (Dews and Wiesel, '70).

Since the effects of monocular deprivation may be seen following rather brief periods of eye closure (Hubel and Wiesel, '70), it is also possible to examine the extent to which physiological and behavioral recovery may be seen *within* the sensitive period. Hubel and Wiesel ('70) reported that a kitten monocularly deprived to the age of five or seven weeks, and then permitted normal binocular vision for some months, showed a surprisingly small recovery of physiological function in the cortex, despite the fact that the deprived eye does gain considerable behavioral capabilities (Dews and Wiesel, '70). In contrast, Blakemore and Van Sluyters ('74) and Movshon ('76a) showed that forcing a similarly deprived kitten to use its deprived eye *alone*, even for a few weeks, causes a marked and sometimes total shift in cortical ocular dominance toward the initially deprived eye. These reverse-sutured kittens also show clear recovery of behavioral function when using their deprived eyes (Dews and Wiesel, '70; Blakemore and Van Sluyters, '74; Movshon, '76b).

These results, and others concerned with the morphological consequences of early deprivation (Wiesel and Hubel, '63a; Kupfer and Palmer, '64; Guillery, '72), have been interpreted to indicate that during the sensitive period there is a competitive interaction between the afferents from the two eyes at the level of the visual cortex. If the two eyes are prevented from working together to activate cortical neurons, then the eye that is more effective in driving a particular cell comes to drive that cell exclusively; the other eye becomes largely or totally ineffective (Hubel and Wiesel, '65; Sherman et al., '74). Once the influence of an eye over a cell is established, that eye may only be dislodged by artificially giving the other eye a competitive advantage by a procedure like reverse-suturing; such a procedure must take place within the sensitive period in order to be effective (Blakemore and Van Sluyters, '74; Blakemore et al., '76).

In the course of an extended series of experiments examining behavioral recovery from the effects of monocular deprivation (Giffin and Mitchell, '77), we noticed again the phenomenon reported by Dews and Wiesel ('70): kittens allowed binocular vision within the sensitive period following early deprivation show striking behavioral recovery. We therefore decided to compare directly the recovery seen under these conditions with that seen during reversed monocular deprivation (Dews and Wiesel, '70; Movshon, '76b), and to reexamine the extent of physiological recovery in the visual cortex of the same animals. We have briefly presented these results elsewhere (Movshon et al., '77).

METHODS

Animals and rearing conditions

Five kittens were used in these experiments; all four of the kittens that were tested behaviorally were littermates. All animals were caged in a colony room illuminated on a 16-hour/8-hour light/dark cycle, and their health was checked daily. Kittens were routinely vaccinated against enteritis at the age of nine weeks.

At the age of eight days, the right eyelids of each kitten were sutured shut under ketamine anesthesia, using methods similar to those described by Wiesel and Hubel ('63a). During the surgery the eye was infiltrated with a local ophthalmic anesthetic (proparacaine HCl) and antibiotic ointment (aureomycin). At the age of 45 or 60 days, the kittens were anesthetized again and their sutured eyelids parted. At the same time, two of the animals were reverse-sutured—the lids of their left eyes were closed. Animals that had both eyes open during recovery were given the mnemonic suffix B, while those reverse-sutured were given the suffix R. The kittens are hereafter referred to as 45R and 60R (reverse-sutured at days 45 and 60) and 45B and 60B (deprived eye opened at days 45 and 60). Two kittens were reared in the manner of 45B. 45B(1), from the first litter, was tested behav-

iorally, while 45B(2) was not tested, and served as a control for possible effects of behavioral testing on cortical physiology.

The kittens were inspected daily for small "window" openings in their sutured eyelids. Small openings, through which little or no vision can have occurred, were noted and immediately repaired in 60R at the ages of 65 and 97 days; none of the other kittens had any such openings.

The physiological recordings that terminated each experiment were arranged to give roughly equal recovery periods of between seven and eight weeks for each kitten. The kittens' ages at recording were: 45B(1), 100 days; 45B(2), 100 days; 45R, 102 days; 60B, 110 days; 60R, 109 days. All kittens were thus recorded from near the end of the sensitive period (Hubel and Wiesel, '70).

Behavioral testing

Behavioral estimates of the monocular visual acuity of four kittens were obtained at regular intervals during recovery on a jumping stand using procedures that have been detailed elsewhere (Mitchell et al., '76, '77). The kittens were trained to jump down from an elevated platform onto one of two stimuli mounted side-by-side on trapdoors below. The positive stimulus was always a vertical square wave grating (contrast ≈1) whose spatial frequency was the experimental variable; the negative stimulus was a uniform grey field of exactly the same size (at least 14 deg square) and space-average luminance (110 cd/m²) as the grating. Kittens were rewarded for correct performance with beef baby food and brief gentling; punishment usually was administered by merely withholding these rewards, but occasionally the trapdoor under the negative stimulus was opened and the kitten allowed to fall roughly 30 cm to the floor. The positions of the stimuli were reversed in pseudo-random sequence from trial to trial; the long runs present in true random sequences tended to lead to the establishment of side preferences.

Once the kitten had mastered the discrimination with a grating of one spatial frequency, the animal was given ten trials at a higher frequency and this procedure repeated until performance fell below criterion level (7 correct jumps in 10 trials). Spatial frequency was altered between trials either by raising the jumping stand (to a maximum of 1 m) or by changing the photographic patterns. Frequency-of-seeing curves generated by this method are rather steep (e.g., fig. 2), so estimates of spatial resolution are not strongly affected by a particular choice of threshold criterion.

Behavioral testing began between 10 and 14 days prior to the end of the initial deprivation period, ensuring that the animals were well trained at the time that measurements were first made in the deprived eye. Measurements were made daily for the first few weeks of recovery, and less frequently thereafter.

When testing the deprived eye of 45B(1) and 60B, the other eye was covered with a large black contact occluder. We checked regularly to ensure that the animal could not see around the edge of the occluder by constricting the pupil with a miotic (pilocarpine HCl) or by covering the whole eye with a patch. No change in performance ever accompanied these manipulations. Control experiments showed that the visual acuity of 45B(1) and 60B measured binocularly was identical to that measured with the deprived eye occluded, so we usually took binocular acuity measures as an index of the acuity of the nondeprived eye in these kittens.

Physiological recording

Our methods for obtaining single unit recordings from the visual cortex of acutely prepared, anesthetized cats have been described elsewhere (Cynader and Berman, '72; Cynader et al., '76). Cats were initially anesthetized with intravenous pentobarbital sodium, an endotracheal tube was emplaced, and the animals paralyzed with gallamine triethiodide given intravenously as required. The skull was exposed and a square flap of bone (approximately 5 mm square) removed over the central projection of area 17; the dura was not opened.

During recording, light anesthesia was maintained by artificially ventilating the animal with a mixture of N_2O and O_2 (70:30), and intravenous anesthesia was discontinued. The animal's body temperature was maintained near 38°C with a thermostatically controlled heating pad, and end-tidal P_{CO_2} was monitored continuously and maintained near 4.5% by varying the rate of the artificial respiration pump.

Contact lenses were chosen by retinoscopy to focus the eyes on a tangent screen 145 cm distant; the lenses contained 3 mm artificial
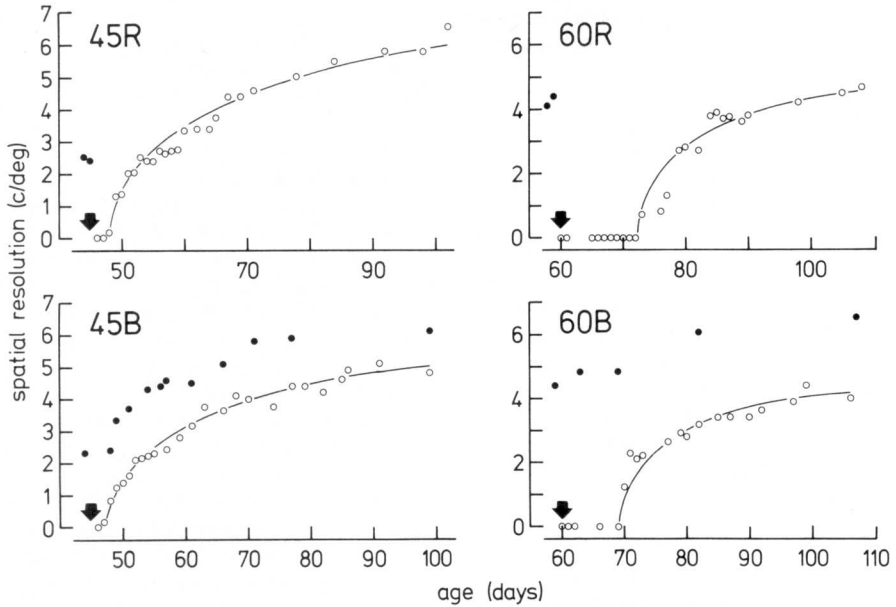
Fig. 1 The recovery in visual acuity in four kittens deprived of vision in one eye until day 45 or 60, and given recovery with reverse-suturing (suffix R) or binocular vision (suffix B). Filled symbols indicate performance measured through the initially open left eye in each case; open symbols indicate performance measured through the initially deprived right eye. Solid arrows indicate the end of the initial period of deprivation. Each data point represents the highest spatial frequency of grating for which the kitten jumped correctly seven times in ten trials on a given day. For comparison, note that the visual acuity of a normal kitten over these ages corresponds very closely to that measured through the initially open eyes of 45B and 60B (solid symbols, lower pair of graphs; Mitchell et al., '76). The smooth curves are fitted by eye through the data points.

pupils to decrease scattered light and increase depth of focus.

Single units and multiple-unit background activity were isolated in area 17 with glass-coated platinum-iridium microelectrodes (Wolbarsht et al., '60), driven hydraulically through the intact dura into the underlying cortex. We adopted the sampling procedure of Stryker and Sherk ('75), sampling units evenly throughout the cortical penetration at intervals of approximately 100 μm, in order to minimize the bias of our recorded population. Although these methods were originally devised to sample evenly from the finely spaced orientation columns in the cortex, their use here ensured that the number of neurons sampled from a given eye dominance column was proportional to its extent.

The receptive fields of single cortical units were examined using flashed and moving slits, edges and spots of light, and most units were classified as simple, complex, hypercomplex or non-oriented in accordance with standard criteria (Hubel and Wiesel, '62; Movshon, '76a; Cynader et al., '76). Non-oriented cortical units were distinguished from afferent fibers from the lateral geniculate nucleus (LGN) by the latters' concentric receptive field organization, monocular drive and brief action potentials. For each unit, we noted ocular dominance, using the 7-point scale of Hubel and Wiesel ('62), orientation and direction selectivity, and other significant receptive field characteristics. The responses of all units were simply judged by listening to their activity relayed over an audiomonitor; no quantitative analytical methods were used. We occasionally encountered units for which we could devise no effective visual stimulus; these units, like those identified as afferent LGN fibers, were excluded from the analysis.

At the end of the recording session, the animal was sacrificed with Nembutal and perfused through the heart with Ringer's solution followed by 10% buffered formalin. In some cases, blocks of the cortex containing the electrode tracks were cut, frozen, sectioned at 40 μm, and stained with thionin, in order to reconstruct the electrode penetrations. Blocks containing the LGNs were also

cut, sectioned and stained, in order to examine these nuclei for morphological changes.

RESULTS

Behavioral observations

Prior to the termination of the initial period of deprivation the visual behavior of the animals, tested through the open eye, appeared normal in all respects. Not only did they possess normal visually guided behavior, but their acuity as measured on the jumping stand was identical to that of normal animals of comparable ages (Mitchell et al., '76).

In dramatic contrast to the excellent visual behavior mediated by the initially open eye, all of the animals initially exhibited the very profound behavioral deficits described by Wiesel and Hubel ('63) when tested through their deprived eyes, appearing blind in all respects. When tested on the jumping stand the animals were unable to discriminate an open door from a closed door on which a grating with a 4-cm period was placed. When the platform was set very low, only a few centimeters above the trapdoor, the animal could reach out until its front paws touched the wooden divider that separated the two trapdoors; using this as a support it would then reach out with each paw in turn to feel for the closed trapdoor. Only after it had found the door with its paw would the kitten cautiously emerge from the platform onto the trapdoor. If the platform was set slightly higher so that the animal could no longer reach out to the divider, it would leap onto the closed door or fall through the open hole with equal frequency.

After from 1 to 12 days, depending on the animal, there was a sudden dramatic improvement in the animal's visual behavior when using the deprived eye. This was usually first observed on the jumping stand where the animal would demonstrate its ability to discriminate an open from a closed trapdoor on the basis of visual cues alone. Often within the same day the kitten was able to successfully discriminate a coarse grating from a grey uniform field of the same average luminance. After this point it was possible to estimate the animal's acuity with the procedure outlined above.

Figure 1 shows the recovery following monocular deprivation of the visual acuities of the deprived (open circles) and non-deprived (filled circles) eyes of the four animals that
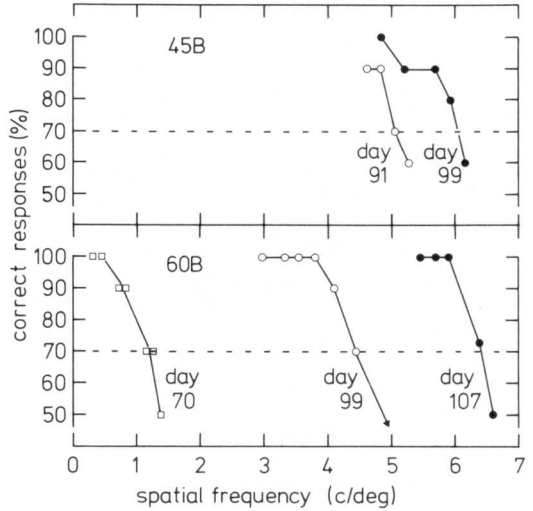

Fig. 2 Sample frequency-of-seeing curves obtained from the two kittens given binocular vision during recovery. The symbol convention is as in figure 1: open symbols represent performance using the initially deprived eye; filled symbols represent performance using the initially open eye. The two curves for 45B represent his best performance through his initially open (day 99) and initially closed (day 91) eyes. The three curves for 60B represent his performance through the deprived eye on the first day on which he could perform the task at all through that eye (day 70), his best performance through that eye (day 99), and his final performance through his initially open eye (day 107). The dashed lines indicate our criterion for threshold performance (70%).

were tested behaviorally. Each data point shows the spatial frequency of the grating for which the animal was correct on 70% of the trials, estimated from frequency-of-seeing curves generated from each daily session. A curve has been fitted by eye to the data for the deprived eye of each animal. Figure 2 shows typical frequency-of-seeing curves obtained at several different stages of recovery from both the deprived (open circles) and non-deprived (filled circles) eyes of 45B and 60B. Since these curves were always very steep the acuity on any day could be titrated extremely precisely.

All of the animals showed a remarkable recovery of vision in the deprived eye, including those that simply had the eyelids of the deprived eye opened. In fact, the most surprising feature of the behavioral findings was the close similarity between the recovery of vision in the deprived eye of the "binocular" kittens 45B and 60B and that of the two reverse-sutured animals. Both of the kittens that were monocularly sutured until 45 days of age ap-
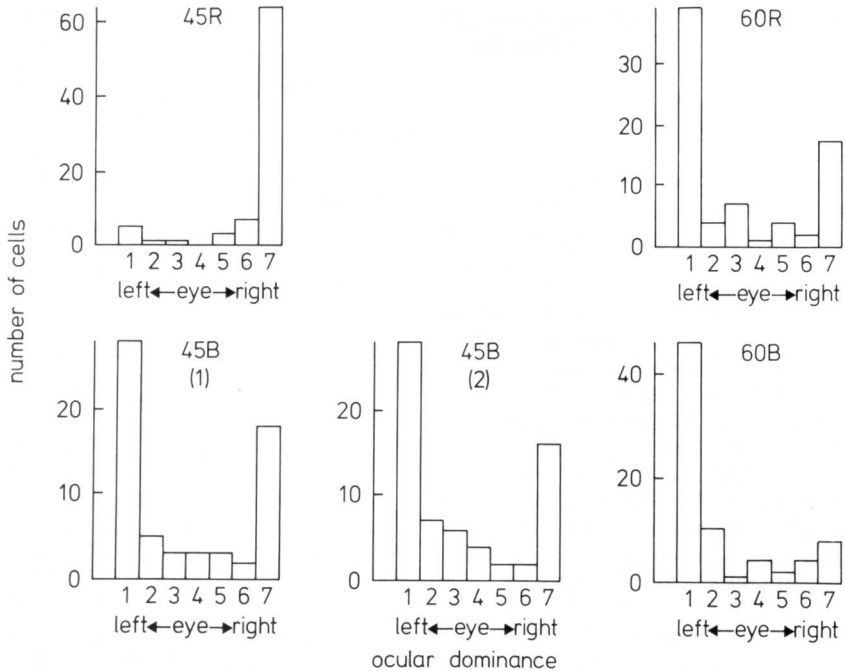
Fig. 3 Ocular dominance histograms obtained from the five experimental kittens. The ocular dominance classification we used was that of Hubel and Wiesel ('62), but since unit samples from the two hemispheres did not differ systematically, we have pooled them and displayed the data as if all units were recorded from the right hemisphere, contralateral to the initially open left eye.

peared blind in the deprived eye for the first 24 hours but shortly thereafter 45B(1) was able to discriminate a very coarse grating from a grey uniform field. On the other hand, 45R did not recover vision for three days. Vision progressively improved in a very similar manner in both animals for the next few weeks but thereafter the acuity of 45R increased slightly faster than that of the deprived eye of 45B(1). At the time of recording the visual acuity of 45R (6.6 cycles/deg) was comparable to that of a normal kitten of a similar age. The final acuity of the deprived eye of 45B(1), 4.9 cycles/deg, was discriminably lower than that of the other eye, as may be seen from an inspection of the upper panel of figure 2, which shows frequency-of-seeing curves for the best sessions of testing of each eye of this animal.

The kittens that remained monocularly sutured until day 60 showed no sign of vision in their deprived eye for a considerably longer time (10 days) than was the case with the other two animals. Although both kittens showed signs of vision after this time, 60R re-

mained unable to discriminate a grating from a uniform field for a further three days. As with the other animals, the subsequent progressive improvement in vision over the next month was almost identical in the two animals, although once again the final acuity of the reverse-sutured kitten, 60R (4.7 cycles/deg) was very slightly higher than the acuity of the deprived eye of 60B (4.4 cycles/deg). Therefore, at the time of physiological recording, the acuities measured through the deprived eyes of these animals were about 30% lower than that of a normal animal of a similar age.

Physiological observations

We recorded from 359 cortical units in five cats. In each cat, we recorded approximately half of our sample of units in each hemisphere. The electrode penetrations were all angled medially down the interhemispheric segment of the postlateral gyrus in order to sample from a number of ocular dominance columns (Hubel and Wiesel, '65; Movshon, '76a). We found no significant differences be-

tween the samples of units obtained from the hemispheres ipsilateral and contralateral to the deprived eye, so the data were pooled.

Figure 3 shows the ocular dominance histograms obtained from each of the five cats studied. The three left-hand histograms show the recovery obtained after monocular deprivation to day 45; the right-hand histograms show recovery after deprivation to day 60. The upper pair of histograms show the results for kittens forced to use their initially deprived eyes by reverse-suturing; the lower histograms show the results of recovery when the deprived eye was opened. The data we obtained from the two reverse-sutured kittens are similar to those previously reported by Blakemore and Van Sluyters ('74). At the age of 45 or 60 days, when the reverse lid-suture was performed, virtually all neurons in these kittens had been dominated by the initially open left eye, and would thus have fallen in ocular dominance group 1 (Hubel and Wiesel, '70; Blakemore and Van Sluyters, '74; Movshon, '76a). Following reverse-suturing at the age of 45 days, it may be seen that the vast majority of cortical neurons had switched ocular dominance; 74 of 81 units (91%) were dominated by the initially deprived eye. Even after reverse-suturing at the age of 60 days, 23 of 74 units (32%) were dominated by the initially deprived eye.

The kittens allowed to use both eyes following early monocular deprivation also showed considerable physiological recovery. The data from the first of the two kittens that had their deprived eyes opened at day 45 (45B(1)) shows that the initially deprived eye had reestablished control of nearly half of the cortical neurons sampled (23 of 62: 37%). It occurred to us that this kitten had been subjected to daily behavioral testing through the initially deprived eye, during which time the initially open eye was, of course, covered. The kitten, then, had had a certain amount of reversed deprivation during the recovery period. Moreover, it seemed possible, as suggested by Chow and Stewart ('72), that the extent of recovery seen following deprivation might be greater if the kitten was rewarded for using its deprived eye. We therefore recorded from another animal, reared identically, but not subjected to any behavioral testing; the ocular dominance histogram for this animal (45B(2)) reveals that there was little, if any, physiological effect of the behavioral testing: 20 of 65 units

(31%) were dominated by the initially deprived eye. Even following deprivation to day 60, we found considerable recovery of function: 14 of 75 units (19%) were dominated by the deprived eye. In contrast, in monocularly deprived kittens given no recovery period, fewer than 5% of units are dominated by the deprived eye (Wiesel and Hubel, '63b, '65a).

Note should be taken of the results of Stryker and Shatz ('76), who showed that if special techniques are used to record from the small neurons of layer IV in the visual cortex of monocularly deprived cats, substantial influence from the deprived eye may be detected. Our results on recovery are not likely to be contaminated by these neurons, since our electrodes yields results after monocular deprivation similar to those originally reported (Wiesel and Hubel, '63b, '65a), and since the recovery we observed was confined neither to the middle cortical layers nor to the simple and non-oriented cells reported by Stryker and Sherk ('76) to preserve functional connections to the deprived eye.

This recovery of function consequent to binocular visual experience following early deprivation contrasts in both form and magnitude with that seen by Hubel and Wiesel ('70). In their experiments, in two kittens given extended periods of binocular recovery from the age of 37 days (and also tested behaviorally: Dews and Wiesel, '70), approximately one-fifth of the cortical neurons were dominated by the deprived eye; in one kitten, deprived to day 51, approximately one-tenth of neurons changed ocular dominance. Hubel and Wiesel ('70) also reported that most of the neurons in their kittens that changed ocular dominance following early deprivation possessed unusually unselective and unresponsive receptive fields, many of which were insensitive to contour orientation. In our experiments, the majority of units, irrespective of eye dominance, possessed qualitatively normal orientation selective receptive fields. We did encounter a few units whose orientation selectivity was abnormally broad or that lacked orientation and direction selectivity altogether, but these units showed only a slight tendency to be dominated by the deprived eye; most of them were binocularly driven, unlike the other, more normal units that we encountered. The unselective units apart, we could find no tendency for units of one or the other of the normal types to be
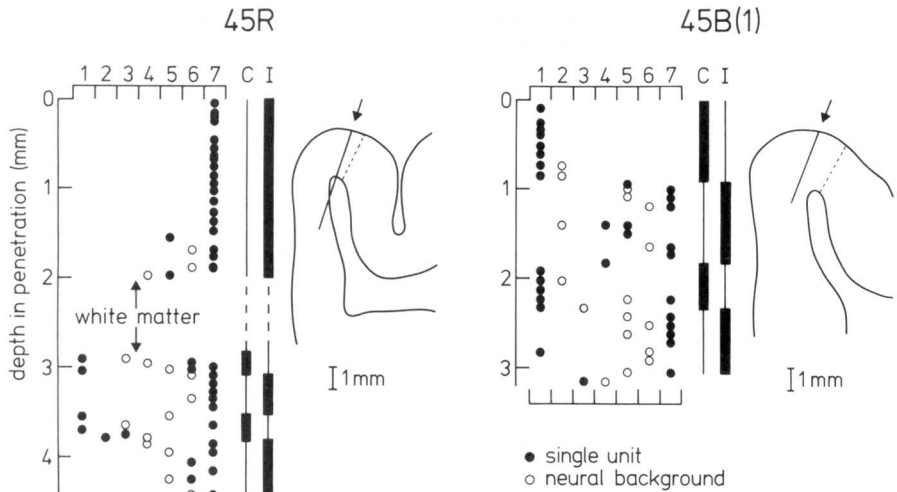
Fig. 4 Diagrammatic representations of two microelectrode penetrations through the right hemispheres of two of the kittens initially deprived until day 45. Each point indicates the depth in the electrode penetration and the ocular dominance (Hubel and Wiesel, '62) of a single cortical neuron (solid symbols) or, where it differed from the nearest neuron, the ocular dominance of the unresolved neural background activity (open symbols). The vertical strips labelled C and I indicate physiologically defined ocular dominance columns dominated by the contralateral or ipsilateral eye; the borders of these columns were derived from the recording data shown on the left of each part of the figure. The tracings to the right of the summary graphs are taken from the histological coronal sections of the cortex containing the electrode tracks, which are indicated by solid lines and arrows; the dashed lines indicate the positions of the borders between area 17 and area 18. Note that in both penetrations, neurons in group 7 could only be driven through the initially *deprived* right eye.

more strongly dominated by one eye or the other; all unit types appeared to have switched ocular dominance to the same extent in each animal.

None of our kittens, even those that showed substantial shifts in cortical eye dominance, possessed many units that could be binocularly activated. As is usual in kittens with reduced binocularity, neurons were aggregated into groups dominated by one eye or the other—the ocular dominance columns of Hubel and Wiesel ('65). It has been demonstrated, both physiologically and anatomically in deprived and reverse-sutured animals, that the sizes of these ocular dominance columns are closely related to the degree to which the eye in question dominates the cortex as a whole: in monocularly deprived cats and monkeys, columns devoted to the deprived eye shrink: in reverse-sutured kittens, the reappearance of influence from the deprived eye is accompanied by an expansion of columns devoted to the deprived eye (Shatz et al., '75; Hubel et al., '77; Movshon, '76a).

Figure 4 shows the sequences of ocular dominance that we encountered in our electrode penetrations through the right hemi-

spheres of two kittens deprived to day 45. The left-hand side of the figure shows the penetration from 45R. The right, initially deprived eye was strongly dominant throughout most of the penetration; we encountered only two small regions in which the contralateral, initially open left eye dominated the neurons and unresolved neural background activity. These physiologically defined ocular dominance columns are indicated by the blocks in the columns labelled C(ontralateral) and I(psilateral). The right-hand side of the figure shows a similar diagram derived from a penetration in 45B(1). It may readily be seen that the columns devoted to the two eyes were roughly equal in extent, and that the initially deprived, ipsilateral eye had reestablished firm control over extended regions of the cortex.

The low level of binocularity seen in these kittens was quite striking, and appears at first sight to be rather unexpected, particularly in those animals given normal binocular experience following deprivation; it might be anticipated that any recovery of influence by the deprived eye would be accompanied by the reestablishment of something resembling the

original pattern of binocular connections. Hubel and Wiesel ('70) reported a similar reduction in binocularity in their experiments on recovery from monocular deprivation, and suggested that the binocular connections in these kittens might be more susceptible to abnormal visual experience than monocular connections and thus show less recovery. There is, however, another reason why kittens given binocular vision following early deprivation might not be expected to redevelop cortical binocularity: monocular deprivation is known to produce abnormalities of interocular alignment, which would result, after the eyes are both opened, in the binocular recovery period being a period of strabismus. We therefore estimated the positions of the visual axes in our kittens from the positions of the receptive fields and optic disks in the two eyes as plotted on the tangent screen. In each of the three kittens given binocular vision following monocular deprivation, there appeared to be a convergent strabismus, of approximately 6° in one kitten, and between 9° and 10° in the other kittens. It is therefore not surprising that few units in these kittens could be binocularly activated: the period of binocular recovery was, in all probability, a period of strabismus as well, a condition that alone greatly reduces cortical binocular interaction (Hubel and Wiesel, '65).

DISCUSSION

Neural and behavioral recovery

The recovery of vision that was observed in the initially deprived eye in all our animals was very extensive. This was particularly noteworthy in the case of 45R, who possessed nearly normal visual acuity in the initially deprived eye at the time of physiological recording even though this eye had received no visual input all during the first 45 days of life. In confirmation of earlier studies (Blakemore and Van Sluyters, '74; Movshon, '76b), the restoration of vision that we observed in the deprived eye of the two reverse-sutured kittens was accompanied by marked physiological recovery. But the most surprising aspect of our results was the extent of both the behavioral and physiological recovery in the two animals, 45B and 60B, that simply had the sutured eyelids parted at 45 and 60 days of age, respectively. The behavioral recovery of these kittens was in fact only marginally less good than that of the reverse-sutured animals. Although the degree of physiological recovery

was rather less than that observed in the comparable reverse-sutured animals, its extent was nevertheless dramatic. A substantial proportion of neurons recorded from these animals could be influenced through the deprived eye; over half in the cases of 45B(1) and 45B(2) and nearly two-fifths in 60B.

It is clear from comparisons among the kittens that the two eyes' visual acuities do not simply relate to the observed cortical ocular dominance distributions (cf. figs. 1 and 3). Despite marked differences in the numbers of cells driven by their deprived eyes, for example, 60B and 60R did not differ greatly in acuity; nor did 45B and 45R show much more substantial differences. There is, of course, no special reason for thinking that the *number* of responsive neurons connected to an eye should determine acuity measured through that eye. Rather, it is likely that the *spatial resolving properties* of the most sensitive units will determine the animal's performance on our tasks. Although we made no quantitative measurements of the spatial resolution of the neurons we recorded, most of them had receptive fields of roughly normal size and stimulus selectivity, irrespective of the eye that drove them. It has recently been reported that monocular deprivation impairs the spatial resolution of geniculate neurons in cats (Maffei and Fiorentini, '76), and it may be that our results merely reflect limits of resolution imposed by changes in the character of the geniculate afferent relay. These effects may recover less quickly or completely than cortical ocular dominance, and may thus be responsible in part for our behavioral observation of reduced acuity in the deprived eyes of our kittens.

Binocular competition

Our results are not readily compatible with any simple notion of "binocular competition." That hypothesis states that during the sensitive period, LGN terminals driven by the two eyes compete for control of postsynaptic space on the cortical neuron. During normal development, the two eyes are usually activated together, preserving and strengthening cortical binocular interaction. In the absence of this cooperation, persistently greater functional activity in LGN terminals receiving input from one eye allows that eye to increase its effectiveness in driving a cortical cell, at the expense of the effectiveness of terminals driven from the other eye (Hubel and Wiesel, '65; Sherman et al., '74). This scheme ac-

counts for the classic data on monocular deprivation, alternate monocular occlusion and strabismus (Wiesel and Hubel, '63b; Hubel and Wiesel, '65), as well as the consequences of reverse-suturing (Blakemore and Van Sluyters, '74; Movshon, '76a), in which the initially deprived eye is placed artificially at a competitive advantage after a period of occlusion. It cannot account for the recovery observed in 45B(1), 45B(2) and 60B—in these cases, the deprived eye was opened without reversing the lid suture, and consequently was never at a competitive advantage. Nevertheless, its ability to drive cortical neurons increased strikingly (fig. 3).

We suggest that in addition to binocular competition based on functional interaction, there is another factor that allows functional connections an advantage in reinnervating targets to which they were initially predisposed, and thus influences the final state of binocular connectivity in the cortex. Very young monkeys and kittens seem to possess ocular dominance columns that are qualitatively similar to those in adult animals, though perhaps not fully-formed (Wiesel and Hubel, '74; Blakemore et al., '76; Hubel et al., '77; Rakic, '77). Monocular deprivation causes the columns devoted to the deprived eye to shrink away from the cortical regions they once occupied, while columns driven from the open eye expand to take their place (Hubel et al., '77; Movshon and Dürsteler, '77). It was clear during our experiments that the deprived eyes of 45B(1), 45B(2) and 60B recovered influence only in clearly delimited regions of our microelectrode penetrations (e.g., fig. 4), and it seems unlikely that these regions reflect anything other than the original, innate ocular dominance columns, passively reestablished by functional connections returning to the terminal regions they once occupied, or to which they were originally predisposed.

A tendency for regenerating fibers to return preferentially to their original innervation sites has been reported for retinotectal afferents in goldfish and frogs (Sperry, '63; Yoon, '72; Levine and Jacobson, '75). Such a mechanism is also evident in neuromuscular connections, where preferential innervation of "slow" or "fast" twitch muscles by "slow" or "fast" fibers may be observed. A "slow" or "fast" nerve fiber may even effectively reinnervate its own muscle in the presence of competing, foreign innervation, and in so doing

displace the abnormal input (Hoh, '75; Schmidt and Stefani, '76). It may be fruitful to view the encroachment onto a new cortical territory by the open eye after a period of monocular deprivation as similarly "foreign" innervation. Here, as at the neuromuscular junction, effective reinnervation by the "native" input could occur without a competitive *advantage* based on functional activity— removal of the artificial competitive *disadvantage* produced by eye closure would be sufficient. A process of this kind would go much farther toward explaining the recovery we observed in kittens given binocular experience after deprivation than would conventionally defined binocular competition.

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