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Phil. Trans. R. Soc. Lond. B 1977 **278**, 411-424
doi: 10.1098/rstb.1977.0051

Phil. Trans. R. Soc. Lond. B. **278**, 411–424 (1977) [411]
Printed in Great Britain

Functional aspects of plasticity in the visual system of adult cats after early monocular deprivation

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Responses to visual stimuli and to electrical stimulation of the optic chiasma were analysed in neurons of the lateral geniculate nucleus, visual cortex and superior colliculus in monocularly deprived cats with different post-deprivation periods. If the cats had both eyes open in their post-deprivation period (1 year) no recovery from the effects of early deprivation was found in the responses of neurones in all 3 visual structures. In cats with a post-deprivation reverse closure we found an increase in the proportion of Y-cells recorded in the early deprived layer of LGN when compared to the Y-cell proportion found in the same layers immediately after the deprived eye was opened. In neurons of the visual cortex and superior colliculus the functional abnormalities remained unaltered. The late closure of the non-deprived eye for up to 3 years did not effect neurons normally activated through that eye.

Removal of the non-deprived eye unmasked connections of the deprived eye's pathway onto neurons in the visual cortex and the superior colliculus. The neurons showed no specificity for the direction of movement or the orientation of visual stimuli. This recovery from deprivation was greater after enucleating the cats at the age of 6 months than at 18 months after birth. In the lateral geniculate nucleus of these cats the proportion of Y-cells in the recorded sample driven by the deprived eye had recovered to the value of normal cats.

The difficulties in relating these physiological findings to results from morphological or behavioural studies are discussed.

Introduction

Depriving one eye of visual experience has well-documented effects on the development of the visual system in young kittens. If monocular deprivation lasts through the first 3–4 months after birth, abnormalities in neurons of the visual system are permanent (Hubel & Wiesel 1970; Blakemore & van Sluyters 1974). Such abnormalities are as follows: (1) Cells in the layers of the lateral geniculate nucleus receiving the fibres from the deprived eye shrink by up to 40 % and the relative recording probability of Y-cells† in these layers is reduced in comparison to the non-deprived layers (Wiesel & Hubel 1963*a*; Sherman, Hoffman & Stone 1972). (2) In the visual cortex almost all cells can be influenced only through the experienced eye (Wiesel & Hubel 1963*b*; Blakemore & van Sluyters 1974). (3) In the colliculus about half of the cells can still be influenced by the deprived eye, although their responses become unspecific for the direction of movement (Hoffmann & Sherman 1974). Binocular competition for synaptic

† Based on electrophysiological criteria, the cat's retinal ganglion cells have been classified into three functional groups called W-, X- and Y-cells. X- and Y-cells constitute the main retinal projection to layers A and A_1 of the LGN. W- as well as X- and Y-cells project to layer C. W- and Y-cells project into the retino-collicular pathway (see results).

contacts was suggested as a model to account for the abnormalities described. Fibres of relay cells from the deprived layers of the lateral geniculate nucleus fail to contact cortical cells. The cells in the LGN shrink and it is found with this shrinkage that Y-cells are recorded less frequently. The visual cortex becomes dominated by the non-deprived eye, thus there is no cortical influence on the superior colliculus when the deprived eye is stimulated (Wiesel & Hubel 1965*a*; Sherman *et al.* 1972; Hoffmann & Sherman 1974).

Are all these changes really permanent, even if the animal is left to recover from the deprivation for a long time and if the animal is forced and trained to use its deprived eye in testing situations (Ganz, Fitch & Satterberg 1968; Ganz & Fitch 1968; Dews & Wiesel 1970; Chow & Stewart 1972)? We investigated a group of cats which had a reverse suture after their period of monocular deprivation, i.e. the deprived eye was opened and the non-deprived eye was closed by lid suture for another two years. These animals had shown a remarkable recovery. A report of their visual behaviour is available (van Hof-van Duin 1976). It seemed worth while to undertake a reinvestigation of the visual structures which had suffered as a result of deprivation in order to compare physiological and behavioural effects in the same animals. In a second group of experiments the influence of the non-deprived eye on the possible recovery of vision with the deprived eye was varied in long post-deprivation periods with either both eyes open (group A), a reverse suture (group B) or removal of the non-deprived eye (group C).

Data will be presented to show that in the lateral geniculate nucleus the recovery from the decrease in the number of recordable Y-cells is weakest in group A cats and strongest in group C cats. The only clear evidence for improvement from the state of monocular deprivation in neurons of the visual cortex and of the superior colliculus was found in the cats with the non-deprived eye enucleated. Even in these cats, however, the visual responses of cortical and collicular neurons to stimuli presented through the initially deprived eye were far from normal.

Materials and methods

Subjects

Eleven cats were raised under the condition of monocular deprivation. The lids of one eye were sutured together before their natural opening after birth. After 6–12 months the lids were parted and in 6 animals, single cells of the visual cortex (VC) and the lateral geniculate nucleus (LGN) were studied electrophysiologically in an experiment from which the cats were allowed to recover. The well-established effects of monocular deprivation were found in all 6 cats. After the period of deprivation, the cats were divided into 3 groups. In group A, 2 cats were left with both eyes open for 12 months before the second recording. For group B, a reverse suture was performed on 2 cats after the first recording session and on the other 5 cats without a recording session. The deprived eye (called 'early deprived' in the following) was left open and the other eye (called 'late deprived' in the following), which had previously viewed normally, was sutured shut for 1–3 years before the next recording. In two more cats (group C), the non-deprived eye was enucleated after 6 months deprivation of the other eye, which was then left open for another year.

Preparation, recording and stimulation

We have previously described our methods (Hoffmann 1973; Hoffmann & Sherman 1974) and will only briefly outline them here. Cats were anaesthetized for surgery by an intravenous injection of 0.5 ml of 5% thiopental sodium (Trapanal) and the trachea was intubated through

the mouth. Animals were then immobilized by a continuous infusion with 6 ml/h of saline containing 20 mg Flaxedil and artificially ventilated during the experiment with $N_2O - O_2$ (70 %: 30 %). Under sterile conditions a small incision was made in the skin on the skull and a small hole was drilled through the bone above the stereotaxic position of the recording site. After 6–10 h of recording, the electrode (Insl-X varnished tungsten wire) was withdrawn, the hole in the skull was sealed with bone wax and the muscle and skin sutured back. Normally the cats recovered within 12 h and were placed back in the animal quarters and treated for one week with chloramphenicol. At the final recording session, stimulating electrodes were placed just above the optic chiasma, which was then stimulated by 50–100 μs wide electrical pulses. The recording sites were marked by microlesions (5 μA, 10 s) and verified histologically in Kluver–Barrera stained 10 μm thick brain sections. The LGN was stained with cresyl violet for cell size analysis. Visual stimuli were spots and slits of light projected via a double mirror system onto a tangent screen 143 cm in front of the cat. The stimuli were moved through up to 45° of visual angle to either side of the vertical zero meridian by deflecting the light beam from mirrors mounted on voltage controlled galvanometers. On-line post-stimulus time histograms were accumulated from the spike responses of the visual neurons.

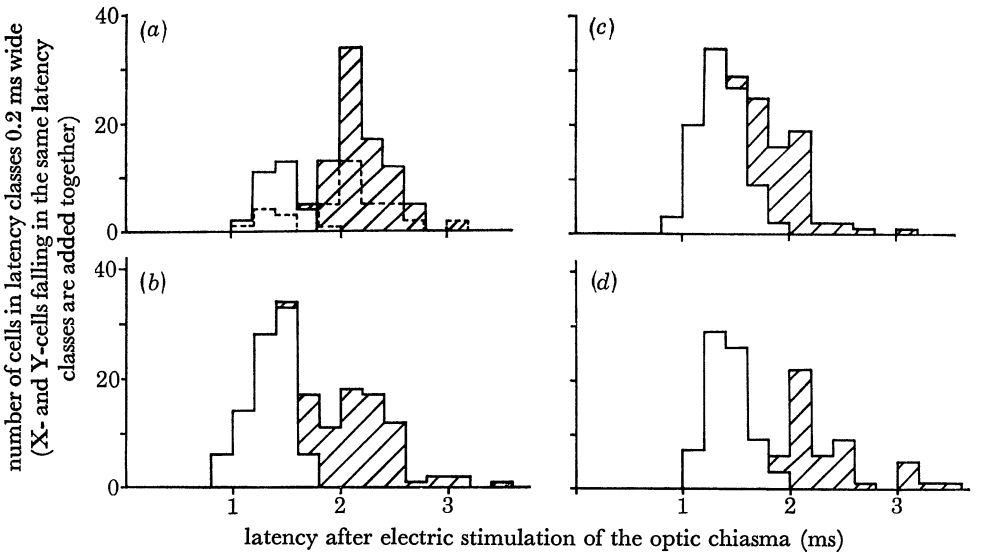

FIGURE 1. Y-cells (white bars) and X-cells (hatched bars) were plotted according to their afferent latencies after electric stimulation of the optic chiasma. Latencies shorter than 1.5 ms can mostly be taken as clear evidence for Y-cells. In (*a*) a reduced ratio of cells with Y-latencies versus cells with X-latencies is shown for recordings in the deprived laminae of cats with both eyes open for recovery. Below the dotted line: cells recorded before acute enucleation (see text). In (*b*) (deprived layer after reverse suture) and (*d*) (deprived layer after removal of the non-deprived eye) the relative number of cells with Y-type latencies was close to the value in normal layers as well as close to the value in the non-deprived layer after reverse suture (*c*).

RESULTS

(*a*) *Changes in the lateral geniculate nucleus* (*LGN*)

Relay-cells in the LGN were classified as X- and Y-cells following the criteria given previously (Hoffmann, Stone & Sherman 1972). Electrical stimulation was not used in the first recording after the deprivation but was in all other experiments.

In the binocular segment of the normal cat's LGN (not including the area centralis representation) we find about equal numbers of X- and Y-cells (Cleland, Dubin & Levick 1971; Hoffmann *et al.* 1972). After early monocular deprivation a drop in the relative recording probability of Y-cells versus X-cells in the deprived part of the LGN was reported earlier (Sherman *et al.* 1972) and confirmed in this study. Less than 25 % of the recorded LGN cells in the deprived layers are Y-cells (table 1 column I, II).

TABLE 1. THE SIGNIFICANCE OF DIFFERENCES IN X/Y RATIOS RECORDED IN THE LGN OF MONOCULARLY DEPRIVED CATS AFTER VARIOUS POSTDEPRIVATION CONDITIONS

The number of X and Y cells recorded is shown in the top line. Yates corrected χ^2-values are given below. Significantly less Y-cells were recorded in deprived layers than in non-deprived layers of cats without recovery or with both eyes open for recovery but this difference became insignificant after reverse suture or cross enucleation (values in italics). The ratio of Y-cells recorded in the early deprived layers did not increase significantly after both eyes were left open for recovery but the ratio became significantly larger after reverse suture and cross enucleation (values in brackets). The X/Y ratio in the non-deprived layers was not altered by the various post-deprivation conditions (values marked by an asterisk).

	I	II	III	IV	V	VI	VII	VIII
X/Y ratio	107/20	43/76	83/31	7/28	75/86	57/94	47/75	37/44
	without recovery		both eyes open		reverse suture		cross enucleation	
LGN-lamina	early deprived	non-deprived	early deprived	non-deprived	early deprived	late deprived	early deprived	normal
I	—	*57.80*	(4.05)		(41.71)		(53.22)	
II				2.52*		0.02*		1.45*
III				*29.05*				
V						*2.14*		
VII								*0.75*

$P \leqslant 0.001$; $\chi^2 > 10.83$. $P \leqslant 0.01$; $\chi^2 > 6.64$. $P \leqslant 0.05$; $\chi^2 > 3.84$.

Relay-cells in the LGN of the 2 cats in group A were recorded at the time when the deprived eye was opened. Six Y-cells and 29 X-cells were found in the deprived layer. No significant increase in the relative frequency of recorded Y-cells in the early deprived layers was found in the same animals after both eyes had been open for one year (31 Y-cells: 83 X-cells = 27 %) (figure 1*a*). In the non-deprived layer, 26 Y-cells and 7 X-cells were found at the first and 28 Y-cells and 7 X-cells at the second recording (table 1, column III, IV).

Group B was made up of 5 cats. At the time of opening the deprived eye, we recorded 8 Y-cells and 46 X-cells in the deprived layers of 2 of the 5 cats, avoiding the monocular segment. In comparison, 33 Y-cells and 26 X-cells were found in the non-deprived layers. After the eyes had been reverse sutured for 1–3 years, a significant increase in the relative frequency of Y-cells was found in the early deprived layers of all 5 cats. The Y:X ratio was almost identical in the early (53 %; 86 Y-cells:75 X-cells) and in the late deprived layer (62 %; 94 Y-cells:57 X-cells) (figures 1*b* and 1*c* respectively) (table 1, column V and VI).

In the binocular segment of the deprived LGN layers in the 2 cats of group C, we found 6 Y-cells and 32 X-cells and in the non-deprived layers 17 Y-cells and 10 X-cells. One year after cutting the optic nerve of the non-deprived eye, 75 Y-cells and 47 X-cells driven by the deprived eye were recorded in the LGNs (figure 1*d*). The relative frequency of recorded Y-cells thus increased to 61 %, a value such as that found in normal or non-deprived layers, which is significantly higher ($P < 0.01$ in a χ^2-test) than after the deprivation (table 1, column VII and I). The data and the χ^2-values (Yates corrected) for the differences between various groups are given in table 1.

In the 2 monocularly deprived cats of group A, we recorded the LGN again 1 day and 14 days after the optic nerve was cut. No significant increase in the recording probability of Y-cells could be noted when comparing the data from before cutting the optic nerve (9 Y-cells: 30 X-cells) with those from after cutting it (22 Y-cells: 53 X-cells) (figure 1*a*).

If one eye is destroyed in normal adult cats no change in the relative frequency of recorded Y-cells can be found acutely or one year later. In 2 such animals we recorded 44 Y- and 37 X-cells (table 1, column VIII).

(*b*) *Changes in the visual cortex*

As reported by others for similar experiments after a deprivation period of more than 4 months, the deprived eye had almost no access to cells in the binocular part of the visual cortex. In the 7 cats of group A and B no recovery could be found in the visual cortex even after long forced usage or training of the deprived eye. In the experiments on the 5 cats in group B, a total distance of 61 050 μm was traversed in the visual cortex by 25 microelectrode penetrations made either perpendicularly or obliquely to the surface. Approximately 400 visually active units were recorded and tested for their ocularity. Almost all of them were exclusively driven by the late deprived eye and had normal receptive field properties. The receptive fields were located all over the binocular visual field from the area centralis to about 40° eccentric to it. A number of units which were driven by the deprived eye clearly had fibre-like spikes and concentrically organized receptive fields and were recorded at depths from the cortical surface indicating that the electrode tip was situated in the optic radiation. These units were counted as afferent fibres from the lateral geniculate nucleus. No more than 10 units were positively identified as cells in the visual cortex with input from the deprived eye and only 1 of these was binocularly driven. This unit was selective for the direction of movement and the orientation of a long light slit. Two more of the remaining 9 monocular cells were direction and orientation sensitive, though relatively broadly tuned. Directions and orientations perpendicular to the optimal were still effective. All other cells were non-oriented and not direction selective but had low spontaneous activity and responded only to velocities of stimulus movement typical for normal cortical cells.

In the group C cats, a different picture emerged after the normal nerve had been cut. We searched for cells driven by the early deprived eye in 22 penetrations, in which the electrode traversed 58 600 μm in the visual cortex. In each of the two cats more than 200 units were recorded in 2 recording sessions. In 12 of the 22 penetrations we found visual activity from the deprived eye in a total of 60 cells in the cortex contra- and ipsilateral to the deprived eye. This activity was found in clusters during the penetrations and from the histological reconstruction of 4 electrode tracks it appeared to be in and below layer IV of the visual cortex. Again, units which were probably LGN fibres were excluded from the sample of 60 cells.

Only 2 out of the 60 units were direction selective and one appeared orientation specific. All the other cells had receptive field properties like the rarely encountered non-oriented cells of the normal cat's visual cortex. They were not direction selective or orientation specific (51 of 53 tested) (figure 2*a*). All cells tested had on-, off- or on-off-responses to stationary flashing spots of light. The significant majority (40 of 50 tested) gave off-responses only. Four had on-responses. 35 cells responded phasically, 9 tonically. 6 cells including the two direction selective cells gave on-off-responses (figure 2*b*).

The cells were clearly distinct from afferent LGN fibres in that they had zero or low

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spontaneous activity (34 or 37 cells measured) (figure 2*c*). 39 of the cells activated by the deprived eye were also tested for their latencies to electrical shocks applied to the optic chiasma. 18 cells responded to such stimuli and the results are plotted in figure 2*d*. The latencies were within the range of normal data. Monosynaptic activation by Y fibres can be suggested in several cases. Units not activated by visual or electrical stimulation were identified by their spontaneous activity or injury discharges when they were destroyed by the advancing electrode.

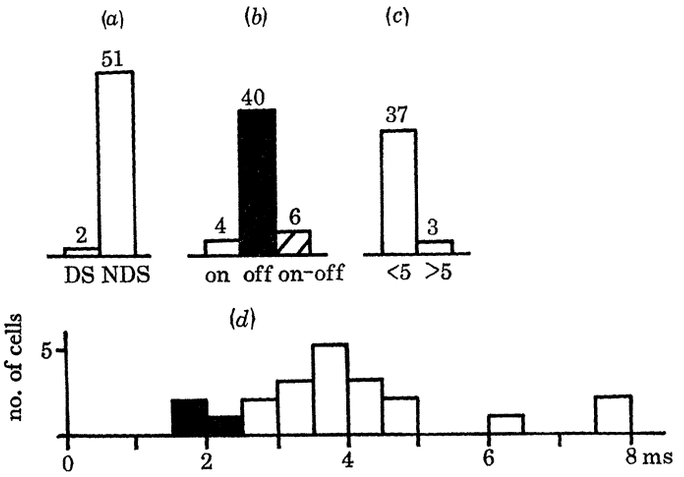

FIGURE 2. Cells recorded in area 17 and 18 of the visual cortex could be activated by the deprived eye after the non-deprived eye had been enucleated. (*a*) numbers of direction selective (DS) and of non-direction selective (NDS) cells. (*b*) numbers of cells giving either on- (white bar), off- (black bar) or on-off (hatched bar) responses to flashing stationary light stimuli. (*c*) numbers of cells with zero to low (< 5) or high (> 5) frequencies of spontaneous spike discharges. (*d*) frequency distribution of response latencies after electrical stimuli applied to the optic chiasma (OX). Black bars: examples of OX-latencies measured in LGN-fibres projecting to the visual cortex. White bars: OX-latencies measured in cortical cells.

To control the effects of the animals' age and the time after enucleation on the cortical recovery, the non-deprived eye was removed in the 2 cats of group A when they were 18 months old in an acute experiment. First these cats were recorded one year after the deprived eye had been opened. In 7 electrode penetrations 120 cortical cells were recorded over a total penetration length of 16 000 μm. In each of three penetrations a single cell was found to be clearly driven by the deprived eye. All the other cells were driven by the non-deprived eye. In one of the cats the optic nerve of the non-deprived eye was cut while the electrode was recording cells in the visual cortex. In this particular penetration visual responses appeared almost immediately after the nerve was cut. The three units analysed showed no spontaneous activity, had phasic off-responses to stationary flashing light and were not sensitive to changing direction or orientation of movement. In the following 24 h, visual activity was found in two out of six other penetrations. The activity was restricted to very few units and mostly could only be detected in unresolved background activity. During this search the electrode travelled more than 7000 μm through the visual cortex. In the second cat the optic nerve was cut at the end of the first recording session after the post-deprivation period with both eyes open. Three days after cutting the nerve we recorded 106 cells in 3 electrode tracks over a total penetration length of 10 700 μm. Only one cell was found to be clearly driven by the deprived eye. Data for all 3 groups of cats are summarized in table 2.

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TABLE 2. NUMBER OF NEURONS IN THE BINOCULAR SEGMENT OF VISUAL CORTEX AND SUPERIOR COLLICULUS INFLUENCED BY THE DEPRIVED EYE IN CATS WITH DIFFERENT POST-DEPRIVATION PERIODS

neurones in	with input from	post-deprivation period: both eyes open	reverse suture	cross enucleation
visual cortex ipsi- and contralateral to the deprived eye	deprived eye	3	9	60
	both eyes	—	1	unresponsive: 400
	non-deprived eye	120	400	
superior colliculus contralateral to the deprived eye	deprived eye	—	35	85
	both eyes	—	94	unresponsive: 20
	non-deprived eye	—	101	
superior colliculus ipsilateral to the deprived eye	deprived eye	—	—	52
	both eyes	—	18	unresponsive
	non-deprived eye	—	72	not counted

The data show that very few cells in the visual cortex can be driven by the deprived eye immediately after the non-deprived eye is enucleated when the cats are 18 months old.

Removing one eye in the normal adult cat had no effect either acutely or chronically on the response properties of cells in the visual cortex tested through the other eye. This was tested in 45 cells in 6 penetrations in 3 cats.

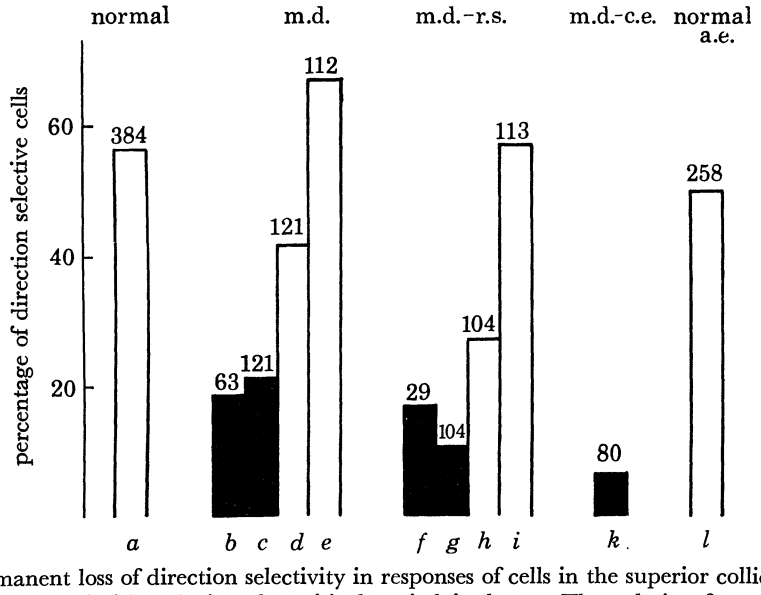

FIGURE 3. The permanent loss of direction selectivity in responses of cells in the superior colliculus when the eye tested was deprived of vision during the critical period is shown. The relative frequencies of direction selective cells in the colliculi of normal and monocularly deprived cats are compared. *a*, cells tested through either eye in normal cats. *b–e*, cells recorded after 6–12 months of monocular deprivation (cf. Hoffmann & Sherman 1974). *f–i*, cells recorded after 6–12 months of monocular deprivation followed by 1–3 years of reverse suture in which the animal was forced to use its deprived eye. No improvement in direction selectivity in the responses evoked through the deprived eye could be found. *b*, *f*, cells responsive only to the deprived eye. *c*, *g*, binocular cells tested through the deprived eye. *d*, *h*, the same binocular cells tested through the non-deprived eye. Note that 50% of these cells show direction selectivity only when tested through the non-deprived eye. *e*, *i*, cells responding only when tested through the non-deprived eye. *k*, cells tested through the deprived eye after the non-deprived eye was enucleated 1 year before the experiment. *l*, cells tested through the intact eye after the other was enucleated in a normal adult cat 1 year before the experiment. ■, deprived eye tested. □, non-deprived or normal eye tested. Abbreviations: m.d., monocularly deprived; m.d.-r.s., reverse suture; m.d.-c.e., cross enucleated; normal a.e.: enucleation in a normal adult cat.

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(*c*) *Changes in the superior colliculus*

In the binocular segment of the superior colliculus (SC) of the normal cat a high proportion of neurones is binocularly driven and 60 % of them are direction selective, mostly preferring movements away from the area centralis (figure 3*a*). Collicular neurones respond over a broad range of stimulus velocities. 50 % of the cells prefer velocities only up to 10°/s, 30 % respond to velocities up to 50–100°/s and 20 % respond to all velocities up to jerking movements (500°/s).

Monocular deprivation has different effects on the colliculus contralateral and ipsilateral to the deprived eye. The retinotectal pathway to the contralateral colliculus seems nearly unaffected and, unlike in the visual cortex, more than half of the units can be driven by the deprived eye. Nevertheless, there is a marked skewing of the ocular dominance distribution towards the non-deprived eye. This trend is much stronger in the colliculus ipsilateral to the deprived eye. As in the visual cortex, almost all cells are driven by the non-deprived eye. The activity from the deprived eye seems to be concentrated in both colliculi on the more superficial neurons in any electrode penetration. The deeper neurones are mostly exclusively driven by the non-deprived eye. In both colliculi the direction selectivity is reduced to 20 % if tested through the deprived eye (figure 3*b*, *c*). The velocity tuning of the cells was not significantly altered by the deprivation (cf. Hoffmann & Sherman 1974).

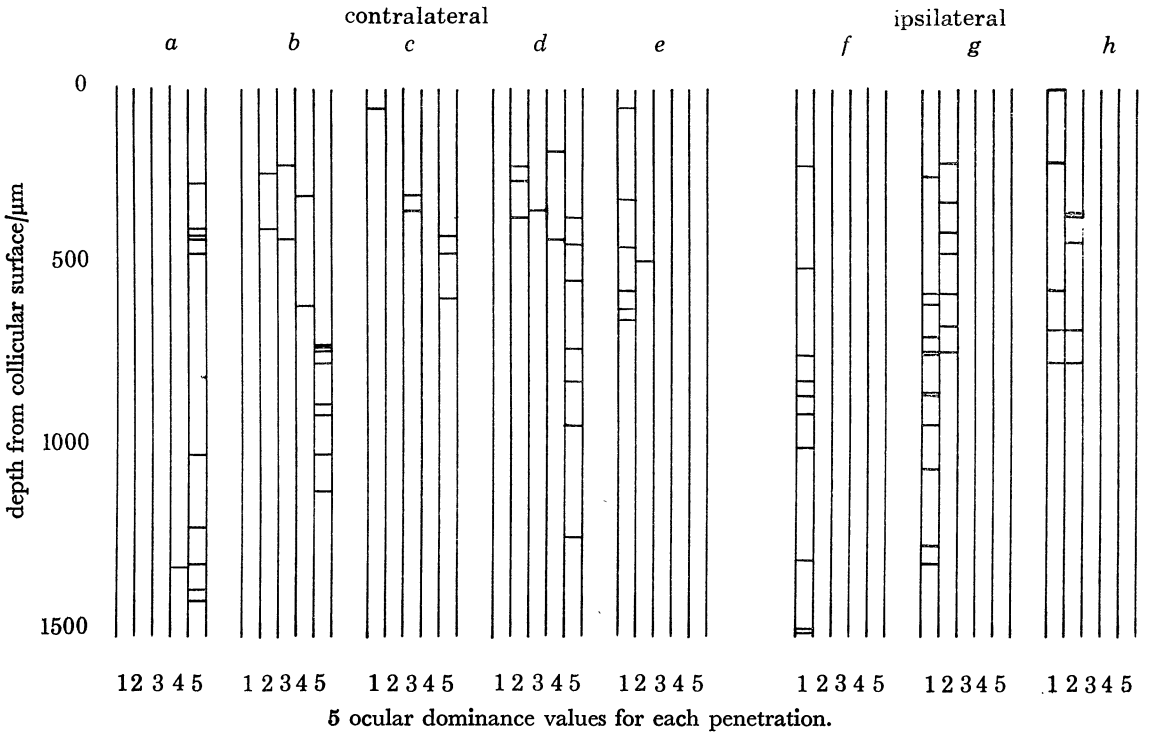

FIGURE 4. Representative ocular dominance distributions in single penetrations through both superior colliculi of one monocularly deprived cat after 2 years reverse suture in which the cat was forced to use the deprived eye show that the early deprived eye mostly activated cells only in the upper part of the stratum griseum superficiale. *a*–*e*, deprived eye is contralateral; *f*–*g*, deprived eye is ipsilateral to the colliculus recorded. 1, exculsive drive from the contralateral eye; 2, strong drive from the contralateral eye and weak drive from the ipsilateral eye; 3, equally strong drive from both eyes; 4, weak drive from the contralateral eye and strong drive from ipsilateral eye; 5, exclusive drive from the ipsilateral eye.

Cats in groups A and B were similar in that the post-deprivation period either with both eyes open (A) or with reverse suture (B) had no effect on the changes induced by the early visual deprivation. Activity from the early deprived eye was restricted to the superficial neurons in the contralateral and still almost absent in the ipsilateral colliculus (figure 4). Nevertheless, in every penetration through the contralateral colliculus, activity from the deprived eye could be found coming to a total of 129 units of the 230 recorded in 19 penetrations. In the ipsilateral colliculus the deprived eye was found to activate neurons only in 3 out of 11 penetrations (18 out of 90 analysed neurons) (see data in table 2). This high proportion of 20 % was presumably found because a search was made for penetrations with activity from the deprived eye.

Direction selectivity when tested through the deprived eye was still very low (16 selective compared to 117 non-selective neurons) (figure 3*f*, *g*). When tested through the non-deprived or late deprived eye, the responses of 65 cells were selective and of 48 cells non-selective for the direction of stimulus movement (figure 3*h*, *i*).

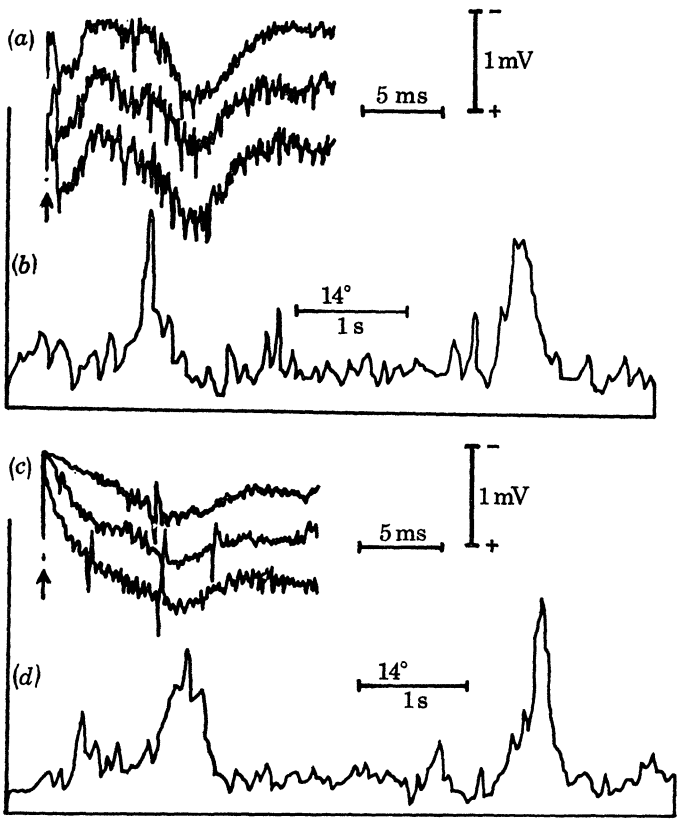

FIGURE 5. The oscilloscope traces of evoked potentials from the deeper part of stratum griseum superficiale elicited by electrical stimulation of the optic chiasma show that a clear potential can be evoked in the colliculus contralateral (*a*) and ipsilateral (*c*) to the deprived eye. The non-deprived (left) eye was enucleated 1 year before the experiment. The well known evoked potential reflecting the post-synaptic activity elicited by the slow W-fibre input has its maximum in both colliculi 9 ms after the stimulus was applied to the optic chiasma: stimulus onset is marked by arrows. Post-stimulus time histograms for horizontal movement of a 2° diameter light spot taken from multi-unit activity (*b* + *d*) present additional evidence that visual responses can be elicited through the deprived eye in the lower part of stratum griseum superficiale contralateral (*b*) and in the colliculus ipsilateral (*d*) to the deprived eye after removal of the non-deprived eye. The velocity of movement was 14°/s and the movement went 45° of visual angle to either side of the vertical O-meridian. Left half of the histogram: movement from right to left on the screen; right half: movement from left to right. The strength of visual response is not scaled in spikes/second because we recorded from more than one unit.

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In the two cats in group C, 11 penetrations were made through the colliculus contralateral and 5 penetrations through the colliculus ipsilateral to the deprived eye (data are summarized in table 2). Contrary to the recordings in the colliculus of cats in groups A and B, visual activity was found in all 5 penetrations through the ipsilateral colliculus after the non-deprived eye had been removed one year before recording (figure 5*d*). The strengthening of the retinal input from the deprived eye to the ipsilateral colliculus was confirmed through electrical stimulation of the optic chiasma. The field potential (figure 5*c*) recorded in the colliculus ipsilateral to the early deprived eye was larger than ever found in this pathway of normal or monocularly deprived cats (cf. figures 5*c* and 6*b*, *c*). In the colliculus contralateral to the deprived eye visual activity was recorded in 4 out of 11 penetrations at a depth greater than 1000 μm (figure 5*a*, *b*). Thus fibres from the deprived eye could now drive cells deeper in the colliculus than found in cats of group A and B (figure 4). Of the single cells recorded in these 16 penetrations, 5 out of 80 analysed were direction selective (figure 3*k*).

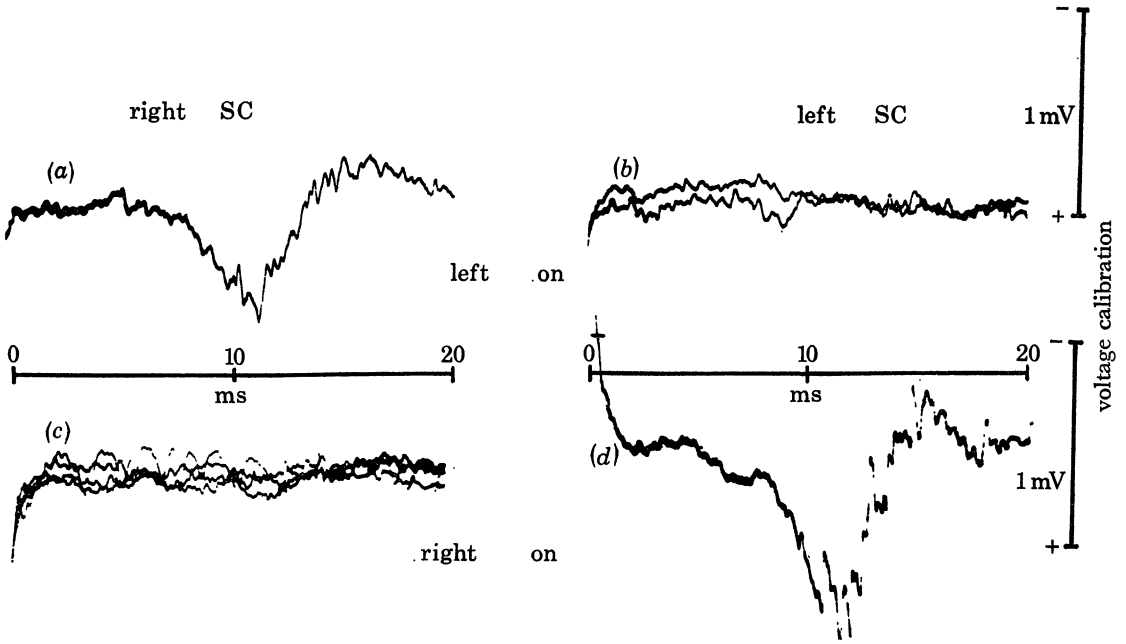

FIGURE 6. Oscilloscope traces of evoked potentials recorded in the superior colliculi of a cat in which the right eye was deprived. At the same time one pair of stimulating electrodes was placed on the optic nerve behind the right eye and another pair behind the left eye. Thus the evoked potential elicited by contralateral and by ipsilateral optic nerve stimulation could be recorded at the same recording site. From both optic nerves (deprived: $c+d$, non-deprived: $a+b$) a strong field potential can be elicited in the contralateral ($a+d$) but not in the ipsilateral colliculus ($b+c$). Single cells, however, could be driven in both colliculi from the ipsilateral optic nerves (cf. Hoffmann & Sherman 1974).

In the two MD cats of group A, the activity of collicular cells was also recorded after acute transsection of the optic nerve of the non-deprived eye. Only in one out of five penetrations through the ipsilateral colliculus could we find activity from the deprived eye. No obvious immediate changes at the collicular level could be observed after acute transsection of the non-deprived nerve in adult, 18 month old cats.

The direction selectivity and other receptive field properties in collicular cells remained unaltered after removing one eye in *normal* adult cats (figure 3*l*). However, the input from

the intact eye to the ipsilateral colliculus seemed strengthened. Field potentials recorded in the colliculus after electrical stimulation of the ipsilateral optic nerve were much clearer and larger than ever recorded in the colliculus of normal cats when the ipsilateral optic nerve was stimulated.

Discussion

How do visuomotor behaviour and pattern discrimination of monocularly deprived cats relate to neurons in the visual cortex and superior colliculus?

After 6–12 months of monocular deprivation, cats had to use their deprived eye either together with their non-deprived eye or alone due to a reverse suture. In a third group, the non-deprived eye was enucleated to try to force the system toward a maximum reorganization for vision with the deprived eye. In an extensive study on the cats with a reverse suture, the visuomotor coordination was found to be impaired even after a forced usage of the deprived eye for 2–3 years, whereas pattern discrimination was found to be largely intact (van Hof-van Duin 1976). This result is basically in agreement with the reports by Dews & Wiesel (1970) and Spear & Ganz (1975). The new neurophysiological data gathered in the LGN and superior colliculus of monocularly deprived cats by Sherman *et al.* (1972) and Hoffmann & Sherman (1974), plus the expectation of finding signs of neuronal recovery after long training periods even in the visual cortex, led us to screen the visual system for an increase in number and specificity of neurons activated by stimulation of the early deprived eye. The assumption was that this increase would correlate with the excellent performance in pattern discrimination. In cats with post-deprivation reverse suture or both eyes open, we found no evidence for recovery of neuronal functions in the visual cortex or in the superior colliculus (see table 2). Our results in these structures do not confirm the idea that improved vision with the deprived eye after long forced usage relates to more active or stimulus specific neurons (Chow & Stewart 1972; cf. Wiesel & Hubel 1965*b*).

Only after the non-deprived eye was enucleated in 6 month old animals did we observe an increase in the number and responsiveness of neurons driven by the deprived eye in the visual cortex and in the superior colliculus. This was found in both brain hemispheres. Krantz, Spear & Smith (1976) report that this increase occurred within 12 h of enucleating the non-deprived eye. We did not observe this rapid improvement in 18 month old animals. This may suggest that, after the critical period, the degree of recovery due to the removal of the non-deprived eye decreases between the ages of 6 and 18 months. In normal adult cats, clear evidence for a strengthening of a 'masked' input was found in the superior colliculus. The evoked potential recorded after electrical stimulation of the ipsilateral optic nerve was significantly clearer and larger after the contralateral optic nerve had been destroyed 6 months before the experiment. Thus, the effects seen after enucleating the non-deprived eye may not be specific for post-deprivation recovery but reflect a general plasticity in the superior colliculus of the adult cat.

A similar rapid unmasking followed by a slower development of novel connections after destruction of the afferent system, which normally dominates a set of neurons, has been shown in the rat thalamus and in the cat spinal cord by Wall & Merrill (1972). In our case, no explanation in terms of synapses can yet be given for the 'new' functional connections of the deprived visual pathway.

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Changes in the LGN and cortico-geniculate or intrageniculate influences

The changes found in the LGN of reverse sutured cats cannot be explained easily by the hypothesis that abnormalities in the deprived layers of the LGN are caused by the failure of LGN terminals in the binocular competition for cortical synaptic sites (Guillery 1972). The proportion of Y-cells in the early deprived layers of reverse sutured cats becomes almost identical to that in the non-deprived or late deprived layers, although the LGN terminals cannot have made effective contacts in the visual cortex. A mechanism acting at the subcortical level between the LGN layers as suggested by Garey, Fisken & Powell (1973) may play a more important role for the LGN deprivation effect than binocular competition at the cortical level. If the non-deprived eye was not closed in the post-deprivation period, significantly less, if any, recovery in the Y-cell proportion was found in the deprived LGN layers. On the other hand, enucleating the non-deprived eye caused an even greater reversal in the deprivation effect on the LGN than reverse suture. Again these results are consistent with the hypothesis that interaction between the LGN layers rather than interaction between LGN and visual cortex controls the mechanism which causes the differences in the recorded Y-cells proportions. The evidence that binocular interaction affects the postnatal development of Y-cells in the cat's LGN presented by Sherman, Wilson & Guillery (1975) does not exclude the possibility that this interaction takes place between the LGN layers.

Must there be a specific loss of Y-cells in the deprived LGN?

On the basis of our results one has to reconsider the idea of a Y-cell loss in the deprived LGN layers. In the original report, only 6-Y cells (compared to 64 X-cells) were found in the binocular part of the deprived layers. This result was confirmed recently by Sherman *et al.* (1975) and also in the present study. A higher proportion of Y-cells (20 %) is given in both studies. It seems possible to record more Y-cells in the deprived layers than we had originally thought. One only has to use other types of microelectrodes than micropipettes. The variables in the method of sampling the proportions of different cell types in the retina with microelectrodes were described by Stone (1973) and Levick & Cleland (1974). Their results, together with those of Wässle, Levick & Cleland (1975), show that Y-cells are recorded at a much higher relative frequency in the peripheral retina ($> 50\,\%$) than in the area centralis ($< 10\,\%$), although the absolute ratio of Y-cells to all the other retinal ganglion cells is fairly constant across the retina. Morever, the fact that the recorded Y-cell frequency is inversely correlated with the impedance of the microelectrode used makes it impossible to be certain that the change induced in the LGN by monocular deprivation is a true loss of Y-cells. One has to give more weight to the earlier suggestion (Sherman *et al.* 1972) that the shrinkage in the size of all cell somata in the binocular segment of deprived LGN layers could cause the relative decrease in the number of recorded Y-cells. Such an effect can be seen in the retina with the concurrent decrease in the diameter of all ganglion cell somata and decrease in the number of recorded Y-cells. The retina could serve as a model to understand the 'Y-cell loss' after deprivation, but it is difficult to interpret the recovery in the recordability of Y-cells after reverse suture with the same model. No evidence for an increase in the deprived cells' size due to reverse suture was found (Holländer, personal communication) although clearly different physiological results were obtained from the same material before and after reverse suture (see table 1). One possibility, however, is that the actual proportion of Y-cells in the LGN is as small as in the retina (3 %) and the increased size

of Y-cells after reverse suture cannot be observed against the background of the greater number of other cells. A detailed statistical analysis of large samples should clear up both this point and the discrepancy with earlier reports on morphological recovery (Chow & Stewart 1972).

Conclusions

If cortical area 17 and 18 are destroyed, the pattern discrimination ability in monocularly deprived cats is lost for their deprived eye (Spear & Ganz 1975). On the basis of our results, we have to face the fact that the animals have to rely on a proportion of 10 in 400 cells in their visual cortex for perfect pattern discrimination with the deprived eye. The superior colliculus contralateral to the deprived eye alone cannot maintain the function of pattern discrimination but plays a role in localizing objects in the hemifield ipsilateral to the deprived eye (Sherman 1974; von Hof-van Duin 1976). In both structures, visual cortex and superior colliculus, no neuronal changes can be observed for the deprived eye except that elimination of the non-deprived pathway by enucleation may unmask existing connections or allow reinnervation of vacant synaptic sites by the deprived pathway. Only in this context could we find evidence for plasticity in the visual system of the adult cat after deprivation.

The uncertainty about the deprived LGN as to whether a proportion of cells sampled with microelectrodes is representative for the absolute number of these cells makes it difficult to discuss the relevance of recorded neuronal subsets for morphological changes or impairment of behaviour.

We are indebted to Dr J. van Hof-van Duin for the generous access to her data on the visuomotor behaviour and pattern discrimination of monocularly deprived cats and for supplying us with the tested and trained animals for this study. We should like to thank Ms L. Kleudgen, Dr A. Schoppmann and Mr G. Weckbart for their help during the course of the second group of experiments and N. Beckhaus for secretarial help.

This work was supported by DFG Grants SFB 50 A 1.3 and Ho 450/4 to K.-P. Hoffmann and M.R.C. Grant Ma 5201 to M. Cynader.

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