Exp Brain Res (1987) 68: 525–532

Experimental Brain Research

Effects of monocular strobe rearing on kitten striate cortex

J.P. Rauschecker and W. Schrader*

Max-Planck-Institut für biologische Kybernetik, Spemannstr. 38, D–7400 Tübingen, Federal Republic of Germany

Summary. Monocular deprivation in kittens does not lead to an ocular dominance shift in striate cortex if the visual stimuli do not contain contours. In the present study we sought to find out whether an ocular dominance shift is produced if the visual environment does contain contours but is devoid of motion. Six kittens were reared with one eye occluded in a visual environment that was lit only by the light of a stroboscope (2 flashes per sec). Exposure was started at 5–6 weeks of age after dark-rearing from birth and extended until 8–12 weeks of age for 8 h per day. The rest of the time was spent in total darkness. Thus, the animals were completely deprived of vision in one eye, while the other eye experienced only stationary flashing contours. Single units in area 17 of these animals were studied and compared to normally reared cats. In all six animals ocular dominance was clearly shifted towards the eye with strobe experience. The ocular dominance shift showed, however, the following interdependencies with other parameters: neurones that responded to stationary flashing test stimuli were nearly always dominated by the strobe eye; neurones that responded only to moving bars or edges remained binocular. In the normal control animals the ocular dominance distribution was similar for both groups of cells. Track analysis according to cortical lamination revealed that neurones in infragranular layers consistently showed a weaker OD shift towards the strobe eye than neurones in supragranular layers (including layer 4). Response latencies to stationary flashing stimuli were significantly shorter in the strobe-reared animals than in the normal controls. Orientation tuning was normal in all animals. Directional tuning was reduced after monocular strobe experience, but not by the same amount as described after *binocular* strobe rearing. The present results demonstrate that monocular visual experience reduced to stationary flashing contours is sufficient to produce on ocular dominance shift in striate cortex. This adds further support to existing notions about the role of nervous activity for changes in cortical connections. Cortical responses to afferent stimulation and the resulting correlated activation of pre- and postsynaptic neurones seem to be a prerequisite for a stabilization of synaptic connections.

Key words: Cat – Visual cortex – Stroboscopic exposure – Monocular experience – Motion deprivation

Introduction

Most neurones in the visual cortex of the normal cat or kitten are responsive to stimulation of both eyes (Hubel and Wiesel 1962). Wiesel and Hubel (1963, 1965) have demonstrated that single cells in striate cortex can be driven from only one eye if the other eye had been sewn shut or occluded by an opaque contact lens during early postnatal development. Later studies have shown that the visual input to the stimulated eye has to contain contours if this eye is to gain dominance over the cortical neurones (Singer et al. 1977; Wilson et al. 1977). Diffuse light presented to one eye, even if temporally modulated, does not produce a shift of ocular dominance. Since cortical neurones rarely respond to such changing Ganzfeld illumination, while most neurones in the lateral geniculate nucleus do (Hubel and Wiesel 1962), these results suggest that correlated cortical activity must play a role in changes of binocularity. This has been confirmed recently by directly blocking activity in the visual cortex with TTX (Reiter et al. 1986).

* Present address: Universitäts-Augenklinik, D–7800 Freiburg, FRG

Offprint requests to: J.P. Rauschecker (address see above)

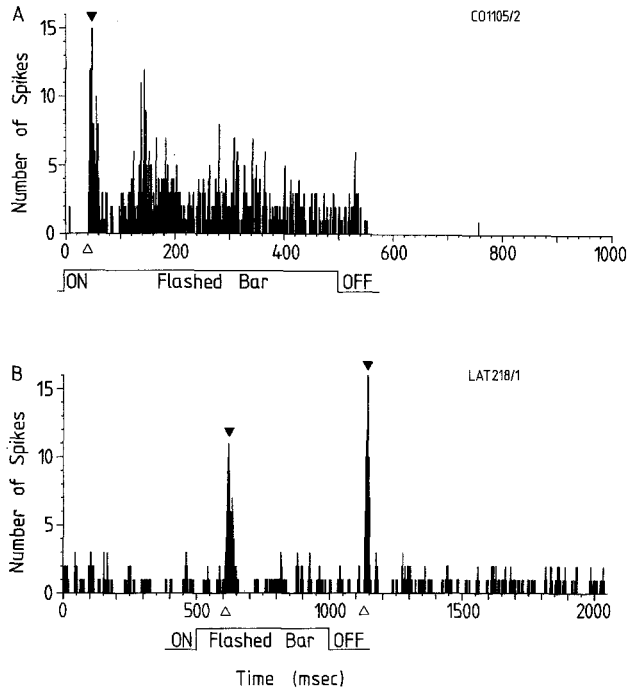

Fig. 1A, B. Examples of neuronal responses from area 17 of normal cats to a stationary bar flashed on the receptive field in the optimal orientation (bin width of the histograms: 1 ms). Response latencies were determined as described in Methods. Onset latencies are indicated by open, peak latencies by filled arrow heads. **A** ON-response of a cortical simple cell. The stimulation was presented 30 times starting with "light on" at time 0. The light bar was switched off after 500 ms. The onset latency of this cell was 42 ms, peak latency 48 ms, which made this unit one of the fastest-responding cells that we encountered. **B** Mixed ON-/OFF-response of a cortical complex cell. Response latencies were longer than 100 ms, which is not unusual for complex cells (onset/peak ON-response: 106/120 ms, OFF-response: 126/140 ms

The importance of correlated activity between pre- and post-synaptic neurones for plastic changes in the visual cortex is also suggested by the outcome of experiments combining monocular occlusion with visual experience restricted to contours of one orientation (Cynader and Mitchell 1977; Rauschecker and Singer 1979, 1981; Carlson et al. 1986). Cortical neurones change their ocular dominance as a function of orientation preference, which is typically thought of as a postsynaptic, cortical response property.

While most cortical neurones do not respond to temporally modulated Ganzfeld illumination, most of them do respond to stationary flashed bars or edges (Hubel and Wiesel 1962). Assuming that the same is true for inexperienced kittens, we have designed the present study, in which we have combined monocular deprivation with visual experience restricted to stationary flashed contours. We have reared kittens in a stroboscopically illuminated environment with one eye occluded, in order to see whether an ocular dominance shift can be produced in striate cortex. In particular, we wanted to compare any resulting ocular dominance shift for cortical units that are responsive and those that are unresponsive to stationary flashed bars. A clear correspondence was found between these two properties, which we interpret within the same framework of rules for synaptic modification that we have stated previously (Rauschecker and Singer, 1981). In order to have baseline data for direct comparison, we also analyzed visual cortical cells in normally reared cats with stationary flashed test stimuli.

Methods

Rearing conditions

In order to make the present study as comparable as possible to previous studies (Singer et al. 1977; Rauschecker and Singer 1979, 1981) we reared the six experimental animals in a totally dark room prior to exposure, which started at 5–6 weeks of age. From then on the dark-room (which was equipped with a double-door arrangement) was illuminated with a stroboscope (flash duration: 9 μs, flash frequency: 2 Hz, contrast: 100%, mean luminance: 10 cd/m^2) for 8 h/day. During this time one eye of the kittens was covered with a black contact lens that was inserted while the animals were in the dark. Additionally, black adhesive tape was put over the eye to ensure that the lens remained in place.Thus the animals experienced only briefly-flashing stationary contours through the other eye until the recording experiment, which was performed between 8 an 12 weeks of age. The total exposure time varied between 80 h and 240 h in the different kittens (see Table 1).

Surgery and recording

Conventional methods were used in all cases to prepare the animals for single unit recording. This was done in a blind procedure, i.e. it was unknown to the experimenter which eye had been exposed. Double-barrelled micropipettes were used for recording and (in 3 kittens) iontophoretic track marking, one barrel being filled with 1.5 M K-citrate and the other with a 5% HRP solution in 0.2 M KCl and 0.05 M Tris buffer (pH 7.6). Only well-isolated single-cell responses were taken for analysis. Oblique penetrations (N = 13) of at least 30 deg inclination were made through the postero-lateral gyri (P3, L1.5) of both hemispheres, in order to avoid a sampling bias imposed by the ocular dominance columnar system of visual cortex. While some of the tracks did go down the medial bank, receptive field locations always remained within 10–15 deg eccentricity. Initial anaesthesia was done with 10 mg/kg ketamine (Ketanest) i.m. combined with 0.01 ml xylazine (Rompun, 5%). Premedication consisted of 0.1 ml subcutaneous atropine sulfate (1%). A venous catheter was placed in one of the forearm veins and anaesthesia continued with 1 mg/kg · h sodium pentobarbital (Nembutal) i.v. throughout the experiment. Muscle paralysis was achieved with gallamine triethiodide (Flaxedil). Artificial respiration was performed through a tracheal cannula with a mixture of 70/30 nitrous oxide/oxygen. It has been shown that this condition assures sufficient anaesthesia of the animals (Hammond 1978). For nutrition Ringer's solution with 5% glucose

Table 1. Summary of results from individual animals with monocular strobe exposure. OD: ocular dominance

Animal	Exposure Period (wks)	Exposure Duration (hrs)	Age at recording (wks)	No. of OD determined (ipsi/contra to occluded eye)	OD distribution (strobe eye [1+2]/both eyes [3]/occluded eye [4+5] Total	Responsive to stationary flashed bars	Unresponsive	Supra-granular	Infra-granular
SF1	6–10	120	10	27 (27/ 0)	18/ 1/ 8	–	–	–	–
SF2	6–12	240	12	56 (28/28)	45/ 4/ 7	–	–	–	–
SF3	6– 9	80	10	35 (0/35)	20/ 3/12	14/0/2	3/ 3/2	–	–
SF4	6–12	180	12	12 (12/ 0)	10/ 1/ 1	1/0/0	1/ 0/0	7/0/0	3/1/1
Str1	5– 8	80	8	37 (13/24)	21/10/ 6	16/1/2	1/ 6/4	16/6/3	5/4/3
Str2	5–12	220	13	18/(12/ 6)	12/ 2/ 4	7/0/2	2/ 2/2	5/0/2	0/0/2
				185/(92/93)	126/21/38	38/1/6	7/11/8	28/6/5	8/5/6
					N = 185	N = 45	N = 26	N = 39	N = 19

was given through a gastric catheter. The physical state of the animal was monitored by means of EKG, EEG, intrapulmonary pressure, and expiratory CO_2 content. EKG and EEG were also used to control the state of anaesthesia.

Visual stimulation

Atropine and neosynephrine were instilled in the eyes and their refractory state was determined using a Rodenstock refractometer. Optical correction with spectacle lenses focussed the eyes on a tangent screen 1 m away onto which visual stimuli were projected. Retinal landmarks were monitored by means of a Zeiss fundus camera. Visual stimuli were generated by an optic bench and consisted of bars, edges and spots of light that were moved over the receptive field in various directions or were kept stationary on the receptive field and switched on and off with a frequency of 0.5 to 2 Hz. Although receptive fields were not always specifically classified into "simple" or "complex" (Hubel and Wiesel 1962), care was taken to find any discrete on- and off-regions and assess their responses to stationary stimulation separately. Peri-stimulus time histograms (PSTH) of the single unit responses to these stimuli were generated on a PDP 11/34 computer. Figure 1 shows two examples of responses to stationary flashed bar stimuli. Onset latencies were determined from these histograms by fitting a tangent to the rising side of the response peak and measuring the point of intersection with the average level of spontaneous activity that was determined from the stimulus-free portions of the PSTH (Cleland and Enroth-Cugell 1970).

Ocular dominance, preferred orientation, orientation and direction tuning, responsivity to moving vs. stationary flashed stimuli and flash response latencies were determined quantitatively from such histograms measuring peak responses in spikes/s and total number of spikes in a defined interval. In addition, when the response was clear, hand plotting of these parameters was used. Ocular dominance (OD) was rated in five classes: 1, 2 = response exclusively or predominantly from the eye with strobe exposure; 3 = equal response from both eyes; 4, 5 = response predominantly or exclusively from the totally deprived eye. Very strict criteria were used to define OD classes 1 and 5: even only occasional spikes elicited by stimulation of the non-dominant eye (or inhibition) caused the cell to be classified as 2 or 4. For a rating as class 3 the responses from the two eyes were not allowed to differ by more than 20%.

Orientation preference and tuning were measured to the nearest multiple of 22.5 deg. Those orientations of a bar stimulus that just failed to elicit a response determined the width of orientation tuning. The length and width of the bar stimuli were adjusted such that they elicited maximal response; e.g. in cells with discrete on- and off-areas the width of the bar was the same as that of these areas and the length at least as long as the receptive field (or longer, if there was no end inhibition). For direction selectivity three classes were formed in the following way: Class I cells responded only to one direction of movement within about 30 deg, and practically not to the opposite direction (response ratio greater than 10 : 1), class II responded better to one direction of movement than to the opposite direction (ratio greater than 2 : 1), and class III responded about equally to both, or in the case of non-oriented cells, to all directions. Response strength was rated in five grades ranging between 1 and 5 for the weakest and best responses respectively (For all definitions compare Rauschecker and Singer 1981; Rauschecker and Harris 1983).

Histological processing

At the end of an experiment the cats were deeply anaesthetized and perfused transcardially with 4% formalin solution. The brains were removed and cut on a freezing microtome for track reconstruction. In all cats a standard Nissl staining procedure was applied that was often sufficient to retrieve the penetrations. In six electrode tracks from the strobe-reared animals and three tracks from the controls iontophoretic HRP-injections were made in addition through the recording micropipette at the end of each penetration and at least two other locations on the way back; the HRP deposits were visualized by the tetramethyl-benzidine (TMB) method of Mesulam (1978). Their diameters varied between 50 and 100 μm and the centre of injection could always be clearly identified (see Fig. 1 in Rauschecker et al. 1987).

Results

Activity from striate cortex neurones in six cats with monocular strobe experience was recorded extracellularly. In two of these animals only ocular dominance of cortical neurones was determined, in the remaining cats cortical units were analyzed in more detail, including responsivity to stationary flashed bars (four cats) and laminar origin (three cats). In addition, results from five normally reared cats over 3 months of age served as control data.

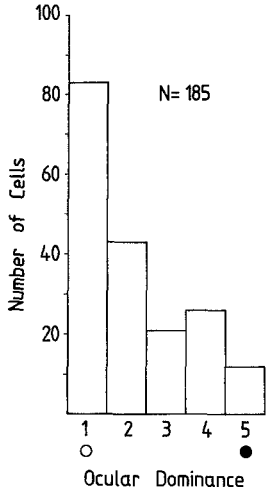

Fig. 2. Ocular dominance distribution of neurones in striate cortex from six kittens reared with one eye open in an environment lit by stroboscopic illumination with a frequency of 2/s. The other eye was occluded with a black contact lens that prevented all vision. Ocular dominance classes are defined as follows: 1, 2 = exclusively/predominantly driven by the eye with strobe exposure; 3 = equally driven by both eyes; 4, 5 = predominantly/exclusively driven by the totally deprived eye. Open and closed symbols refer to open and closed eye, respectively

1. Ocular dominance

The first aim of the present study was to determine whether monocular experience with a 2 Hz strobe lit environment is at all sufficient to induce an ocular dominance (OD) shift towards the open eye. Figure 2 shows for the pooled data from all six cats that this was indeed the case. The results from the single animals were all consistent in showing a similar degree of OD shift (see Table 1): more than two thirds of the cells (126/185 = 68%) were exclusively or predominantly driven by the eye with strobe experience (OD classes 1 and 2); only 21% (38/185) were dominated by the eye that had been occluded. As might be expected, the ocular dominance shift towards the strobe eye was slightly stronger in the hemisphere ipsilateral to the strobe eye).

The shifted ocular dominance distribution in the cats with monocular strobe exposure was in clear contrast to the data from the normal cats, where the distribution was symmetrical between left and right eye, as described in classical studies (Hubel and Wiesel 1962): 29 out of 93 cells for which OD was determined were dominated by the right eye, 31 by the left eye.

2. Responses to stationary flashed stimuli

The next main point was to correlate ocular dominance after monocular strobe exposure with the neurones' ability to respond to stationary flashed contours. Seventy-three neurones in four of the strobe-reared and 114 in normal cats were explicitly tested for this property: First the optimal orientation of a moving bar stimulus was determined. Then the bar was flashed on different parts of the receptive field in this orientation. It was noted whether the stimulus elicited a response and whether this response was of the on-, off- or mixed on-/off-type. If discrete on- and off-regions were found, the responses were analysed separately for each subfield. Responses were determined quantitatively by averaging peri-stimulus-time histograms (see Fig. 1). Flash frequency was 0.5, 1 or 2 Hz, flash duration was mostly 500 ms, but shorter flash durations (down to 1 ms) were also used.

Table 2. Number of cells with different response latencies to flashing bar stimuli in normal cats and cats with monocular strobe experience (MSE)

	Response latency (ms)			
	$T_1 \leq 50$	$60 \leq T_2 \leq 90$	$T_3 > 90$	Total
Normal	27	62	20	109
MSE	12	8	2	22

In the cats with monocular strobe exposure two thirds of the cells tested for flash responses could be driven with such stimuli (48/73 = 66%). No particular preference for the 2 Hz flash frequency was found nor was there a noticeable difference between the responses from the two eyes in binocular units. The proportion of flash responses did not differ significantly from that found in the normal control animals (89/114 = 78%, $\chi^2 = 2.846$, df = 1, $p < 0.1$). In neither group a flash response was found that was better than the response to moving stimuli. Cells that did not respond to moving bar stimuli never responded to stationary ones.

Flash latencies. Onset latencies of the responses to stationary flashing stimuli were determined quantitatively from computer-generated PSTH's (see Methods and Fig. 1) for 22 cells in 2 of the strobe-reared cats and were compared to those of 109 cells in the control animals. In the strobe-reared cats a lack of response latencies between 80 and 100 ms was found, which were frequently seen in normal cats. The median latency was 43 ms in the strobe-reared animals and 65 ms in the controls. For statistical testing latencies were grouped into three categories (Table 2): T1 smaller than or equal to 50 ms; T2 between 60 and 90 ms; T3 greater than 90 ms. Despite the limited number of latencies measured in strobe-reared cats the difference between the two

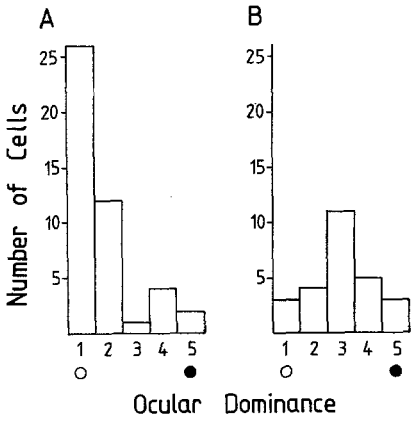

Fig. 3A, B. Ocular dominance of cortical neurones as a function of the ability to respond to stationary flashed bars of light. Neurones that, in the recording experiment, responded to such stimuli were mostly dominated by the eye with strobe experience (**A**). Neurones that responded only to moving contours retained a normal ocular dominance distribution (**B**)

distributions was clearly significant ($\chi^2 = 7.827$; $p < 0.02$; df = 2).

Flash responses and ocular dominance. Next, the responsivity to flash stimuli was correlated with ocular dominance. It was found that neurones responding to stationary flashed bars were nearly always dominated by the strobe eye (Fig. 3A). Neurones that did not respond to stationary flashed stimuli but only to moving bars, showed a normal ocular dominance distribution with a majority of binocular neurones (Fig. 3B). This was consistently so for all animals (see Table 1). The overall difference between the two distributions was highly significant ($\chi^2 = 27.792$; df = 4; $p < 0.0001$). The argument naturally holds also the other way round: when tested with stationary flashed bars 84% of the cells dominated by the strobe eye (OD 1 and 2) responded to this kind of stimulation, while only 27% of the rest (OD 3–5) did.

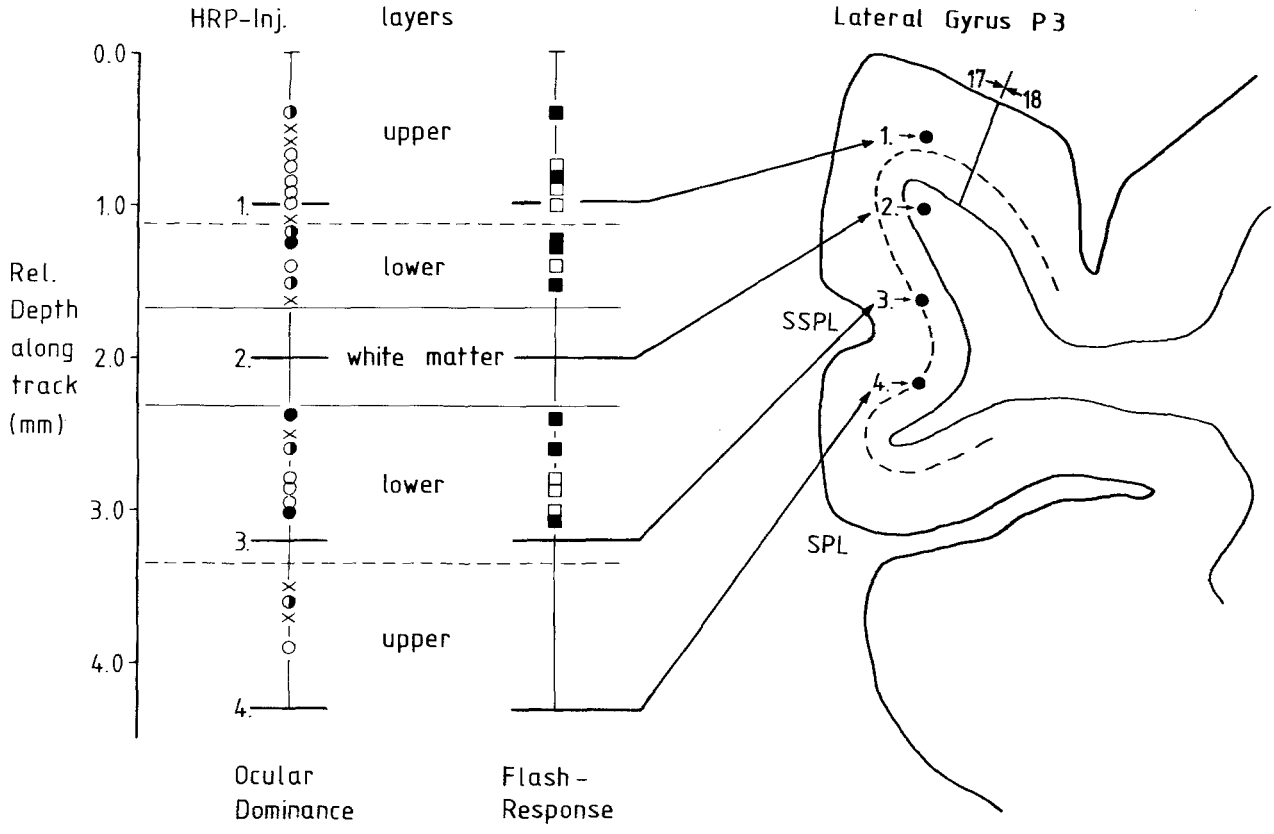

Fig. 4. Example of a track reconstruction through area 17. Four deposits of HRP (labelled 1 to 4) are drawn as black dots. The dashed line indicates the border between cortical layers IV and V. The single neurones encountered and their properties are shown on the left side. Open circles indicate ocular dominance classes 1 or 2, filled circles classes 4 or 5, half-filled circles class 3 (for definitions see Fig. 2). Crosses indicate visually unresponsive or incompletely analysed cells. Open squares indicate units that responded to stationary flashed stimuli, filled squares correspond to units that did not. The close correlation between ocular dominance and responsiveness to flashes as well as the stronger OD shift in upper layers can be seen quite clearly in this example. SPL, SSPL = splenial and suprasplenial sulcus

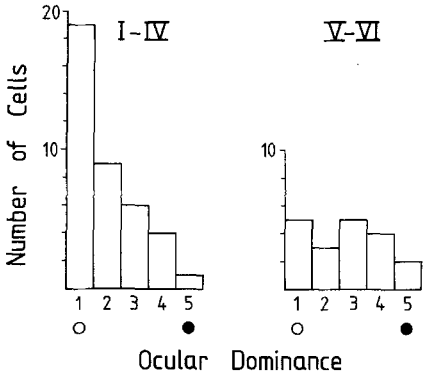

Fig. 5. Ocular dominance as a function of cortical layers. In six penetrations a precise reconstruction was performed with regard to cortical lamination using HRP marking, and ocular dominance of recorded cells was related to supra- and infra-granular layers, respectively. Relatively more neurones remained binocular or dominated by the occluded eye in infragranular layers

In the normal cats the ocular dominance distribution for the two groups of cells were, however, rather similar to each other. The proportion of monocularly activated units was only slightly higher among the cells that responded to flash stimulation (19/70 = 27%) than in units that did not (5/23 = 22%). Accordingly, only a somewhat larger percentage of monocular than binocular units responded to flashed bars (19/24 = 79% as compared to 51/69 = 74%).

3. Laminar analysis of the ocular dominance shift

A track analysis of the cells in each penetration was performed on Nissl stained sections. All penetrations were situated in area 17. A crude depth analysis in the first two experiments on cats with monocular strobe experience revealed that cells in the upper half of any one penetration (corresponding on average to more superficially situated cells) invariably showed a much clearer ocular dominance shift than cells in the deeper part of a penetration ($\chi^2 = 12.602$; df = 4; $p < 0.01$; see also Rauschecker et al. 1981). Tracks recorded later during the course of an experiment showed the same difference as earlier ones.

In order to see whether this corresponded to a laminar difference in the ocular dominance shift, careful track reconstructions from brain sections were performed in 3 subsequent experiments. Small HRP deposits (50–100 μm diameter) were placed iontophoretically at different depths along the electrode track, in order to identify the laminar distribution of neurones. Six penetrations could be retrieved unequivocally. An example is shown in Fig. 4. When ocular dominance distributions were drawn separately for neurones from supragranular (including layer IV) and infragranular layers, in all six penetrations a clearer OD shift was found for layers I to IV, the overall difference from layers V/VI being significant at the 5% – level (Fig. 5; $\chi^2 = 4.990$; df = 2).

This difference in OD shift was not accompanied by a difference in response quality. In upper portions of all tracks 19.5% of the cells (26/133) were visually unresponsive and average response strength was 2.6; in deeper parts of the electrode penetrations the corresponding numbers were 21.2% (21/99) and 2.7.

4. Orientation and direction selectivity

Previous studies on *binocular* strobe rearing have reported a dramatic reduction of direction selectivity in visual cortex (Cynader et al. 1973; Cynader and Chernenko 1976; Pasternak et al. 1985). In addition, one study using a very low strobe frequency of 0.5 Hz in two animals reported a reduction of orientation selectivity (Cynader et al. 1973). We therefore also measured these properties for most single units in our cats with *monocular* strobe rearing. Orientation tuning was practically unchanged in all our experimental animals: 72% (107/148) of the cells displayed narrow orientation selectivity (± 45 deg or less), which is in the normal range (87 of 119 tested in our normal cats, i.e. 78%). Interestingly, 68% (120/177) of the units in our experimental animals also showed directional selectivity (class I or II as defined in Methods). This proportion is significantly lower than in our normal controls (114 of 140 tested = 81%), but the loss is not as dramatic as is the case after binocular strobe rearing.

Discussion

Ocular dominance after monocular strobe rearing

The results of this study show that an ocular dominance (OD) shift in striate cortex of kittens can be produced if they are reared in a 2-Hz strobe environment with one eye occluded for 8 h per day between 6 and 12 weeks of age. This effect is in marked contrast to that of rearing kittens in a diffuse, temporally modulated Ganzfeld illumination, where no OD shift is obtained (Singer et al. 1977). The state of cortex at the outset of exposure was the same in both studies (initial dark rearing after birth was employed to shift the exposure period to an age when kittens are less dependent on their mother for survival). Therefore, the most reasonable explanation compatible with both results is the following: most neurones in striate cortex of cats, dark-reared

or normal, do *not* respond to diffuse changing light, but *do* respond to stationary flashing contours. Since neurones seem to depend on postsynaptic activity for ocular dominance changes to occur (Rauschecker and Singer 1979, 1981; Reiter et al. 1986), an OD shift is observed after monocular strobe rearing, but not after monocular exposure to diffuse contrasts. In this respect, the study by Daniels et al. (1984) is more akin to that of Singer et al. (1977) than to our present one, because it used dim low-contrast flickering illumination (0.01 cd/m^2) with a sluggish onset (500 ms) and consequently received no OD shift.

Our conclusion about the postsynaptic gating of OD changes is strengthened by the finding of a tight correlation between OD and responsiveness to stationary flashing bars of light. Among neurones capable of responding to such stimuli an almost perfect OD shift was found, while in neurones that would not respond to these stimuli a binocular distribution was retained.

The only alternative interpretation of the present data would be that strobe stimulation of one eye led to an "instruction" of cells connected to this eye such that they learned to respond to stationary flashed stimuli. This appears unlikely, because no particular preference was found for the 2 Hz strobe frequency that the kittens had experienced, nor did binocular units show a difference between the two eyes in their responsiveness to flashes. The only piece of evidence that could be seen in favour of an "instructive" effect is the relative decrease of response latency to flashed bar stimuli in the strobe-reared animals. Although this difference is highly significant, the overall sample size is too small to make a strong point.

Layer specificity and behavioral consequences

In the first three experiments a differential effect of monocular strobe exposure on neurones in different recording depths was found. More superficially recorded cells were more clearly dominated by the exposed eye than units in deeper recording sites. This difference was not related to the time elapsed during the experiment nor to RF eccentricity. An actual layer-specific effect was then confirmed by careful track reconstruction using iontophoretic HRP marking. We have previously speculated (Rauschecker 1984) that it might be corticotectal cells in layer V that did not change their ocular dominance, because they have been reported to respond preferentially to moving stimuli (Palmer and Rosenquist 1974). In addition, the finding of Leventhal and Hirsch (1980) that their F-cells occur almost exclusively in layers V/VI may be of particular importance for our present finding. F-cells respond preferentially to faster moving stimuli and may therefore not be activated adequately by stationary strobe stimulation.

Since the subcortically projecting infragranular layers (Lund et al. 1975) can be assumed to subserve important functions for visuomotor tasks, it would be interesting to see whether the behavioral deficits after strobe rearing (Hein et al. 1970; Pasternak and Leinen 1986) are specifically related to a generally stronger affection of infragranular layers by strobe rearing.

From our present data on the orientation and direction selectivity of cortical units it appears that rearing kittens in a strobe environment with only *one* eye open has less devastating effects than *binocular* strobe rearing (Cynader et al. 1973; Cynader and Chernenko, 1976; Pasternak et al. 1985). This may have to do with the known interdependence between binocularity and feature selectivity (Fregnac and Imbert 1978; Leventhal and Hirsch 1980). However, other explanations are also conceivable: It is not clear whether similar criteria were used in all studies to assess direction selectivity. Exposure duration could be another factor: in most studies with binocular strobe rearing prolonged steady exposure of several months was used. Only one study (Olson and Pettigrew 1974) exposed their kittens just for a few weeks at the beginning of the sensitive period and reported no difference in the percentage of directional units as compared to normal controls. Certainly, our results cannot be due to an untight darkroom: in that case no ocular dominance shift would have occurred at all, because the animals had both eyes open outside exposure sessions.

In summary, monocular deprivation of moving contours during the sensitive period by rearing kittens in a strobe-lit environment with one eye occluded produces a shift of ocular dominance in striate cortex neurones. The shift does not occur, however, equally in all neurones, but is different depending on the cell's filter properties and laminar origin. These dependencies are best explained by the following hypothesis: At the outset of strobe-rearing there are fixed classes of units that differ in their responsiveness to stationary flashed stimuli. Activation of the afferent visual pathway by specific activity patterns then leads to synaptic changes and their subsequent consolidation in those local networks that are best attuned to these patterns, i.e. where the correlation between pre- and postsynaptic activity is maximal (Hebb 1949; Rauschecker and Singer 1979, 1981; Rauschecker and Hahn 1987).

Acknowledgements. We wish to thank Profs. Horace B. Barlow and Wolf Singer for commenting on an earlier version of the

manuscript, and Dr. Michael von Grünau for participating in two of the experiments. Special thanks are due to Sabine Hahn for technical assistance and for editing the manuscript, and to Andrea Opper for help in rearing the kittens. The present study was partially supported by the Deutsche Forschungsgemeinschaft (SFB 307-C7 "Neurobiologie des Verhaltens").

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Received December 12, 1986 / Accepted July 21, 1987