

## EVIDENCE FOR LONG-TERM FUNCTIONAL PLASTICITY IN THE VISUAL CORTEX OF ADULT CATS

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### SUMMARY

1. Vision was investigated with behavioural and electrophysiological techniques in three groups of cats: (a) two normally raised kittens in which one eye was rotated at an age of 3 months, (b) three adult cats in which one eye had been rotated and the other closed 6 months prior to recording, (c) two adult cats in which first one eye had been rotated and the other closed and subsequently, after one year, the rotated eye had been closed and the normal eye re-opened. The latter two cats were investigated 6 and 12 months after reverse suture, respectively. All adult cats were at least 2 years old when operated on for the first time.

2. Behavioural analysis revealed that the kittens of the first group no longer used the rotated eye for fixation, visuo-motor behaviour being impaired when tested through this eye. Binocularity was found to be disrupted to nearly the same extent as in kittens made strabismic at the beginning of the critical period. In addition, ocular dominance was shifted towards the normal eye.

3. The adult cats in the second group developed a virtually complete neglect of the visual modality subsequent to a period of severely disturbed visuo-motor behaviour.

4. These behavioural abnormalities were associated with clear alterations in the functional state of striate cortex. Only 47% of the recorded cells could be driven with light, the majority of these reactive neurones yielding only sluggish responses to optimally aligned stimuli. The ocular dominance distribution showed a significant reduction of binocular cells but gave no indication of a shift in ocular dominance towards either of the two eyes. Moreover, contrast sensitivity as assessed with pattern-evoked potentials was significantly reduced.

5. The remaining two animals that were reverse sutured after the visual neglect had developed showed complete behavioural recovery when tested through the re-opened normal eye. However, this recovery was not instantaneous and occurred only after the cats had been forced to use their visual sense.

6. Behavioural recovery was paralleled by an increase of cortical reactivity to normal levels and by a marked increase in binocularity. This gain increase of excitatory transmission was, however, selective for neurones dominated by the normal eye, leading to a bias in ocular dominance towards this eye.

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7. The observed modifications in the functional state of striate cortex indicate that reversible changes in the gain of excitatory transmission can still occur beyond the end of the classical critical period. These long-lasting changes in synaptic efficiency appear to follow the rules postulated by Hebb for adaptive synaptic connexions.

#### INTRODUCTION

It is commonly believed that in the visual cortex experience can induce permanent changes of neuronal response properties during a critical period of early development. Just when experience can induce such changes has so far been investigated only with the paradigm of monocular deprivation (Hubel & Wiesel, 1970; Blakemore, 1976; Blakemore & Van Sluyters, 1974; Blakemore, Garey & Vital-Durand, 1978; Olson & Freeman, 1978, 1980). Recently Cynader & Mitchell (1980) showed that raising kittens in the dark before monocular deprivation can considerably extend the period during which striate cortex is susceptible to monocular deprivation. Thus, the period during which cortical plasticity is demonstrable does depend on the way in which experience is manipulated.

The hypothesis leading to the present investigation was that paradigms other than monocular deprivation might be capable of revealing long-term plasticity even in adult striate cortex. Rather than merely deprive the system of its natural input, we manipulated retinal signals in a way that we thought would force the visual system to change. As in the preceding study (Singer, Tretter & Yinon, 1982) we employed surgical eye rotation, expecting that the mismatch between retinal co-ordinates and other sensory-motor maps would disturb visually guided behaviour of adult cats at least to the same extent as it did in kittens. The results, some of which have been published in short form previously (Singer, Yinon & Tretter, 1979*c*), confirm our expectancy and demonstrate a remarkable degree of functional plasticity in the mature visual system.

#### METHODS

In five adult cats we sutured closed one eye and rotated the other eye surgically. We also rotated one eye in two 12-week-old kittens, but left the other eye open. At the time of surgery all the adult cats were at least two years old and had been in our colony for at least six months. The surgical procedure and later electrophysiological tests were those described in the preceding paper (Singer *et al.* 1982). The kittens were studied electrophysiologically 3 months after surgery. Three of the adult cats were studied after 6–7 months of experience with only the rotated eye open. The two other cats were studied after 1 year of experience with only the rotated eye open, 1–2 months with both eyes open, and a subsequent period of 6 or 12 months with the rotated eye closed and the normal eye open. Table 1 summarizes each cat's history.

#### RESULTS

##### *Behavioural observations*

The two young cats whose normal eyes had been left open displayed normal visuo-motor co-ordination as soon as they recovered from surgery, but like amblyopic kittens (Ikeda & Tremain, 1979; Singer, von Grünau & Rauschecker, 1980) they used only the normal eye for fixation. When tested with the normal eye occluded,

TABLE 1.

No. of cat	Age at first intervention	Type of first intervention		Interval between 1st and 2nd intervention	Type of second intervention		Interval between 1st intervention and recording
		Right eye	Left eye		Right eye	Left eye	
102	3 months	rot. 60 deg	open	—	—	—	3 months
105	3 months	rot. 45 deg	open	—	—	—	3 months
62	> 2 years	rot. 90 deg	closed	—	—	—	6 months
78	> 2 years	rot. 90 deg	closed	—	—	—	6 months
132	> 2 years	rot. 180 deg	closed	—	—	—	7 months
181	> 2 years	rot. 90 deg	closed	1 year	closed	opened	1½ year
182	> 2 years	rot. 90 deg	closed	1 year	closed	opened	2 years

visuo-motor co-ordination was found to be impaired to about the same extent as it is in kittens which receive the same treatment at 4 weeks of age. On the other hand, the visuo-motor co-ordination of the five adult cats whose normal eye had been closed at the time of eye rotation was even worse than that in 4 week old kittens treated similarly (Singer *et al.* 1982). The cats immediately after surgery and for several weeks showed head nystagmus, stereotyped circling, withdrawal from large visual targets, and false orienting responses. We also observed signs of severe emotional distress for the first time. The cats avoided any kind of interaction and tended to become aggressive or frightened when approached by other cats. These abnormalities faded over time but the cats' avoidance of movement left them distinguishable from their normal colony mates and even from cats binocularly deprived from birth. They also stopped using visual cues to orient or to guide their motor behaviour. They would sometimes approach a smaller target without even noticing it until it touched the head, and then startle. Visually guided placing of the front paws and jumping were also severely disturbed.

In the two cats in which the normal eye was reopened at this stage, we were surprised to observe no spontaneous recovery of visually guided behaviour. The cats continued to ignore their visual sense. Therefore, after a few months we closed the rotated eye, assuming that the elimination of its inappropriate visual signals would allow the normal eye to recover. But it did not. The cats started to recover only when we forced them to use vision by transferring them to another, unfamiliar colony room and by giving them frequent visual tests. Within a few weeks vision appeared to be normal.

### *Electrophysiological results*

*Cats with one eye rotated at 12 weeks and the other eye left open.* Three months after surgical eye rotation, when the two kittens were 6 months old, we recorded the discharges of 156 units from striate cortex. We were able to identify receptive fields for 65% of these cells, most of which (92%) were well tuned for orientation. In binocular cells orientation preferences were identical in the two eyes when related to retinal co-ordinates. As shown in Fig. 1A, binocularity was reduced compared to normal cats: only 10% of the cells responded equally well to stimulation of either eye. Ocular dominance had shifted toward the open normal eye, to the same extent as it did in kittens with one eye rotated at the beginning of the critical period (see Singer *et al.* 1982). However, there were more binocular cells (38%) than in the kittens raised with misaligned visual axes from the beginning of the critical period. Using the same procedure we found only 26 and 25% of cells were binocular in a kitten with one eye rotated at 4 weeks (Singer *et al.* 1982) and in kittens made strabismic at 4 weeks (Singer, von Grünau & Rauschecker, 1979b).

*Adult cats with one eye rotated, the normal eye closed and no reverse suture.* We recorded from 219 cells in the three adult cats in which the normal eye was closed until the time of recording. 121 units were from the hemisphere contralateral to the rotated eye, but since there were no obvious inter-hemispheric differences, we have pooled data from the two hemispheres. Only 104 (47%) cells could be driven with light stimuli and in the majority of these cells responses were sluggish and fatiguable. Correspondingly, the average indices for response vigour from the closed and rotated

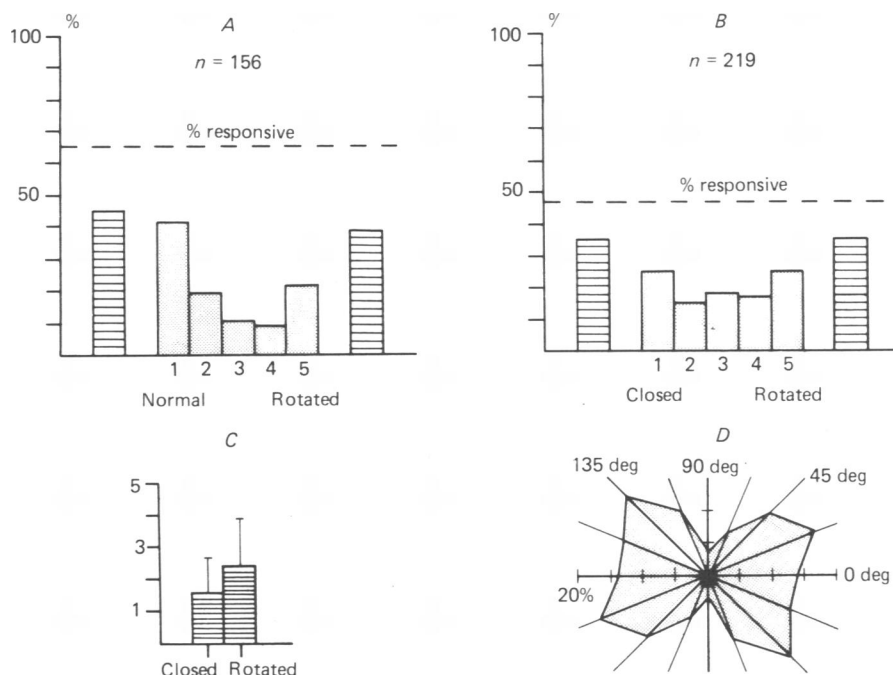


Fig. 1. *A*, ocular dominance (o.d.) distribution (filled columns), percentage of light reactive cells (dashed horizontal line) and percentage of cells excitable from either of the two eyes (hatched columns) from striate cortex of two kittens in which one eye was rotated at 12 weeks of age. The o.d. distribution is calculated in percent of light reactive cells; the percentage of cells excitable from either of the two eyes (hatched columns) are calculated from the sum of o.d. classes 1-4 and 2-5 respectively, and refer to the total sample of analysed cells ( $n = 211$ ). o.d. classes 1 and 5 comprise cells driven exclusively from the normal or the rotated eye, classes 2 and 4 refer to binocular cells with prevailing input from one eye and class 3 contains cells driven equally well from either eye. *B*, o.d. distribution from three adult cats in which one eye was rotated and the other closed 6 months prior to recording. Data are presented in the same way as in *A*. *C*, average indices for the quality of responses obtained from the closed and the rotated eye in the adult cats. Vertical bars show standard deviations. *D*, polar plot of orientation preferences of mappable cells ( $n = 30$ ) in the adult cat in which the open eye was rotated by 180 deg. The 0 and 90 deg vectors correspond to horizontal and vertical orientation preferences, respectively. Orientation preference was classified in eight classes as indicated by the eight vectors. For clearer presentation the distribution was smoothed according to the formula

$$N_{\alpha} = \frac{N_{\alpha} - 22 \text{ deg} + 2N_{\alpha} + N_{\alpha} + 22 \text{ deg}}{4}$$

eye were 1.5 and 2.7, respectively, and thus considerably lower than the average of 3.7 obtained from normal animals (Fig. 1 *C*). In the  $\chi^2$  test both distributions of vigour indices differed significantly ( $P < 0.001$ ) from the distribution in normal cats. As shown in Fig. 1 *B* the proportion of binocular cells was markedly low (50% of reactive cells), but the ocular dominance distribution had remained symmetrical.

All responsive cells had an orientation preference and in binocular cells the preferred orientations and directional preferences were identical in both eyes when related to retinal co-ordinates.

Because of inconsistent responses to stationary stimuli we could classify the type of receptive field only for the few cells ( $n = 33$ ) responding well to light stimuli (vigour classes 3–5). Eighty percent of these cells had simple receptive fields which were small and sharply tuned for orientation. The remaining six cells were classified as complex. All cells but one were dominated by one or the other eye. All other units reacting vigorously to light stimuli could be identified as l.g.n. fibres. They were shared equally by the two eyes and showed no abnormalities.

In the one cat with 180 deg eye rotation but not in the two other cats with 90 deg rotation it also appeared that binocular neurones preferring vertical orientations were under represented (Fig. 1 *D*). Because of the small sample size ( $n = 30$  binocular cells) this bias was not statistically significant, but the trend agrees with findings in kittens with 180 deg eye rotation (Singer, Tretter & Yinon, 1979*a*).

*After reverse suture.* We recorded from 131 units in two cats in which the rotated eye had been closed and the normal eye opened for a period before recording. Since again no inter-hemispheric differences were apparent, data from the two sides were pooled. There was remarkable recovery compared to the cats given no reverse suture, although abnormalities were still apparent. Thus, a normal percentage of cells could be excited by light stimuli (91 %) and more cells could be driven binocularly (75 %). But most of these cells were dominated by the normal eye or driven equally well by either eye. Even fewer cells were dominated by the rotated eye than in the cats given no reverse suture (Fig. 2 *A*). In line with these selective changes in excitability, the vigour index for responses from the normal eye was nearly normal while that for responses from the rotated eye was higher than in the cats given no reverse suture but still significantly ( $P < 0.001$ ) lower than in normal cats (Fig. 2 *B*).

As in cats given no reversal, all responsive neurones were orientation selective. There was no significant asymmetry in the distribution of preferred orientation and the preferences in the two eyes were identical with respect to retinal co-ordinates. With two exceptions, the monocular cells had simple fields with either single or juxtaposed 'on' or 'off' regions.

#### *Contrast sensitivity functions*

We calculated contrast sensitivity functions from evoked potentials elicited by phase alternating gratings as in the preceding article and in our previous studies of cats with squint amblyopia (von Grünau & Singer, 1980). In the cats given no reverse suture, contrast sensitivity was drastically reduced in both eyes and at all spatial frequencies tested. After reversal, contrast sensitivity in the previously normal eye had recovered considerably but not completely. In the rotated eye, contrast sensitivity improved as well, but to a smaller extent. The control data in Fig. 2 show the contrast sensitivity function of the normal eye of a cat suffering from squint amblyopia that was examined with identical methods (von Grünau & Singer, 1980). This control is in the range characteristic of normal adult cats.

### DISCUSSION

#### *Changes in the cats whose normal eyes were open*

These cats lost nearly as many binocular units as kittens in whom unilateral cyclotorsion or strabismus was induced at the beginning of the 'critical period' (Hubel

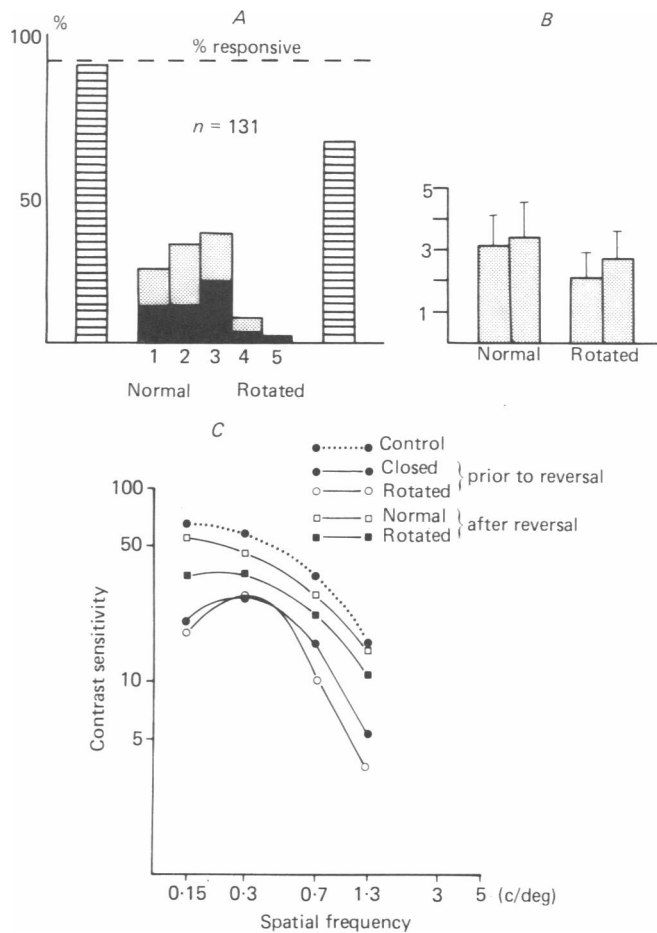


Fig. 2. *A*, ocular dominance distribution of two adult cats which had one eye closed and the other rotated for one year and subsequently, for another 6 and 12 months respectively, had the normal eye reopened and the rotated eye closed. The samples from the two animals are indicated by different shadings, otherwise data are represented in the same way as in Fig. 1 *A* and *B*. *B*, average indices for the quality of responses obtained from the same adult cats through the normal and the rotated eye. Vertical bars indicate standard deviations. The data of the two animals are represented separately, the left columns corresponding to the cat with the shorter survival after reverse suture. *C*, contrast sensitivity functions determined from cortical evoked potentials elicited by phase alternating square wave gratings from a control animal (dotted line) and from the adult cats with one rotated eye recorded prior (circles) and after reverse suture (squares). Spatial frequency and contrast sensitivity are plotted on logarithmic scales on the abscissa and the ordinate, respectively.

& Wiesel, 1965; Singer *et al.* 1979*b*, 1982). Since there is no parametric study using strabismic kittens to define the length of the 'critical period' it cannot be decided whether the relevant aspect of cyclotorsion is not rotation *per se*, but is rather the misalignment of visual axes and associated diplopia. The subnormal percentage of cells reacting to light, the shift in ocular dominance towards the normal eye and the

cats' fixating only with the normal eye, all indicate that the signals from the rotated eye were suppressed as in strabismic kittens which develop amblyopia (Ikeda & Tremain, 1977, 1979; Singer *et al.* 1980). This interpretation accounts for the impaired visual functions of the rotated eye and suggests that long-term suppression can lead to changes in cortical functions beyond the critical period.

*Changes in the adult cats with one eye rotated and the other closed before reversal*

In the striate cortex of these cats the responsiveness of cells to light had markedly decreased. Half of the responsive cells remained binocular, and the distribution of ocular dominance was symmetrical. This indicates that pathways from the rotated eye were disrupted no more than pathways from the normal eye. Disruption probably occurred mainly beyond first order cells and after signals from the two eyes converged. The cells which continued to respond normally had mainly simple and monocular receptive fields, like cells in layer IV (Gilbert, 1977) receiving direct thalamic input (Singer, Tretter & Cynader, 1975; Bullier & Henry, 1979; Henry, Harvey & Lund, 1979). Cells with identifiable complex fields and cells excited equally well by both eyes were markedly under-represented, which suggests that these neurones had been affected selectively. Most of these cells occupy a higher rank in the cortex: they tend to be located outside layer IV (Gilbert, 1977), to be remote synaptically from the thalamus (Singer *et al.* 1975; Bullier & Henry, 1979; Henry *et al.* 1979) or, if they are monosynaptically driven, to receive additional input from intracortical circuits (Singer *et al.* 1975). Thus, the decrease in responsiveness appears to be particularly pronounced beyond the level of first order cells. Further evidence for this interpretation comes from peculiarities of the recovery process and is referred to in the next paragraph.

This apparent inability to disrupt connexions of only the rotated eye at the level of binocular convergence contrasts with the finding in the cats which had the normal eye open. One explanation could be that the simultaneous deprivation of the normal eye had prevented local competition at the site of binocular convergence. The alternative explanation is that plasticity at the level of binocular convergence while persisting beyond the classical critical period still does not last indefinitely.

*The recovery process*

The neglect of vision continued after switching in the normal eye and closure of the rotated eye. This agrees with the above conclusion that the suppression had affected transmission of signals from both eyes probably because pathways were affected beyond the level of binocular convergence. Vision recovered only after we had transferred the cats to an unfamiliar environment and had subjected them to frequent visual testing. Thus, adult cats have to be forced not only for the disruption of visual functions but also for their restitution.

The asymmetric distribution of ocular dominance after recovery indicates that, unlike the initial disruption, the restitution of excitatory transmission has been selective for pathways conveying activity from the normal eye. This excludes that recovery is solely due to a general increase of excitability and indicates that signals from the open eye have selectively improved transmission in the respective activated pathways just as occurs with reverse suture during the critical period. Unlike the



effect of reverse suture during the critical period, however, the closed eye had not at the same time become repressed. On the contrary, this eye drove more cells after reversal than before and this increase of gain occurred exclusively at cells receiving *also* input from the newly opened, normal eye. No recovery had occurred for cells driven by the rotated eye alone. This is best explained by assuming, as stated above, that impairment and subsequent recovery of transmission had occurred beyond the level of binocular convergence. Only in that case can the rotated eye profit from the gain increase which is caused by signals from the newly opened normal eye.

#### *Comparison with plasticity during the critical period*

The decrease of cortical excitability, the reduction of binocularity, the reduced contrast sensitivity and the behavioural alterations following long-term suppression of visual functions in the adult resemble qualitatively and quantitatively the consequences of binocular deprivation from birth (for comparison with b.d. preparations see Ganz, Hirsch & Tieman, 1972; Chow & Steward, 1972; Sherman, 1973, 1977; Singer & Treutter, 1976; Loop & Sherman, 1977; Watkins, Wilson & Sherman, 1978; Smith, Lorber, Stanford & Loop, 1980).

Activity-dependent modifications during the critical period can be explained by Hebbian synapses whose gain changes as a function of the probability of contingent pre- and post-synaptic activity (Rauschecker & Singer, 1979, 1981; Singer, Freeman & Rauschecker, 1981). The same mechanism might account both for the impairment of excitatory transmission after long-term suppression of neuronal responses *and* for the selective improvement of transmission once appropriate signals are again available. The adaptive changes in the adult differ, however, radically from those occurring during early development because they remain reversible once the 'critical period' is terminated. The characteristic feature of the critical period, therefore, is not the existence of adaptive synapses but the existence of a mechanism which *irreversibly* inactivates functionally weakened connexions.

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