

THE IMPORTANCE OF MOVEMENT TO THE DEVELOPING VISUAL SYSTEM*

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Abstract—Cats reared under stroboscopic conditions (frequency 2 Hz; duration 0.2 ms), when only a series of “frozen” retinal images is received and the neural channels responsible for movement analysis are put into competitive disadvantage, show severe deficits in the proportion of direction-selective cells in areas 17 and 18 and markedly abnormal optokinetic nystagmus responses.

INTRODUCTION

The question of how the complexity of the adult nervous system of vertebrates is established has intrigued neurobiologists since the time of Cajal. The topographical relationships which exist within the visual system require a high degree of precision of interneuronal connections. Although the factors which govern the formation of this neuronal circuitry are poorly understood, there is considerable evidence that the process is a dynamic one, which involves a more or less prolonged period of continued reorganization. Two aspects of the developing nervous system deserve special mention in this respect. Firstly there is an overproduction of neurons which compete for survival (Cowan, 1973) and secondly only a fraction of the synapses present in the developing system persist in the adult animal (Changeux and Danchin, 1976; Purves and Lichtman, 1980). The existence during development of prolific numbers of neurons and synapses raises the probability that the precise connectivity in the adult is achieved by the pruning of an initially overelaborated neuronal circuitry.

There is a global consensus that activity in the nervous system is an important factor in determining which neuronal circuits are going

to be eliminated. Given the extension of the dynamic phase of neuronal reorganization after birth, it is very likely that sensory experience, by modulating neural activity, contributes to the precise pattern of connectivity in the adult. Wiesel and Hubel (1963) showed that rearing kittens with one eye closed leads to a contraction of cortical territory normally innervated by that eye. However, closure of both eyes at birth gives rise to much more subtle effects (Wiesel and Hubel, 1965). It therefore seems possible that competition (in terms of activity) between sets of axons rather than just disuse is decisive in determining neuronal organization (Wiesel, 1982).

Activation of neurons at all levels of the visual system depends on the spatial and spatial–temporal parameters of the stimulus. Stroboscopic illumination of the environment (strobe rearing) gives rise to a “frozen” retinal image and puts into competitive disadvantage the neural channels responsible for movement analysis. Spatial–temporal interactions involving sequential activation of adjacent loci on the retina will be abolished and therefore one would predict that neuronal mechanisms such as those described by Barlow and Levick (1965) for detection of direction of movement will be greatly affected. Strobe rearing should therefore constitute a far stronger deprivation paradigm than binocular lid suture, and should above all affect those regions of the brain

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devoted to the analysis of visual movement. Recent results have suggested that area 18 has a privileged role in the analysis of movement (Orban *et al.*, 1981a, b). Area 18 subserving central vision responds to relatively slow stimulus velocities and possesses more velocity-tuned and direction-selective cells, whereas peripheral area 18 has less direction-selective cells, gives higher response levels and responds to higher stimulus velocities. The present series of experiments shows that this cortical specialization is susceptible to disruption in the absence of the experience of visual movement, resulting in a permanent impairment of the visual capacities.

METHODS

Cats were reared from birth in light-tight cages illuminated stroboscopically (frequency 2 s^{-1} ; duration 0.2 ms. The methods used here have been described elsewhere (Orban *et al.*, 1981a, b; Kennedy *et al.*, 1982) and only a brief description will be given here.

Electrophysiological recordings

Single-cell activity was recorded in anaesthetized and paralyzed cats. Direction selectivity and its dependence on stimulus velocity were assessed quantitatively with a multihistogram method. At a given velocity the direction selectivity was measured by the direction index (DI):

$$DI = \frac{\text{response in preferred direction} - \text{response in non-preferred direction}}{\text{response in preferred direction}}$$

Given that DI changes with velocity, the overall ability of the neuron to code direction of movement was measured by a mean direction index (MDI), which is the weighted mean of the DI s at different velocities, weighted by the response strength at the corresponding velocities:

$$MDI = \overline{DI} = \frac{\sum_{i=1}^N R_i DI_i}{\sum_{i=1}^N R_i}$$

where $DI_i = DI$ at each velocity, $R_i =$ net response in the preferred direction, and $N =$ number of velocities tested.

Eye movement recordings

Cats were implanted under anaesthesia with silver-chloride electrodes for recording horizontal eye movements. Two weeks after surgery animals were placed with the head fixed at the center of a drum (1 m diameter) with 10° wide black-and-white stripes. Eye position was monitored on a polygraph. The optokinetic nystagmus (OKN) was tested by rotating the drum around the animal at various velocities ranging from 7 to 80° s^{-1} . Records of eye movements were calibrated (Stryker and Blakemore, 1972). The slope of cumulative eye position gave the average value of the nystagmus velocity.

RESULTS

Electrophysiology

Strobe rearing had a major effect on direction selectivity, reducing the proportion of direction-selective cells in areas 17 and 18 and abolishing the direction selectivity gradient with eccentricity in area 18. Since in both normal and strobe-reared animals the direction selectivity of a considerable number of area 17 and 18 cells (55% in normal and 70% in strobe-reared animals) changes with velocity, it is important to use an index such as MDI , averaging direction selectivity over a large range of velocities, to characterize direction selectivity of cortical cells. In the normal animal the uniform distribution of MDI s (Fig. 1) shows that direction selectivity is a graded property ranging from an MDI of 100, corresponding to a null response in the non-preferred direction, to an MDI of 0, indicating exactly equal response in opposite directions of motion.

In areas 17 and 18 of the normal animal, 65% of the cells had MDI values over 50 and were classified as direction-selective (Fig. 1). Strobe rearing drastically reduced the proportion of direction-selective cells to 22%. The distribution of MDI in areas 17 and 18 of strobe-reared cats shows a gradual decrease in proportion of cells with MDI s over 20 (Fig. 1).

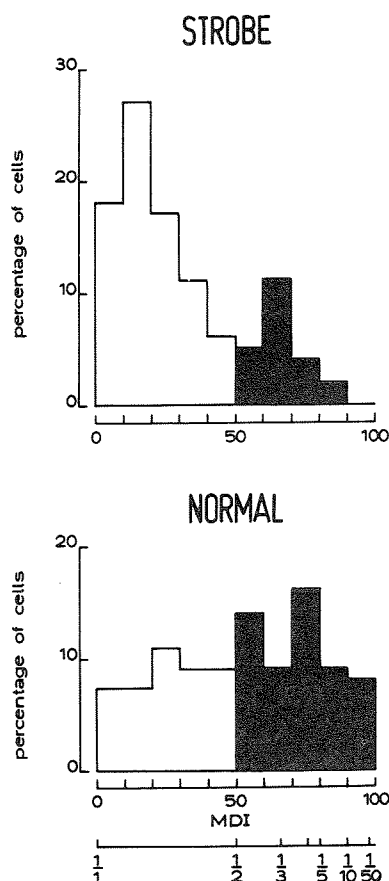


Fig. 1. *MDI* distribution of area 17 and 18 cells in strobe-reared ($N = 82$) and normal ($N = 196$) animals. The ratio between the response in the non-preferred and in the preferred direction is indicated below the corresponding *MDI*; open area indicates non-direction-selective cells, filled area indicates direction-selective cells.

This indicates that the deficit is not a disappearance of a class of cells from the upper end of the *MDI* scale, as would be expected if direction selectivity was an all-or-none property of cortical cells. Rather the deficit is a gradual one, being largest at the far end of the direction selectivity spectrum.

In the normal animal there is a decrease in the proportion of area 18 direction-selective neurons as a function of eccentricity (Fig. 2). In the strobe-reared animal the proportion of direction-selective cells is at an equally low level at all eccentricities. Plotting the *MDI* as a function of eccentricity is a powerful way of illustrating this effect of eccentricity (Fig. 2) since the *MDI* distribution measures the direc-

tion selectivity of all cells including those with a low *MDI* value. In normal cats the median *MDI* decreases from 75 in area 18 subserving central vision to 45 in peripheral cortex. In the strobe-reared animals the median *MDI* is about 25 at all eccentricities. Therefore, what is left of direction selectivity in area 18 is uniformly distributed over the cortex.

Eye movements: monocular OKN

Stimulating only one eye in the normal animal gives a response which, up to 30° s^{-1} , is as strong as the binocularly viewed OKN. At velocities in excess of 30° s^{-1} the gain of monocular OKN (i.e. pursuit eye velocity divided by stimulus velocity) drops faster than does the response to binocular stimulation and at 60° s^{-1} the monocular OKN has a gain not higher than 0.31 whereas at the same velocity the mean gain of the binocular response is 0.64. Not only is the gain lower at high stimulus velocities, but there appears to be a consistent asymmetry according to the direction of stimulation. As expected, a stimulus moving in the temporal–nasal direction elicits a more vigorous response than does a stimulus moving in the nasal–temporal direction. In the normal animal the mean difference in gain between the two directions is around 25%. In the strobe-reared animal this asymmetry is much more pronounced (Fig. 3). Stimuli moving in a temporal–nasal direction at 7° s^{-1} elicit a nystagmus with a mean gain (0.8) only slightly less than that resulting from binocular stimulation (0.9). Stimuli moving in a nasal–temporal direction at the same velocity give a considerably weaker nystagmus which does not exceed a gain of 0.2 and disappears at velocities over 30° s^{-1} . The monocular optokinetic response in the preferred direction falls off much quicker than that following binocular stimulation. At 30° s^{-1} , monocular stimulation in the temporal–nasal direction gives rise to a gain of 0.05 compared to a gain of 0.18 during binocular stimulation at the same velocity.

DISCUSSION

Strobe rearing leads to strong deficits both at the single-cell level and the behavioural level.

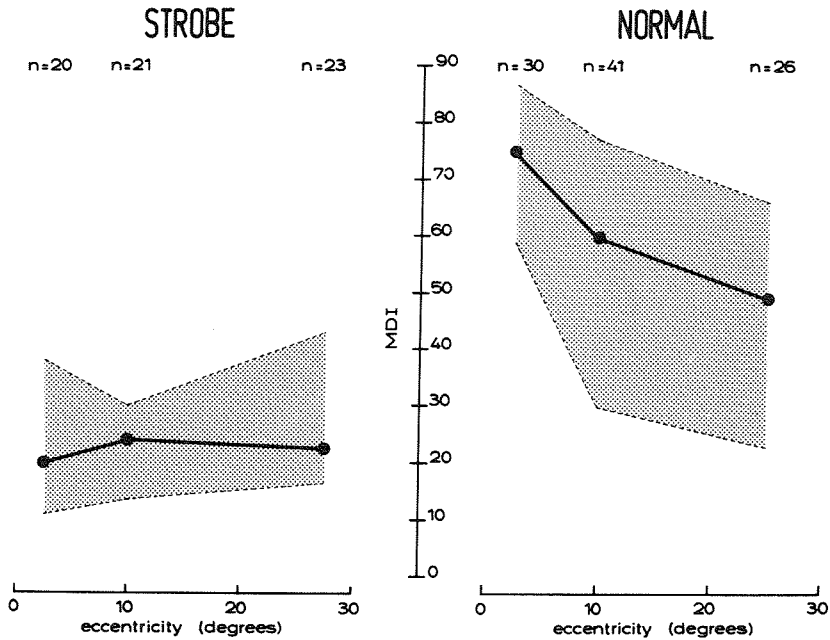


Fig. 2. MDI of area 18 cells plotted as a function of eccentricity in strobe-reared and normal animals. Medians (dots) and the first third quartiles of the distributions are plotted. In the normal animal the correlation was significant ($r = 0.41$, $P < 0.002$). There was no correlation in the strobe-reared cat ($r = 0.11$).

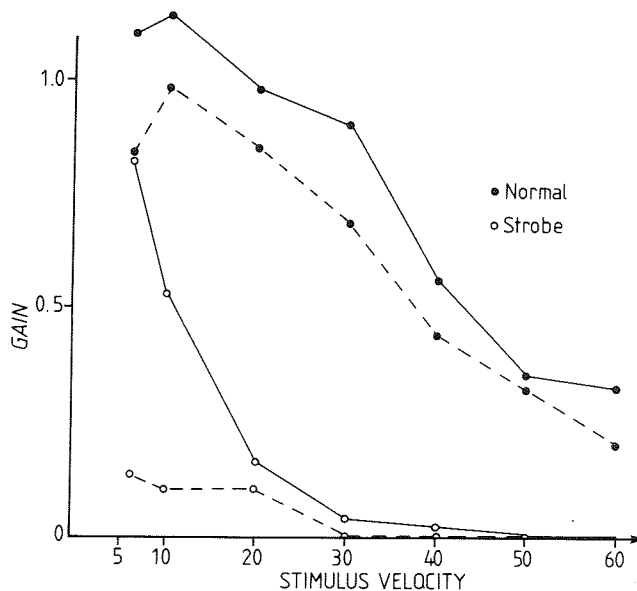


Fig. 3. The gain of the horizontal optokinetic nystagmus following monocular stimulation as a function of stimulus velocity ($^{\circ} \text{s}^{-1}$). Mean values are shown for two measurements made for the normal (filled circles) and strobe-reared animals (open circles). In both sets of animals the mean gain values for temporal-nasal-directed stimuli are shown by a continuous line and for nasal-temporal-directed stimuli by a discontinuous line.

There is evidence for two pathways mediating OKN: (1) a largely crossed subcortical pathway in which temporal – nasal-directed stimulation predominates in eliciting a nystagmus and, (2) a cortical pathway which is responsible for a symmetrical oculomotor response (Fukuda, 1959; Braun and Gault, 1969; Wood *et al.*, 1973; Hoffmann and Schopmann, 1975; Montarolo *et al.*, 1981). The visual cortex has been shown to increase the gain of OKN particularly at higher velocities resulting from both directions of horizontal stimulation, although more so for uncrossed fibers and the nasal – temporal direction (Montarolo *et al.*, 1981). The absence of a temporal-directed, monocular OKN in the strobe cat and the drop-off in gain at high velocities of the binocular OKN indicate, therefore, a failure of the cortex to contribute to visually-elicited reflex eye movements.

The asymmetrical response of the monocular OKN could be linked to the lack of direction-selective neurons at the cortical level. It has been suggested by Tauber and Atkin (1968) that optokinetic symmetry has developed in relation to foveal organization. A symmetrical response would provide better conjugate performance of the two eyes and result in improved binocular vision. It may be, therefore, that in strobe-reared cats, where there is no specialization of cortex subserving the area centralis, the need or the capacity to elaborate a symmetrical monocular OKN is compromised.

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