Cortical Effects of Daily Sequential Stimulation of Right and Left Eyes in the Kitten

R. D. Freeman and C. R. Olson
School of Optometry, University of California, Berkeley 94720, CA, USA

Summary. Beginning near the peak of the sensitive period to monocular deprivation, kittens were reared in darkness except for daily sessions during which the left eye was exposed first followed immediately by an equal amount of right eye exposure. The notion was that the sequence of stimulation may be an important determinant in cortical representation of each eye. Although study of single neurons in area 17 showed that nearly all cells were monocular, no systematic imbalance was found in the numbers of units controlled by each eye.

Key words: Monocular deprivation — Kitten visual cortex

The two eyes normally influence approximately equal numbers of cells in the kitten's striate cortex, but neural pathways from an eye that is not allowed normal visual input may be selectively impaired (Wiesel and Hubel 1963, 1965; Hubel and Wiesel 1970). Although the effects of this process have been well documented, the underlying cellular mechanisms remain to be elucidated. It would be instructive if this functional advantage of one eye over the other could occur in a situation where there is no interocular difference in visual experience. This could happen if visual exposure is alternated equally between the right and left eyes, but the sequence of stimulation causes unequal control of cortical neurons. The first eye that is exposed might dominate if, e.g., stimulation causes an immediate and lingering suppression of conduction through pathways from the other eye. Alternatively, assuming that the kitten spends a period of time in darkness following the second monocular exposure, the first eye that is exposed could obtain a functional disadvantage as follows. Suppose that stimulation produces a trace which is consolidated after a delay into a strengthening of the activated pathways. In this case, if stimulation of an eye abolished traces resulting from immediately preceding exposure of its mate, one would expect the second eye that is exposed to dominate a majority of cortical neurons.

We have examined the possibility that imbalanced cortical control by the two eyes may result even when each has the same quality and quantity of visual exposure. Normally reared kittens were placed in a darkroom at 4 weeks postnatal. Each day they were brought into a lighted room while monocularly occluded with a large opaque contact lens placed in the right eye for one hour and then immediately in the left eye for another hour. During this entire period, they were prevented from sleeping. At the end of the second hour, they were returned to the darkroom.

After a rearing period of 16 or 46 days, extracellular responses in striate cortex were studied. Kittens were prepared for physiological study using standard methods (Freeman 1978a). Under suitable anaesthesia, a femoral vein and the trachea were cannulated and the dura was exposed over area 17. Procedures were used to monitor expired CO₂, body temperature, EKG, and EEG. Tungsten-in-glass microelectrodes were advanced at an angle into the brain and spikes from individual cells were amplified and displayed using a conventional apparatus.

Once spikes from a neuron were isolated, receptive fields were plotted using back-projected, hand-controlled stimuli. Boundaries were recorded and optimal parameters of orientation, direction, velocity, and stimulus dimensions were noted for each eye. After optimal stimulus conditions were determined, the eyes were stimulated alternately to estimate
absolute and relative response strengths. Ocular dominance values were assigned to each responsive cell by use of a standard scale (Hubel and Wiesel 1962). Groups 1 and 7 refer to monocular cells dominated by the eye contralateral or ipsilateral, respectively, to the hemisphere that contains the electrode. Intermediate values designate binocular cells controlled primarily (groups 2 or 3), slightly (groups 5 or 6), or equally (group 4) by the contralateral eye. Visually unresponsive units were also noted.

Most cells in the visual cortex of normally reared cats and kittens are binocular (Hubel and Wiesel 1962, 1970; Freeman 1978b). Ocular dominance histograms in Fig. 1a and b show data from normal animals recorded at ages similar to those at which the experimental groups were studied (6.5 and 13 weeks for a and b, respectively). Results shown in Fig 1c are for another control animal, normally reared until 4 weeks postnatal, and then dark-reared until 8.5 weeks postnatal except for daily binocular exposure sessions for 1–2 h during which both eyes were open. As the figure suggests, the ocular dominance data for this cat are well within the normal range. Results in Fig. 1d–g are from four experimental animals, alternately occluded during successive daily sessions with the right eye always occluded first. The appearance of inter-animal variability with respect to which eye dominates the majority of cells probably is attributable to sampling problems rather than to any genuine inter-animal differences. Certainly, when the results from all four experiments are pooled (Fig. 1h), neurons dominated by the two eyes are quite evenly balanced. Therefore, we conclude that any competitive advantage bestowed on one eye or the other by the conditions of our experiment must be very subtle. It should be noted that all kittens displayed a marked breakdown of binocular connectivity, with most

Fig. 1a–h. Ocular dominance histograms are shown for control and experimental cats. Abscissae represent subjective classifications based on the relative influence that stimulation through a given eye has on a cell’s activity. If a unit is activated through only one eye, it is group 1 or 7. The other groups indicate binocular activation of varying balance (see text for further description). The category “u” indicates cells that were isolated but visually unresponsive. Results in a and b are for normal animals aged 6.5 and 13 weeks, respectively. Those in c are for a kitten normally reared to 4 weeks and then dark-reared with daily periods of binocular exposure. Data in d and e are from kittens reared for 16 days with daily periods of alternate monocular exposure. Histograms shown in f and g are from kittens reared similarly, but for 46 days of alternate occlusion. In all cases, the left eye was exposed first and electrodes were placed in the contralateral hemispheres, as indicated by the arrows. The data of d, e, f and g are combined to form the dotted histogram shown in h.