DEVELOPMENT OF ORIENTATION-SPECIFIC NEURONAL RESPONSES
IN FERRET PRIMARY VISUAL CORTEX

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Neurons in the primary visual cortex of higher mammals respond best to light-dark borders at particular orientations. These orientation-specific responses are present at birth in the monkey (Hubel et al., 1977), and can be recorded by the end of the first postnatal week in the cat (Hubel and Wiesel, 1963; for review see Fresean and Imbert, 1984). Since it is difficult to perform electrophysiological recordings in very young animals, we have chosen to study the development of oriented visual cortical responses in the ferret. The ferret visual system is quite similar to that of the cat (Law et al., 1988), but the ferret is born approximately three weeks earlier in development (Linden et al., 1981).

In order to study the normal development of orientation selectivity, we have looked at response properties of primary visual cortex neurons in ferrets of different ages. Radial microelectrode penetrations were made through cortical area 17 in anesthetized, paralyzed animals, and extracellular responses of neurons to moving light bars were recorded. Orientation tuning histograms were compiled, showing the responses of each neuron to 36 different stimulus orientations. Since orientation tuning is a circular function with a period of 180°, we quantified the degree of orientation selectivity of each neuron by fourier transforming the data from the tuning histograms, and taking the percentage of the total harmonic power which was found at the second harmonic as a measure of orientation selectivity (Worgotter and Rysel, 1987). The measure correlates very well with the degree of orientation selectivity subjectively determined by examining the orientation tuning histograms, with neurons having greater than 10% of total power at the second harmonic showing clearly oriented responses.

The earliest age at which visual cortical responses could be recorded was postnatal day 23, a developmental stage comparable to day of birth in the cat (Linden et al., 1981). At this age no clearly orientation-specific responses were
found in primary visual cortex, although a small number of cells may have shown slight orientation bias. This immature state, with few if any oriented cortical cells, persisted through the 5th postnatal week. During postnatal week 6 a larger percentage of cells showed orientation specificity, and by postnatal week 7 cortical responses had matured to an adult-like state, with approximately 50% of cells showing clear orientation preference.

To determine whether this development of oriented responses occurs through an activity-dependent mechanism, we silenced cortical neuronal activity during the time that orientation was maturing. The sodium channel blocker tetrodotoxin (TTX) was infused into area 17 through a 30 ga. cannula connected to an osmotic minipump (Alzet 2001). Infusion of $2.3 \times 10^{12}$ moles/hr TTX was found to silence all neuronal activity in an area extending approximately 5 to 10 mm from the cannula tip. TTX infusion was begun during the 4th postnatal week when oriented responses are not seen in cortex, and continued through post-natal week 7 by which time oriented responses similar to those seen in adult animals would normally be present. Four days after the infusion was terminated, neurons within the TTX-treated area were found to respond vigorously to visual stimulation, but these responses were not orientation selective. Neurons in the opposite (untreated) cortex showed a distribution of orientation selectivity identical to that in normal adults (Mann-Whitney U: $p=0.50$, data not shown). These results are shown in Figure 1.

![Graph showing distribution of orientation selectivity.](image)

**Fig. 1.** Histograms showing the distributions of orientation selectivity of neurons in primary visual cortex of TTX-treated ferrets. Data from neurons in the control (untreated) cortex are plotted to the left of zero, data from the TTX-treated cortices are plotted to the right. Higher values of orientation selectivity (calculated as described in the text) indicate more selective responses.
The distribution of orientation selectivities seen in the cortices of 7-8 week old animals treated with TTX starting during postnatal week 4 was statistically indistinguishable from the distribution seen in normal animals at 4 weeks of age (Mann-Whitney U; p=0.17; data not shown) suggesting that the activity blockade produced by the TTX treatment maintained the cortical neurons in an immature state. Thus the normal development of orientation specificity in ferret primary visual cortex neurons appears to depend on the presence of neuronal activity.

In normal adult ferrets, afferents projecting to a single orientation column have receptive fields covering an elongated region of space aligned with the preferred orientation of cortical cells in that column (Chapman et al., 1991). It is not clear whether this arrangement of afferents is a cause or a consequence of cortical cell orientation specificity, and the relative contributions of subcortical inputs versus intracortical connections to oriented cortical responses are not known. It will be of interest to study the development of this arrangement of afferent input to a cortical orientation column, and to determine whether the alignment of afferents seen in normal adults is also found in the animals which lack orientation selectivity because their normal cortical development has been disrupted by activity blockade.

REFERENCES


