

# Quantitative Study of Cortical Orientation Selectivity in Visually Inexperienced Kitten

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## SUMMARY AND CONCLUSIONS

1. Extracellular recordings were made from single units in the visual cortices of six kittens deprived of experience with pattern vision by binocular lid suture.

2. Selectivity for stimulus orientation was quantitatively assessed in 98 units; 90 responded selectively to the orientation of a moving bar stimulus, the remainder responding nonselectively or too poorly to classify. Cells in these visually inexperienced kittens were similar in their degree of selectivity for orientation to cells tested in adult cats. However, responses tended to be weaker and somewhat more erratic.

3. About half the cells in this sample responded to both directions of stimulus motion at the optimal orientation. Most of those responding to only one direction of motion were considered orientation rather than direction selective because they responded more strongly or more selectively to a moving bar than to a moving spot.

4. Cells appeared to be organized within the cortex in a pattern similar to that found in adult cats, with cells in one column selective for the same orientation, and adjacent columns having similar preferred orientations.

5. It is concluded that selectivity for stimulus orientation in the cat's visual cortex is innately determined.

## INTRODUCTION

After describing the highly selective response properties of cells in the visual cortex of the adult cat (9, 12) Hubel and Wiesel explored the development of these cell properties. Studying single units in very young visually inexperienced kittens, they concluded that the response properties of cells in the cat's visual cortex are, to a large extent, innately determined (10). This conclusion has recently been challenged by a number of experiments on visually inexperienced kittens, in which no cortical cell re-

sponses were found to be selective for stimulus orientation (3, 13; R. F. Spencer and P. D. Coleman, personal communication), or only a few selective cells were found (2, 4-6, 17).

In the experiments reported here we have reinvestigated, using quantitative techniques, response properties of cortical cells in kittens deprived of experience with pattern vision. The selectivity of cells for stimulus orientation was examined using a computer driven optical display. With this method, quantitative measures of orientation selectivity and response strength could be obtained and compared directly with data from adult cats. We found that most cells in the visually inexperienced kitten did respond selectively to the orientation of moving bar stimuli, with a degree of selectivity similar to that found in the normal adult cat. Furthermore, the cortical organization characteristic of adult cats, in which the cells in one vertical column respond selectively to the same stimulus orientation and neighboring columns have similar preferred orientations (9, 11, 12), also appeared to be present in these visually inexperienced kittens.

## METHODS

### *Animals and rearing*

Six kittens from three litters were used. Each kitten was deprived of patterned visual experience by binocular lid suture performed before the age of natural eye opening. The eyes remained closed until the kitten was between 22 and 29 days old, when the recording experiment was done. When we were ready to start recording unit responses, the eyelids were cut open and the eyes were refracted, using contact lenses, onto a tangent screen at 57 inches (145 cm) distance. Especially in younger kittens, poor optics made refraction difficult and uncertain, and 2.5-mm artificial pupils were sometimes used to improve focus. One unit was recorded in each of three additional kittens (24-31 days old) which were used primarily for another experiment (19). These were raised in a

dark, light-tight room where they were placed before the time of eye opening. Two normal adult cats were also studied using similar techniques for comparison with the kittens.

### *Recording and visual stimulation*

Surgery was carried out under either Fluothane anesthesia or Fluothane followed by intravenous pentobarbital, and heart rate was monitored during this period. One foreleg vein was cannulated to allow continuous infusion with a mixture of 5% dextrose in Ringer solution (0.75 ml/kg·h) and Flaxedil (10 mg/kg·h) for paralysis; a tracheal cannula was inserted, and a 4 mm x 8 mm craniotomy drilled. A short Plexiglas cylinder cemented to the skull served both as a recording chamber and as a means of rigidly attaching the skull to a stereotaxic frame; neither eye, ear, nor mouth bars were used. The kitten was then paralyzed and artificially respired with a mixture of 75% N<sub>2</sub>O and 25% O<sub>2</sub>, and the pump rate and volume were adjusted to maintain end-tidal CO<sub>2</sub> close to 4% (Beckman LBI medical gas analyzer). Rectal temperature was also monitored and kept at 37.5°C with a heating pad. Intramuscular doses of dexamethasone (0.2 mg) were administered at least twice during the experiment.

Single-unit responses were recorded using platinum-iridium electrodes with exposed tips 25–35 μm long and 2–3 μm in diameter. A dural flap was reflected over the midline, and the electrode was positioned by eye over the exposed visual cortex so that it would travel down the medial bank of the lateral gyrus or along the crown of the lateral gyrus inclined 40°–70° in the parasagittal plane. All recordings were made within the region of the visual cortex representing the central 10° of the visual field. To verify electrode locations, we perfused the four kittens from which most of our data were obtained with 10% formalin in saline, and examined 30-μm frozen sections stained with cresyl violet for the electrolytic lesions marking the end of each penetration. One penetration was found in area 18 and the rest were located in area 17 (12, 15).

We studied quantitatively all cells which responded reliably enough to determine receptive-field locations. To assess response properties, location of each unit's receptive field and its preferred stimulus orientation, length, width, and velocity were first determined by hand using light stimuli projected through an optic bench onto the tangent screen. Then a bar or edge stimulus controlled by a PDP-11 computer was swept across the receptive field in a random sequence of 24 different orientations, 15° apart. In one kitten (*K22*), and in the three

dark-reared kittens, some orientation-tuning histograms were compiled using only 12 stimulus orientations, 30° apart. Usually three, or occasionally six or nine, sequences were presented, each in a different random order. The computer calculated the mean and standard deviation of the responses to each orientation, and these data were displayed on a Tektronix type 611 oscilloscope in the form of an orientation-tuning histogram such as that presented in Fig. 3. These data were also stored on magnetic tape, and copies of all orientation-tuning histograms were later printed out.

### *Data analysis*

The responses of a typical orientation-selective unit give rise to two bell-shaped peaks in the orientation-tuning histogram (see Fig. 3). Both peaks are centered at the optimal orientation, and represent opposite directions of stimulus motion. Units responding to only one direction of stimulus motion produce orientation-tuning histograms with only one peak. The width of the higher peak in the orientation-tuning histogram can be used as an index of a unit's selectivity for orientation. A highly selective unit generates a narrow peak, indicating that the response falls off rapidly as stimulus orientation is varied from optimal.

The measurements of Campbell et al. (7) indicated that the response of cortical cells decreased linearly with changes in stimulus orientation on either side of the optimal orientation, and therefore that the peak of the orientation-tuning histogram could be well fitted by an inverted V. These authors have expressed cortical cells' selectivity for orientation as the half-width at half-height of this inverted V of best fit.

Our measurements on cells in the adult cat have shown that the peak of most cells' orientation-tuning histograms may be fitted equally well with a Gaussian curve as with an inverted V (unpublished observations). We have, therefore, computed for each of our cells the best Gaussian fit to the mean response at each point tested within 100° of the optimal orientation, using a least-squares error criterion weighted by the reciprocal standard error of the mean response at each point. We then used the "standard deviation" parameter of this Gaussian curve as a measure of selectivity for orientation. This measure corresponds closely to the half-width at 0.6 height of the peak in the tuning histogram, and thus gives a value for orientation-selectivity which is 0.8 times the value calculated by the method of Campbell et al. (7). The Gaussian fit was poor for some cells in our sample, as indicated by a large residual

variance left unaccounted for by the Gaussian curve. For these cells we measured the half-width at 0.6 height directly, using a linear interpolation between the mean response data points (similar to ref 21 but weighted by standard deviations). This second procedure had the disadvantage that variability in the response at the optimal orientation could produce large changes in our estimate of selectivity. These procedures only estimated orientation selectivity, rather than giving precise measurements. However, estimates of selectivity appeared equally good for data from kittens and from adults, so that our comparison is not affected by the imprecision of the measurements. Taking the factor of 0.8 into account, our distribution of orientation selectivity in adult cats (Fig. 6A) matches that of Campbell et al. (7) very closely.

The fact that responses were sampled at stimulus orientations 15° apart introduces a potential inaccuracy into this measurement of orientation selectivity. The optimal orientation of a highly selective unit might lie in between two of the orientations tested, so that the cell's optimal response would not appear in the orientation-tuning histogram. Therefore, this method is adequate to determine orientation selectivity only for those units whose half-widths at 0.6 height were 10° or more. For the 10 cells in our kitten sample which were tested with stimulus orientations 30° apart, this half-width is doubled.

## RESULTS

### *Visually inexperienced kittens*

**ORIENTATION SELECTIVITY.** In the six binocularly sutured kittens, quantitative data were obtained from 90 cortical cells which responded selectively to the orientation of a moving bar stimulus. In both areas 17 and 18, cells showing such selectivity were extremely common, accounting for over 90% of the responsive units.

An electrode penetration taken in area 17 of a 24-day-old kitten is reconstructed in Fig. 1, in which each cell encountered is represented by an orientation-tuning histogram. Here most of the units responded selectively to a preferred orientation of a bar stimulus, responding very poorly or not at all to the orthogonal orientation.

Responses from area 18 are illustrated in Fig. 2 in which, again, all the cells recorded in one electrode penetration are represented by orientation-tuning histograms. In this penetration, taken in a 22-day-old kitten, all but one unit responded selectively to stimulus orientation. In addition, cells were recorded with approximately uniform frequency along the electrode

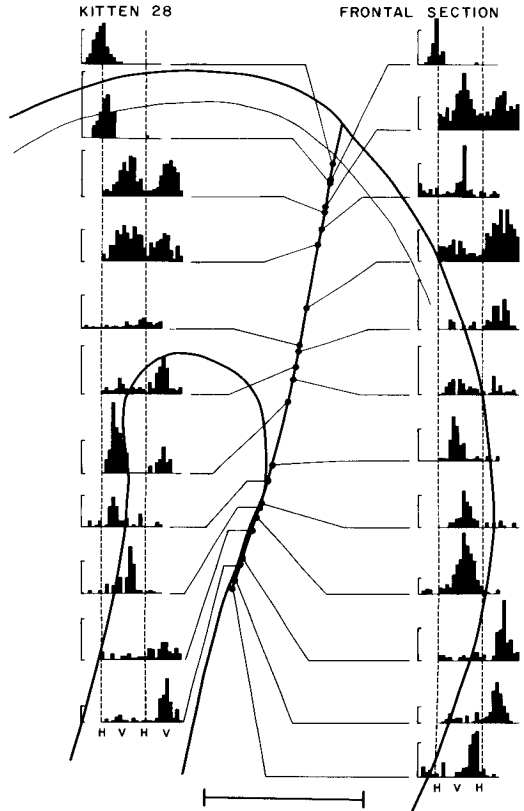


FIG. 1. Coronal section containing electrode track in area 17 of a 24-day-old kitten. Scale is 1 mm. Every cell isolated in this penetration is represented by one orientation-tuning histogram, and the location of each cell is marked by a dot on the reconstructed track. In each orientation-tuning histogram, the abscissa shows orientation of the stimulus bar, the left-hand H representing a downward moving horizontal bar and the right-hand H an upward moving bar; similarly, the left-hand V indicates a vertical stimulus moving from right to left. The ordinate shows mean response in spikes per stimulus sweep; calibration bars indicate a response level of five spikes for each histogram.

penetration, suggesting that the electrode did not traverse any large regions of unresponsive cortex (see also Fig. 4).

Seven cells selective for orientation were studied by hand, but lost before orientation-tuning histograms could be made. Quantitative data were obtained for another seven units which responded too erratically or too poorly to classify (e.g., the fifth orientation-tuning histogram in the left column of Fig. 1), and for one cell which responded well to visual stimuli, but showed no marked orientation selectivity (the second orientation-tuning histogram of Fig. 2). Finally, a few completely unresponsive cells,

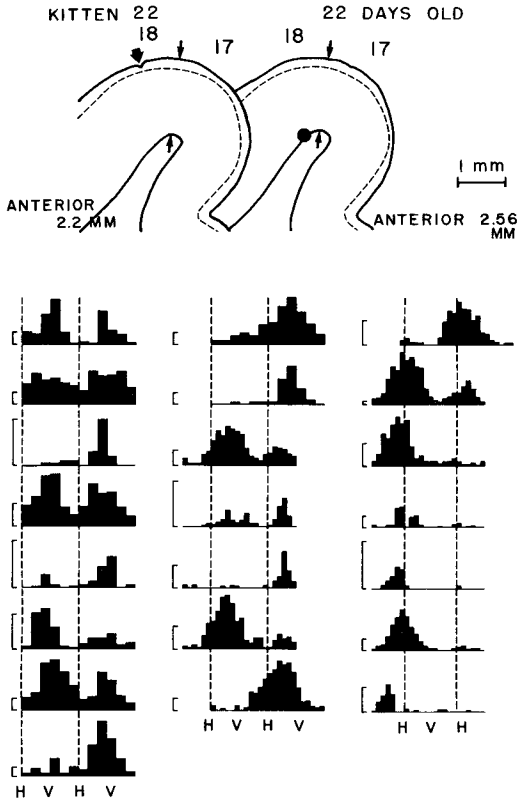


FIG. 2. *Above*: coronal sections, one at Horsley Clarke anterior 2.2 mm, indicating electrode entry point by heavy arrow and the other at Horsley-Clarke anterior 2.56 mm, containing electrolytic lesion (black dot) at end of penetration. Small arrows mark the border between areas 17 and 18. *Below*: every cell encountered in this penetration is represented by one orientation-tuning histogram, in the order in which they were recorded. Calibration bars indicate a response level of five spikes per sweep for each histogram. Other details in legend to Fig. 1.

located by their spontaneous activity, were encountered in some penetrations.

In kittens of comparable ages (2–5 wk), other studies have reported that some cortical cell response properties can be modified by brief periods of visual experience (13, 18, in paralyzed kittens; 3, 5, 13, 16, in alert kittens). It is conceivable, then, that the visual experience acquired by kittens during these experiments was sufficient to cause innately nonoriented cells to become selective for stimulus orientation.

Two observations suggest, however, that the selectivity for stimulus orientation which we observed in these kittens was not due to experience acquired during the recording session. First, such selectivity was both as common and

as pronounced at the beginning of each recording experiment as at the end. Second, in the three dark-reared kittens and in one lid-sutured kitten, it was possible to determine the orientation selectivity of one unit before the kitten was allowed any other visual experience. This was done by leaving the kitten's eyes closed until the first cell had been located by its spontaneous activity; the eyes were then opened, and an orientation-tuning histogram was immediately compiled for that cell. All of these cells did respond selectively to stimulus orientation, as illustrated in Fig. 3 for a cell which responded best to a moving horizontal bar. It thus seems unlikely that the specificity in the response properties of these cells resulted from experience acquired during the recording experiment.

**FUNCTIONAL ARCHITECTURE.** Not only were most cells selective for the orientation of a bar stimulus, but they were arranged in the cortex in an orderly fashion according to preferred orientation, as in the adult cat (11). Cells lying in a column normal to the cortical surface had approximately the same preferred orientation. Cell columns were also organized so that neighboring columns generally had similar pre-

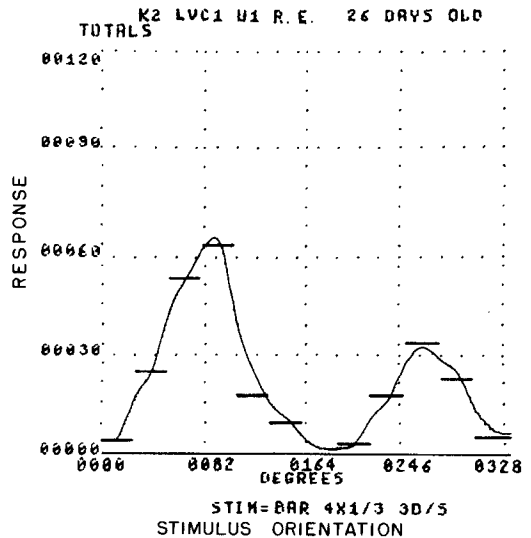


FIG. 3. Photograph of orientation-tuning histogram displayed on CRT screen for the first cell recorded in a 26-day-old dark-reared kitten. The kitten's eyes were opened for the first time immediately prior to compiling this histogram. Total number of spikes (ordinate) are plotted as a function of stimulus orientation (abscissa);  $0^\circ$  on the abscissa represents a vertical bar moving right to left;  $90^\circ$ , a horizontal bar moving down;  $180^\circ$ , a vertical bar moving from left to right, etc. Each of the 12 stimulus orientations appeared a total of 5 times during the stimulus sequence.

ferred orientations. This meant that an electrode penetration which crossed many columns encountered a sequence of cells showing a gradual and progressive change in preferred orientation. The three electrode penetrations in Fig. 4, taken from three different visually inexperienced kittens, show this sort of systematic and progressive change in preferred orientation through the cortex. We commonly found that adjacent cells had opposite preferred directions of stimulus motion but shared the same preferred orientation, indicating that columns are organized according to stimulus orientation rather than direction of motion.

A clustering of cells according to eye preference was also evident in the kittens, as in the adult cat (9). However, unlike results found in the adult, the ocular dominance distribution for our sample of kitten cells was flat and showed no peak at group 4 (which is composed of cells influenced equally from the two eyes). Although most kitten cells were binocular, a large number were dominated by one or the other eye. We do not know whether this finding indicates any significant loss of binocularity compared to the younger animals studied by Hubel and Wiesel (10) since our samples were small and, in most animals, were taken from only one relatively short penetration.

**ORIENTATION SELECTIVITY OR DIRECTION SELECTIVITY?** One possible method to dissociate orientation selectivity from direction selectivity is to test cell responses to stationary, flashed bars or edges. However, there are two

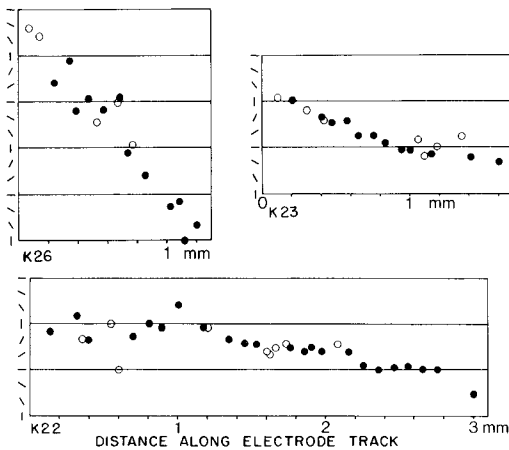


FIG. 4. Electrode penetrations from three different binocularly sutured kittens (K22, 22 days; K23, 24 days; K26, 23 days old). Abscissas show the location of each recording site along the electrode track, and ordinates show the preferred orientation at each site. Filled circles represent isolated single units, and open circles represent activity from multiple units.

difficulties in using this procedure. First, a small error in centering a flashing bar on the receptive field can make a cell not selective for stimulus orientation appear to be so; precise centering of the stimulus is less critical when it is swept across the entire receptive field. Second, many kitten cells which respond reliably to moving bars give a weak or erratic response, or no response, to flashes. Because of these difficulties we used only moving stimuli for quantitative assessments of orientation selectivity.

Of our sample of 90 selective units, 49 responded to two opposite directions of motion of a bar stimulus at one orientation, with little or no response at the orthogonal orientation. These units are clearly not direction selective; we considered them to be selective for stimulus orientation. Of those units which responded to only one direction of motion of a bar stimulus (41 of 90), 30 were also tested with spot stimuli (the remainder were lost before both the bar and spot histograms were completed). The bar and spot responses for all the unidirectional units in one typical penetration are illustrated in Fig. 5. The majority of the unidirectional units (22 of the 30 tested) responded either much more strongly or in a more selective fashion to the bar than to the spot stimulus, even when the spot stimulus was equal in luminance and area to the bar. We conclude that the response of these cells depended on the shape of the stimulus rather than merely on its direction of motion, indicating that these units are orientation selective.

#### *Comparison of kitten with adult cat*

Several response properties of cortical cells in these visually inexperienced kittens were compared quantitatively with those found in the adult cat. Orientation selectivity was determined by measuring the width of the peak in the orientation-tuning histogram for each unit (see METHODS). In Fig. 6A, distributions of orientation selectivity for cells from these kittens and cells from adult cats are compared. The leftmost bin in these histograms includes all units more narrowly tuned than  $8^\circ$ ; our measurements could not accurately distinguish among these. Thus we cannot rule out the possibility that a few cells from the adults are much more selective than any found in the kitten. However, adult cortical cells in this sample were, overall, only slightly more selective (median  $17^\circ$ ) for stimulus orientation than those in visually inexperienced kittens (median  $21^\circ$ ), and the ranges of orientation selectivity found in the kittens and in the adults overlap completely.

The most striking difference between cortical

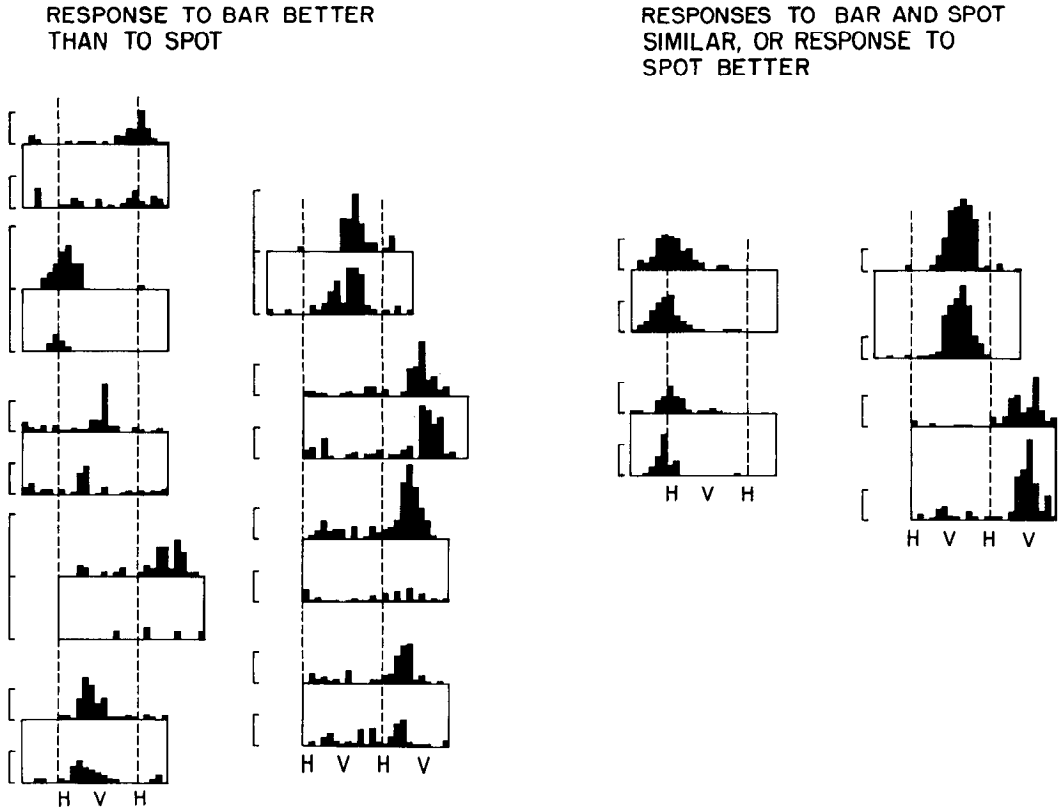


FIG. 5. Comparison of single-unit responses to moving bars and moving spots in a 24-day-old kitten. Each pair of orientation-tuning histograms was compiled from one cell, the top one using a bar stimulus and the bottom one using a spot of equal area. All units recorded in this kitten which responded to only one direction of stimulus motion, and which were held long enough to obtain both bar and spot histograms, are represented here. Calibration bars indicate a response level of 5 spikes/sweep for each histogram.

cell responses in visually inexperienced kittens and in adult cats is the relative weakness of responses in the kittens (10). As a measure of each cell's peak response strength in both kittens and adults, we used the mean number of spikes elicited by one sweep of an optimally oriented bar stimulus through the receptive field. Distributions of peak response strengths for this sample are compared in Fig. 6*B*. Most of the kitten cells responded to one stimulus sweep with fewer than 12 spikes (median = 6 spikes), while the median value for the adult cells was 13 spikes/sweep. The kitten cells, in the median, responded less than half as strongly as our comparable sample of adult cells. In addition, the kitten cells were more variable in their responses than the adult cells, with the median coefficient of variation (standard deviation divided by mean of the responses to three stimulus sweeps) for optimal orientation being 0.44 for the kittens and 0.34 for the adults.

We also found that the kitten's physiological

state was much more critical in obtaining responsive cells than is the case in the adult. Slight changes in oxygen consumption detected with the  $\text{CO}_2$  meter often were correlated with increasing numbers of sluggish, erratic, or unresponsive cells recorded along the electrode penetration. Under these conditions, we generally ended the experiment.

#### DISCUSSION

A large majority (90 of 98) of the cortical cells which we studied quantitatively in kittens deprived of visual experience responded selectively to the orientation of a bar stimulus. More than half (49 of 90) responded to two opposite directions of motion and gave little or no response to the orthogonal direction. Of the unidirectional cells (41 of 90), most which were tested with both a moving bar and a moving spot, responded preferentially to the bar (22 of 30); that is, they responded either much more strongly or more selectively to the bar than to

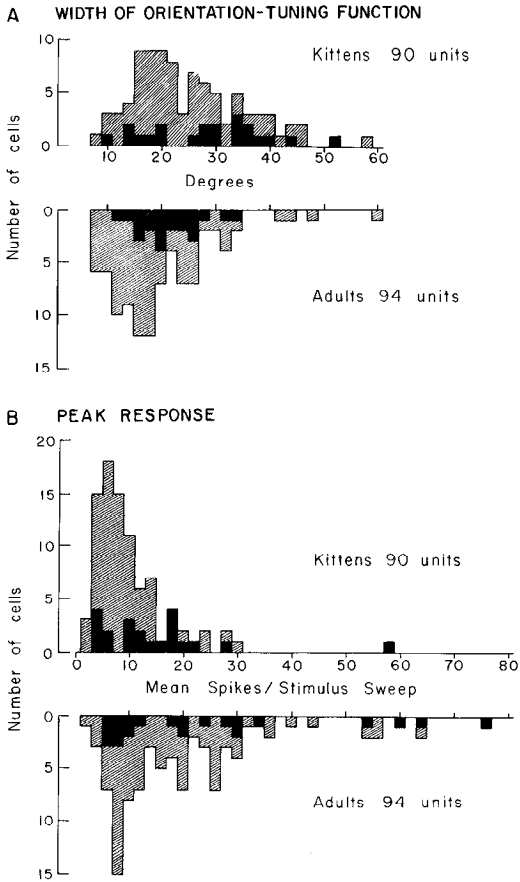


FIG. 6. Comparisons of response properties of cells in lid-sutured kittens with cells in adult cats. Hatched regions indicate cells in area 17; filled regions indicate cells in area 18. Height of each bin in histograms indicates the total number of cells (sum of those in areas 17 and 18). *A*: orientation selectivities of isolated units (see METHODS) are plotted on abscissa. Median value for kitten cell sample is  $21^\circ$ , and median for adult cat sample is  $17^\circ$ . *B*: peak response strength, measured as mean number of spikes elicited by one sweep of an optimally oriented stimulus, is indicated along abscissa. Median value for kitten cell sample is 6 spikes/sweep and median for adult sample is 13 spikes/sweep.

the spot. These data suggest that selectivity for stimulus orientation is innately determined in the cat, as Hubel and Wiesel (10) concluded from studying kittens younger than ours. Furthermore, the degree of selectivity of the cells recorded in the inexperienced kitten is quantitatively similar to that found in cells of the normal adult cat.

This conclusion could be criticized by arguing that the visual experience given each kitten during the recording session was sufficient to

cause cells to become orientation selective, while in the absence of any visual experience they would have shown no specificity. There are several reports of extremely rapid development of stimulus-selective response properties after brief periods of exposure in young, visually inexperienced kittens (3, 5, 13, 16, 18). However, in the animals studied in this experiment, we could find no evidence of this sort of change. Cells recorded early in the experiment were as selective for stimulus orientation as cells recorded later. Furthermore, at the start of each recording experiment, it was possible to determine the orientation selectivity of the first cell encountered before the kitten had had any other visual experience, and these cells also responded selectively to stimulus orientation. Finally, the orderly arrangement of cells across the cortex according to preferred orientation, which was evident when the electrode crossed many cortical columns, seems unlikely to have been produced by the visual stimulation the kitten received during the course of the recording session.

Results reported here are not in agreement with those of a number of recent studies from other laboratories. These studies found that most (2, 4, 5, 6, 17) or all (3, 13; R. F. Spencer and P. D. Coleman, personal communication) cortical cells in the visually inexperienced kitten were unselective for stimulus orientation. This discrepancy may be explained in part by differences in the ages of animals studied, since there is some evidence that prolonged deprivation causes degenerative changes in the cat's visual system (22). Differences in methods may also account to an unknown extent for this discrepancy.

The similarities between adult cortical cell properties and those found in visually inexperienced kittens seem remarkable when one considers the anatomical immaturity of the young kitten's visual system. The optics of the kitten's eye from birth at least through the 3rd wk appear, when assessed ophthalmoscopically, to be very poor because of a relatively opaque membrane, the tunica vasculosa, lying behind the lens (20); how seriously this degrades the image on the retina is unknown. The optic tract is also considerably different from that of the mature cat: at 2 wk of age, only 24% of the fibers are myelinated, although by 4 wk, myelination has progressed to include 80% of the fibers (14). Myelination in the visual cortex itself does not begin to appear until the 4th wk (8). The cortex contains a lower synaptic density in the kitten than in the adult, the number of synapses per cell being about 30% of that in the adult at 2

wk, and rising to 80% by 4 wk (8). Finally, some intracortical projections are reported not to appear until the middle of the 2nd wk or beginning of the 3rd wk (1). In many respects, then, the young kitten's visual system is radically different from that of the adult.

The rapid increase in optic tract myelination, the appearance of myelin within the cortex, the sharp rise in synaptic density, the development of various intracortical connections, and the clearing of the kitten's optics between 2 and 4 wk of age all suggest that cell response properties might be considerably more adult in the 4-wk-old kitten than in the kitten at 3 wk. However, we found no apparent differences between responses in a 22-day-old kitten and responses in older kittens up to 29 days.

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