Effects of early experience upon orientation sensitivity and binocularity of neurons in visual cortex of cats

(orientation preference/receptive field/velocity sensitivity/X and Y cells/ developmental neurobiology)

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ABSTRACT   The class of neurons within the visual cortex of normal adult cats that has the smallest receptive fields (≤ 2.25 degrees^2) and that responds only to low rates of stimulus motion ($\leq 50°$/sec) responds preferentially to lines oriented about either the horizontal axis ($\pm 22.5°$) or the vertical axis ($\pm 22.5°$). In animals reared without exposure to patterned visual stimulation, many of these cells display orientation preferences but are activated monocularly. In contrast, in normal animals, neurons that have larger receptive fields or that respond to higher rates of stimulus motion do not exhibit a similar bias in the distribution of their orientation preferences. Cells of this type, studied in animals reared without exposure to patterned visual stimuli, are activated binocularly but do not display orientation preferences.

Three classes of cells have been identified in the retina and in the dorsal lateral geniculate nucleus (LGNd) of the cat: X cells, Y cells, and W cells. During postnatal development these three neuron types are not affected equally by visual stimulation—the populations of X cells and W cells in the cat's visual system appear to be less dependent than the population of Y cells upon sensory stimulation for the maintenance or for the development of normal function (1–5). The manner in which these differences in experience sensitivity in the retina and LGNd affect cortical development, however, remains unclear (6).

To examine further the role that early visual experience plays in the development or maintenance of the response properties of cortical neurons, we have compared cells in the visual cortex of normal cats with those in cats reared from birth for prolonged periods without exposure to patterned visual stimuli. We now report that the class of cortical cells found in normal cats that has the smallest receptive fields and that responds only to relatively low rates of stimulus motion responds preferentially to horizontal and to vertical lines. These cells appear to be insensitive to early experience for the development or maintenance of orientation sensitivity but appear to be sensitive to such experience for the development or maintenance of binocularity. Many neurons of this type studied in cats raised without patterned visual stimulation display orientation preferences but are activated monocularly. The remaining neurons in normal animals—cells that have larger receptive fields or that respond to rapid stimulus motion—display no convincing bias in the distribution of their orientation preferences. These cells appear to be sensitive to early experience for the development or maintenance of orientation selectivity but appear to be insensitive to such experience for the development of binocularity. In cats deprived of exposure to patterned visual stimulation for extended periods neurons of this type exhibit no obvious orientation preferences but, as in normal animals, most of these cells can be activated by visual stimulation of either eye.

Abbreviation: LGNd, dorsal lateral geniculate nucleus.

METHODS

Eight normal adult cats and three cats deprived of exposure to patterned visual stimuli from birth to 10–12 months of age were studied. Two of the pattern-deprived cats were reared entirely in total darkness (dark-reared). The third cat was also housed in the dark from birth to 11 months of age except that in its second month of life it was removed from the dark daily and placed in an illuminated environment while it wore a mask such that each eye could view a blank white field (diffuse-reared). This animal received 6 hr of diffuse stimulation each day for a total of 73 hr.

Animals were prepared for electrophysiological recording in a conventional manner (6–9). Insl-X-coated tungsten microelectrodes were used to record the action potentials of cortical cells (10). The electrode was moved at an oblique angle through the cortex and was advanced at least 75 μm between units to reduce sampling bias by recording from many different columns of orientation-sensitive cells (11). Responses of units were amplified and single units were isolated in a conventional manner (8, 12). Significantly, while advancing the electrode, we presented a wide range of visual stimuli to include, in our sample, units with low spontaneous activity, small receptive fields, and distinct preferences for slow stimulus motion (8).

Once a unit was isolated, a number of its response characteristics were assessed with the aid of a hand-held projector—receptive field size, preferred orientation, the range of orientations eliciting a response, preferred direction, and ocular dominance. Subsequently, an optical display capable of presenting moving line-shaped stimuli at various speeds, directions, and orientations was used to determine the maximal stimulus velocity that elicited a reliable response from the unit (cutoff velocity).

For this study we defined a neuron's *receptive field* as the area in visual space within which a visual stimulus elicited a response. For most cells, the "minimum response field" was plotted by using light bars and both light and dark edges in a manner similar to that described by Barlow *et al.* (13). If a neuron's receptive field could not be determined adequately in this fashion (if the cell responded erratically or the limits obtained did not delineate a positive area) we moved light bars as well as light and dark edges of various sizes and shapes into and out of the cell's receptive field in an effort to determine a region within which responses could be evoked. If all attempts to define a positive receptive field failed, the unit was excluded from our analysis of field size. The receptive fields of most cells were plotted both before and after the determination of the unit's cutoff velocity. If the field size determined initially could not be reproduced reliably, the unit was not included in our analysis. By utilizing these procedures, receptive fields were determined for 93% of the units studied.
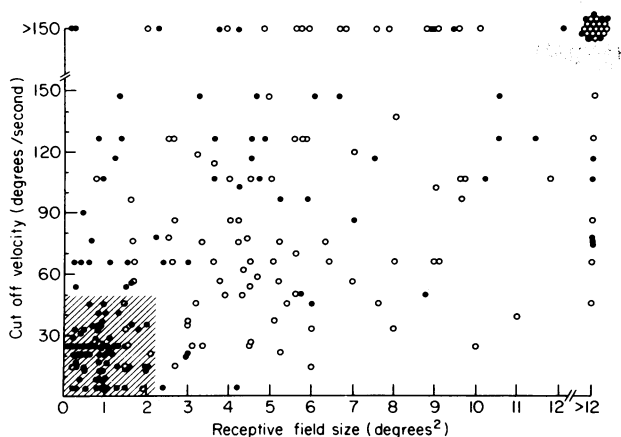
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FIG. 1. Receptive field sizes and cutoff velocities of cortical neurons preferring either horizontal (±22.5°) lines or vertical (±22.5°) lines (solid circles) and either 45° (±22.5°) lines or 135° (±22.5°) lines (open circles).

To estimate the preferred orientation as well as the range of orientations over which a cell would respond, an elongated stimulus was moved at a constant velocity through the neuron's receptive field. After each pass through the receptive field, the orientation of the stimulus was changed systematically until moving it through the response field produced no detectable response. This stimulus orientation was defined as one of the cell's orientation limits. The second orientation limit was then determined by changing the orientation of the mapping stimulus systematically in the opposite direction until a stimulus orientation was again reached for which responses could not be detected. The *preferred orientation*, the stimulus orientation to which the cell gave its strongest response, generally lay midway between the two orientation limits [it has been suggested that this procedure decreases the effects of experimenter bias on the determination of the preferred orientation of cortical neurons (14)]. The angle between the two orientation limits defines the cell's *width of tuning*.

The maximal stimulus velocity to which a cell would respond (*cutoff velocity*) was determined as follows. Long, light bars moving in the preferred direction and oriented appropriately were presented to the dominant eye and moved through the cell's receptive field at a velocity that was controlled by the experimenter. The velocity of the stimulus was first increased gradually (from 1°/sec to a maximum of 150°/sec) until responses could no longer be detected. After a pause to allow the unit to recover, the stimulus velocity was decreased gradually from 150°/sec until the cell resumed responding. If different values were obtained for these tests, the greater of the two velocities was considered to be the cutoff velocity for the unit. To verify this measurement, stimuli moving either at the cutoff velocity or slightly above or below it were moved across the cell's receptive field with suitable pauses between trials to permit recovery of the unit. The entire procedure was repeated if a discrepancy was observed at this point. For units with low spontaneous activity the output of an audio monitor was used to determine the velocity at which the cell ceased to respond. If a cell's spontaneous activity was sufficiently high to make this determination difficult, the unit's evoked and spontaneous discharge rates were determined and compared by using a digital counter.

RESULTS

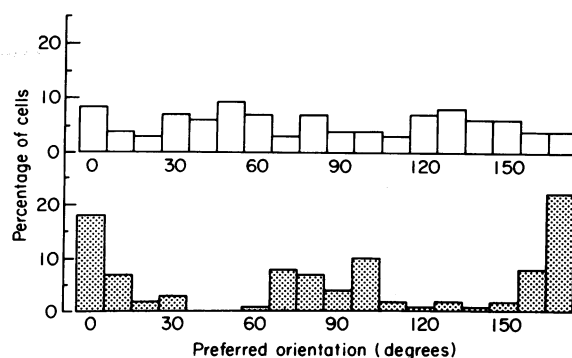**Normal Cats.** We sampled neurons along 14 oblique electrode penetrations through the visual cortex of eight normal

FIG. 2. Distribution of the orientation preferences of cortical neurons having both receptive fields ≤2.25 degrees² and cutoff velocities ≤50°/sec (shaded bars) and distribution of the orientation preferences of cells with receptive fields >2.25 degrees² and/or cutoff velocities >50°/sec (open bars).

cats. For most of these animals, histological examination of the cortex could be carried out and all electrode tracts that were reconstructed were within area 17. We determined the receptive field characteristics of 282 single units in normal adult cats. As reported by others, most cortical neurons examined were responsive to visual stimulation (97%), selective for orientation (92%), and could be influenced by stimuli presented to either eye (83%) (7, 8). Also in agreement with earlier reports, the preferred orientations of cortical units recorded during most penetrations were observed to vary gradually and systematically as the electrode was advanced obliquely through the visual cortex (11, 15).

We also observed a relationship among the receptive field size, the cutoff velocity, and the orientation preference of cortical cells (Fig. 1). Specifically, a majority of neurons that had both a small receptive field (≤2.25 degrees²) (1 degree² ≅ 0.3 mstereradian) and a low cutoff velocity (≤50°/sec) responded best to either horizontal (±22.5°) or vertical (±22.5°) stimuli (χ^2; $P < 0.001$) (Fig. 2). In contrast, among those cells in our sample that had larger receptive fields (>2.25 degrees²) or responded to stimuli moving rapidly (>50°/sec), a more even distribution of orientation preferences was evident (Fig. 2).

The high spontaneous activity and the broad orientation tuning of some cortical cells made the determination of their response characteristics difficult. In particular, neurons with large receptive fields or high cutoff velocities tended to respond to a wider range of stimulus orientations than did cells with small fields and low cutoff velocities (SEM, $P < 0.001$). To see if this significantly affected the results reported here, we examined separately units in both classes which displayed no spontaneous activity and which had a tuning width of ≤50°. These neurons would be expected to have half-widths of 12.5° or less (16–18). Preferred orientation, receptive field size, and cutoff velocity could be determined readily and quite unambiguously for this subset of units in our sample. This analysis confirmed that most cells with small receptive fields and low cutoff velocities preferred lines oriented either horizontally or vertically (χ^2; $P < 0.001$) and that there was no bias in the distribution of orientation preferences of cells having large receptive fields or high cutoff velocities. We conclude from this that errors in the determination of preferred orientation, receptive field size, or cutoff velocity are unlikely to significantly affect the relationships that we have observed among these three parameters.

Cells with small receptive fields and low cutoff velocities were found to be concentrated in cortical areas subserving central vision (Fig. 3). Most neurons displaying these properties
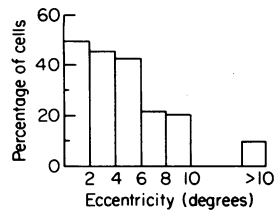
FIG. 3. Visual field distribution of neurons having cutoff velocities $\leq 50°$/sec and receptive fields ≤ 2.25 degrees^2.
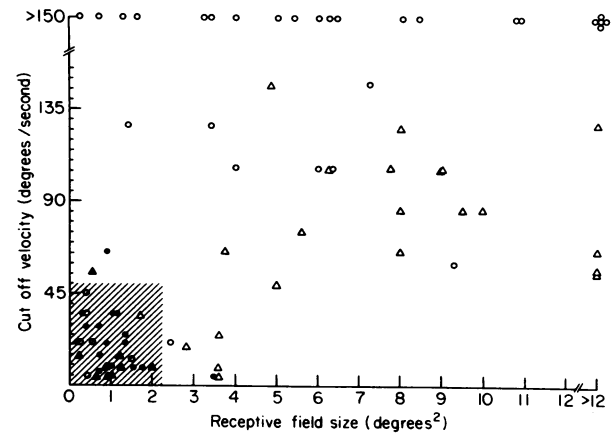

FIG. 4. Receptive field sizes and cutoff velocities of orientation selective neurons (solid circles and triangles) and of visually responsive cells displaying no obvious orientation preferences (open circles and triangles) in long-term pattern-deprived cats. Circles and triangles represent cells recorded from two dark-reared cats and a diffuse-reared cat, respectively.

responded best to horizontal or to vertical lines regardless of their position in the cortex. On the other hand, cells with larger receptive fields or higher cutoff velocities were encountered more frequently in cortical areas subserving the peripheral visual field, though many cells of this type were encountered at all eccentricities. Finally, as reported by others (7, 8), when all neurons we studied were considered together, no convincing bias in the distribution of preferred orientations was evident at any eccentricity.*

Pattern-Deprived Cats. We also studied a sample of 184 cortical units along 10 electrode penetrations through the visual cortex of a group of cats deprived of exposure to patterned stimuli (19). As in our sample of normal adult cats, all of the reconstructed electrode tracts in these animals were within area 17.

Consistent with earlier reports, we observed that many cortical cells sampled from pattern-deprived cats did not display the specificity of response typical of neurons studied in normal animals (20). In particular, over half of the neurons recorded from these animals either failed to respond to any of the visual stimuli presented or responded indiscriminately to various stimuli: they displayed no obvious preferences for the shape, orientation, or direction of movement of any stimulus presented. The remaining cells were either direction-selective (30%) or orientation-selective (15%) (21, 22). Most significantly, nearly all orientation-sensitive cortical cells in these animals had small receptive fields (≤ 2.25 degrees^2), responded only to stimuli moving slowly (cutoff velocities $\leq 50°$/sec), and responded best to either horizontal or to vertical lines (χ^2; $P <$ 0.001) (Fig. 4). Orientation-sensitive neurons were found at all eccentricities studied ($0°-17°$ from the estimated projection of the *area centralis*). Furthermore, in contrast to normal adult cats in which only 12% of the cells with small receptive fields and low cutoff velocities were activated monocularly, most cells of this type (70%), regardless of eccentricity, responded to stimulation of only one eye in deprived animals (Fig. 5).

Neurons that had larger receptive fields or that responded to more rapidly moving stimuli were affected differently by deprivation of patterned visual stimulation. In particular, most cells of this type studied in pattern-deprived cats displayed no evidence of normal orientation selectivity (93%) and a majority (73%) were activated binocularly. This proportion is similar to that observed in normal adult cats in which 80% of these cells respond to stimulation of either eye (Fig. 5). Finally, the proportion of cells of this type encountered at all eccentricities studied was lower in pattern-deprived cats than in normal cats.

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* Preliminary evidence indicates that the cells with small receptive fields and low cutoff velocities that we have described are concentrated in or above layer IV of the striate cortex. Cells with larger fields or higher cutoff velocities, however, were also encountered within these laminae. This organization appears compatible with the gradual shifts in the orientation preferences of cortical cells we observed during the course of most of our oblique electrode penetrations.

DISCUSSION

We have observed that the class of cells in the normal cat's visual cortex that has the smallest receptive fields and that responds only to stimuli moving slowly, responds preferentially to lines oriented about either the horizontal axis ($\pm 22.5°$) or the vertical axis ($\pm 22.5°$). Many of these cells are activated monocularly and display orientation preferences after extended periods of visual deprivation. The remaining cells—neurons in normal animals that have larger receptive fields or respond to more rapid stimulus motion—do not exhibit a similar bias in the distribution of their orientation preferences. Cells of this type
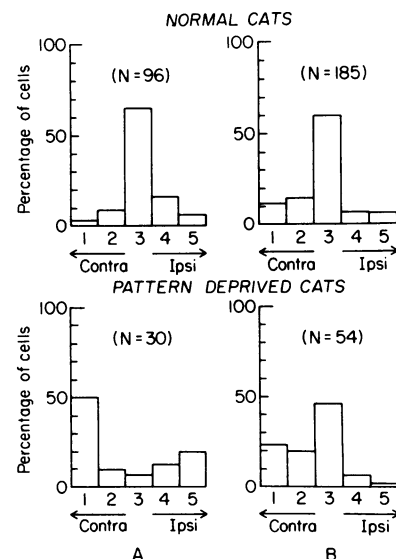

FIG. 5. Ocular dominance distributions of cells having receptive fields ≤ 2.25 degrees^2 and cutoff velocities $\leq 50°$/sec (*Column A*) and of cells with larger receptive fields and/or higher cutoff velocities (*column B*) in normal cats (*Top*) and in pattern-deprived cats (*Bottom*). Ocular dominance groups are defined as follows: group 1, cells activated only by the contralateral eye; group 2, cells activated by both eyes with the contralateral eye being strongly favored; group 3, cells activated by both eyes with the responses evoked by the two eyes being comparable; group 4, cells activated by both eyes with the ipsilateral eye being strongly favored; group 5, cells activated only by the ipsilateral eye.

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do not display orientation preferences and are activated binocularly in cats reared for a prolonged period without exposure to patterned visual stimulation.

Results consistent with our findings have been reported by Pettigrew *et al.* (*8*). These experimenters observed that a preponderance of simple unimodal direction-selective cells located near the cortical projection of the *area centralis* respond preferentially to either horizontal or vertical lines. Because these cells were reported to have the smallest receptive fields of all neurons studied and were observed to prefer stimuli moving slowly, they may be similar to our sample of cells with small receptive fields and low cutoff velocities. In addition, Blakemore and Van Sluyters (*22*) observed a predominance of neurons responding best to either horizontal or vertical lines in the visual cortex of one cat exposed only to a blank white cylinder during rearing (*24*). Finally, Blakemore and Van Sluyters (*22*) and Buisseret and Imbert (*24*) have reported that most orientation-sensitive cells in the cortex of visually deprived kittens are activated monocularly.

A number of explanations could account for the absence of orientation-selective cells having large receptive fields and/or high cutoff velocities in animals deprived of patterned visual stimulation. We think that the most likely of these are: (*i*) Most cortical cells may be orientation-sensitive in visually inexperienced kittens; prolonged pattern deprivation causes cells with large receptive fields or high cutoff velocities to lose their innate orientation preferences while many cells with small fields and low cutoff velocities retain their intrinsic preferred orientations after such deprivation. (*ii*) Only cortical neurons with large receptive fields and high cutoff velocities require early visual experience for the development of normal orientation sensitivity; prolonged pattern-deprivation eliminates early experience and thus prevents these neurons from becoming selective for orientation. To differentiate between these two possibilities, it is necessary to know the extent to which these different cell types are orientation selective in the inexperienced kitten cortex. Unfortunately, many conflicting reports exist in this area (*21–25*). Furthermore, changes in the cortical physiology of young kittens have been reported to occur during acute recording sessions (*26, 27*), making the interpretation of the distribution of the orientation preferences of cortical cells observed in young animals even more difficult.

Cortical neurons with small receptive fields that are selective for slow stimulus motion reportedly receive afferent inputs from X cells in the LGNd whereas cells with larger receptive fields that are responsive to stimuli moving rapidly are reported to receive inputs from LGNd Y cells (*28*). Our results, therefore, suggest that certain X cells axons terminate on a class of cortical cells that is insensitive to early experience for the development of orientation sensitivity and that responds best to horizontal and vertical stimuli. The axons of Y cells, on the other hand, may terminate on neurons that require early patterned visual experience for development or maintenance of orientation selectivity and that do not exhibit a biased distribution of orientation preferences. (A contribution of afferent inputs from LGNd W cells to the groups of cells we have described cannot be ruled out because the response properties of cortical cells with W-cell afferents have not been determined.) Consistent with this, we have found that the relative number of cortical neurons with small receptive fields and low cutoff velocities is high near the cortical projection of the *area centralis* and is low in more eccentric regions while the relative frequency of cells having larger receptive fields or higher cutoff velocities is relatively low near the projection of the *area centralis* and increases in portions of cortex subserving peripheral regions of

the retina. These findings are consistent with the reported inhomogeneities in the distributions of X cells and Y cells in both the retina and the LGNd (*1*). In addition, our finding that the relative proportion of cells with large response fields and high cutoff velocities is reduced by early binocular deprivation is compatible with the suggestion that Y cells in the LGNd are affected most severely by this procedure (*1–5*). Furthermore, since cells with small receptive fields and low cutoff velocity are activated monocularly in pattern-deprived cats, and possibly also in visually deprived kittens (*22, 24*), their sensitivity to binocular competition still remains to be demonstrated. Our results do, however, lend support to the hypothesis that Y cells in the LGNd are affected severely by binocular competition (*1, 3*).

It has been suggested that simple cortical cells receive inputs from LGNd X cells while complex cortical cells receive LGNd Y cell afferents (*29*). This suggestion has, however, been challenged (*30*). The present study was not designed to approach this question directly. However, since many cortical neurons remain uncategorized according to the classification system proposed by Hubel and Wiesel and since simple cells, complex cells, and uncategorized cells can display receptive fields larger than 2.25 degrees^2 (*7, 31*) it is unlikely that one of the two groups we have described consists only of simple cells while the other consists only of complex cells. In fact, our own observations suggest that the class of cells with small fields and low cutoff velocities we have described consists mainly of certain simple and hypercomplex cells with these response properties while the other group of cells we have characterized contains both simple and complex cells with larger fields or higher cutoff velocities.

A number of reports suggest that the relationships reported here for the cat can be generalized to other species. In particular, Mansfield (*32*) observed a preponderance of cells preferring either horizontal or vertical lines only near the cortical projection of the fovea in the monkey; a similar anisotropy was not evident in more eccentric regions. Apparently, these cells receive inputs from neurons analogous to X cells found in the cat's visual system because the great majority of ganglion cells near the primate fovea are of the tonic type but fewer cells of this type are observed in the peripheral retina (*33–35*). Furthermore, virtually all orientation-sensitive rabbit retinal ganglion cells prefer lines oriented either horizontally or vertically, have small receptive fields, prefer slow stimulus motion, and are concentrated near the visual streak (*36, 37*). Finally, most orientation-sensitive ganglion cells in the pigeon's central retina prefer lines oriented horizontally and have small receptive fields (*38*). The presence of cells of this type in the retina in some species and in the visual cortex in others may reflect an evolutionary centralization in the processing of certain visual information.

We suggest a functional significance for the class of cortical cells with small receptive fields and low cutoff velocities that we have characterized. Specifically, these neurons may mediate the preferential response characteristic of the visual systems of many species, including man, to horizontal and vertical contours. The observations that the anisotropic response of the human visual system is greatest at the fovea, decreases with increasing eccentricity, appears to be mediated by cells with small receptive fields, and is not observed when subjects are tested with rapidly flickering stimuli that should not activate neurons with a low cutoff velocity (temporal sensitivity) are all compatible with this suggestion (*32, 39, 40*).

It has been suggested that the localized biased distribution of cortical cell orientation preferences observed in the primate

visual cortex (32) results from an early visual environment dominated by horizontal and vertical contours (32, 41). Recently, however, we and others have challenged this view (6, 42). On the basis of our present results, we now suggest that the visual system's preferential response to horizontal and vertical patterns is determined intrinsically and reflects the response properties and distribution of certain cortical neurons, possibly a subset of those cells that receive afferent inputs from X cells in the LGNd.

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