40° nasal or from 20° to 80° temporal; this region corresponds to the ring scotoma. At 80° temporal for both patients, the sensitivity values were 2.5 log units below the normal mean. The data in the middle panel present a similar picture; sensitivities at fixation were reduced by 1 log unit. Again, there was a precipitous drop of sensitivity at 10°; with a ring scotoma from 10° to the far periphery.

The upper panel illustrates the log threshold ratios of the two stimuli along the horizontal meridian. As described previously, if rods are responsible for the detection of both lights, the threshold ratio will have a value of approximately 2 log units; if cones are responsible for the detection of both lights, the log ratio will have a value close to zero. These differing ratios are determined by the differing shapes of the rod and cone spectral sensitivity functions. In the upper panel of Fig. 1, the log ratios in the central 10° were close to the cone-determined value, and in the far periphery the log ratios were close to the rod-determined value.

Discussion. As demonstrated in the upper panel of Fig. 1, the log ratios for the central 10° are near 0; consequently, we may conclude that only cones detected both lights and that rods are making no contribution to detection. In the far periphery the log ratios are near 2; these data indicate that the rods detected both lights and therefore the rod sensitivity, relative to the cone sensitivity, must be nearly normal. (Because there is a 2.5 log unit sensitivity depression in this retinal region for the blue-green light (lower panel, Fig. 1), we can conclude that the far peripheral rods and cones are not normal but that both probably are reduced in sensitivity by the same factor, thus preserving the normal sensitivity relation.)

The above data indicate that (1) because of the threshold ratios, there probably are no functioning rods within the central 10°; (2) because the foveal cones are reduced in sensitivity by 1 log unit (middle panel, Fig. 1) and both patients have a strong blue-yellow color vision defect, the foveal cones are abnormal; (3) because of the mid-peripheral ring scotoma, there probably are no functioning mid-peripheral rods or cones; and (4) because absolute sensitivities are reduced in the far periphery, because rod-determined threshold ratios are obtained, and because the photopically measured far peripheral field is intact, there must be functioning, albeit abnormal, rods and cones both. These conclusions are in point-by-point agreement with the conclusions of the electron microscopic study by Szamier et al. It is not possible to draw conclusions from our psychophysical studies regarding outer segment length or integrity or other specific morphologic features.

The agreement between psychophysical data and electron microscopic data for X-linked RP additionally supports conclusions regarding other types of RP reported earlier. We previously described two other subcategories of RP based on this psychophysical methodology, which may be characterized broadly as a diffuse rod sensitivity loss for one group and localized rod-cone sensitivity losses for a second group. In this study, the mutual corroboration of psychophysical and histopathologic data for X-linked RP heightens our confidence in the predictive value of similar psychophysical tests for other forms of RP.

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Key words: retinitis pigmentosa, dark adaptation, inherited retinal dystrophies, absolute thresholds

REFERENCES


Spatial periodicities of periodic complex cells in the visual cortex cluster at one-half octave intervals. DANIEL A. POLLEN AND STEVEN E. FELDON.

Within individual penetrations in the visual cortex, spatial periodicities of periodic complex cells differ by either one-half or one octave. When data are pooled from neurons subserving the central visual area in many cats, the results indicate that spatial periodicities cluster at one-half octave intervals over a 2½-octave range (0.95 to 5.4...
Periodic complex cells in the striate cortex are the first neurons along the geniculocalcarine pathway which scan sufficiently large sections of the visual field to be involved in spatial pattern recognition over appreciable subsections of visual space. These cells usually respond with a series of five to seven evenly-spaced (i.e., periodic) excitatory responses superimposed upon an increased baseline level of activity when an optimally oriented narrow slit is moved across the receptive field in the preferred direction. The periodicity is spatial because the number of peaks across corresponding spacings within the receptive field remains fixed when the velocity of the moving slit is tested over a one- to two-octave range. Similar cells have also been reported by others. Spatial frequency-selectivity studies of periodic complex cells have recently been reported. Responses of these cells to moving sinewave gratings consist of components modulated by the moving grating superimposed upon unmodulated levels of activity. Spatial frequency-selectivity studies based upon evaluation of mean firing levels show a cyc/deg. Thus a relatively small number of such channels spaced at regular intervals along a logarithmic scale within each orientation column may suffice for this stage of spatial processing.

Fig. 1. A, Average-response histogram generated by a complex cell as a narrow slit of light (width 0.1°) at the preferred orientation moves across the receptive field in the preferred direction. B, Fourier transform of average response histogram in A shows a peak at 2.7 cyc/deg, indicating spatial periodicity of periodic excitability pattern. Amplitude of the periodic component has been normalized at unity. C, Histogram shows distribution of spatial periodicities for 56 periodic complex cells in area 17 and 12 such cells in area 19 (shaded areas) arranged in 1/4-octave wide bins. D, Dots connected by solid lines indicate values of spatial periodicity found within the same cortical penetration. Dots connected by broken lines indicate values of spatial periodicity found within adjacent penetration. Examples of penetrations from eight different experiments in area 17 and one study in area 19 (lowermost set of points) are shown. When successive cells were found in area 17, usually in close proximity to each other, the first cell encountered had the lower periodicity. The reverse was seen for the penetration in area 19.
Fig. 2. Smoothed histogram was constructed by representing each of the 68 data points as a triangle function centered at its spatial periodicity value with a full bandwidth at half amplitude of 1/6 octave. The triangle functions were then summed to produce this histogram, which shows essentially the same spacings seen in Fig. 1, C.

broadly tuned curve peak about one octave below the value of the periodicity determined in single-slit studies. This result is consistent with a contrast-sensitivity study of such cells by Ginsburg et al.,\textsuperscript{2} in which their published illustration shows the contrast sensitivity peaking just over one octave below the spatial periodicity found in their single-slit study.

However, estimates of spatial-frequency selectivity based upon evaluation of only modulated levels of activity indicate two preferred spatial frequency bands. A broadly tuned band with a full bandwidth of over one octave peaks at about one octave below the narrow-band spatial frequency. A narrowly tuned band with a full bandwidth at half amplitude of about 0.5 octave peaks at the same spatial frequency as the spatial periodicity determined in single-slit studies. Similarly narrowly tuned channels have been found in the human visual system at spatial frequencies of 20 cyc/deg or higher.\textsuperscript{6} Cavanagh\textsuperscript{7} recently proposed that the adaptation results of Blakemore and Campbell\textsuperscript{8} could be explained on the basis of neurons with the spatial frequency characteristics of the modulated responses of periodic complex cells.\textsuperscript{9}

In previous work there was a preliminary suggestion that spatial periodicities may cluster at one-half octave intervals.\textsuperscript{9} Therefore we would now like to test further this suggested relationship and to determine whether there is any relationship between spatial periodicities of complex cells within a cortical orientation column.\textsuperscript{9} In addition, we have compiled a histogram showing the distribution of spatial periodicities from the present study and from recent studies in area 17\textsuperscript{7} and area 19\textsuperscript{9} carried out for other purposes.

Methods. The experiments were performed in 10 cats initially anesthetized with halothane for surgery and maintained under 70\% N\textsubscript{2}O-30\% O\textsubscript{2} for light anesthesia and analgesia during recording. The full experimental details for anesthesia, surgery, eye fixation, cell classification, and other techniques may be found elsewhere.\textsuperscript{1} Either tungsten in glass\textsuperscript{10} or Parylene insulated microelectrodes with tip exposures of 9 to 18 μm were used.

In essence, the experiment consisted in isolating a periodic complex cell, mapping its receptive field very carefully, determining the preferred orientation and directional selectivity to within 5°, and then moving a narrow slit of light at constant velocity across the receptive field. The single cell responses were summed over at least 20 sweeps to generate an average response histogram of 100 bins. Bin widths were generally chosen so that at least 10 to 15 bins were used to analyze each cycle of periodic activity. The spatial periodicity of the average response histogram was then determined by discrete Fourier analysis. The accuracy of this measurement depended upon the estimate of the receptive field width which could be measured to within 6%, i.e., within less than one-eighth octave.
Fig. 3. A and B, Nissl and Loyez stains, respectively, mark the recording site (arrows) of a periodic complex cell in the lower part of layer II with a spatial periodicity of 1.97 cyc/deg. Lesion was made by passing 3 μA current (electrode tip negative) for 4 sec. The deeper lesion was made to mark the end of the penetration. C and D, Nissl and Loyez stains, respectively, mark the recording site (arrows) of a periodic complex cell in layer III with a spatial periodicity of 1.37 cyc/deg in another experiment. Lesion was made by passing 3 μA for 4 sec.

All penetrations were made in cortical areas subserving the central 5° of the visual field. In general, only one or two periodic complex cells were found in a single penetration, but on occasion three or four were found. The number found in a single penetration probably underestimates the number actually present, since it is often difficult to satisfactorily isolate the action potentials of complex cells from each other, particularly in the superficial layers where they are most often found.

Results. An example of an average response histogram indicative of the receptive field profile for a periodic complex cell is shown in Fig. 1, A. The spatial periodicity of the periodic component was determined by Fourier analysis of the field profile (Fig. 1, B). A histogram has been assembled to show the spatial periodicities of 56 periodic complex cells in area 17 and 12 periodic complex cells in area 19 (Fig. 1, C). The histogram shows clusters of periodicity values that seem separated from each other by approximately one-half octave intervals. The sample of cells from area 19 is limited; even so, periodicities cluster in the same range as in area 17.

A separate test was carried out to determine whether the clustering was independent of the intervals we selected for compiling the histogram. Each of the 68 data points was represented as a triangle function centered at its spatial periodicity value with a full bandwidth at half amplitude of one-eighth octave. The 68 functions were then
summed, producing a smoothed histogram (Fig. 2) which showed essentially the same spacings seen in Fig. 1, C. A frequency analysis of the smoothed histogram showed that most of the power in its Fourier spectrum could be attributed to a distribution based on one-half octave spacings. There is very little likelihood that the observed clustering occurred by chance, given the number of cells \((n = 68)\) in the population.

Within individual penetrations in area 17 in which preferred orientation remained unchanged, spatial periodicities differed by values close to either one-half or one octave (Fig. 1, D). Cells were considered to belong to the same orientation column when their orientation and directional preferences within a given penetration remained within 5° of each other.

These results from both our pooled data and individual penetrations in the same animal show a tendency for spatial periodicities to occur at integral multiples of one-half octave steps. Thus spatial periodicities are represented at evenly spaced intervals along a logarithmic scale. The favored values of periodicity are close to 0.95, 1.35, 1.91, 2.70, 3.92, and 5.4 cyc/deg. The intervals between clusters are four times larger than the maximal possible error for any given measurement. The higher values, 2.7 to 5.4 cyc/deg are more likely to be found at posterior frontal planes —3 to —5 mm, the lower values being more frequently found at —2 to —3 mm levels.

Histologic verification of recording sites for periodic complex cells in the present work has indicated that they are most often found in the superficial cortical layers. When the superficial layers were penetrated very carefully, we have frequently found such cells within the lower part of layer II (Fig. 3, A and B) or among the middle-sized pyramidal cells of layer III (Fig. 3, C and D). On occasion we have also found periodic complex cells in layer V.

**Discussion.** The present findings demonstrate a clustering of spatial periodicities of periodic complex cells at even intervals along a logarithmic scale within cortical orientation columns. It is not yet known how these cells are built up from antecedent visual neurons. A model of the periodic complex cell based upon inputs from overlapping On- and Off-center cells with preferred spatial frequencies one octave below the periodicity found in response to a single moving slit will be considered elsewhere. Such a model suggests that the basic subunits comprising periodic complex cells have preferred spatial frequencies one octave below the range of spatial periodicities reported here, but the one-half octave scaling would not be altered.

The quantal-like clustering of spatial periodicities at regular intervals along a logarithmic scale may reflect a principle of significance to both the structure of the visual system and the function of these cells in spatial information processing. These data also suggest that a relatively small number of such channels within each orientation column may suffice for this stage of spatial processing.

We are very grateful to Professor Richard Kronauer, who first urged us to examine our records to see whether such clustering was present. We thank Dr. Bryan Andrews for his helpful suggestions and criticisms and Peter A. Bridgman for excellent technical assistance.

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**Key words:** visual cortex, cat, periodic complex cells, spatial periodicities

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The activities of ouabain-sensitive (Na-K-) and ouabain-insensitive ATPases were determined in 3.6 mM calcium-containing and calcium-free media. Three lens tissue segments were studied: the epithelium/capsule segment, the anterior cortical segment and the posterior cortical segment. In the presence of calcium, the Na-K-insensitive ATPases were determined in 3.6 mM calcium. The activities of ouabain-sensitive (Na-K-) and ouabain-insensitive ATPase activity in each segment were measured, in both 3.6 mM calcium and calcium-free EGTA media.

In a recent study, Delamere and Paterson showed that the rabbit lens in vitro rapidly depolarized in a calcium-free environment. This effect was shown to be the result of an increase in lens permeability to sodium. Such a permeability effect was shown to be the result of an increase in lens cation levels. Since such changes were not observed, we were interested to learn whether the lens cation pump, as evidenced by Na-K-ATPase activity, was significantly affected by the levels of calcium employed in the media. The Na-K-ATPase activity in several tissues has previously been shown to be inhibited by calcium. Since Neville et al. have shown that significant Na-K-ATPase activity is present in the lens cortex as well as in the lens epithelium, we examined the influence of calcium on this enzyme in the lens epithelium, anterior cortex and posterior cortex. The effect of calcium on the ouabain-insensitive fraction of the total ATPase was also examined in these lens segments.

Methods. New Zealand albino rabbits weighing approximately 2 kg were killed by cervical dislocation, and the eyes were enucleated. The lens was removed by a posterior approach to the globe and freed of zonules and adhering vitreous.

An epithelial segment, consisting of the lens epithelium and capsule, was removed from the lens by making an equatorial incision through the lens capsule and peeling the capsule together with the adhering epithelial layer away from the cortex. Segments of the anterior and posterior lens cortex were obtained by cutting out a 7 mm diameter core from the lens and separating the anterior and posterior cortical tissue away from the nucleus. The segments from paired lenses were pooled in tissue samples were run in duplicate.

The total ATPase activity of each lens tissue suspension was determined by a modification of the method of Bon ting et al. with the solutions given in Table I. This assay relies upon determining the amount of phosphate released from the breakdown of ATP by spectrophotometrically measuring the color reaction with ammonium molybdate and ferrous sulfate. Appropriate standards and tissue blanks were run in parallel with tissue samples. All samples were run in duplicate.

The total ATPase activity and ouabain-insensitive ATPase activity were obtained from the amount of phosphate released in the absence and presence of ouabain, respectively. The ouabain-sensitive Na-K-ATPase activity was obtained from the difference between the total and the ouabain-insensitive ATPase activities.

By this method, total ATPase, Na-K-ATPase, and ouabain-insensitive ATPase activity in each segment were measured, in both 3.6 mM calcium and calcium-free EGTA media.

Results. The activity of the ouabain-sensitive

Table I. Composition of solutions used in ATPase assay (mM/L)

<table>
<thead>
<tr>
<th>Epithelial segment</th>
<th>Cortical segments</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
</tr>
<tr>
<td>Tris ATP*</td>
<td>3</td>
</tr>
<tr>
<td>MgCl₂</td>
<td>3</td>
</tr>
<tr>
<td>KCl</td>
<td>5</td>
</tr>
<tr>
<td>NaCl</td>
<td>116</td>
</tr>
<tr>
<td>Tris</td>
<td>34</td>
</tr>
<tr>
<td>Ouabain</td>
<td>—</td>
</tr>
<tr>
<td>EGTA*</td>
<td>1</td>
</tr>
<tr>
<td>CaCl₂</td>
<td>—</td>
</tr>
</tbody>
</table>

All solutions were adjusted to pH 7.4 at 36°C.

*Tris ATP (Sigma No. A3877), CaCl₂, and EGTA were added to stock solutions immediately prior to each experiment.

The K⁺ concentration in the solutions used for the cortical segments was adjusted to compensate for the larger amount of K⁺ in these segments.

EGTA was added to ensure a calcium-free environment. It was noted, however, that there was no significant difference between ATPase activity measured in calcium-free solution and that measured in calcium-free solutions containing EGTA.