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TEMPORAL CONTRAST SENSITIVITY AND CORTICAL MAGNIFICATION

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Abstract—We measured temporal and spatial contrast sensitivity functions of foveal and peripheral photopic vision at various locations in the nasal visual field. Sensitivity decreased monotonically with increasing eccentricity when it was measured by using the same test gratings at different eccentricities. When the gratings were normalized in area, spatial frequency, and translation velocity by means of the cortical magnification factor M so that the calculated cortical representations of the gratings became equivalent at different eccentricities, the temporal contrast sensitivity functions became similar at all eccentricities. The normalization was effective under all experimental conditions that included various kinds of temporal modulation from 0 to 25 Hz (movement, counterphase flicker and on-off flicker) and different threshold tasks (detection, orientation discrimination, and discrimination of movement direction), independently of the subjective appearances of the gratings at threshold. We conclude that central and peripheral vision are qualitatively similar in spatiotemporal visual performance. The quantitative differences observed without normalization seem to be caused by the spatial sampling properties of retinal ganglion cells that are directly related to the values of M used in the normalization.

INTRODUCTION

Some aspects of photopic visual performance seem to bear remarkably simple relations to the neuroanatomy of the visual system. Human visual acuity and resolution, for example, appear to be directly proportional to the linear cortical magnification factor M (Cowey and Rolls, 1974; Rovamo and Virsu, 1979) that indicates how many millimeters on the striate cortical surface correspond to 1 deg of visual angle at different locations in the visual field. On the other hand, the spatial contrast sensitivity functions of various visual field locations can be made similar by scaling the spatial properties of the test gratings so that the gratings produce equivalent cortical representations at different locations as calculated by means of M (Rovamo *et al.*, 1978; Virsu and Rovamo, 1979) or the just resolvable distance (Koenderink *et al.*, 1978). Because M is probably directly proportional to the linear density (frequency) of retinal ganglion cells (Drasdo, 1977; Rovamo and Virsu, 1979), the relations valid with respect to M can be extended to the spatial sampling properties of the ganglion cells.

As Lennie (1977) has pointed out, the simple relations between visual performance and the overall anatomical measures are surprising because there are different classes of ganglion cells that project to several areas of the brain and may have different distributions over the retina. Even though it now appears that X and Y ganglion cells of the cat are quite similarly distributed at least at eccentricities smaller than 20 deg (Peichl and Wässle, 1979), they may be dissimilarly distributed in the rhesus monkey (De Monasterio and Gouras, 1975; De Monasterio, 1978). In addition, visual information is processed in several prestriate cortical areas that may have different progressions of magnification and different functional roles (Zeki, 1978).

In general, the physiological findings have supported the common assumption that central and peripheral vision are qualitatively different, central vision being specialized for pattern and peripheral vision for temporal analysis (Ikeda and Wright, 1972; Sharpe, 1974; Scobey and Horowitz, 1976). Patterns and temporal events are supposedly processed by different kinds of channels, sustained for patterns and transient for movement and flicker (Kulikowski and Tolhurst, 1973).

Considering these complications, it is possible that the relations between visual performance and gross anatomical measures are valid only when a single class of cells or channels mediates the visual responses. Therefore, we extended our previous studies of spatial contrast sensitivity to the temporal domain. We measured contrast sensitivity at various temporal frequencies and with different types of modulation in three threshold tasks hoping to find conditions under which the normalization based on M would fail because the failures could give hints on the functions of different classes of cells. We found no such condition. The results indicated that the normalization based on M makes temporal contrast sensitivity functions similar at different eccentricities as was previously reported for spatial contrast sensitivity functions.

METHODS

The methods were the same as in Virsu and Rovamo (1979) and are only briefly described here.

Apparatus and procedures

The subject fixated binocularly a small point of green light in a dark room; a bite board aided steady fixation. Sinusoidal gratings were generated under computer control on a white cathode-ray screen (HP1300A/P4) that was masked to display a semicircular area. Frame frequency was 50 Hz and this made it possible to present apparently smoothly drifting gratings up to a drift rate of 18 Hz. At 25 Hz movement could also be seen under some conditions, but its direction was arbitrary because the modulation was then actually in counterphase (spatial phase shifts in subsequently presented gratings were 180 deg).

The other eye's view was masked so that the display screen was visible to one eye only. The natural pupil used had a diameter of about 6.5 mm. The average luminance of the screen was continuously 10 cd/m^2. Hence, the average retinal illuminance was about 330 td, which corresponds to 1060 scotopic td on our display. The adaptation level was photopic.

Contrast sensitivity was measured by determining the inverse of threshold contrast for a series of spatial and temporal frequencies. The thresholds were estimated by using a computer-controlled forced-choice method that indicated the contrast required for a probability of 0.84 of correct choices. In detection tasks, the subject had to decide during which one of two sound signals a grating was presented. In the discrimination of movement direction the subject indicated to the computer in which one of two opposite directions of movement the grating presented was drifting. In orientation discrimination the subject indicated after each presentation whether the sound signal heard was accompanied by a horizontal or vertical grating.

Three experienced subjects participated in the experiments. Their monocular Snellen decimal acuities were better than 1.4. Only one subject wore corrective lenses; the others were emmetropic.

Stimulus normalization

The eccentricities studied were 0, 1.5, 4, 7.5, 14 and 30 deg on the nasal half of the horizontal visual-field meridian. They were measured from the nearest edge of the semicircular grating field (see Fig. 1B). The values of M for these eccentricities were obtained from the equation presented by Rovamo and Virsu (1979) and were, from 0 to 30 deg, 7.99, 5.34, 3.44, 2.28, 1.37 and 0.625 mm/deg.

In order to calculate the cortical properties of stimulus gratings, the following equivalences were obtained by considering M as the scale of mapping from retina onto the striate cortex:

(1) Cortical length = ML mm, where L is length measured in deg in retinal images.

(2) Cortical spatial frequency = $M^{-1}F$ c/mm, where F is retinal spatial frequency in c/deg.

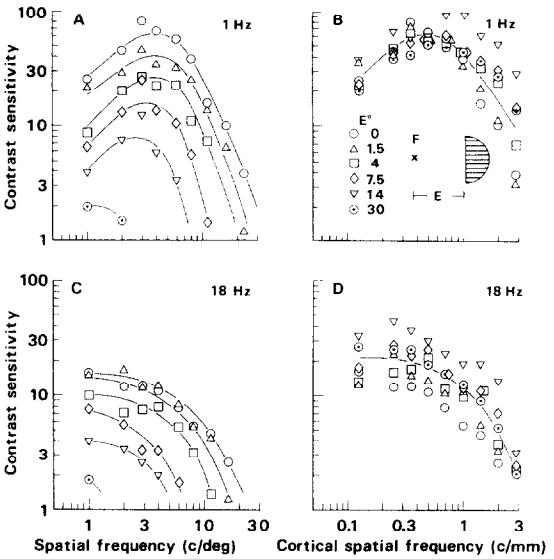

Fig. 1. Contrast sensitivity as a function of spatial frequency and eccentricity in the nasal visual field for two drift rates (1 and 18 Hz). The eccentricity was varied and measured as indicated in the inset of B; at $E = 0$ deg, the fixation point (F) was in the middle of the chord. The subject's task was to detect the presentation of drifting gratings exposed for 1 sec. In A and C, the gratings were *retinally equivalent*, that is, the same gratings were shown at all eccentricities for each spatial frequency. Viewing distance was 458 cm and the radius of the semicircular grating was a constant 1 deg. The retinal spatial frequency varied as shown on the abscissae. In B and D, the gratings were normalized so that they were *cortically equivalent*, that is, the retinal images were made larger with increasing eccentricities by changing the viewing distance so that it was always 57.3M cm. The radius of the grating was then a constant 7.99 mm in calculated cortical terms. Retinally it was 1 deg at $E = 0$ deg, and 1.50, 2.32, 3.50, 5.81, and 12.8 deg at the increasing eccentricities indicated in B. Spatial frequency varied in cortical terms as shown on the abscissae in c/mm. Retinal spatial frequency varied for each function from 0.125M to 2.88M c/deg at each eccentricity. Subject: P.L.

(3) Cortical stimulus area = M^2A mm^2, where A is retinal area in deg^2.

(4) Cortical translation velocity = MV mm/sec, where V is retinal translation velocity in deg/sec. For drifting gratings, translation velocity (deg/sec) is equal to drift rate (Hz) divided by spatial frequency (c/deg).

(5) Cortical drift rate (modulation frequency at a fixed point) and temporal frequency of flicker in Hz are the same as the corresponding retinal values.

The stimulus descriptions could be given in terms of the receptive field frequency of retinal ganglion cells because it is directly proportional to the values of M used here, but the present system was selected to describe the results of scaling because it is simpler.

As far as the properties of retinal images are represented by the visual field descriptions directly, the equivalences imply that similar cortical representations are obtained at different eccentricities if the same gratings are viewed at different distances so that

the viewing distance is a constant multiple of the value of M for each eccentricity. This method of scaling or stimulus normalization for obtaining equivalent cortical representations was used in the present study and the descriptions listed above were applied in the data analysis. The method is not exact because involuntary eye movements and the optical defects of the eye prevent an accurate correspondence between retinal images and visual field stimuli. The inaccuracies are most serious at small eccentricities where the values of M are high and small retinal deviations lead to relatively large cortical deviations, in direct proportion to M. On the other hand, the equivalences are not exact even for retinal images because M decreases nonlinearly with eccentricity and because scatter is introduced by neural connections. The inaccuracies of the stimulus description are small in comparison with the systematic variance caused by experimental manipulations, however.

RESULTS AND DISCUSSIONS

Spatial contrast sensitivity at different temporal frequencies

Our previous studies included measurements of spatial contrast sensitivity functions with drifting gratings, but the temporal frequencies used were only 0 and 4 Hz. The results of Fig. 1 extend the temporal frequencies to 1 and 18 Hz.

When gratings were presented and described in the conventional manner, so that retinally similar test gratings were presented at all eccentricities, contrast sensitivity and spatial resolution decreased rapidly with eccentricity, as in Fig. 1A and C. The maximum sensitivities reached in Fig. 1 (and in subsequent experiments) are relatively low due to the small size of gratings and nonoptimal spatiotemporal frequency combinations, but nevertheless sensitivity differences reaching $2 \log_{10}$ units can be seen between central and peripheral vision. When the gratings were normalized for similar cortical representations (Fig. 1B and D), the maximum differences were reduced at low and medium cortical spatial frequencies down to a range of $0.3 \log_{10}$ units or less at 1 Hz, and to $0.5 \log_{10}$ units at 18 Hz. The remaining variability does not indicate a systematically decreasing sensitivity with increasing eccentricity.

At high cortical spatial frequencies, the foveal sensitivity was lower than average. This was expected because the eye optics attenuates contrast strongly only at high retinal spatial frequencies. These were required for producing high cortical spatial frequencies in the fovea, but in the periphery low, relatively unattenuated spatial frequencies produced high cortical spatial frequencies.

The results shown in Fig. 1 are not the neatest ones we have obtained so far, and it is possible that the values of M were not optimal for the subject because the results at 14 deg eccentricity are clearly deviant from the others. At any rate, the normalization was reasonably successful both at 1 and 18 Hz. This is interesting because these two drift rates should selectively favor the sustained and transient channels (see Kuljkowski and Tolhurst, 1973; Kulikowski, 1975). According to subjective observations, the detection was based on perceiving flicker or movement at low spatial and high temporal frequencies, and on pattern at high spatial and low temporal frequencies. These differences were irrelevant to the success of the normalization.

The results do not support the assumption that the peripheral retina would be specialized for the detection of moving stimuli (cf. Hilz, Rentschler and Brettel, 1980). Fovea and periphery behaved similarly at all cortical spatial frequencies, and the changes observed without normalization were monotonic under all conditions.

We have now evidence that the normalization based on M is effective at least at four temporal frequencies between 0 and 18 Hz. This suggests that the normalization is effective for the whole spatiotemporal contrast sensitivity surface, studied previously only in central vision (see Robson, 1966; Kelly, 1977). The subsequent experiments test the validity of this generalization for a large variety of temporal conditions and in different threshold tasks.

Temporal contrast sensitivity at low and high spatial frequencies

Figures 2 and 3 show contrast sensitivity as a function of temporal frequency for spatial frequencies differing by factor 16. When the same test grating was presented at different drift rates at increasing eccentricities (Figs 2A and 3A), contrast sensitivity decreased similarly with eccentricity at all temporal frequencies. No evidence for a better movement or flicker sensitivity in the periphery was obtained.

When the gratings shown at different eccentricities were spatially normalized for similar cortical representations (Figs 2B and 3B), the different temporal contrast sensitivity functions formed a single function for all visual-field regions studied. The systematic decrease of sensitivity with eccentricity was replaced by a variability whose range is about $\pm 0.2 \log_{10}$ units. The simplification gained by the normalization was most striking at high spatial frequencies: 12 c/deg gratings could not be detected at all at eccentricities of 14 and 30 deg in Fig. 3A, but after normalization these eccentricities yielded results similar to those of the fovea in Fig. 3B.

The upper abscissae in Figs 2B and 3B indicate the cortical translation velocities of the drifting gratings in mm/sec. If the translation velocities are plotted in retinal terms as in Figs 2C and 3C, it becomes evident that the cortical rather than retinal velocities must be matched in order to obtain similar contrast sensitivities.

Hence, if two stimuli moving at different retinal loci in the visual field are to be compared, it is not sufficient to match their cortical sizes for equal visibility,

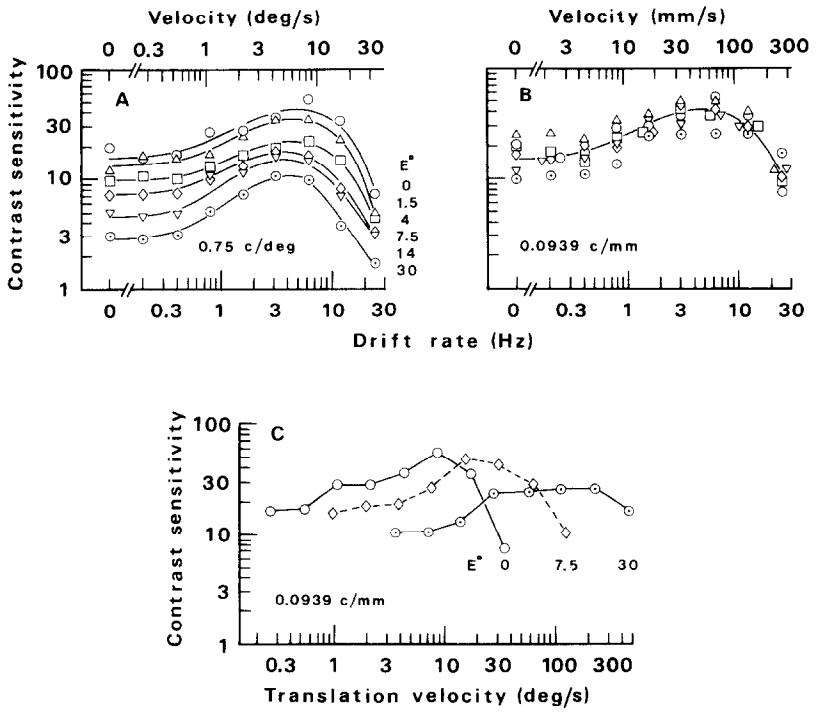

Fig. 2. Temporal contrast sensitivity at low spatial frequencies as a function of drift rate, translation velocity and eccentricity in the nasal visual field. The subject's (J.R.) task was to detect the presentation of horizontal gratings drifting upwards; the gratings were shown for 1.5 sec at each trial. The symbols are as in Fig. 1 for various eccentricities. (A) The same grating of 0.75 c/deg was presented at all eccentricities but at different drift rates and translation velocities as indicated on the lower and upper abscissae. Viewing distance was 344 cm and the radius of the semicircular grating subtended 1.33 deg. (B) The calculated cortical representations of the gratings were similar at all eccentricities and only the drift rate and translation velocity varied. The experiment was otherwise like in A, but viewing distance varied as a function of eccentricity so that the calculated cortical spatial frequency was a constant 0.0939 c/mm and display radius was 10.6 mm. The viewing distance was 43.1M cm, display radius $10.6M^{-1}$ deg, and retinal spatial frequency was 0.0939M c/deg at each eccentricity. (C) Data from figure B are replotted as a function of retinal translation velocity for three eccentricities (0, 7.5, and 30 deg). The results of other eccentricities would look similar but differently located on the abscissa; they are omitted for clarity.

but also their cortical translation velocities must be the same. This is automatically taken care of with normalized moving gratings when their drift rates (in Hz) are the same because translation velocity is inversely proportional to spatial frequency.

Effectiveness of normalization in different threshold tasks

The well-known distinction between sustained and transient channels was first introduced by Keesey (1972) to explain the different thresholds for seeing flicker or a flickering line in the same stimulus constellation depending on temporal frequency. Later, large differences have been reported for flicker and pattern thresholds in the perception of gratings at some combinations of spatial and temporal frequency (Kulikowski and Tolhurst, 1973; Kulikowski, 1975). This distinction is relevant here because it is usually assumed that the two types of psychophysically identified channels are represented by different kinds of visual cells, X for sustained and Y for transient.

The contrast sensitivities reported in Figs 1–3 were measured with a detection task. Fig. 4 shows a replication of the experiments of Figs 2 and 3 with a task that required discrimination of the direction of movement (up or down). If channels specialized for the analysis of movement exist, they should be utilized in this task. The results were essentially the same as in the detection experiments, except that contrast sensitivity was now lower at high spatial frequencies. The normalization was as effective as in the detection task. Evidently the success of normalization is not limited to tasks that can be solved by utilizing pattern channels only.

Figure 5 presents results from experiments in which an orientation discrimination task was compared with the detection task. Normalized gratings were used as stimuli at a low (A–C) and high (D–F) calculated cortical spatial frequency at the nearest-edge eccentricities of 0 and 30 deg, and three different kinds of temporal modulation were applied. In the detection task (open symbols), any feature of the gratings could serve as the cue that led to the probability of 0.84 of correct responses. At low spatial frequencies, the relevant cue was flicker or movement because they had then the lowest thresholds. The orientation-discrimination task

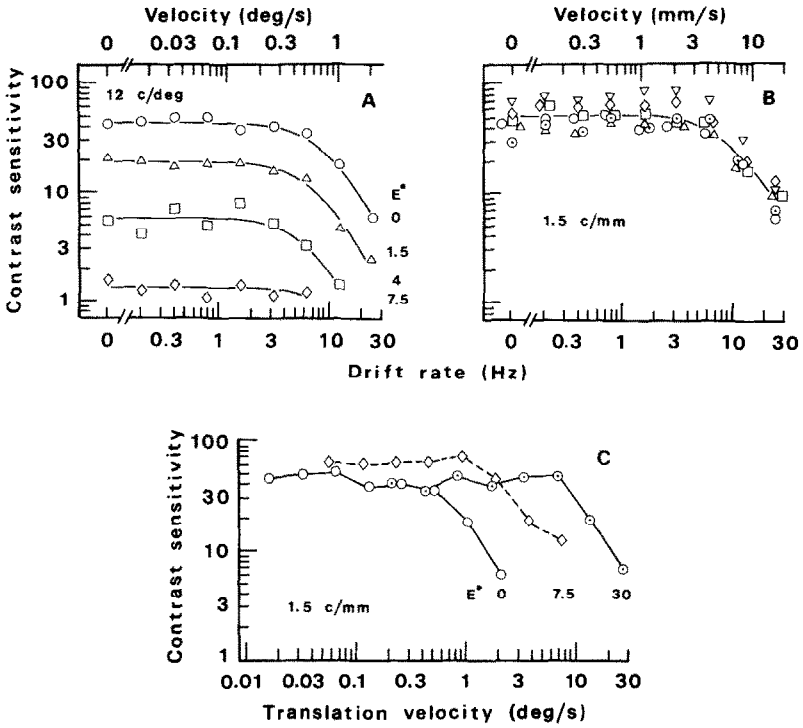

Fig. 3. Temporal contrast sensitivity functions at high spatial frequencies as a function of drift rate, translation velocity and eccentricity in the nasal visual field. The legend of Fig. 2 explains all details, except that the constant retinal spatial frequency in A is 12 c/deg, and the constant cortical frequency in B is 1.50 c/mm (1.50M c/deg on the retina).

(filled symbols) measured the perception of pattern in the objective sense that a definite feature, horizontal vs vertical orientation, had to be correctly identified with the probability of 0.84.

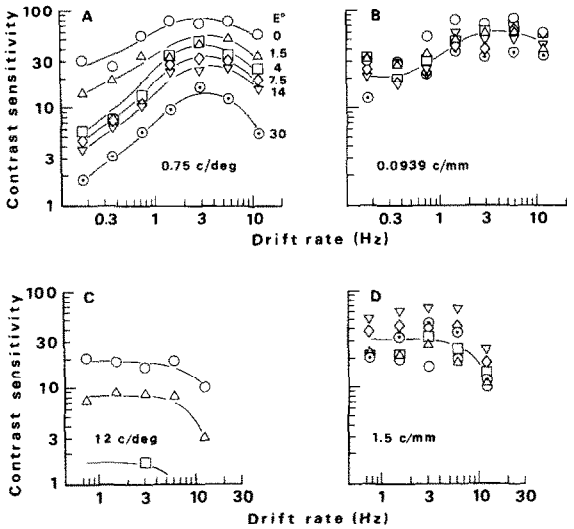

Fig. 4. Temporal contrast sensitivity at low (A and B) and high (C and D) spatial frequencies and at different nasal eccentricities. The subject's (P.L.) task was to indicate whether the horizontal gratings presented for 1.5 sec drifted up or down. In A and C, the gratings were retinally similar at different eccentricities. In B and D, the gratings were normalized for similar cortical representations. Other details are as in Figs 2 and 3.

The normalization procedure worked well under all spatiotemporal conditions. The sensitivities measured in the periphery (squares) were similar to foveal values (circles) everywhere: the largest single difference (*in* Fig. 5A) was $0.5 \log_{10}$ units and all other differences were smaller. Considering the possible variation of single thresholds for the same subject measured in different sessions, we do not regard any single difference smaller than $0.3 \log_{10}$ units statistically significant, although the variances recorded within sessions may suggest a much smaller value. Without normalization, contrast sensitivity at 30 deg would have been much lower or impossible to measure as in Figs 2–4.

The temporal contrast sensitivity functions measured with drifting or counterphase-flickering gratings were quite similar (compare A and B, and D and E). In on-off flicker (C and F), the sensitivities at high flicker frequencies were higher than for other types of modulation and about half those of the lowest frequencies as would be expected on the basis of temporal averaging of contrast (Virsu and Nyman, 1974).

The differences between the contrast sensitivities in the two tasks, detection and orientation discrimination, were negligible. Perhaps the reason for this unexpected result was that we used a criterion-free forced choice method in which a single, easily identifiable feature of the grating was sufficient for producing correct responses.

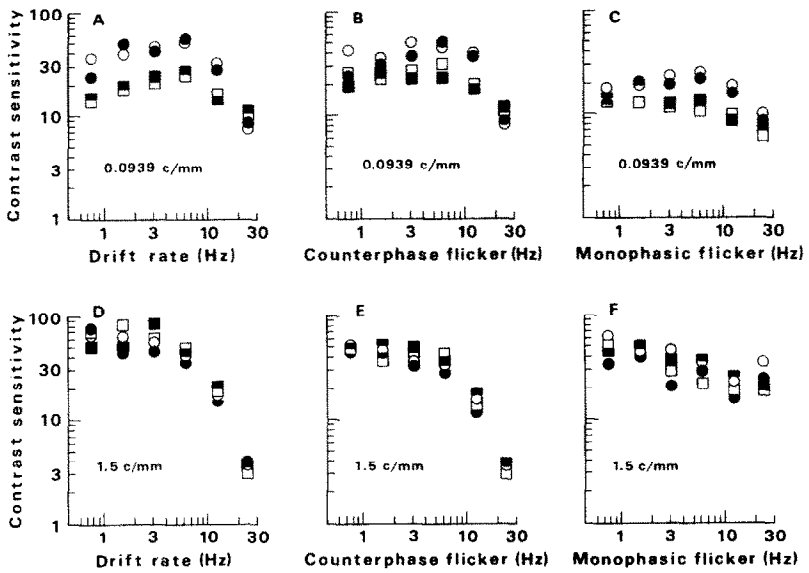

Fig. 5. Temporal contrast sensitivity functions measured with foveally and peripherally presented gratings in two different threshold tasks and at two cortical spatial frequencies. The types of temporal modulation and their frequencies are indicated on the abscissae. The gratings were normalized for similar calculated cortical representations at the two eccentricities that were 0 deg (open and filled circles) and 30 deg nasal (open and filled squares). Cortical spatial frequency was 0.0939 c/mm in A–C. The retinal spatial frequencies were then 0.75 and 0.059 c/deg for the fovea and periphery, and the radii of the semicircular gratings subtended 1.33 and 17.0 deg. In D–F, the cortical spatial frequency was 1.5 c/mm, and the retinal frequencies were 12 and 0.94 c/deg. The normalization was performed by viewing the gratings at a distance of 344 cm for the fovea and 26.9 cm for the periphery. The gratings were presented for 1.28 sec at each trial. The task of the subject (R.N.) was either to detect the presentation of flickering horizontal gratings (open symbols) or to discriminate between flickering horizontal and vertical gratings (filled symbols).

GENERAL DISCUSSION

We had previously shown that spatial contrast sensitivity functions can be made similar for all regions of the visual field by means of a simple scaling or normalization operation that makes the calculated cortical representations of the stimulus gratings independent of eccentricity. In the normalization, the spatiotemporal features of the gratings, such as spatial frequency, area, and translation velocity are scaled so that they get for each location of the visual field cortically corresponding values calculated by means of M. The present results add to these findings a complete spectrum of temporal frequency variation and make possible the generalization that the normalization based on M works similarly in photopic vision for the whole spatiotemporal sensitivity surface, independently of the type of temporal modulation, perceptual appearances of gratings at threshold, and with a considerable variation in the threshold task. The results of Koenderink *et al.* (1978) indicate that the critical flicker fusion frequency measured with moving gratings at different eccentricities agrees with this generalization.

The success of the normalization depends probably on the simple anatomical relations that seem to exist between receptive field size, receptive field density of retinal ganglion cells, and M. Fischer (1973) showed that ganglion cell density and average receptive field size in the cat retina are so related that there is the same constant number of receptive field overlaps at all retinal locations. The recent results of Peichl and Wässle (1979) essentially corroborate Fischer's findings separately for X and Y cells, except that they found the coverage of X cells larger in the area centralis than elsewhere as should be expected on the basis of light spread in the eye. The constant coverage implies an inverse proportionality between the receptive field center area (deg^2) and ganglion cell density (receptive fields/deg^2), that is, the increase of field size and decrease of field density with eccentricity compensate each other. On the other hand, M^2 is directly proportional to the areal density of retinal ganglion cells (fields/deg^2) in the cat and monkey (see Rovamo and Virsu, 1979). The receptive field area in the monkey cortical cells is approximately inversely related to M^2 (see Hubel and Wiesel, 1974), as it should be to match the retinal relations in the striate cortex.

Hence, when two gratings presented at different retinal loci are normalized by M, the spatial properties of the gratings are similarly related to the receptive field size and density at all locations in the visual field. Therefore, the stimuli are analyzed by similar numbers of visual cells and with corresponding postretinal sampling relations beginning from the retinal ganglion cells. Since the primary visual cortex is uni-

form in its cytoarchitecture (Hubel and Wiesel, 1977), the number of relevantly stimulated cortical cells grows in a direct proportion to the cortical area stimulated by a grating and similarly at all eccentricities for the normalized stimuli. The number of relevantly stimulated visual cells seems to be a critical determinant of contrast sensitivity because, below a saturation limit, contrast sensitivity can grow hundredfold as a power function of the cortical area stimulated by the test gratings (Virsu and Rovamo, 1979). Sensitivity measured with non-normalized gratings decreases progressively towards the periphery because fewer visual cells are stimulated due to the decrease of receptive field density and increase of field size.

There are many possible complications in this simple schema, of course. For example, the possible change of signal to noise ratio with receptive field size is not taken into account, and chromatic stimuli may cause additional complications. The present results indicate that the existence of different cell classes and projection sites in the brain is not a serious complication, however. Perhaps the different types of cells are similarly distributed at different eccentricities (cf. Schiller and Malpeli, 1977), or the speculations presented for the functions of the cells are premature. The specialized projection areas in the prestriate cortex may be complementary in their magnifications and functions.

At any rate, the results obtained with normalized gratings indicate that the spatiotemporal postretinal visual processes and mechanisms are qualitatively similar for all retinal locations, in agreement with the anatomical uniformity of the striate cortex. If there were qualitative differences between central and peripheral visual processes, it would hardly be possible to equalize visual performance in a variety of situations simply by equalizing the spatial sampling conditions with respect to retinal ganglion cells. The apparently poor quality of peripheral vision normally observed is probably a consequence of the low sampling density and large sampling apertures of visual cells in the periphery.

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