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RESEARCH NOTE

THE SIZE OF THE POOL FOR BLEACHING ADAPTATION IN HUMAN ROD VISION*

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Abstract—We present new psychophysical estimates of the size of the rod pool for bleaching adaptation in the human retina. We estimate that at 5 deg nasal eccentricity in the human retina the size of the adaptation pool for rods is between 5 and 7.5 min arc. This estimate is compatible with the extent of the dendritic spread of rod bipolars located in this region of the primate retina and with the area occupied by roughly 50 rods in this parafoveal region of the human retina. Thus a candidate for the site of adaptation is the bipolar cell whose receptive field is comprised of approx. 50 rods. These estimates represents the lowest measurements to date of the size of the adaptation pool for rods.

Adaption   Rods   Bleaching

INTRODUCTION

Thresholds can remain elevated long after light stimulation has been removed. The loss of sensitivity in the areas directly exposed can be linked to protracted neural and photochemical changes in these retinal areas, and the recovery of sensitivity is familiarly known as dark adaptation. There is considerable evidence to support Rushton's idea (1965) that for human vision the effects of adaptation are evident mainly at a neural site which combines the signals of many rods and which he called the "adaptation pool." The elegant experiment of Rushton and Westheimer (1962) appeared to show that the loss of sensitivity after a bleach is not solely confined to the bleached area but spreads uniformly throughout areas extending up to 30 min arc away from the bleaching locus. Andrews and Butcher (1971) and Barlow and Andrews (1973), however, presented evidence for a decline in the desensitizing effects of a bleach with distance away from the bleaching site. Their evidence is consistent with a nonuniform spread of the effects of bleaching adaptation. More recently, MacLeod, Chen and Crognale (1989) have estimated the size of the

pool using experimental methods which eliminate the contaminating effects of eyemovements. The latest set of experiments have yielded a smaller estimate for the size of the bleaching pool, about 10 min arc of visual angle at 10 deg eccentricity as compared to the 30 min arc of visual angle estimated at 4.5 deg eccentricity by Rushton and Westheimer (1962). In this report we provide an estimate for the spread of adaptation which is yet smaller. We estimate, on the basis of the results from two observers, that the size of the rod pool is between 5 and 7.5 min arc.

We compared the return of sensitivity after spatially uniform bleaches and grating bleaches which were equated for total flux. We used the same test stimulus, a uniform circular spot, after the patterned bleaches as well as after the uniform bleach. For a particular spatial frequency of the grating bleach, if adaptation is pooled over less than half the extent of a bar width, then the return of sensitivity, measured with the uniform test, should be more rapid after the grating bleach than after the uniform bleach, since the unexposed areas after the grating bleach have retained their sensitivity, whereas all areas have been exposed, albeit to half as much light, after the uniform bleach. As the spatial frequency of the grating bleach is made finer, fewer receptive fields can escape

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some desensitization and the time course of dark adaptation becomes more prolonged until finally, the course of dark adaptation matches that after the uniform bleach of equal flux, and we can assume that the extent of the size of the adaptation pool has been matched by the grating stimulus. At this point, adaptation cannot be pooled over an area less than the period of the grating, and a lower limit on the size of the adaptation pool has been set.

METHODS

Stimuli were presented by a two-channel, Maxwellian-view optical system. Illumination was provided by a 200 W quartz-iodide bulb. An artificial pupil, 3.2 mm in diameter was placed in the plane of the Maxwellian image. The observer's head was held steady by an anchored bite bar. A 30 cm focal length lens imaged the lamp filament at high magnification on the artificial pupil so that one coil of the filament filled the pupil. The dimensions of the bleaching pattern were defined by a field stop located 72 cm away from the observer, between the observer and the lens. A beamsplitter was mounted in such a way that it could be removed during the bleach exposure then quickly and precisely returned into position to bring in the test beam. The advantage of this procedure was that there were no optical components between the bleaching stimulus and the observer; thus any degradation in the retinal image was attributable solely to the optical components of the eye. Accommodation and fixation were aided by a desaturated orange fixation grid. The bleach and the test were centered at an eccentricity of 5 deg in the nasal retina.

The bleaching pattern was either uniformly white or composed of black and white squarewave grating patterns of varying spatial frequencies produced by photographic slides. The bleaching field subtended 4 deg of visual angle. The test was uniformly white and of 1 deg in visual angle. Lights were measured with an E.G.&G. silicon photodiode placed in the plane of the pupil.

The two authors served as observers. Each had better than 20/20 visual acuity.

RESULTS AND DISCUSSION

The results of these experiments are summarized in Figs 1 and 2. Figure 1 shows the course of dark adaptation after a uniform bleach and after grating bleaches of bar widths 5 min arc (6 cycles deg^{-1}) and 7.5 min arc (4 cycles deg^{-1}) for Observer CC. Each bleach delivered the same total flux. The course of rod dark adaptation after the uniform bleach is seen to match that after the grating bleach of 5 min arc bar widths, indicating that for the rods, there is no evidence of modulation of sensitivity loss with this spatial frequency. The recovery of sensitivity after the grating bleach of bar width 7.5 min arc is more rapid than after the uniform bleach, indicating that at distances only 3.75 min arc (half the grating bar width) removed from a bleaching site, there is a breakdown in the pooling of adaptation for this observer. Thus, the lower limit on the size of the pool for CC is between 5 and 7.5 min arc. Setting 5 min arc as the lower bound for the size of the pool is complicated by the effects of optical scatter. Although the 5 min grating bleach produces an identical dark adaptation function when compared to the uniform bleach of equal flux, we cannot necessarily conclude that these results are therefore consistent with a lower bound of 5 min arc for the adaptation pool. Optical scatter, as well as pooling, could contribute to this equivalence. An examination of the early portion of the cone branch of the dark adaptation function gives an indication that optical scatter alone cannot give a complete account. If optical scatter had produced a uniform smear of the light and dark bars of this grating, then the return of sensitivity after this grating bleach should match that after the uniform bleach in cone dark adaptation, as well as for the rods. This does not appear to be the case. Hence, the coincidence of the rod portions can be viewed as being not entirely due to optical scatter.

The results of Fig. 2, by similar arguments, allow the lower bound for the size of observer MH's rod pools to be set at 5 min arc. For this observer, the rod portion of the dark adaptation function after a grating bleach of bar width 5 min arc (6 cycles deg^{-1}) shows a consistent divergence from the result after a uniform bleach matched for total flux, indicating a more rapid return of sensitivity after the grating bleach as compared to the uniform bleach.

A possible difficulty with the logic leading to these estimates of a restricted spread of adaptation is that the visual signal regulating adaptation may involve a nonlinearity, which could cause a divergence between the dark adaptation curves measured after the grating bleach and the
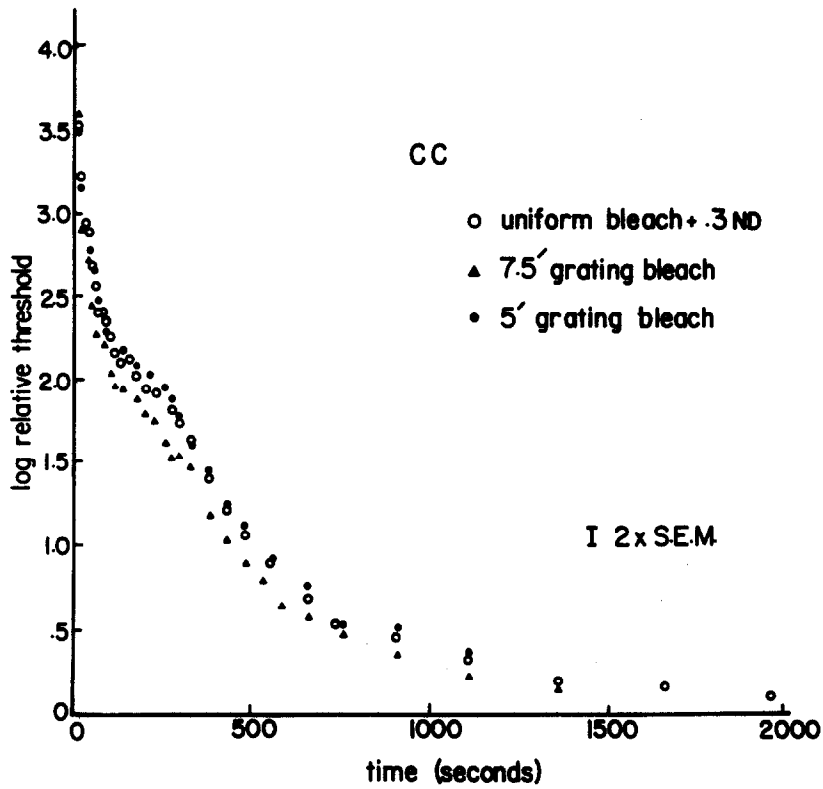
Fig. 1. Shown in this figure are thresholds for detecting a uniform test spot after a uniform bleach (open circles), a grating bleach of 7.5 min arc bar width (closed triangles) or a grating bleach of 5 min arc bar width (closed circles) as a function of time after the bleach. All bleaches were equated for total flux. The recovery of sensitivity in the rod branch of the function after the uniform bleach is shown to coincide with that measured after the 5 min arc grating bleach, but the course of adaptation measured after the coarser grating bleach of 7.5 min arc is more rapid. The size of the rod pool for CC lies between 5 and 7.5 min arc.
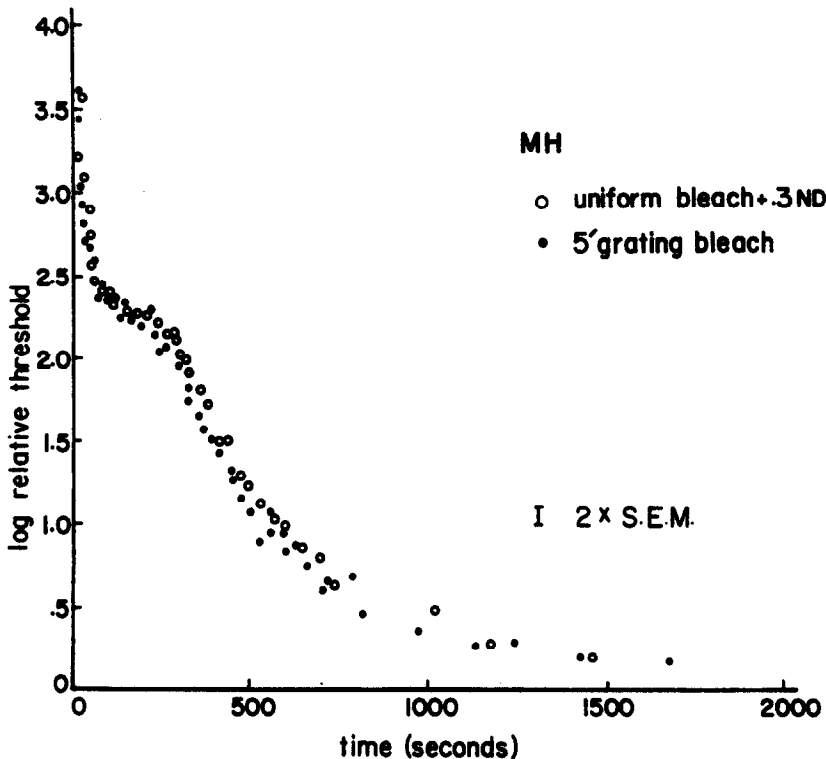

Fig. 2. Shown in this figure are results for observer MH. Symbols and procedures are as in Fig. 1. Since the return of sensitivity in the rod system after a 5 min arc grating bleach is more rapid than that after a uniform bleach of equal flux, the lower limit on the size of the rod pool for MH is 5 min arc.

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uniform bleach, regardless of the nature of pooling of adapting signals. A compressive nonlinear relationship between light intensity and the amount of pigment bleached would, on its own, lead to less pigment bleached, on average, after the grating bleach. Although this possibility cannot be completely discounted, we note that, whenever measurements of the sensitivity loss after the grating bleach diverged from those after the uniform one, a patterned afterimage was observed. This observation is, of course, inconsistent with complete pooling of adaptation.

The question naturally arises as to why our results are consistent with a considerably smaller size for the rod adaptation pool as compared to the early results of Rushton and Westheimer (1962) who used bleaching stimuli identical to ours to estimate 30 min arc as the size of the pool in this same region of the retina. According to Rushton and Westheimer's logic, the desensitizing effects of these distinct bleaches could be compared only if appropriate tests, matching in the areas of the retina they stimulated and in total flux, were employed. To this end, they used a uniform test after the grating bleaches and a square-wave grating test matching the profile of the grating stimulus after the uniform bleach, and reasoned that these measured equal amounts of desensitization when they were matched for total flux at threshold. Under these conditions, they measured identical time courses for the recovery of sensitivity after a grating bleach of period 30 min arc and after a uniform bleach matched in total flux. Since this result would be obtained for adaptation pool sizes of 30 min arc or less, Rushton and Westheimer's (1962) experiment sets an upper bound for the size of the pool. It should be noted that Rushton and Westheimer (1962) reported inter-observer differences and chose Observer RLG, upon whose results the 30 min arc estimate was based, because his large pool size made it easier to discount scattered light as a significant factor. Barlow and Andrews (1973) who used stabilized images and as test probe, a thin line centered on either a bleached or unbleached strip, showed that the desensitization produced in the center of a light bar was tenfold greater than that produced in the center of a dark bar for gratings of 30 min arc bar widths. Thus, even if thresholds are determined by the pooling of signals from bleached rods across 30 min arc in this region of the retina, Barlow and Andrews showed that the

desensitization across the extent of this summation pool is nonuniform. MacLeod et al. (1989), whose methods were designed to eliminate smearing due to eyemovements, have more recently established a pool size of 10 min arc at an eccentricity of 10 deg, as compared to our measurements of 5–7.5 min arc which were made at 5 deg of retinal eccentricity.

Psychophysical evidence (e.g. Ransom-Hogg & Spillmann, 1980) points to larger summation areas for rod vision, approx. 30 min arc for this retinal region, as compared to the considerably narrower extent of spread of adaptation we measure, indicating that adaptation occurs prior to the site of summation. A number of animal studies (e.g. Cicerone & Green, 1980, 1981 for rat; Enroth-Cugell & Harding, 1980 for cat) have also shown that, after a bleach, significant adaptation occurs in the rod system prior to the site of pooling of excitatory signals which form the center response of retinal ganglion cells. Assuming this also holds for the primate, then the bipolar cells, by virtue of their location in the neural chain, would be a reasonable locus for the site of pooling of adaptation. Anatomical studies on the outer plexiform layer of the rhesus monkey retina indicate that the dendritic fields of rod bipolar cells for this region of retina span approx. 15–30 μm (Polyak, 1941; Boycott & Dowling, 1969; Kolb, 1970). This compares reasonably well with our estimate for the rod adaptation pool, which on the basis of Le Grand's (1957) theoretical eye, can be converted into distances on the retina of 24–36 μm. Furthermore, using Osterberg's (1935) estimate of rod density in this region of the retina, our estimated area for the pool corresponds to that occupied by approx. 50 rods.

In summary, we estimate that at 5 deg nasal eccentricity in the human retina the size of the adaptation pool for rods is between 5 and 7.5 min arc. This estimate is compatible with the extent of the dendritic spread of rod bipolars located in this region of the primate retina and with the area occupied by roughly 50 rods in this parafoveal region of the human retina. Thus a candidate for the site of adaptation is the bipolar cell whose receptive field is comprised of approx. 50 rods. These estimates represents the lowest measurements to date of the size of the adaptation pool for rods.

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