Effects of Enucleation of the Fixating Eye on Strabismic Amblyopia in Monkeys

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The effects of enucleation of the fixating eye on the visual function of the deviating eye were studied in two rhesus monkeys with strabismic amblyopia. An esotropia was surgically induced when the monkeys were approximately 1 mo of age, and the fixating eyes were then enucleated at age 3 yr 11 mo. Four measures of visual function (photopic increment–threshold spectral sensitivity, scotopic spectral sensitivity, spatial modulation sensitivity, and temporal modulation sensitivity) were determined for both eyes prior to enucleation and for the deviating eyes over an 11-month period following the surgical removal of the fixating eye. Both monkeys showed some recovery of contrast sensitivity of their deviating eyes. The extrapolated cut-off values for their spatial modulation sensitivity functions increased from .27 to 2.8 c/deg for one animal and from .28 to 6.3 c/deg for the other. The extrapolated cut-off frequencies for the temporal modulation sensitivity functions of both animals showed an increase of 20-25 Hz compared to the pre-enucleation values. The spectral sensitivity functions of one monkey recovered to near normal values following enucleation, while both the photopic and scotopic functions of the other animal remained at pre-enucleation levels. Overall, the results of the experiments indicate that the removal of the fixating eyes of monkeys with strabismic amblyopia can result in significant improvements in the functional capacity of their deviating eyes. Invest Ophthalmol Vis Sci 27:246–254, 1986

Interocular suppression mechanisms are generally considered to play an important role in the subnormal visual acuity of amblyopic eyes. In addition to being involved in the development of amblyopia, suppression mechanisms may also continue to affect the vision of the amblyopic eye after the organism is past the “critical period” for visual system development. For example, several studies have shown that the nondeprived eyes of monocularly lid-sutured cats continue to exert an inhibitory or suppressive influence upon the deprived eyes well past the classical critical period. Moreover, psychophysical studies of human amblyopes have demonstrated that inhibitory binocular interactions are present in adult subjects and that the visual acuity of the amblyopic eye sometimes improves following the loss of the nonamblyopic eye.

The role of post-critical period suppression is probably not the same in all types of amblyopia. In our previous study of stimulus deprivation amblyopia, it was shown that enucleation of the nondeprived eye did not result in any recovery of visual function in the amblyopic eye over a 9-mo recovery period. These results indicate that post-critical period interocular inhibition did not substantially affect the functional capacity of an eye with severe stimulus deprivation amblyopia. However, it is possible that abnormal binocular interactions may be more important in other forms of amblyopia such as strabismic amblyopia. Therefore, the present study was undertaken to investigate the effects of enucleating the fixating eyes on the visual capability of the amblyopic eyes in monkeys reared with surgically induced, unilateral esotropia. Prior to the removal of the fixating eyes, the sensory deficits of the deviating amblyopic eyes, as assessed by psychophysical measures of spatial and temporal modulation sensitivity and increment–threshold spectral sensitivity, were quite similar to those resulting from monocular deprivation produced by lid suture. Therefore, any recovery seen for these strabismic amblyopes following enucleation of the fixating eye can be directly compared to the previous results for stimulus deprivation amblyopes.

Materials and Methods

All of the experimental and animal care procedures conformed to the ARVO Resolution on the Use of Animals in Research and were strictly in adherence with the NIH guide for the Care and Use of Laboratory Animals.
Animals (NIH Publication No. 80–23). The subjects for the experiments were two well-trained rhesus monkeys (*Macaca mulatta*). Experimental esotropia was induced when the animals were 3–4 wk of age (see Table I for the pertinent details of the treatment sequence) using surgical procedures similar to those previously described. The resulting strabismus was inconstant, constant, and unilateral with an angle of deviation in excess of 50 prism diopters. In order to facilitate psychophysical testing, the angle of deviation was reduced by a second surgical procedure when the animals were approximately 1 yr of age. Immediately following the second surgery, both animals were nearly orthotropic. The eye position of one of the animals (subject 7606) remained straight throughout the duration of the experiments, but within the first year following the second surgery the other animal (subject 7605) developed a secondary exotropia of 15–20 prism diopters which was subsequently constant in magnitude and direction. The fixating right eyes of both monkeys were enculated under aseptic operating room conditions using standard surgical procedures when they were 3 yr 11 mo of age. Both monkeys recovered from the surgery without any apparent adverse physiological or behavioral effects.

The refractive errors were determined under cycloplegia at one year intervals by retinoscopy and with an infrared optometer (Bausch and Lomb Ophthalmotron; Rochester, NY). The refractive error measurements at ages 1 yr 1 mo (at the time of eye alignment surgery) and at 3 yrs 11 mo (at the time of enucleation) are presented in Table II. It is interesting that the spherical equivalent refractive errors of the deviating eyes were nearly constant over this period while the refractive errors of the fixating eyes changed 2.25 to 2.50 diopters in the less hyperopic (7905) or more myopic (7906) direction. The refracting right eyes of both monkeys were enculated under aseptic operating room conditions using standard surgical procedures when they were 3 yr 11 mo of age. Both monkeys recovered from the surgery without any apparent adverse physiological or behavioral effects.

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The monkeys viewed all of the stimuli through natural pupils. The fixation behavior of the subjects was not objectively monitored during the experiments.

The apparatus and methodology have been previously described and were identical to those of our previous study of the effects of enucleating the nondeprived eye on stimulus deprivation amblyopia. The contrast sensitivity stimuli were generated on the CRT of an oscilloscope using standard methods. The stimulus field subtended a 4° visual angle at the 114 cm viewing distance and had a mean luminance of 40 cd/m². In the spatial modulation sensitivity experiments, the detection stimuli were stationary vertical sinusoidal gratings presented for 500 msec with square-wave onset and offset properties. In the temporal modulation sensitivity experiments, the luminance of the entire screen was sinusoidally modulated about its mean luminance to produce a uniform field flicker. The viewing duration for the flickering stimuli was 1 sec.

The optical system used in the spectral sensitivity experiments was a 2-channel Maxwellian view system with a 2.5-mm exit pupil. The source for both channels was a 1000-W, heat-filtered xenon arc lamp. The background and test fields subtended visual angles of 10° and 2°, respectively. The test flash duration was 50 msec. The monochromatic test stimuli, obtained by a Jarrel–Ash Mark X monochromator (Fisher Scientific; Orangeburg, NY) with a 10-nm half-band width, were superimposed on a 3000 troland achromatic background in the photopic sensitivity studies. For the scotopic sensitivity studies the background channel was blocked, and the spectral test stimuli were presented to the dark-adapted eye.

Threshold estimates were determined by a descending methods of limits using a criterion response–time paradigm. The monkeys were trained to press and hold down a response lever at the beginning of each trial, which was signalled by the onset of an auditory cue. The lever press initiated a variable interval foreperiod.

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**Table 1. Treatment sequence**

<table>
<thead>
<tr>
<th>Subject</th>
<th>Date of birth</th>
<th>Age at eye alignment</th>
<th>Age at enucleation</th>
</tr>
</thead>
<tbody>
<tr>
<td>7905</td>
<td>2/26/79</td>
<td>34 days</td>
<td>1 yr 1 mo</td>
</tr>
<tr>
<td>7906</td>
<td>3/8/79</td>
<td>24 days</td>
<td>1 yr 1 mo</td>
</tr>
</tbody>
</table>

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**Table 2. Vision characteristics of subjects**

<table>
<thead>
<tr>
<th>Subject</th>
<th>Eye</th>
<th>Refractive error at eye alignment</th>
<th>Refractive error at enucleation</th>
<th>Extrapolated spatial frequency cut-off values</th>
<th>Extrapolated temporal frequency cut-off values</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>pre-enucleation</td>
<td>post-enucleation</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>34 c/deg</td>
<td>93 Hz</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.27 c/deg</td>
<td>33 Hz</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.8 c/deg</td>
<td>58 Hz</td>
</tr>
<tr>
<td>7905</td>
<td>OD-fixating</td>
<td>+5.50 –1.50 X 135</td>
<td>+2.00 DS</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>OS-deviating</td>
<td>+0.50 –2.00 X 180</td>
<td>–0.50 X 120</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7906</td>
<td>OD-fixating</td>
<td>plano</td>
<td>–2.50 DS</td>
<td>26 c/deg</td>
<td>84 Hz</td>
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<tr>
<td></td>
<td>OS-deviating</td>
<td>–7.00 DS</td>
<td>–6.50 –2.00 X 180</td>
<td>0.28 c/deg</td>
<td>43 Hz</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>6.3 c/deg</td>
<td>64 Hz</td>
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the linear, subtractive-interaction equations proposed by Sperling and Harwerth. The curve superimposed on the data of the deviating eyes (filled circles). The curves drawn through the data for the fixating eyes and at long wavelengths for the deviating eyes were derived from the linear, subtractive-interaction equations proposed by Sperling and Harwerth. In contrast, the spectral sensitivity data for the deviating eyes (filled circles) are not adequately described by “typical” photopic spectral sensitivity functions and, in comparison to the data for the fixating eyes, exhibit about a 2-log unit reduction in sensitivity for the middle wavelengths. These spectral sensitivity functions are, in most respects, similar to those obtained for monkeys with stimulus deprivation amblyopia. The data for wavelengths shorter than 570 nm form a broad spectral sensitivity function which has a peak in the 500–510 nm region and which is well-described by the CIE scotopic luminosity function as represented by the curve drawn through the data points), even though the function was determined at a moderately intense photopic adaptation level (3000 td). The data for wavelengths longer than 570 nm deviate from the scotopic luminosity function (as represented by the curve drawn through the data points), even though the function was determined at a moderately intense photopic adaptation level (3000 td). The data for wavelengths longer than 570 nm deviate from the scotopic luminosity function suggesting that photopic mechanisms, although reduced in sensitivity, determine the spectral sensitivity over the long wavelength region of the spectrum. Although the photopic mechanisms revealed at the long wavelength end of the spectral sensitivity function cannot be identified with certainty, the data points can be adequately fit by functions similar to those used to describe the long wavelength sensitivity of the fixating eye. If such an interpretation of the data is correct, it suggests that both the long- and middle-wavelength sensitive cones are involved in the determination of long wavelength spectral sensitivity.

In an attempt to define more clearly the nature of the photopic mechanisms underlying the long wavelength sensitivity in the amblyopic eyes, a set of selective chromatic adaptation experiments were conducted. The results for blue light adaptation (Oriel narrow-band interference filter, 480 nm peak wavelength) are presented in Figure 2. Data are shown for adaptation levels of 3000 td (circles), 9000 td (squares), and 27,000 td (triangles). The shapes of the spectral sensitivity func-
tions for the 3000 and 9000 td blue light adaptation levels are virtually identical to the functions for the 3000 td achromatic adaptation condition (Fig. 1, filled circles). Moreover, even with the threefold increase in the adapting field intensity, there was no appreciable reduction in sensitivity (the two lower curves in Fig. 2A–B were each displaced downward by 0.5-log units for clarity). However, with an additional threefold increase in adapting field intensity the spectral sensitivity curves became flatter and, as illustrated by the three curves superimposed on the data, the shapes are compatible with the explanation that for the 27,000 td blue background the spectral sensitivity is determined by the upper envelope of the 3 individual cone receptor mechanisms. Although the intense blue adaptation suggests the presence of three color vision mechanisms, the adaptation properties of the deviating eye are clearly abnormal since, in the normal eye, this level of blue light has been shown to be sufficient to selectively adapt the short- and middle-wavelength sensitive cones and to reveal the isolated sensitivity function of the long-wavelength sensitive cones.28

The spectral sensitivity functions obtained after enucleation of the fixating eyes are shown for subject 7906 in Figure 3 and subject 7905 in Figure 4. There is an obvious difference between the two monkeys in the recovery effects following enucleation of the fixating eye. For subject 7906 (Fig. 3) the earliest spectral sensitivity measurements demonstrated a 1-log unit increase in sensitivity and a change in the shape of the function from an apparently rod dominated function to a 3-peaked cone dominated function that is very similar in shape to the function which had previously been measured for the fixating eye under these conditions. Subsequent sensitivity measurements for the deviating eye of subject 7906 confirmed that even though the shape of the spectral sensitivity curve is essentially normal, the absolute sensitivity of the amblyopic eye is still approximately 1 log unit lower than was found for the fixating eye. In contrast, the post-enucleation spectral sensitivity measurements for subject 7905 (Fig. 4) do not show any evidence of recovery. The function determined in the second wk after enucleation of the fixating eye (panel A) is at approximately the same level of sensitivity as the pre-enucleation function, and the only substantive difference between the pre- and post-enucleation data is that the photopic intrusion at long wavelengths is absent in the post-enucleation curves. The later spectral sensitivity determinations (Fig. 4, panels B–D) reveal a small increase in sensitivity during the first 3 mo after enucleation of the fixating eye but, in general, the shapes of the curves were essentially constant over the 9-mo period in which the sensitivity was followed. Therefore, the increment-threshold spectral sensitivity experiments show that enucleation of the fixating eyes of monkeys with strabismic amblyopia can result in considerable recovery, but that this outcome is not consistent since the sensitivity of the second animal remained essentially at pre-enucleation levels.
SUBJECT: 7S03
A. 1  WEEK 5 POST-ENUCLEATION

Fig. 4. Post-enucleation increment-threshold spectral sensitivity functions for subject 7905 for a 3000 td achromatic background. Data are shown for the four post-enucleation periods indicated on the graphs.

Scotopic Spectral Sensitivity

A difference in recovery between the two animals, similar to that found for the photopic mechanisms in the increment–threshold spectral sensitivity experiments was also found for the animals’ scotopic mechanisms (Fig. 5). Prior to enucleation of the fixating eyes, the sensitivities of the scotopic mechanisms of the deviating eyes (filled circles) were 3–3.5 log units lower than those of the fixating eyes (open circles). When the dark-adapted spectral sensitivity functions were measured 5 wk after enucleation of the fixating eyes, complete recovery of scotopic sensitivity had occurred for subject 7906. The post-enucleation sensitivity for his deviating eye, represented by the diamonds in Fig. 5, was at the same level as the pre-enucleation data for his fixating eye. However, the scotopic sensitivity for the other subject changed very little from the pre-enucleation levels at either 5 wk (diamonds) or 11 mo (squares) after enucleation. Therefore, spectral sensitivity measurements involving both the photopic and scotopic mechanisms are in agreement in showing significant recovery of visual function for one subject (7906) and an absence of recovery for the other subject (7905).

Spatial Modulation Sensitivity

The effects of enucleation of the fixating eyes on the spatial modulation sensitivity of the deviating eyes are presented in Figure 6. The pre-enucleation data (Panels A and B), as previously reported, 19 show that esotropia surgically induced at 1 mo of age causes a profound reduction of contrast sensitivity in the deviating eyes. The extrapolated cut-off spatial frequencies for these functions (see Table 2) are more than 6 octaves lower for the deviating eyes than for the fixating eyes of both animals. The spatial modulation sensitivity functions determined at 3 wk (diamonds), 3.5 mo (squares), 6.5 mo (triangles), and 9.5 mo (inverted triangles) after enucleation of the fixating eyes are shown in the lower panels of Figure 6. For comparison purposes, the pre-enucleation data for the deviating eyes (filled circles) have also been replotted along with ±1.0 SD of these data. The data for subject 7906 show only a very small improvement at 3 wk post-enucleation, but between 3 wk and 3.5 mo a relatively large increase in contrast sensitivity was evident. Thereafter, the functions are relatively constant with an extrapolated cut-off spatial frequency of 6.3 c/deg (approximately 20/100 Snellen acuity) for the function determined 9.5 mo after enucleation. However, even though the range of spatial frequencies which the animal could detect increased from 0.3 c/deg to 6 c/deg, the function is very flat on the low spatial frequency side and the peak of the function is more than 1.0 log unit below the pre-enucleation values for the fixating eye. Typically, contrast sensitivity functions have a more pronounced low spatial frequency roll-off, even if the subject is amblyopic and
their contrast sensitivity function exhibits a cut-off spatial frequency similar to that demonstrated by this subject.19,20,31

The post-enucleation spatial modulation sensitivity data for the other subject (Fig. 6D) are generally similar to those of subject 7906 except that the time course was slower and the final cut-off spatial frequency was lower (2.8 c/deg or approximately 20/215 Snellen acuity). Therefore, even though the spectral sensitivity experiments failed to show any recovery of visual function for subject 7905, the spatial modulation sensitivity functions show a definite, though incomplete, recovery following enucleation of the fixating eye.

Temporal Modulation Sensitivity

The results of the investigation of temporal modulation sensitivities following enucleation of the fixating eyes are presented in Figure 7, using the same format as that used for the spatial modulation sensitivity results (Fig. 6). The pre-enucleation data (Panels A and B) have also been previously reported30 and show a lower temporal modulation sensitivity for the deviating eyes than for the fixating eyes at all temporal frequencies (the extrapolated cut-off temporal frequencies are listed in Table 2). The extent of recovery of temporal modulation sensitivity of the deviating eyes following enucleation of the fixating eyes is shown for the two animals in panels C and D of Figure 7 for post-enucleation intervals of 1 mo (diamonds), 4 mo (squares), 7 mo (triangles), and 10 mo (inverted triangles). The temporal contrast sensitivity measurements show some recovery of function for all temporal frequencies for both animals, but the most significant changes were observed for the higher temporal frequencies. The extrapolated cut-off temporal frequencies from the final functions determined 10 mo after the enucleation surgery demonstrate that the temporal resolution limit had increased by 20–25 Hz for both animals. However, the final temporal modulation sensitivities for the deviating eyes were still approximately 0.4 log units below those obtained for the fixating eyes at all temporal frequencies. Therefore, both the temporal modulation sensitivity data and the spatial modulation sensitivity data are consistent in showing measurable, but incomplete, recovery of visual function for the deviating eyes, presumably as a result of removing the suppressive influences of the fixating eyes.

Discussion

The results of these experiments have shown that enucleation of the fixating eye can produce a marked
improvement in the functional capacity of a strabismic subject’s deviating amblyopic eye. The improvement was observed in both animals for measures of spatial and temporal modulation sensitivity, but only one animal showed recovery for measures of spectral sensitivity. It is puzzling that one animal (subject 7906) showed substantial recovery of both photopic and scotopic spectral sensitivity functions, while the other animal (subject 7905) failed to exhibit any improvement above the pre-enucleation levels. Kratz and Lemkuhle have also reported that enucleating the nondeprived eye does not result in the recovery of visual function in some kittens with stimulus deprivation amblyopia. They hypothesized that their intersubject variability probably was a result of differences in the duration of the initial period of deprivation and the age at which the nondeprived eye was enucleated. However, in the present study the ages at which strabismus was induced and at which the fixing eyes were subsequently removed were essentially the same for both subjects. Moreover, the spectral sensitivity functions for both animals were nearly identical prior to the enucleation surgery, and ophthalmoscopic observations of the posterior segments of the monkeys’ eyes also indicated that they were both normal and free from pathology.

The recovery of contrast sensitivity for subject 7905 without the concurrent recovery of spectral sensitivity is somewhat difficult to explain. Since it is generally considered that, in comparison to spatial information, color information is processed at relatively peripheral sites in the nervous system, one would not expect to observe any recovery of spatial vision in subjects with altered spectral sensitivity caused by a limiting anomaly early in the ascending visual pathway. However, like the anomalous spectral sensitivity functions previously observed in monkeys with severe stimulus deprivation amblyopia, the alterations in spectral sensitivity observed in these esotropic subjects are similar in nature to those manifested by monkeys that have had their visual cortices surgically removed. Since the inputs from the deviating eyes are substantially reduced in monkeys reared with an esotropia, it is reasonable to hypothesize that prior to enucleation when these strabismic monkeys were forced to use their deviating eyes, they were behaving like functionally decorticate monkeys. If that is the case, then the differences in recovery of spectral sensitivity between subjects 7905 and 7906 following enucleation of the fixing eyes may reflect differences in the degree of influence attained by the deviating eyes at some cortical level rather than differences in recovery at more peripheral sites in the visual pathway.

Following the experiments reported here, a subsequent investigation (Crawford, in preparation) employing cytochrome oxidase staining methods revealed that the horizontal extent of the ocular dominance columns for the deviating eyes in layer IVc of the striate cortex were the same for both subjects 7905 and 7906. It is not known to what extent that these column measurements reflect the functional integrity of connections from the deviating eyes to either infragranular or supra-granular layers within the striate cortex or to other cortical areas. Investigation of specific cortical areas which appear to be specialized for processing color information, e.g., the cytochrome rich “blobs” of the striate cortex or cortical area V4 may reveal differences in recovery between subjects 7906 and 7905. However, based on the available evidence, it is impossible to explain the difference in the recovery patterns for the two esotropic subjects.

The results of the present studies may be contrasted with our previous investigation of stimulus deprivation amblyopia, although these comparisons should be viewed with some caution since the number of animals in each study was too small to access the variability of these findings. Prior to enucleation of the dominant eye, the contrast sensitivity and spectral sensitivity deficits were very similar for the two groups of ambyopes. However, following enucleation of the dominant eye, neither of the subjects with stimulus deprivation amblyopia showed any measurable recovery of visual function, while in the present study the subjects with strabismic amblyopia both demonstrated significant recovery, especially in their spatial (Fig. 6) and temporal resolving (Fig. 7) capabilities. The differences in the results of the two studies suggest that different neural mechanisms are involved in the two types of amblyopia; but it should also be noted that there were differences in the ages of the animals at the time of enucleation (57 mo for the lid sutured monkeys vs 47 mo for the strabismic monkeys), a difference which has been considered an important factor for cats. However, since both the esotropic and lid-sutured monkeys were well past the critical period at the time of enucleation, we feel that the different recovery patterns observed in lid-sutured and strabismic monkeys reflect different neural mechanisms. In this respect, the findings of the present experiments are in accord with clinical evidence that inter-ocular suppression is more important in strabismic amblyopia than in anisometropic or stimulus deprivation amblyopia. Clinicians have also observed that patients with strabismic amblyopia, who are well past the critical period of development, will often show considerable recovery of visual acuity if their good eye is lost as a result of injury or disease.

With respect to the degree and extent of recovery of spatial modulation sensitivity, the present results from
strabismic monkeys are in better agreement with the results of other investigators’ experiments with monocularly deprived cats\textsuperscript{6–10} than our previous experiments with monocularly deprived monkeys.\textsuperscript{17} Most of the experiments with cats reared with monocular lid suture have shown that the proportion of neurons in the striate cortex which responded to stimulation of the deprived eye increased dramatically following enucleation of the non-deprived eye.\textsuperscript{6–8} In accord with the physiological findings, in cats a considerable amount of behavioral recovery in visual acuity has also been reported for the deprived eyes following the enucleation of the nondeprived eyes,\textsuperscript{9,10} although there have also been some exceptions.\textsuperscript{45} Therefore, removal of inhibitory influences of the non-amblyopic eye of either species results in some recovery of visual function in some types of amblyopia, but the time course for recovery appears to be much more rapid for cat\textsuperscript{7,9} than monkey. In cats recovery occurs immediately after enucleation of the nondeprived eye,\textsuperscript{6,7} but in monkey, recovery occurs much more slowly (see Fig. 6). Therefore, in cat the post-enucleation recovery appears to reflect the immediate release from an active inhibitory process, while in monkey the improvement of contrast sensitivity may be more related to the forced usage of the deviated eye. In this sense, the improvement in resolution capability for the monkey may be similar to the improvement of visual acuity of human amblyopes during orthoptic treatment. These differences indicate that different recovery mechanisms are involved for different species or types of amblyopia and further experimentation is required to determine which aspects of early abnormal visual experience, eg, age of onset, degree of amblyopia, etc, are most important in determining which aspects of visual function may recover if suppression is eliminated.

Key words: amblyopia, strabismus, animal psychophysics, monkeys, contrast sensitivity, spectral sensitivity, enucleation

References


