The Relationship Between Binocular Rivalry and Strabismic Suppression


Increment-threshold spectral sensitivity functions were determined for normal observers during binocular rivalry and for esotropic observers during strabismic suppression and under viewing conditions that normally induce binocular rivalry. Depending on the spatial and temporal properties of the test stimulus, the normal observers exhibited a wavelength-specific loss in sensitivity during the suppression phase of rivalry, which suggests that binocular rivalry differentially attenuates the sensitivity of the chromatic mechanisms relative to the luminance mechanisms. In contrast, regardless of the test stimulus dimensions, the esotropic observers did not manifest a wavelength-specific loss in sensitivity either during strabismic suppression or under conditions that normally induce binocular rivalry. The different patterns of suppression shown by the normal and esotropic subjects suggest that strabismic observers do not demonstrate normal binocular rivalry, and that strabismic suppression and normal binocular rivalry suppression are mediated by different neural mechanisms. Invest Ophthalmol Vis Sci 26:80–87, 1985

The phenomenon of suppression is characterized by an inability to perceive normally visible objects in all or part of the visual field of one eye. Suppression occurs under binocular viewing conditions and is considered to represent an interocular inhibitory process that prevents visual information from the “suppressed” eye from reaching the threshold for conscious perception. Suppression phenomena occur in individuals with normal binocular vision as well as in individuals with anomalous binocular vision. For example, when dissimilar targets that cannot be fused into a single percept are presented simultaneously to corresponding retinal areas in the two eyes of an observer with normal binocular vision, the observer experiences an unstable alternating suppression of information from each eye, a phenomenon called binocular rivalry. Suppression is also commonly exhibited by strabismic observers. Many individuals with strabismus of early onset reduce or eliminate the distressing sensory aspects of their eye misalignment (diplopia and confusion) by suppressing the conflicting visual information from specific regions of the deviated, nonfixating eye.

Because both binocular rivalry suppression and strabismic suppression result in the functional loss of visual information from one eye during binocular viewing conditions, it has been hypothesized in the classic and more recent literature that binocular rivalry suppression and strabismic suppression are related. If binocular rivalry suppression and strabismic suppression are related, it is reasonable to assume that common neural mechanisms may underlie both forms of suppression. To date, little is known about the nature of the mechanisms that are responsible for binocular rivalry and strabismic suppression. Measurements of the changes in visual sensitivity produced by binocular rivalry suppression and strabismic suppression would provide a way to characterize and compare the underlying mechanisms responsible for these two types of suppression. In a previous study, we measured the spectral sensitivity of the eyes of normal observers during binocular rivalry and found a wavelength-specific loss in sensitivity, which suggested that binocular rivalry suppression differentially attenuates the sensitivity of the chromatic mechanisms relative to the luminance mechanisms. Because of the distinctive, wavelength-specific loss of visual sensitivity during binocular rivalry, spectral sensitivity measurements appear to provide a reliable means for characterizing and comparing the nature of the inhibitory states associated with binocular rivalry and strabismic suppression. Therefore, in the present study, we compared the spectral sensitivity functions obtained for normal observers during binocular rivalry with the functions obtained for esotropic observers.
during strabismic suppression and under conditions that normally induce binocular rivalry. The results clearly demonstrate that different mechanisms are involved in normal binocular rivalry and strabismic suppression.

Materials and Methods

Subjects

Five strabismic individuals, demonstrating constant unilateral esotropia of early onset, mild amblyopia (Davidson-Eskridge visual acuity chart\(^4\)), no stereopsis (Tittmus Stereo Test), and normal color vision (A.O.-HRR Pseudoisochromatic Plates) were used as subjects in the strabismic suppression experiments. All of the strabismic observers exhibited harmonious anomalous retinal correspondence on the Bagolini striated glass test\(^7\) but normal retinal correspondence when viewing targets in the haploscope used in the present study. The visual characteristics of the strabismic observers are summarized in Table 1. Ten individuals with normal visual acuity (20/20 or better in each eye), color perception, and binocular vision were used as subjects for the binocular rivalry experiments. Two of the authors served as normal subjects, however, all of the other observers were naive with respect to the purpose of the experiment. Each observer had clear media, normal fundi, and were appropriately corrected for any refractive errors.

Table 1. Visual characteristics of the strabismic observers

<table>
<thead>
<tr>
<th>Observer no.</th>
<th>Age/sex</th>
<th>Eye</th>
<th>Refractive status</th>
<th>Fixation status of deviating eye (visuonscopy)</th>
<th>Binocular status</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>22/F</td>
<td>OD*</td>
<td>plano</td>
<td>20/40</td>
<td>Unsteady central</td>
</tr>
<tr>
<td></td>
<td></td>
<td>OS†</td>
<td>plano</td>
<td>20/15</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>23/F</td>
<td>OD</td>
<td>+4.50 – 0.75 x 100</td>
<td>20/22</td>
<td>Unsteady central with nasal drift 0.5 deg</td>
</tr>
<tr>
<td></td>
<td></td>
<td>OS</td>
<td>+4.50 – 1.00 x 75</td>
<td>20/30</td>
<td>Constant 2° left esotropia</td>
</tr>
<tr>
<td>3</td>
<td>26/M</td>
<td>OD</td>
<td>+0.75 – 0.25 x 70</td>
<td>20/20</td>
<td>Unsteady 1° nasal</td>
</tr>
<tr>
<td></td>
<td></td>
<td>OS</td>
<td>+6.50 – 0.50 x 23</td>
<td>20/20</td>
<td>Eccentric fixation</td>
</tr>
<tr>
<td>4</td>
<td>25/M</td>
<td>OD</td>
<td>-6.75 DS‡</td>
<td>20/30</td>
<td>0.5 deg nasal eccentric fixation</td>
</tr>
<tr>
<td></td>
<td></td>
<td>OS</td>
<td>-6.25 DS</td>
<td>20/20</td>
<td>Constant 3° right esotropia</td>
</tr>
<tr>
<td>5</td>
<td>36/M</td>
<td>OD</td>
<td>-1.25 – 1.25 x 52</td>
<td>20/25</td>
<td>Unsteady central</td>
</tr>
<tr>
<td></td>
<td></td>
<td>OS</td>
<td>-2.00 – 0.50 x 05</td>
<td>20/20</td>
<td>Alternating esotropia noted since early childhood.</td>
</tr>
</tbody>
</table>

* OD = right eye; OS = left eye.
† Dioptric sphere.
‡ Dioptric sphere.

Apparatus and Procedures

The stimuli that were used to induce binocular rivalry and strabismic suppression were high-contrast, square-wave gratings with a fundamental spatial frequency of 2.8 cycles per degree and a space-averaged luminance of 5.9 cd/m\(^2\). The gratings were surrounded by a 0.5-deg dark border to form a square pattern that subtended 5.7 deg. The grating patterns were embedded in a spatially homogenous 19-deg field, with a luminance of 17 cd/m\(^2\).

For the binocular rivalry experiments, a vertical grating was presented to the eye that was to be tested and a horizontal grating was presented to the other eye. A mirror stereoscope was used to present the orthogonally oriented grating patterns to corresponding points in the two eyes. For the esotropic observers, this necessitated adjusting the stereoscope so that the two grating patterns coincided with the observer’s subjective angle of squint. The dark borders surrounding the gratings provided a strong cue for fusion and both the normal and strabismic observers reported that the borders were perceived as single. However, in agreement with previous studies of binocular rivalry, the strabismic (see references 8 and 9) as well as the normal observers reported an alternation of visibility between the vertical gratings seen by the tested eye and the horizontal gratings seen by the other eye. The observers reported that at times the entire field for one eye was suppressed completely.
but that usually the composite pattern consisted of regions of vertical bars interspersed with regions of horizontal bars.

For the strabismic suppression experiments, vertically oriented gratings were presented to both eyes rather than the orthogonally oriented gratings utilized to induce binocular rivalry. Vertically oriented gratings were used because, as Schor9,10 has demonstrated, similar patterns that fall on corresponding points and that normally stimulate sensory fusion are the optimal stimuli for inducing strabismic suppression. The vertical grating patterns contained cues for monitoring suppression (small, nonpaired, horizontal black bars) and were viewed in the mirror stereoscope adjusted for the esotropic observers' subjective angle of squint. For individuals with normal binocular vision, the patterns used to induce strabismic suppression were fused easily into a stable, single percept, and the suppression cues for each eye were always visible. Although the strabismic observers also reported a single percept, the presence of a suppression scotoma in the deviating eye was noted by the disappearance of the corresponding suppression cues.

A single channel optical system consisting of a heat-filtered 250 W tungsten-halogen light source, a monochromator (10-nm bandpass), an electronic shutter, neutral density wedges, a variable aperture, and the appropriate focusing lenses was used to project a spectral test probe onto the center of the vertical gratings seen by the left eyes of the normal observers. For the strabismic observers, the test probe was projected onto the area of the grating pattern corresponding to the suppression scotoma of the deviating eye (usually about 1 deg into the nasal field). The onset of the stimulus was controlled by the observers who were instructed to trigger the test probe by depressing a button either during the appropriate phase of rivalry or during strabismic suppression. Due to the dynamic nature of these suppression phenomena, especially binocular rivalry, stimulus presentations that occurred when the area of the grating pattern corresponding to the position of the test probe was not completely visible (eg, during rivalry dominance) or completely suppressed (eg, during rivalry suppression) were repeated until the observer was confident that the stimulus had been presented at the appropriate time.

Detection thresholds for the test probe were determined using an ascending method of limits. At the start of each ascending series, the intensity of the stimulus was reduced well below the observer's detection threshold. The intensity of the stimulus was increased in 0.1 log unit steps following trials in which the observer failed to detect the stimulus. The lowest stimulus intensity at which the observer detected the test probe was defined as the observer's threshold. The stimulus intensity was reduced subsequently about 0.4 to 0.5 log units and the next ascending threshold series was initiated. Three of the normal observers and all of the strabismic observers thresholds were measured at 20-nm intervals for stimulus wavelengths between 420 and 680 nm. Six threshold estimates were determined for each stimulus wavelength with the order of presentation (ie, ascending or descending) counterbalanced from session to session. The log of the reciprocal of the number of quanta associated with the geometrical mean of the six threshold estimates determined over two to three experimental sessions was plotted against the wave-number of the test stimulus to produce spectral sensitivity functions for each of the viewing conditions. For the normal observers, spectral sensitivity functions were obtained for the dominance and suppression phases of binocular rivalry, and for a nonrivalrous monocular viewing condition (the untested eye was occluded). For the esotropic observers, spectral sensitivity functions were obtained for the deviating eye under monocular viewing conditions (ie, non-suppressed control condition), when both eyes viewed similarly oriented patterns (ie, during strabismic suppression) and when both eyes viewed orthogonally oriented patterns (ie, during rivalry suppression). Since the shape of the spectral sensitivity function is dependent on the spatio-temporal characteristics of the test stimulus, these sets of spectral sensitivity functions were obtained for three different test probe sizes and durations (0.35 deg and 5 msec; 0.85 deg and 20 msec; 1.2 deg and 50 msec).

Because the interpretation of the results of this study depend to some extent on the consistency of the wavelength-dependent sensitivity loss reported previously in normal observers during binocular rivalry5, detection thresholds were measured for all 10 normal subjects for two stimulus wavelengths (450 nm and 560 nm) during the dominance and suppression phases of rivalry and under monocular viewing conditions. Ten threshold measurements were obtained for each observer for all of the stimulus conditions. The stimulus wavelengths used in this experiment were selected because our previous study5 indicated that for the specific test probe dimensions used in this portion of the study (0.85 deg and 20 msec), rivalry suppression reduced the sensitivity for stimulus wavelengths shorter than about 480 nm to a much greater extent than for wavelengths longer than 480 nm. Therefore, a comparison of the effects of rivalry suppression on the 450 nm and 560 nm stimuli should provide an indication of the consistency of the wavelength-dependent nature of rivalry suppression.
Fig. 1. Increment-threshold spectral sensitivity functions obtained from two normal observers. Functions are shown for the following three test-probe dimensions: 50 msec, 1.2 deg (circles); 20 msec, 0.85 deg (squares); and 5 msec, 0.35 deg (diamonds). For clarity of presentation, the functions for the 50 msec, 1.2-deg test probe have been displaced upward 1.4 log units. Open symbols, filled symbols and half-filled symbols represent data for the monocular control condition, rivalry suppression, and rivalry dominance, respectively. Each data point represents the geometrical mean of six threshold estimates. The standard errors of the mean were typically less than 0.05 log units. The functions drawn through the data for reference represent either the functions derived from the linear-subtractive interaction model of spectral sensitivities proposed by Sperling and Harwerth, or functions determined for normal observers in a previous study using flicker methods.

Results

Normal Rivalry Suppression

Figure 1 illustrates increment-threshold spectral sensitivity functions determined for two of the normal observers during binocular rivalry and under monocular viewing conditions using three different test-probe durations and field sizes. The results obtained for all of the normal observers confirm and extend our previous investigation of the spectral characteristics of binocular rivalry. The data indicate that the shapes of the spectral sensitivity functions obtained under the monocular viewing conditions (open symbols) and the dominance phase of rivalry (half-filled symbols) are identical for all of the stimulus durations and field sizes. However, depending on the spatial and temporal characteristics of the test probe, the spectral sensitivity functions for the suppression phase of rivalry (filled symbols) differ markedly in shape from the functions obtained during the dominance phase of rivalry and during the monocular viewing condition. For example, for the larger test fields and longer viewing durations (circles and squares), stimulus dimensions that normally bias detection toward chromatic or opponent-color mechanisms, the dominance phase and monocular control functions exhibit three maxima of sensitivity at approximately 440, 530, and 610 nm and conform to the linear, subtractive-interaction model for spectral sensitivity proposed by Sperling and Harwerth. But, in contrast, for the same test-probe dimensions, the suppression phase data are described adequately by a function obtained with flicker methods (ie, a unimodal luminosity function with a peak at about 550 nm). The only departure of the suppression-phase data from the luminosity function occurred for the 50 msec, 1.2 deg stimulus (circles). For one of the normal observers (panel A) the suppression-phase data for the shortest wavelengths (420 and 440 nm) appear to conform to the absorption spectrum of the short-wavelength sensitive cones. These differences in the shapes of the spectral sensitivity functions for the dominance and suppression phases of rivalry are not apparent for test probe dimensions that normally bias detection toward luminance mechanisms. For instance, for the 5 msec, 0.35-deg test probe (diamonds), the data obtained for all three viewing conditions conform to the shape of functions obtained by flicker
BINOCULAR RIVALRY
NORMAL OBSERVERS

DOMINANT PHASE
SUPPRESSION PHASE

LOG RATIO

0.6

0.4

0.2

0

-0.2

0.2

0.4

0.6

0.8

1

450nm
560nm

STIMULUS WAVELENGTH

Fig. 2. Log ratio of the mean (±SE) increment thresholds obtained for the 10 normal observers during binocular rivalry (open bars, rivalry dominance; filled bars, rivalry suppression) and the nonrivalrous monocular viewing conditions. Data are shown for the 450- and 560-nm stimuli. The test probe dimensions were 20 msec and 0.85 deg.

methods although the subjects' spectral sensitivities were usually lower during the suppression phase of rivalry.

The wavelength-dependent nature of the rivalry suppression exhibited by normal observers for the longer and larger test stimuli is emphasized in Figure 2. The mean (±1 SE) increment thresholds obtained for the 10 normal observers for the dominance and suppression phases of rivalry are plotted in histogram form relative to the thresholds obtained under monocular viewing conditions. Data shown above the dashed zero line indicate that the subjects' sensitivity during binocular rivalry was lower (ie, higher thresholds) than that for the monocular viewing condition and vice versa. For both the 450 nm and 560 nm stimuli, the mean thresholds measured during the dominance phase of rivalry did not differ significantly from the mean monocular thresholds (450 nm: t(9) = 1.40, P = 0.145; 560 nm: t(9) = 0.144, P = 0.138).

As expected, the mean thresholds for the suppression phase of rivalry were significantly higher than the monocular thresholds for both the 450 nm (t(9) = 10.98, P < 0.0001), and 560 nm stimuli (t(9) = 5.31, P < 0.001). However, a comparison of these sensitivity losses clearly indicates that rivalry suppression reduced the normal observers' spectral sensitivity for the 450-nm stimulus significantly more than it did for the 560-nm stimulus (t(9) = 6.50, P < 0.0001). This result confirms our previous investigation of the spectral characteristics of binocular rivalry and further suggests that this wavelength-selective aspect of rivalry suppression is a characteristic of observers with normal binocular vision.

Strabismic Suppression

Typical increment-threshold spectral sensitivity functions measured during monocular viewing conditions (open symbols) and during binocular viewing conditions that produce strabismic suppression (filled symbols) are shown in Figure 3 for two of the esotropic observers. The strabismic observers' spectral sensitivity functions obtained for monocular viewing conditions are qualitatively comparable to the normal observers' monocular spectral sensitivity functions. For example, the data for the test probes with the larger field sizes and longer durations (circles and squares) are adequately described by functions derived from Sperling and Harwerth's subtractive-interaction model of spectral sensitivity.13 For the 5 msec, 0.35-deg test probe (diamonds), the data conform to a unimodal luminosity function.

Although all of the esotropic observers exhibited lower spectral sensitivities under binocular viewing conditions when the test probes were restricted to the deviating eye's suppression scotoma, the shapes of the spectral sensitivity functions for the monocular control condition, and for the strabismic suppression condition are similar regardless of whether the test probe dimensions favored detection by the chromatic mechanisms or by the luminance mechanisms. Therefore, in contrast to the wavelength-dependent loss in sensitivity exhibited by normal observers during the suppression phase of binocular rivalry, the loss of sensitivity associated with strabismic suppression in our esotropic observers appears to be independent of the stimulus wavelength. The different patterns of sensitivity loss associated with rivalry suppression for normal observers and strabismic suppression for esotropic observers are illustrated in Figure 4. In this figure, the mean loss of sensitivity produced by strabismic suppression in the five esotropic observers (open circles) and by rivalry suppression in the three normal observers (filled circles) is plotted as a function of wavelength for the 20 msec, 0.85-deg test probe. Also included in Figure 4 are rivalry suppression data obtained from one of our normal observers in a previous study4 (filled circles, dashed line). The loss of sensitivity obtained during rivalry suppression for normal observers is obviously dependent on the stimulus wavelength, whereas the function for the esotropic observers indicates that strabismic suppression pro-
duces an equal reduction in sensitivity for all stimulus wavelengths (slope = 0.0002 ± 0.04, least squares criterion). The differences between normal rivalry suppression and strabismic suppression are particularly apparent in the short wavelength region of the spectrum where rivalry suppression results in a dramatic reduction in spectral sensitivity.

Rivalry Suppression in Strabismic Observers

When similar objects are presented to corresponding points in the two eyes of observers with strabismus of early onset, regions in the normally deviating eye are almost constantly suppressed. When, however, dissimilar objects, objects that induce binocular rivalry in normal observers, are presented to the two eyes of a strabismic observer with little or no amblyopia, the observer experiences an alternating suppression of each eye. Because the temporal characteristics and the phenomenal description of the alternating suppression produced by rivalrous stimuli are similar, we wondered if our strabismic observers, like our normal observers, would demonstrate a wavelength-dependent loss of sensitivity when suppression was produced by rivalrous stimuli. To answer the question, spectral sensitivity functions were measured for the esotropic observers' deviating eyes during the suppression pro-
Fig. 5. Increment-threshold spectral sensitivity functions for the deviating eye of an esotropic observer for monocular viewing (open circles) and for the suppression phase of binocular rivalry (orthogonal gratings, filled circles). The stimulus subtended 0.85 deg and was presented in 20 msec flashes. The lower inset shows the log ratio of the sensitivity obtained during the monocular and binocular (suppression phase) viewing conditions. For comparison, the difference function obtained for binocular rivalry for a normal observer is also included in the inset.

duced by rivalrous stimuli (ie, orthogonally oriented gratings presented to the left and right eyes were used to produce suppression). Thus, in this experiment the methods and stimuli were identical to those used to assess rivalry suppression in our normal observers.

Figure 5 illustrates typical increment-threshold spectral sensitivity functions determined for the deviating eye of an esotropic observer for monocular viewing conditions (open circles) and during the suppression produced by the rivalrous stimuli (filled circles). Although the strabismic observers reported an alternating suppression of each eye when they viewed the orthogonally oriented patterns, the shapes of the spectral sensitivity functions determined for the suppressed, deviating eyes were identical to those obtained under monocular viewing conditions. The lower inset in Figure 5 shows that the sensitivity of the deviating eye was reduced by the suppression initiated by the rivalrous stimuli; however, the reduction in sensitivity was approximately constant for all stimulus wavelengths. Clearly the strabismic observers failed to demonstrate the dramatic reduction in sensitivity for short wavelength stimuli characteristic of rivalry suppression in normal observers.

Discussion

The similarity between the normal observers' increment thresholds obtained under monocular viewing conditions and those obtained during the dominance phase of rivalry indicates that the subjects' spectral sensitivity was essentially normal during rivalry dominance. However, in agreement with previous investigations of increment thresholds during binocular rivalry, all the normal observers demonstrated some reduction in sensitivity during rivalry suppression. More importantly, for test probe dimensions that normally biased detection toward the chromatic mechanisms, rivalry suppression resulted in a wavelength-dependent loss in sensitivity that was associated with a change in the shape of the suppressed eye's spectral sensitivity function. If it is assumed that the shape of the spectral sensitivity function indicates the type of psychophysical mechanism that dominates detection, the alterations in the shape of the spectral sensitivity function observed during binocular rivalry indicate that rivalry suppression in normal observers involves a selective reduction in the sensitivity of chromatic mechanisms relative to luminance mechanisms. As a consequence of the differential attenuation of chromatic and luminance mechanisms, the magnitude of the suppression measured with a test probe will depend not only on stimulus wavelength but potentially on a variety of stimulus variables (eg, background luminance, stimulus size, and duration, etc.), which normally affect spectral sensitivity.

In contrast to the mechanism-specific loss in sensitivity demonstrated by normal observers during binocular rivalry, the esotropic observers exhibited an approximately equal reduction in the sensitivity of both the chromatic and luminance mechanisms during strabismic suppression. Schor's has shown previously that the optimal stimuli for inducing binocular rivalry suppression and strabismic suppression are different. Our experiments quantitatively show that the types of information suppressed during binocular rivalry in normal observers and strabismic suppression in esotropic observers are also different. Thus, it seems unlikely that normal binocular rivalry and strabismic suppression are mediated by identical mechanisms.

In agreement with previous investigations of binocular rivalry in amblyopic subjects, the esotropes reported an alternating suppression of each eye under rivalrous conditions. However, the alternating suppression process initiated in the esotropic observers by the orthogonally oriented grating patterns did not result in a wavelength-specific loss of sensitivity. The differences in the patterns of suppression demonstrated in Figure 5 by the strabismic and normal observers...
under rivalrous viewing conditions indicate that the esotropic subjects did not experience normal binocular rivalry. Instead, the pattern of sensitivity loss exhibited by the esotropic subjects was identical for the parallel and orthogonally oriented grating patterns. Therefore, it appears that the esotropes manifested a form of strabismic suppression under rivalrous conditions.

In summary, the results indicate that adults with constant esotropia of early onset do not demonstrate normal binocular rivalry and that strabismic suppression is not simply a form of normal binocular rivalry with different temporal characteristics. However, the present study does not disprove the commonly held view that binocular rivalry is an important phase in the development of strabismic suppression, ie, the facultative suppression of Worth.1

Key words: binocular rivalry, strabismus, suppression, spectral sensitivity, binocular vision, chromatic mechanisms, luminance mechanisms

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References