

Suprathreshold Contrast Sensitivity in Experimentally Strabismic Monkeys

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Human strabismic amblyopes show deficits in spatial vision that can be revealed in a variety of visual tasks. In particular, they show a reduced sensitivity to contrast for a wide range of spatial frequencies. The ability of strabismic amblyopes to process contrast information at levels well above detection threshold is less well understood and somewhat controversial. In the course of investigating the neural basis of strabismic amblyopia we studied contrast processing both at and above detection threshold in experimentally strabismic monkeys (*Macaca nemestrina*). First we trained them to perform a contrast *detection* task and measured their contrast sensitivity for a wide range of spatial frequencies. Then we trained them to *discriminate* between two gratings that were identical except for their contrast. We show that these monkeys exhibit deficits in both tasks. The deficits in the contrast discrimination task cannot be solely attributed to their deficit at threshold.

Strabismus Amblyopia Contrast sensitivity

INTRODUCTION

Strabismus is a misalignment of the optical axes. It is a condition often associated with amblyopia in the human population (von Noorden, 1967; Ciuffreda, Levi & Selenow, 1991). Amblyopia is commonly defined as a loss of visual acuity in one or both eyes that is associated with no detectable pathology (von Noorden, 1985). Human strabismic amblyopes have been shown to have deficits in spatial vision that are revealed in a large variety of visual tasks. These include a lower Snellen acuity (Sireteanu, Fronius & Singer, 1981; Bradley & Freeman, 1985; Levi & Klein, 1985), a reduced sensitivity to contrast at threshold (Hess & Howell, 1977, 1978), an impairment in many hyperacuity tasks (Levi & Klein, 1982; Bedell, Flom & Barbeito, 1985; Flom, Simpson & Jiang, 1991), a reduced ability to process motion information (Levi, Klein & Aitsebaomo, 1984) and deficits in their ability to process spatial phase information (Pass & Levi, 1982; Lawden, Hess & Campbell, 1982; MacCana, Cuthbert & Lovegrove, 1986).

To understand the neural basis for amblyopia it is necessary to study a satisfactory animal model. Evidence has accumulated in recent years to support the view that monkeys made strabismic near birth develop spatial vision deficits similar to those of humans with strabismic amblyopia (e.g. von Noorden & Dowling, 1970; Kiorpes, Carlson & Alfi, 1989; Kiorpes, 1992). In particular, several studies have shown that monkeys with experimental strabismus show abnormalities in their ability to detect contrast that are similar to those of human amblyopes (Harwerth, Smith, Boltz, Crawford & von Noorden, 1983; Kiorpes, 1989; Kiorpes, Kiper & Movshon, 1993). Like human strabismic amblyopes, they suffer from a loss of contrast sensitivity for a wide range of spatial frequencies. Although losses in the low spatial frequency range have been reported (Harwerth *et al.*, 1983), the reduced sensitivity is particularly marked for medium and high spatial frequencies.

These studies measured contrast detection thresholds but did not provide any information about the processing of contrast at suprathreshold levels in the visual system of experimentally strabismic monkeys. Several studies of suprathreshold contrast processing in human strabismic amblyopes have been done and the conclusions differ depending on the psychophysical task that was used. Despite being severely impaired at threshold levels, the contrast matching ability of human strabismic amblyopes was found by Hess and Bradley (1980) to be normal for suprathreshold stimuli. In their studies, the subjects used the method of adjustment to match the contrasts of two sinusoidal gratings, one presented in each eye. Subjects with strabismic amblyopia were able to match the contrasts extremely well as soon as the reference contrast was above detection threshold.

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However, other researchers tested contrast discrimination in strabismic amblyopes for a wide range of spatial frequencies and found a significant impairment at all the frequencies and contrast levels tested (Ciuffreda & Fisher, 1987). These authors used a two-alternative forced-choice procedure to measure the contrast increment thresholds of their subjects' non-deviated and deviated eyes and found elevated thresholds in the deviated eyes for all the conditions of their experiment. Levi, Harwerth and Manny (1979) had also shown an abnormality for the detection of high contrast sinusoidal gratings in strabismic amblyopes using a reaction time paradigm. Strabismic subjects showed longer reaction time to detect the stimuli when they used their amblyopic eyes. In addition, the reaction time vs stimulus contrast curves of deep amblyopes lack the biphasic shape typically observed in normal subjects. Their results are in agreement with a previous study by Levi and Harwerth (1978) which showed that visually evoked potentials in strabismic amblyopes presented with flashing high contrast gratings had a lower amplitude and a phase lag compared to those of normal subjects.

The present study investigates the ability of monkeys with experimental strabismus to process luminance contrast information. In the first experiment, we measured the animals' ability to detect patches of sinusoidal gratings vignetted by a two-dimensional Gaussian window. We obtained contrast detection thresholds for a range of spatial frequencies that allowed us to estimate the parameters of the contrast sensitivity function (CSF) for each eye of each subject. In the second experiment, we asked the subjects to discriminate between two patches of grating that were identical except for their contrast. The subjects had to indicate which of two gratings had the highest contrast. In a similar experiment, Smith, Harwerth, Levi and Boltz (1982) showed that the suprathreshold contrast discrimination abilities of normal monkeys are similar to that of human observers. The contrast discrimination functions of these animals showed facilitation effects at contrasts just around detection threshold and masking effects for higher contrasts. We found that our strabismic monkeys showed deficits in both tasks and that these deficits resemble those of human strabismic amblyopes. These results have been presented in preliminary form (Kiper, Kiorpes & Movshon, 1990).

METHODS

Subjects

Four monkeys (*Macaca nemestrina*) were subjects in the experiments described in this study. Three of these animals were made strabismic early in life while one grew' up with normal visual conditions and was used as a control subject for all the experiments. The three strabismic animals were made esotropic by transection of the lateral rectus muscle and resection of the medial rectus muscle of the left eye (see Kiorpes *et al.*, 1989). All the procedures to induce strabismus were performed under ketamine hydrochloride anesthesia. Informal observations of the animals' eye movements showed that the resulting ocular motility was good and that they were able to hold fixation with their operated eyes.

The subjects' age of onset of strabismus, refractive errors, angle of deviation and grating acuity are shown in Table 1. The clinical history of some of these subjects and behavioral measures of their visual acuity have been published elsewhere (Kiorpes *et al.*, 1989, 1993; Kiper, 1994). For all subjects the refractive errors and accommodative ranges were checked behaviorally (Kiorpes & Boothe, 1984). The errors were small enough to be within the subjects' accommodative range and all subjects were therefore tested without correction.

All the data presented in this study were collected when the subjects were older than 1 yr, an age when most visual functions in the primate have approached or attained adult levels (Boothe, Dobson & Teller, 1985). The care and housing of the animals conformed to the *NIH guide for the care and use of laboratory animals.*

Psychophysical methods

All the stimuli used in these experiments were generated by a computer and displayed on monitors placed in front of the animal. The stimuli were generated on a high resolution monitor (Mitsubishi Diamondscan HL6605, normal persistence phosphors) with a resolution of 750×480 pixels driven by a personal computer (Zenith 386) equipped with a AT&T Truevision Vista graphics board. All the stimuli were presented on a grey background with a mean luminance of 60 cd/m². The vertical refresh rate was fixed at 60 Hz. The screen subtended from 11.5 to 40 deg according to the viewing distance of the animal.

TABLE 1. Visual characteristics and spatial resolution of the subjects used in this study

Nam	e	Age at surgery (days)	Refraction (D)	Angle of esotropia (prism D)	Spatial resolution (c/deg)
GH	Right eye		+1.00 + 0.50+90		29.7
	Left eye	45	+1.00 + 0.50 * 90	19	19.0
FT	Right eye		+ 1.75 s.		21.6
	Left eye	22	+1.75 + 0.25 * 180	23	6.6
HC	Right eye		+ 2.25		24.2
	Left eye	86	+2.25 + 0.5 + 180	11	12.5
TJ	Right eye				17.9
	Left eye				18.0

The spatial resolution estimates were extrapolated from the contrast sensitivity curves measured for each animal.

Contrast detection. For the first experiment, the target stimulus was a two-dimensional patch containing a sinusoidally modulated grating that had to be discriminated from a uniform field of equal space-averaged luminance. The target was vignetted by a Gaussian window with a standard deviation of 0.75 deg. When the spatial frequency of the grating was below 1 c/deg the standard deviation of the Gaussian window was raised to 1.5 deg to display a minimum of three cycles of the grating pattern. The mean luminance of the stimuli, equal to that of the background, was 60 cd/m^2 . For one subject (FT) the standard deviation of the Gaussian window was 2.5 deg. Preliminary experiments had shown that this subject would not perform well with smaller stimuli. One may speculate that this subject has oculomotor abnormalities such as unsteady or eccentric fixation that could have contributed to her poor performance with small stimuli but since we did not monitor oculomotor behavior quantitatively, we do not have a definitive answer to that question.

The animal, who was seated inside in a testing cage, was trained to identify the location of the target by pulling one of two bars mounted inside the cage. The spatial frequencies of the stimuli were chosen to span the range visible to the animal in octave intervals. Four to six frequencies were chosen for each eye. The experiments described in this study used the method of constant stimuli. Five contrast values at each spatial frequency were chosen to span the performance range from chance to 100% correct. The stimuli were presented in a randomized block design. Each block contained one presentation of each stimulus, in pseudorandom order. Forty trials per stimulus condition were collected. The monocular data were collected in a counterbalanced fashion.

Contrast discrimination. In the second experiment, the animal was presented with two patches made of a



FIGURE 1. Contrast sensitivity curves for a normal (a) and three strabismic subjects (b, c, and d). For the strabismic subjects the solid symbols represent data from the deviated eye, open symbols from the fellow eye.

vertical sinusoid vignetted by a two-dimension Gaussian. The spatial frequency, size and phase of the patches were identical, but their contrasts were different. The animal was trained to indicate the location of the stimulus with the highest contrast. The negative stimulus had a contrast called the "pedestal", the target's contrast was equal to the pedestal plus an increment. For this experiment, we kept the number of cycles in the stimuli constant at 20 cycles (10 for the lowest spatial frequency), displayed within ± 2 SDs of the Gaussian window.

We measured contrast increment thresholds for three spatial frequencies and a wide range of contrasts. The spatial frequencies were chosen to span the range visible to the animal (as measured by the contrast sensitivity function) and the pedestals ranged from 2 to 64% contrast at regular logarithmic intervals.

Experimental procedure

For all the experiments, the stimulus presentation was controlled by the animal. When the animal put its face in a mask mounted on top of the testing cage the stimuli were displayed. The stimuli remained displayed as long as the face was in the mask and no response was given. The use of such a mask has the advantage of allowing precise control of the viewing distance without having to physically restrain the animal. In addition, it allows monocular viewing by securing a shutter that blocks the view of one eye in front of the mask's eye openings. During all the experiments, the animals viewed the display through their natural pupils.

Correct responses were rewarded by 0.25 ml of diluted (40%) apple juice, incorrect responses were followed by an audible tone which delayed the presentation of the next stimulus. The duration of the tone was under the experimenter's control and was adapted to optimize each animal's performance.

We used a maximum likelihood method to fit the integral of a Gaussian to each set of data (Finney, 1971). This analysis yielded estimates of thresholds' and standard errors of the estimate for each condition. Threshold was defined as the 75% correct point. Contrast sensitivity for a given spatial frequency is defined as the inverse of the contrast threshold for that frequency.

RESULTS

Contrast detection

Figure 1(a) shows the data for the normal subject TJ. The curves fit through the contrast sensitivity data are double exponential functions of the form:

$$k_{s}(\omega k_{\omega})^{\alpha} e^{-\beta \omega k_{\omega}}$$
(1)

where ω is spatial frequency. The four free parameters affect primarily the steepness of the low frequency (α) and high frequency (β) portions of the curve, lateral shifts along the frequency axis (k_{ω}), and vertical shifts along the sensitivity axis (k_s). This function accounts well for our contrast sensitivity data in monkeys (Kiorpes, 1989). The solid circles represent the data obtained with the right eye and the open circles with the left eye. Examination of the shape of the curves obtained from TJ reveals that they have the typical bandpass characteristics that have been described in the literature both with human subjects and monkeys. In addition, TJ's data reveal that this animal showed no significant differences in sensitivity between the two eyes tested independently. The two curves peak at the same spatial frequency (3 c/deg) and have the same shape.

The data obtained from the strabismic subjects are shown in Fig. 1(b, c, d). They differ from the normal data in several respects. Most importantly, the deviated eyes of all three subjects showed a decreased sensitivity for a wide range of spatial frequencies. This loss of sensitivity was especially pronounced at medium and high spatial frequencies. The pattern of contrast sensitivity loss is similar to that reported with human strabismic amblyopes (Hess & Howell, 1977, 1978) and with monkeys made experimentally strabismic in other laboratories (Harwerth *et al.*, 1983). It is important to note that despite these losses in contrast sensitivity, the strabismics' curves also showed the same bandpass



FIGURE 2. Contrast increment thresholds as a function of pedestal contrast for the normal subject TJ at three spatial frequencies. The symbols next to each ordinate represent the detection threshold for that particular spatial frequency. Solid symbols are for the left eye, open symbols for the right eye.

characteristics described above. The double exponential function used to fit the contrast sensitivity data of normal subjects is adequate to capture the characteristics of the deviated eyes' data as well.

Data obtained from the three strabismic monkeys also show that the severity of the deficits is quite variable. While HC and FT showed considerably reduced sensitivities for a wide range of spatial frequencies, GH exhibited relatively mild deficits for most of the spatial frequencies tested. The severity of the deficits induced by strabismus has been shown to depend on a variety of factors such as the size of the deviation, age of onset, fixation pattern and presence of refractive errors (Kiorpes *et al.*, 1989). The same study showed that about 40% of the monkeys raised with experimental strabismus do not develop any visual deficits at all, a proportion similar to that reported in the human population (von Noorden, 1980).

The extrapolation of the contrast sensitivity curve to the spatial frequency axis provides an estimate of the highest spatial frequency that the subjects can resolve at a contrast of one. We will refer to this estimate of spatial resolution as acuity. The extrapolated grating acuities for each subject are shown in the rightmost column of Table 1.

Contrast discrimination

The results of the contrast detection experiments showed that these monkeys with experimentally induced strabismus have deficits for the processing of contrast at threshold levels. To determine whether deficits are present at higher levels of contrast, we measured their ability to discriminate between two stimuli that differed only in their contrasts, and made these measurements at contrast levels well above threshold.

The results of this experiment are shown in Fig. 2 for the normal subject TJ. The functions relating contrast increment thresholds to pedestal contrast have a characteristic shape. This type of function has been observed in normal human subjects by many researchers using similar paradigms (Nachmias & Sansbury, 1974; Legge & Foley, 1980; Kulikowski & Gorea, 1978). Their characteristic features are that at subthreshold pedestal contrasts the increment thresholds fall below detection threshold (the "dipper effect"); for visible pedestal contrasts, increment thresholds rise in proportion to pedestal contrast raised to a power of about 0.6. Both characteristics were present in TJ's data. The symbols plotted next to the ordinate show the increment thresholds on a 0% contrast pedestal, i.e. the detection thresholds. Discrimination performance was best for





FIGURE 3(a,b). Caption on next page.



FIGURE 3. Contrast increment thresholds for the strabismic subjects. Symbols as in Fig. 2.

pedestals around detection threshold. For pedestals of higher contrast, the increment thresholds rose with a slope around 0.5 for TJ.

The dip in the contrast increment data has been documented and discussed in the human literature (Nachmias & Sansbury, 1974; Legge & Foley, 1980; Wilson, 1980). It is important to realize that the dip is to be expected from the shape of the psychometric function for the detection of contrast. In the extreme, hypothetical case of a psychometric function being a step function (where the detection probability is 0 below threshold and 1 at and above threshold), the subject would never detect subthreshold pedestals and therefore always show an increment threshold equal to the detection threshold. Since the increment thresholds are defined as the difference between test and pedestal contrast, the increment thresholds for subthreshold pedestals would decrease with a slope of -1 on these graphs, fall to 0 for a pedestal at threshold, and then rise as a function of pedestal contrast. Because real psychometric functions are not step functions, the observed dips do not show these extreme characteristics.

The data for the strabismic monkeys are shown in Fig. 3. Each animal was tested at three different spatial

frequencies, chosen to be below, at and above the optimal spatial frequency of the previously measured CSF. Note that in some conditions the detection thresholds found in this second experiment differ from those shown previously. Although we do not have a complete explanation for these discrepancies, they are likely due to the differences in stimulus size. For example, for subject FT at the highest spatial frequency. the stimulus size was smaller in the second experiment compared to the first one by a factor of two. As discussed previously, stimulus size has a strong effect on the performance of some strabismic subjects. It is readily apparent that the curves for each eye show the dip and the linear rising portion characteristic of contrast increment threshold functions. It is also clear that in almost all conditions, the increment thresholds were higher in the deviated eye than in the non-deviated eyes. This appeared to be true especially for the high spatial frequencies, although FT showed significant threshold elevations for the 2 c/deg gratings. In agreement with the results of Ciuffreda and Fisher (1987), these strabismic subjects showed deficits in contrast processing at suprathreshold levels. It is interesting to note that the slopes of the rising part of the deviated eyes curves were very similar to those of the normal subject and were all very close to the value of 0.6 that has been frequently reported in the literature (they average 0.57 in the deviated eyes and 0.65 in the non-deviated eyes). Because the slope of the rising part of the curves varies between subjects and depends on the spatial frequency of the target (Bradley & Ohzawa, 1986), it is difficult to further interpret the significance of these values. The point to note is that for each subject at each spatial frequency tested, the slopes were similar in the fellow and deviated eyes. However, it appears that the dips in the deviated eyes functions were shifted to the right. For example, the lowest increment thresholds for subject HC with a spatial frequency of 6 c/deg [Fig. 3(c, top panel)] were for a pedestal contrast of 0.02 in the fellow eye and of 0.08 in the deviated eye. This right shift is to be expected from the elevated detection thresholds in the deviated eyes. It also may be the case that the dips in the deviated eyes are typically shallower than those of the nondeviated eyes. Since we focused here primarily on the processing of contrast at suprathreshold levels, we did not sample the subthreshold range very finely. The apparent differences in depth of the dips might disappear with a larger number of measurements in that range of pedestal contrasts.

The obvious issue to address is that of the relationship between the deficits observed at threshold and those at suprathreshold contrast levels. Because a given pedestal contrast is not equally detectable in the two eyes of the strabismic subjects, one might argue that the deficits observed at suprathreshold levels reflect only this difference in the detectability of the stimuli and do not reveal an abnormality in suprathreshold contrast processing. In fact, several authors proposed that the deficits of strabismic amblyopes in a variety of visual tasks could be accounted for by their deficits in contrast sensitivity (Bradley & Freeman, 1985; Barbeito, Bedell & Flom, 1988; Levi & Klein, 1992). To determine whether the suprathreshold deficits revealed in this study could be accounted for by the contrast sensitivity deficit, we transformed the data in Fig. 3 to express contrast in multiples of detection threshold for each spatial frequency. This is equivalent to showing what the discrimination performance would be if the pedestals were equally detectable (i.e. at equal multiples of detection threshold) in the two eves. If the only deficit of the strabismic monkeys was a deficit in contrast sensitivity, this transformation should superimpose the curves from the two eyes. The result of this analysis is shown in Fig. 4. The solid and open symbols represent the data from the deviated and fellow eye respectively. The triangles next to the ordinate represent the detection thresholds, which are superimposed at a value of 1 by this transformation. This figure shows that the deficits of the three strabismic subjects are reduced by this transformation and even completely disappear for subject HC. However, there are also cases where the deficits are still clearly present, e.g. FT at the middle spatial frequency and GH at the highest spatial frequency. This result demonstrates that the deficits of these animals are not restricted to a reduced sensitivity to contrast at threshold but include an impairment in their ability to process suprathreshold contrasts.

DISCUSSION

The goal of this study was to determine whether monkeys with experimental strabismus displayed deficits in their ability to process contrast at threshold and suprathreshold levels. The contrast detection experiment shows that they exhibit elevated thresholds for a wide range of spatial frequencies. The deficits are particularly marked for medium and high spatial frequencies, as it is typically the case for humans with strabismic amblyopia. This result is in agreement with several other reports for strabismic monkeys (Harwerth et al., 1983; Kiorpes, 1989, 1993). The similarity between the deficits shown in this study and those observed in the human population also confirm that these subjects represent an excellent animal model for the study of strabismic amblyopia (von Noorden & Dowling, 1970; Harwerth et al., 1983; Kiorpes et al., 1989; Kiorpes, 1992).

The contrast discrimination experiment shows that monkeys raised with strabismus can develop deficits in



FIGURE 4(a,b). Caption on next page.



FIGURE 4. Same data as Fig. 3, but with contrast expressed in multiples of detection threshold. The triangles near the ordinates represent both eyes' detection thresholds normalized at a value of 1. Average standard errors for each subjects are shown on the right of each graph. Other symbols as in Fig. 2.

their ability to process contrast information at levels well above detection threshold. Although the contrast matching ability of strabismic amblyopes appears to be normal (Hess & Bradley, 1980; Hess et al., 1983), our findings show that they have abnormalities in their ability to process contrast information at suprathreshold levels. Hess et al. (1983) tested two strabismic subjects using a paradigm similar to that reported in this study. Both subjects performed as well with the amblyopic eye as with their fellow eye for pedestal contrasts well above threshold. It must be noted however that of these two subjects, one was not an amblyope (contrast detection thresholds for the spatial frequencies tested were similar in both eyes) and the other one had only a mild amblyopia. A result similar to that obtained in this study was reported by Ciuffreda and Fisher (1987). These researchers reported elevated contrast increment thresholds for all the spatial frequencies and pedestal contrasts they tested in a population of human strabismic amblyopes. The apparent discrepancy between the conclusions reached by Hess and Bradley (1980) and Ciuffreda and Fisher (1987) is likely to be due to the difference in the measures used in these studies. Ciuffreda and Fisher measured contrast increment thresholds using a spatial two-alternative forced-choice procedure similar to the one used in this study. Hess and Bradley used the method of adjustment and measured the accuracy of contrast *matching* rather than the ability to detect small differences in contrast. Given the differences in these measures, the absence of deficit in one study does not contradict the findings of a deficit in the other. In fact, anomalies in contrast increment thresholds in subjects showing no contrast matching anomalies have been reported previously (Hess, Bradley & Piotrowski, 1983), but only with anisometropic or meridional amblyopes. In any case, when tested under similar conditions, the strabismic monkeys and the humans with strabismic amblyopia showed a similar pattern of loss.

This study also reveals that the deficits observed in these strabismic monkeys cannot be solely attributed to the fact that a given pedestal contrast is not equally detectable in both eyes. Normalization of the contrast increment threshold by the detection threshold at each spatial frequency failed to equate the performances of the two eyes in several cases. The fact that the deficits of strabismic amblyopes cannot be completely accounted for by their deficit in contrast sensitivity has been reported in other studies as well (Kiorpes *et al.*, 1993).

In recent years, a variety of models have been proposed to account for the spatial vision capabilities of the primate visual system (see Graham, 1989 for a review). Most of these models propose that the initial stage of processing consists of linear spatio-temporal filters, each tuned to a narrow range of stimulus spatial frequencies and orientations. According to these models, the contrast information is then processed more centrally through a non-linear stage, often referred to as the non-linear transducer stage (Wilson, 1980). The contrast sensitivity deficits of strabismic amblyopes can be interpreted as indicative of a reduced sensitivity of the initial linear spatial frequency filters. Indeed, there are indications that this may be the case for the monkeys used in this study (Kiper et al., 1992). However, the fact that the contrast increment thresholds of these animals are not equal in both eyes after being normalized by detection threshold suggests that animals with severe amblyopia also have abnormalities in their processing of contrast at more central stages of the visual system. Their internal representation of contrast, or contrast gain, is abnormal throughout the range of visible contrasts. These deficits in contrast gain appear to be present in subjects with severe amblyopia (like subject FT in this study) and are dependent on the spatial frequency of the stimulus [e.g. subject GH shows contrast gain deficits for a spatial frequency of 8 but not 4 c/deg, Fig. 4(a)]. Subjects with less severe amblyopia, like HC in this study or the human subjects of Hess et al. (1983) do not show these contrast gain abnormalities. Thus, the results of this study suggest that in addition to a reduced absolute sensitivity to contrast, monkeys with severe strabismic amblyopia also have a deficit in contrast gain at suprathreshold levels.

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