

Scale-dependent loss of global form perception in strabismic amblyopia

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Amblyopic humans are known to have a range of spatial vision abnormalities. Prior studies have documented amblyopic deficits in global form perception but have typically used only one set of stimulus parameters. Our aim in this study was to examine the extent and nature of global form perception deficits in strabismic amblyopia using a range of spatial scales and pattern types. Glass patterns are random dot stimuli in which the local orientations of paired dots must be integrated over space to yield a global form percept. We measured coherence thresholds for discrimination of pattern structure in translational (linear) and concentric Glass patterns at three spatial scales in two control and six amblyopic observers. We found that sensitivity to Glass patterns depended on both spatial scale and pattern type in all observers. Participants with a history of abnormal early visual experience showed greater interocular threshold difference when the discrimination was based on translational patterns than when it was based on concentric patterns, and the degree of amblyopic loss was greatest at fine spatial scale. Our results show that the nature and extent of global form vision deficits vary substantially with stimulus parameters and are greatest at fine spatial scales.

Keywords: amblyopia, strabismus, Glass patterns, global form

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Introduction

Amblyopia is clinically defined as a deficit in optotype acuity with no clear organic cause, such as retinal or optic nerve damage. It is a developmental disorder that is frequently associated with abnormal visual experience early in life due to strabismus (a misalignment of the ocular axes), anisometropia (an inequality between the two eyes in refractive error), or form deprivation (e.g., from cataract or ptosis). Amblyopia often results in degraded stereopsis as well as spatial vision (see Kiorpes & McKee, 1999; McKee, Levi, & Movshon, 2003). It has long been known that amblyopes suffer losses in contrast sensitivity at a range of spatial scales below the acuity limit (e.g., Hess & Howell, 1977; Levi & Harwerth, 1977). However, contrast sensitivity deficits alone are not sufficient to characterize the full pattern of perceptual deficits associated with amblyopia.

Many recent studies characterizing the nature of amblyopia reveal “higher order” spatial deficits that cannot be easily predicted from low-level deficits such as simple acuity and contrast sensitivity (e.g., Kozma & Kiorpes, 2003; Levi,

Yu, Kuai, & Rislove, 2007; Simmers, Ledgeway, & Hess, 2005; Simmers, Ledgeway, Hess, & McGraw, 2003; Wang, Ho, & Giaschi, 2007). These studies raise questions about the kinds of higher order deficits that exist, as well as the degree to which these deficits can be predicted from low-level spatial visual impairment. In general, tasks that require spatial integration, such as contour integration, reliably show impairment for the amblyopic eyes of human observers with strabismic amblyopia (Hess, McIlhagga, & Field, 1997; Kovacs, Polat, Pennefather, Chandna, & Norcia, 2000; Levi et al., 2007; Simmers et al., 2005; also, Hall, Bauer, & Kiorpes, 2004); the deficits are generally greater than would be expected from the acuity loss. Often performance with the fellow eye is also impaired. A similar pattern of loss has been shown in amblyopic non-human primates (Kozma & Kiorpes, 2003).

Spatial integration and segregation (Mansouri, Allen, & Hess, 2005; Mansouri & Hess, 2006) are essential for important processes in object recognition such as global pattern perception and figure–ground segmentation. Thus, it is important to understand the nature and degree to which these processes are impaired in amblyopia. Most prior studies of spatial integration ability in strabismic amblyopes

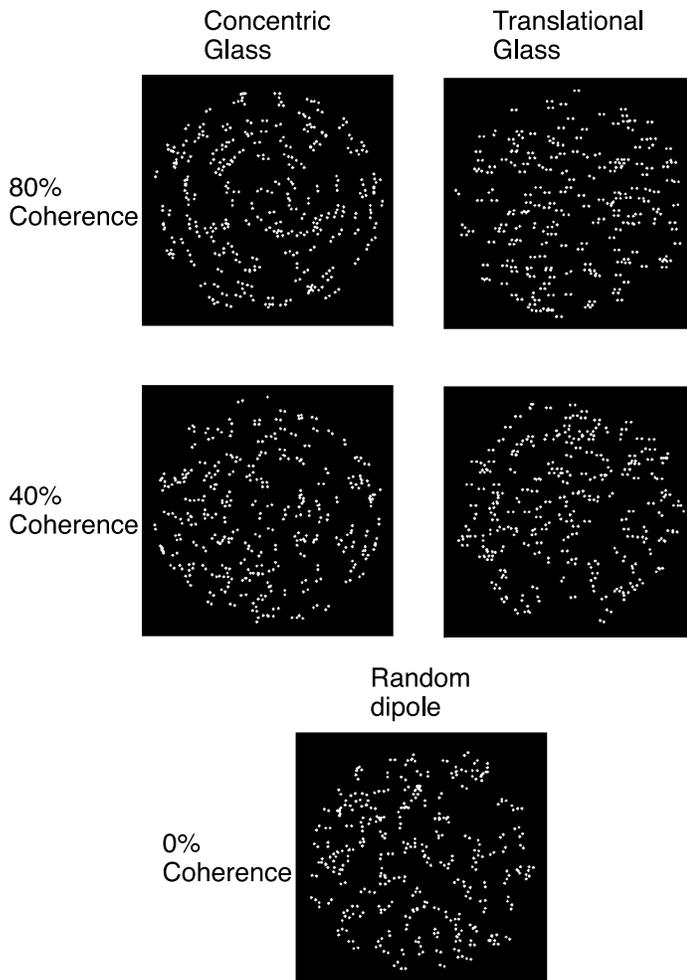


Figure 1. Schematic illustrations of the stimulus types used. We show the two types of Glass patterns: (left column) concentric and (right column) translational, at two coherence levels: (top row) 80% and (middle row) 40%. On each trial, a new Glass pattern stimulus was paired with a unique random dipole comparison stimulus that followed no geometric rule but had the same characteristics as the Glass pattern; one example is illustrated at the bottom. Note that these are schematic illustrations and not copies of the actual stimuli; these patterns each contain 200 dipoles; the actual patterns used contained 1024 dipoles each (see [Methods](#) section); the dot spacing is similar to the fine spatial scale actually used.

have used only a single spatial scale. However, as noted above, the basic spatial deficit in amblyopia varies with spatial scale. Data from animal studies show that deficits in global motion and form sensitivity vary in degree with the underlying spatial scale of the stimulus (Kiorpes, 2006; Kiorpes, Tang, & Movshon, 2006). Recently, one study investigated global contour processing in human amblyopes and found the deficits to depend strongly on spatial scale (Levi et al., 2007). At present, it is unclear what the relationship is between such spatial processing deficits and global form perception.

Glass patterns (Glass, 1969; Glass & Perez, 1973) have previously been used to test global form perception (e.g., Dakin, 1997; Dakin & Bex, 2001; Glass & Switkes, 1976; Kurki, Laurinen, Peromaa, & Saarinen, 2003; Wilson & Wilkinson, 1998; Wilson, Wilkinson, & Asaad, 1997). These stimuli are composed of a random dot pattern, a copy of which has been superimposed after a particular geometric transformation (such as linear translation, magnification, or rotation) has been applied to each dot within the initial pattern (see [Figure 1](#)). Glass patterns are ideal stimuli for studying form processing because the pattern must be perceived as a whole in order for its global form to be identified. Although the paired dots provide local orientation information, it is not sufficient to determine the global structure (Krekelberg, Vatakis, & Kourtzi, 2005; Wilson et al., 1997; Wilson, Switkes, & DeValois, 2004). In previous psychophysical studies, human observers have shown differential sensitivity to different forms of Glass patterns. Wilson et al. reported superior ability to detect concentric Glass patterns, those in which coherent dot pairs lie along a line tangent to one of several concentric circles about the center of the pattern, over patterns with parallel structure, known as translational or linear Glass patterns (Wilson & Wilkinson, 1998; Wilson et al., 1997; also Kurki & Saarinen, 2004). Dakin and Bex (2002) challenged the notion that these abilities actually differ suggesting that the heightened sensitivity for concentric patterns is an artifact resulting from the round aperture in which the stimuli are generally presented. However, Pei, Pettet, Vildavski, and Norcia (2005) showed, using ERPs, that responses to concentric Glass patterns are stronger than responses to linear patterns regardless of the form of the window (see also Alliston, 2004; Wilson & Wilkinson, 2003). The explanation put forward by Wilson et al. was that the differential sensitivity arises from detection of the patterns by different levels of the visual system and from the influence of local versus global pooling mechanisms (Wilson & Wilkinson, 1998; Wilson et al., 1997). These authors proposed that neurons in an extrastriate area such as V4 might subserve the perception of concentric and radial patterns while the weaker global summation for parallel patterns suggested an earlier substrate, perhaps V1/V2.

Clinical support for the idea that V4 neurons are important for detection of Glass patterns comes from a case study showing relatively selective losses for Glass pattern discrimination following damage to the human homologue of V4 (Gallant, Shoup, & Mazur, 2000). In addition, dynamic Glass patterns are more effective at activating areas such as V4 and LOC in humans than they are at activating early visual areas such as V1/V2 (Krekelberg et al., 2005; Ostwald, Lam, Li, & Kourtzi, 2008). Neurophysiological evidence from monkeys (Gallant, Connor, Rakshit, Lewis, & Van Essen, 1996) and imaging data from humans (Wilkinson et al., 2000) support the idea that concentrically organized patterns more strongly activate V4 and other downstream ventral pathway areas than do patterns with parallel structure.

Neurons in V1 and V2 respond only to the local signals in Glass patterns and do not represent the global form (Smith, Bair, & Movshon, 2002; Smith, Kohn, & Movshon, 2007). On balance, there is general agreement that global processing is necessary for the perception of structure in Glass patterns and this kind of global form perception depends on processing of areas in extrastriate cortex, most likely V4 or beyond.

Neurophysiological investigation into the neural mechanisms underlying the basic spatial deficits in amblyopia suggests that correlates emerge early, at the level of V1 (see Kiorpes & McKee, 1999). These neural deficits are correlated with the acuity loss in animal models of amblyopia (Kiorpes, Kiper, O’Keefe, Cavanaugh, & Movshon, 1998; Movshon et al., 1987), but they are not sufficient to account for the full profile of spatial vision losses. The pattern of results suggests that there may be additional neural losses downstream from V1 in extrastriate visual cortex. Recent imaging studies confirm the existence of abnormal activation patterns in striate cortex of amblyopic humans and show increasing deficiencies in higher order cortical areas (Lerner et al., 2006; Li, Dumoulin, Mansouri, & Hess, 2007; Muckli et al., 2006; see also, Anderson & Swettenham, 2006, for review). It is a matter of debate whether the kinds of losses shown in studies of contour integration described above are likely to depend on abnormalities in V1 or elsewhere (see Kozma & Kiorpes, 2003; Levi et al., 2007). Therefore, to probe the nature of higher order form perception losses that are likely to depend on extrastriate cortical function, Glass patterns are a reasonable choice.

A few studies have used Glass patterns to probe the nature of global form deficits following abnormal early visual experience. Lewis et al. (2002) found that human observers with either binocular or monocular form deprivation in early infancy showed elevated thresholds for detecting structure in concentric Glass patterns. Anderson and Swettenham (2006) report increased thresholds for the amblyopic eye of a strabismic amblyopic adult for concentric, radial, and linear dynamic Glass patterns compared to the fellow eye and to the performance of a visually normal control observer; the threshold increase was greatest for the linear pattern. Kiorpes (2006) reported deficits in static Glass pattern perception in amblyopic macaque monkeys. In that study, some impairment was evident for both eyes of the monkeys and the losses were deeper for linear patterns than for concentric ones. Additionally, the depth of the sensitivity losses increased with the underlying spatial scale of the Glass pattern, regardless of the form. Few studies have investigated global form perception tasks at more than one spatial scale in amblyopic humans. One exception is a study by Levi et al. (2007). Their tasks were performed at a number of viewing distances in order to investigate the effect of spatial scale on global contour integration with the eventual finding that global processing deficits in amblyopia do seem to depend strongly on spatial scale. However,

in that study, the spatial scale of both local and global information varied together.

In the present experiment, we measured sensitivity to global structure in translational and concentric Glass patterns. We evaluated the performance of six observers with a history of strabismus, a risk factor for amblyopia, and two observers with normal visual history. We include complete data sets for two control observers since there are little published data on the effects of varying pattern type and spatial scale on coherence threshold in typical human observers. We measured Glass pattern sensitivity at a range of spatial scales, from coarse to fine, for each eye of each observer. The aim of this experiment was to assess the nature of the impairment in global form perception in amblyopia. We found that our strabismic observers were indeed more deeply impaired, as measured by interocular ratio, for translational patterns compared to concentric ones. The losses were largest at the finest spatial scale. Some of these data have been presented in abstract form (Rislove, Hall, & Kiorpes, 2005).

Methods

Subjects

Eight human adults, ranging in age from 19 to 57, participated in this experiment. Two had no history of abnormal visual experience (ages 19 and 54), while six had a history of strabismus early in life, a risk factor for amblyopia. Clinical data from participants with a history of strabismus are presented in Table 1.

We considered Snellen acuity of 20/30 or poorer to be indicative of amblyopia; by this criterion, 5 of the 6 subjects with a history of strabismus were also amblyopic. All participants were experienced at psychophysical tasks prior to the start of data collection; all but two (authors ER and KS) were naive to the purpose of the experiment. Signed informed consent was obtained from each participant. Participants were offered \$25 compensation per laboratory visit. All procedures had received NYU institutional review board approval for use of human subjects in research.

Stimuli

Stimuli were generated on a PC with a Cambridge Research Systems VSG 2/3 graphics board. They were presented on a Silicon Graphics Interface color monitor with a frame rate of 100 Hz at a viewing distance of 1 m. The monitor subtended 22.8×16.7 deg of visual angle at the 1-m viewing distance. The stimulus consisted of two circular patches presented simultaneously, side by side, one of which contained a Glass pattern while the other contained a random dipole pattern. Each patch contained

Participant (age)		Refraction	Snellen acuity	Additional details
ER (21)	OD	−0.75 − 0.50 × 120	20/20	Strabismus surgery age 2.5; patching
	OS	−1.5	20/25	
NK (43)	OD	+1.00 + 1.50 × 90	20/30	Strabismic amblyopia
	OS	−0.75 + 0.75 × 85	20/20	
TW (27)	OD	−1.75 − 0.50 × 90	20/40	Strabismic amblyopia
	OS	−0.75 − 0.50 × 180	20/20	
SK (20)	OD	+6.00 − 0.5 × 135	20/20	Strabismic amblyopia; patching
	OS	+8.00 − 0.5 × 45	20/70	
GH (57)	OD	+3.75S	20/150	Strabismic amblyopia; strabismus surgery age 4.5
	OS	+3.00 − 1.25 × 165	20/20	
SP (55)	OD	−3.5 − 0.50 × 180	20/20	Strabismic amblyopia
	OS	−4.00	20/200	

Table 1. Clinical details of participants with a history of abnormal early visual experience due to strabismus.

1024 dot pairs (dipoles). Static Glass patterns were generated as a mixture of signal and noise dipoles; the mixture on each trial was specified by pattern coherence (see below; Figure 1). The orientation of only the signal dipoles was determined by a geometric transformation such as translation or rotation. Noise dipoles were those that had orientations that did not conform to the underlying geometric function of the pattern; the orientations of these dipoles were randomly generated on each trial. The comparison patch contained an equal number of dipoles to the Glass pattern patch, but the orientations had no defined relationship. The separation between members of a dot pair was the same regardless of whether it was a signal or noise dipole; separation between adjacent dipoles was unconstrained. All patterns were generated anew on every trial.

Each patch had a diameter of 256 pixels, with each pixel corresponding to 1.34 minutes of arc; each stimulus patch subtended 5.7 deg of visual angle in diameter at 1 m. Dots were 2 × 2 pixels; dot density was approximately 80 dots per square degree. The distance between the centers of the two patches was 7.7 deg of visual angle. Two types of Glass patterns were tested at each of 3 spatial scales, corresponding to dot separations: 5.36', 10.72', and 21.44'. Translational (linear) Glass patterns had the appearance of parallel lines, with the dipoles oriented horizontally within the circular window. Concentric Glass patterns had the appearance of a series of concentric circles, with each dot pair being oriented along a line tangent to a circle. Illustrations of stimulus structure are shown in Figure 1. The strength of the pattern structure in the Glass patterns was modulated by varying the coherence of the pattern. To vary coherence, we replaced signal dipoles with noise dipoles, which reduced the perceived strength of the underlying structure. The proportion of dot pairs in the pattern that conformed to the specified geometric transformation determined its coherence; Figure 1 illustrates two coherence levels, for example, 80% (top) and 40% (middle); the bottom panel represents a zero coherence comparison stimulus. Stimulus contrast was near 100%,

with white dots presented against a dark background (90% Michelson contrast).

Behavioral methods

On each trial, either the right-hand or left-hand patch contained a Glass pattern, the other contained a zero coherence random dipole pattern with no defined structure. The observer was seated in a comfortable high-back chair placed at the correct distance (1 m) from the screen; a headrest adjusted for each individual ensured that the viewing distance was correctly maintained. A spatial two-alternative forced-choice task was used, in which participants indicated which patch contained the pattern by pressing one of two buttons on a modified mouse that they held in their lap. Stimulus onset was preceded by a tone (500 Hz). Feedback was given in the form of a different tone, which followed an error; no tone followed a correct response. Trials were essentially self-paced by the observer; observers were encouraged to respond as soon as they had decided whether the right or left patch contained the coherent pattern. Reaction time was not measured. However, if the observer failed to respond within 5 s of stimulus onset, the screen was blanked and a new trial commenced.

Participants wore their own best correction, using that which enabled them to see best at the 1-m viewing distance. Each eye was tested separately, interleaving eyes to avoid fatigue; the non-test eye was covered with an eye patch. For all observers, the dominant eye was tested first to accord the benefit of practice to the non-dominant eye.

We used the method of constant stimuli to determine coherence threshold, the value of dot coherence required to support 75% correct performance. Each coherence threshold was estimated from a minimum of 300 trials; 60–120 trials were collected at each of 4–5 coherence levels chosen to span a performance range of 50% to 100% correct. A minimum of 80% correct at the highest coherence level

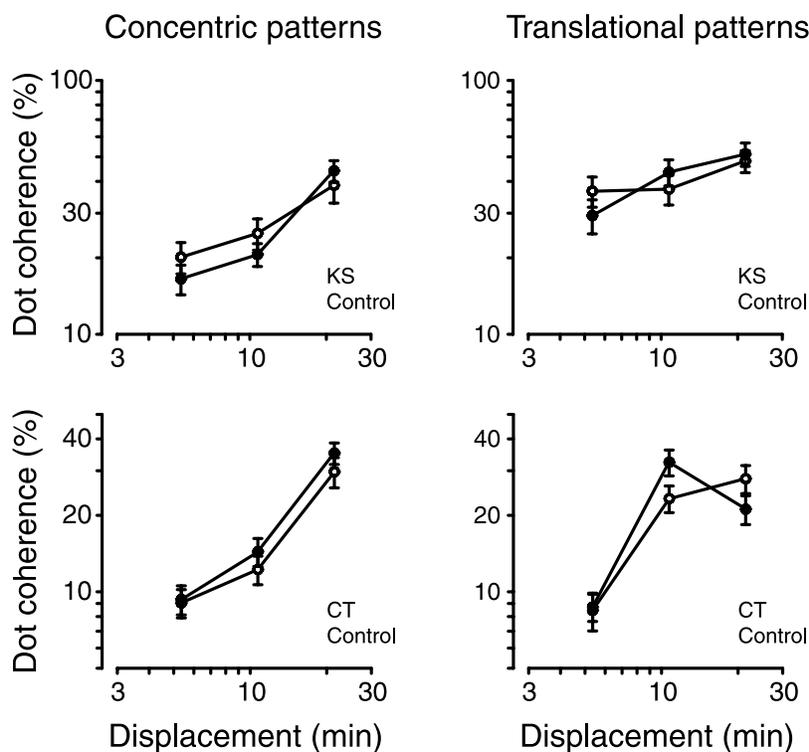


Figure 2. Sample Glass pattern thresholds as a function of dot-pair separation for each eye of the two control observers (KS, age 19, top; CT, age 54, bottom). Thresholds (± 1 SE) for concentric patterns are plotted in the left column; those for translational patterns are in the right column. Open symbols correspond to right eye data; filled symbols represent left eye data. Thresholds generally increase with increasing spatial displacement between paired dots. Neither observer showed a consistent interocular difference across conditions.

tested was required in order for a data set to be accepted for analysis. Threshold coherence and standard errors of estimate were calculated using Probit analysis (Finney, 1971) of the log-transformed data sets. Data collection was counterbalanced across dot separation for each pattern type.

Contrast sensitivity

Full contrast sensitivity functions were also measured for each eye of subjects with a history of strabismus. To measure contrast sensitivity as a function of spatial frequency, horizontal sinusoidal gratings were generated under computer control and viewed on the same monitor as the Glass patterns. The participant's task was to detect the presence of the grating patch on either the right or left side of the screen against a homogenous gray background that matched the grating in space-average luminance. Grating patches were vignetted by a two-dimensional spatial Gaussian. Spatial frequencies ranged from 1.5 to 12 cycles/deg in octave steps at a viewing distance of 1 m. Contrast threshold, the contrast at which performance fell to 75% correct, was established using the method of constant stimuli. Each threshold was estimated from at least 40 trials for each of 4 contrast levels, yielding a minimum of 160 trials per threshold. Threshold values and

standard errors of estimate were obtained by Probit analysis of the log-transformed data sets (Finney, 1971) using a maximum-likelihood technique.

Results

We measured sensitivity to Glass patterns of two types, concentric and translational, at three spatial scales, represented by a range of dot displacements from coarse to fine. Control observers were most sensitive to patterns of fine spatial scale, with generally more elevated thresholds for patterns of coarse spatial scale. Interestingly, amblyopes showed the greatest impairment when tested with patterns of fine spatial scale and were more impaired with translational patterns as compared with concentric patterns.

The general pattern of results is depicted in Figures 2 and 3, which show Glass pattern coherence thresholds as a function of dot displacement for the two control observers and two representative amblyopic observers. Figure 2 shows data for each eye of the two control observers. Observer KS (top) showed a steady increase in threshold with increasing spatial scale for concentric patterns (left column). This trend was less apparent but still present for translational patterns (right column). Her sensitivity was best for concentric patterns at fine spatial scales, and

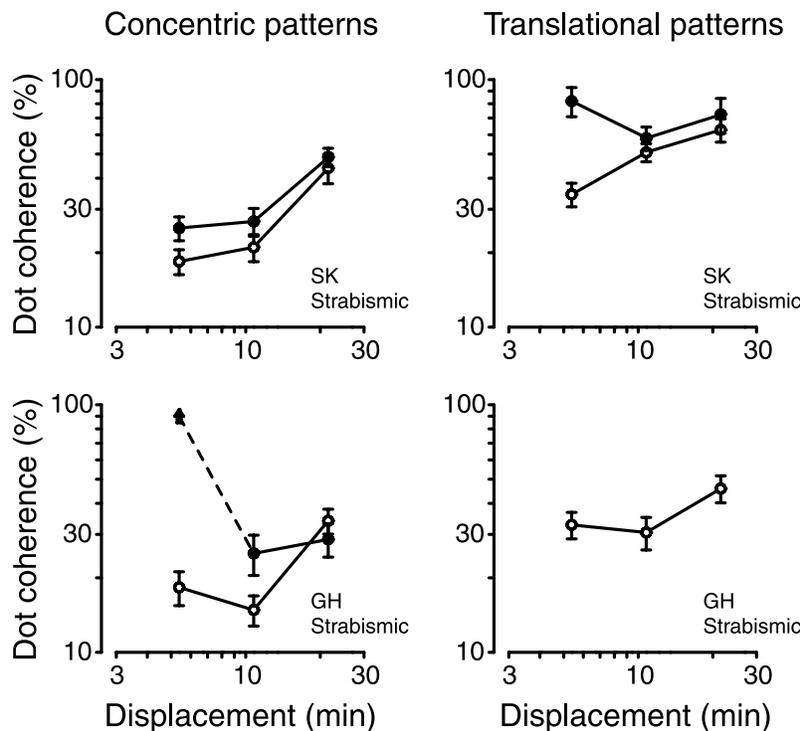


Figure 3. Sample Glass pattern thresholds as a function of dot-pair separation for each eye of the two representative amblyopic observers, (top) SK and (bottom) GH (see Table 1 for participant details). Thresholds (± 1 SE) for concentric patterns are plotted in the left column; those for translational patterns are in the right column. Open symbols correspond to fellow eye data; filled symbols represent affected eye data. SK shows a deficit only at the finest dot displacement tested. Amblyopic eye thresholds for GH are only available for coarse and moderate spatial scales for concentric Glass patterns. She was only able to discriminate the concentric pattern at the finest scale (5.36') at the highest coherence level (90%), indicated by the upward pointing arrow and the dashed line. She was unable to reliably do the task when viewing translational patterns at any spatial displacement with the amblyopic eye.

overall, her thresholds were lower for concentric than for translational patterns. There was no consistent interocular difference across spatial scales for either pattern type. Control observer CT (bottom) also showed the best sensitivity at the finest spatial scale, although he was similarly sensitive to translational and concentric Glass patterns at this spatial scale. Like KS, CT showed no consistent interocular difference across test conditions, and for all but one case (left eye, largest displacement), threshold increased systematically with increasing dot displacement. Note that the ordinate is shifted to a lower coherence range for this observer to accommodate his overall lower thresholds. Variation in absolute sensitivity to dot coherence in Glass patterns across visually normal observers is not an uncommon finding when individual thresholds are reported (e.g., Dakin & Bex, 2002; Kurki et al., 2003; Kurki & Saarinen, 2006; Wilson & Wilkinson, 1998; Wilson et al., 1997, 2004). These studies reported, for moderate dot separation (8 to 10 min), concentric pattern coherence thresholds ranging from about 10% to 32% (mean across studies 18%) while translational pattern coherence thresholds ranged from 17% to 82% (mean across studies 37%).

Figure 3 shows data from two amblyopic observers: mild amblyope SK and deep amblyope GH (see Table 1).

Amblyopic observer, SK (top), exemplified the typical pattern of loss such that the interocular difference in coherence threshold was greatest at the finest spatial scale, where he showed a clear amblyopic deficit for both pattern types. In addition, while he had a clear deficit at the finest dot separation when tested using concentric Glass patterns, his loss was far more substantial when tested with translational patterns. Amblyopic observers showed a similar trend to the controls when viewing with the fellow eye: threshold typically increased from the finest to the coarsest displacement, although the best sensitivity was not always at the finest scale tested (e.g., GH, bottom). Amblyopic observer GH (bottom) showed more dramatic losses than SK. She demonstrated a substantial loss when viewing concentric patterns of moderate spatial scale and was only able to discriminate the pattern structure, as determined by performance above 80% correct, at the highest coherence level (90% coherence) for concentric patterns of fine spatial scale (filled arrow; dashed line). Therefore, we were unable to measure a threshold at that displacement. With translational patterns, she was completely unable to perform the task with her amblyopic eye, performing at chance on all spatial scales, although she was able to successfully discriminate translational structure with the fellow eye.

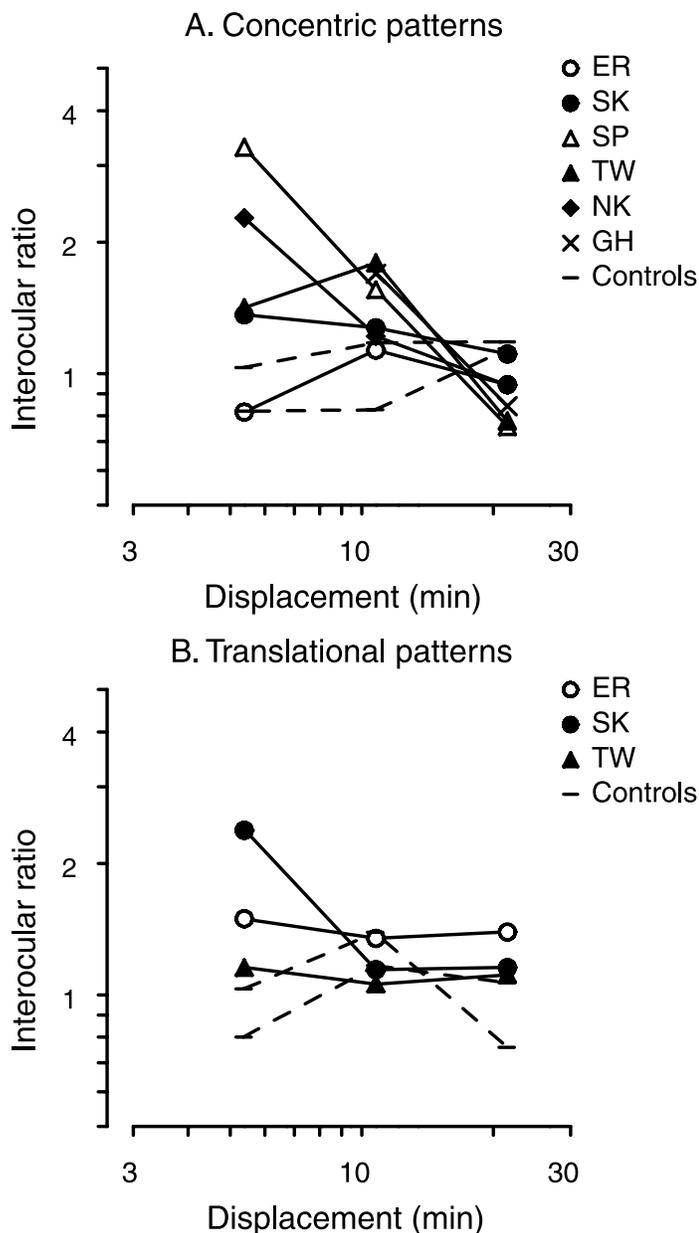


Figure 4. Interocular ratio (amblyopic eye threshold/fellow eye threshold) for Glass pattern sensitivity plotted as a function of dot displacement for each participant with a history of strabismus. (A) IOR for concentric patterns. (B) IOR for translational patterns. Different symbols represent different participants. The data for conditions in which the observer could only do the task with one eye are omitted (by definition); most such cases were with translational patterns (3/6 observers failed), but also note GH with concentric patterns at the smallest displacement. The dashed lines represent IORs for the two control observers, from the data in Figure 2.

To examine the effect of spatial scale on pattern sensitivity in amblyopes more directly, we calculated the extent of the sensitivity loss for each condition tested for each observer. Our measure of sensitivity loss was interocular ratio (IOR; amblyopic eye threshold/fellow eye

threshold). Figure 4 shows the range of sensitivity losses across the three dot separations we tested for concentric patterns (A, top) and translational patterns (B, bottom); IORs for control subjects (from the data in Figure 2) are included as dashed lines. Amblyopic observers generally showed decreasing IOR with increasing spatial scale. In most cases, the largest deficit appeared at the finest dot separation, 5.36 arcmin. This was true for 4 of 6 subjects when viewing concentric patterns and for 2 of the 3 subjects who were able to discriminate translational patterns with both eyes. Note that there is no data point at 5.36 arcmin in Figure 4A for observer GH since we were unable to measure a threshold for that displacement (see above; Figure 3). Observer TW showed the largest deficit at 10.72 arcmin with concentric patterns and, in contradiction to the other amblyopes, showed no substantial deficit with translational patterns. Observer ER showed a different pattern. When viewing concentric patterns, she showed no consistent interocular difference. However, she had a consistent interocular difference in sensitivity to translational patterns of all spatial scales (Figure 4B). It is important to note that ER is not an amblyope based on the Snellen acuity criterion (see Table 1), a result of aggressive treatment as a child. Nevertheless, she shows a deficit on this global task when viewing translational patterns.

Only 3 of 6 observers with a history of strabismus were able to distinguish translational Glass patterns from noise patterns at all three spatial scales when viewing with the amblyopic eye. One of these observers, TW, showed little deficit at any spatial scale while another observer, SK, had a large deficit at the finest displacement. One additional observer (NK) was able to detect the structure in the translational patterns using his amblyopic eye, exceeding 80% correct, only at the highest coherence level with largest spatial displacement. Therefore, we were unable to compute a threshold for that condition or any other spatial scale. However, he could perform well with his fellow eye at all dot displacements. As mentioned earlier, observer GH could appreciate the structure in the translational patterns only with her fellow eye. We were unable to obtain measurable thresholds from either eye of observer SP with translational Glass patterns of any spatial scale. These data show a clear effect of increased perceptual impairment for patterns of fine spatial scale regardless of pattern type and a generally larger loss for translational patterns.

To show the range of variation of coherence sensitivity across observers as well as depth of amblyopic loss, we plot the measured coherence thresholds for each observer for the finest dot displacement in Figure 5. Coherence thresholds for concentric (A, top) and translational (B, bottom) patterns for the 5.36 arcmin displacement conditions are plotted for each eye of each observer; the data for the two control observers are shown in the left-hand panels. As noted earlier, there was considerable disparity in the ability of the two control observers, with no history of abnormal visual experience, to detect Glass patterns of both types. However, the performance level shown by each is solidly

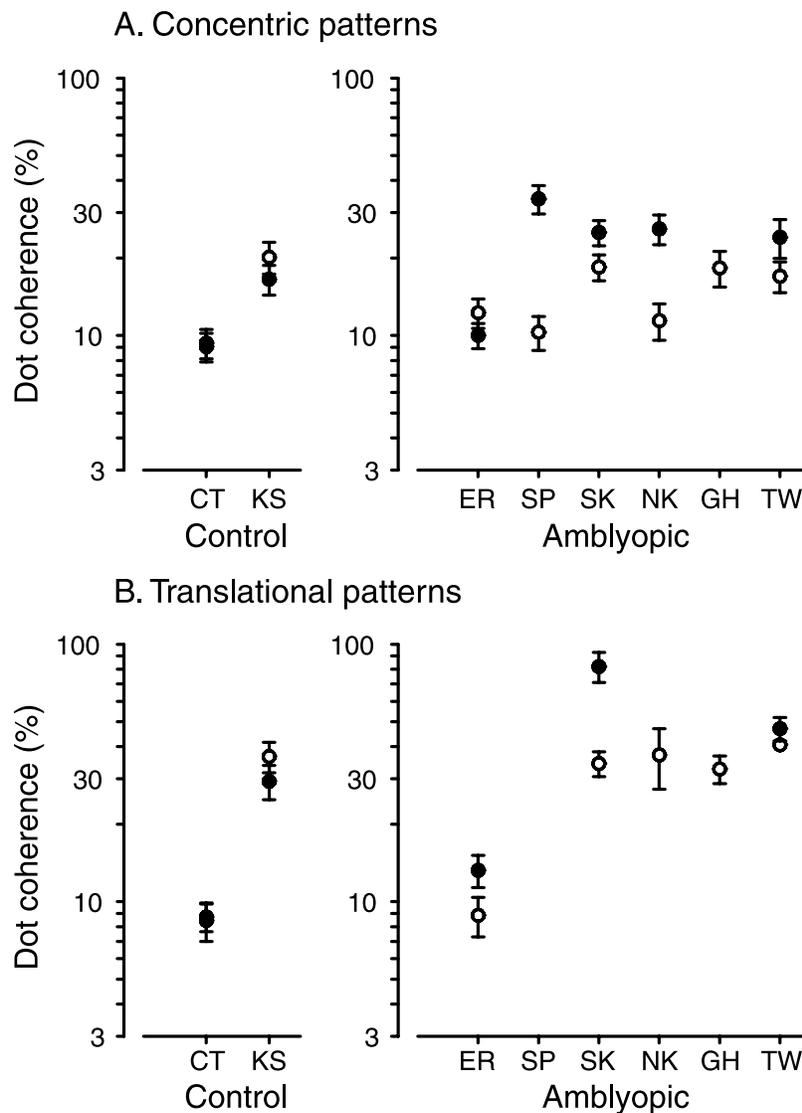


Figure 5. Coherence threshold (± 1 SE) for (A) concentric and (B) translational Glass patterns at fine spatial scale (5.36' displacement) for each eye of each observer. For participants with a history of strabismus, filled symbols correspond to affected eye thresholds; open symbols correspond to fellow eye thresholds. For control observers, open symbols represent right eye data; filled symbols represent left eye data. Missing data reflect the observers' inability to detect the Glass pattern structure under those test conditions (see text for details).

within the range reported in the literature for typical observers. Performance with the fellow eye was in most cases also within the range of the control observers and of typical observers reported in the literature. As was also noted above, we were unable to measure thresholds for the amblyopic eye of two amblyopic observers with translational patterns at any dot separation, and one observer was unable to perform consistently with either eye (SP). For concentric patterns, only observer GH was so impaired that we could not measure her threshold at the finest spatial scale with the amblyopic eye. Finally, observer ER, who was aggressively treated as a child and now has good acuity and contrast sensitivity in both eyes, shows an elevated threshold for detecting the structure of translational but not

concentric patterns when viewing with her amblyopic eye. Overall, our data reveal a particularly strong impairment for translational Glass pattern perception.

Since we found that Glass pattern sensitivity depends on the spatial scale of the pattern tested, we wondered whether or not there was a reliable relationship between contrast sensitivity losses and Glass pattern sensitivity losses. We equated the spatial scale for gratings and Glass patterns based on the neurophysiological findings of Smith et al. (2002, 2007). They used single-cell recordings in macaque V1 and V2 to characterize sensitivity to local orientation cues in Glass patterns. They found peak responses from V1 neurons when two conditions were satisfied: (1) dipole orientation matched that of a given neuron's optimal

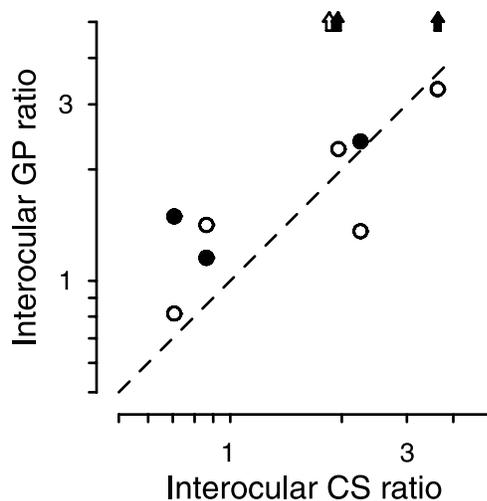


Figure 6. Interocular ratio for Glass pattern sensitivity plotted against interocular ratio for contrast sensitivity for participants with a history of strabismus. IORs are calculated based on Glass pattern data collected with a dot displacement of $5.36'$ and contrast sensitivity data collected with gratings of 6 cpd. Filled circles represent data for translational patterns; open circles represent data for concentric patterns. The dashed line represents a 1:1 relationship. The upward pointing arrows (top of figure) represent the subjects who could not perform the Glass pattern discrimination with both eyes, and hence no Glass pattern IOR could be established. They are plotted against the x-axis, at the IOR corresponding to the observers' contrast sensitivity deficit; filled arrows are for observers who failed only on translational patterns; the open symbol represents the observer who failed with both pattern types (GH).

grating orientation and (2) dot separation between the two dots of a dipole was between one-quarter and one-half of the spatial period of the optimal grating (Smith et al., 2002). Applying this principle to the patterns we tested, in the same manner as Kiorpes and Movshon (2004), the equivalent spatial scales of our patterns are approximately 5.6 cpd (displacement = $5.36'$), 2.8 cpd (displacement = $10.72'$), and 1.4 cpd (displacement = $21.44'$). We compared IOR for Glass pattern sensitivity at the finest spatial scale we tested ($5.36'$) to IOR for contrast sensitivity measured in response to gratings at the closest tested equivalent spatial frequency, 6 cpd. The data are plotted in Figure 6. We plotted only those comparisons for which we were able to measure threshold with both eyes on each metric. The open circles represent the comparisons for concentric patterns and the filled circles represent those for translational patterns; the upward pointing arrows at the top of the figure indicate the cases for which we were unable to measure Glass pattern thresholds.

While the visual impression suggests that the ratios increase together, the large number of failures and the comparatively small population size of our study do not permit us to report a statistical comparison with confidence.

We also examined a simple rank order comparison between Snellen acuity (Table 1) and Glass pattern loss. There was no clear relationship between the two measures.

Discussion

Our aim in this study was to examine the extent and nature of deficits in global form perception in amblyopia. We found that sensitivity to Glass patterns in general and the size of the amblyopic deficit in particular, as based on interocular threshold comparison, depended on the underlying spatial scale and that adults with a history of abnormal early visual experience showed greater impairment for translational patterns than for concentric ones.

For visually normal observers, most previous studies of Glass pattern sensitivity found that concentric patterns were easier to detect than translational patterns (Alliston, 2004; Kurki & Saarinen, 2004; Wilson & Wilkinson, 1998; Wilson et al., 1997). Our results are consistent with those studies in that translational pattern structure was generally more difficult to perceive than concentric pattern structure and deficits were generally larger with translational patterns. However, one control subject (CT) showed similar thresholds for the two pattern configurations at two of the three spatial scales. In addition, one participant with a history of strabismus (ER) showed better sensitivity for the translational pattern at the highest spatial scale with her fellow eye and another (TW) showed little IOR with translational patterns of any spatial scale. One prior study found that thresholds for translational patterns approach those of concentric patterns under some viewing conditions (Dakin & Bex, 2002), although it has been suggested that perceptual learning played some role in these results (Wilson & Wilkinson, 2003). Our participants who performed similarly or better with translational patterns were not more experienced than the others, so it is unlikely that practice explained their different pattern of results. Thus, it is worth recognizing that there are individual differences with respect to the perception of different Glass pattern configurations.

No prior study has evaluated the effect of pattern type and spatial scale on the amblyopic deficit. Only a few studies have used Glass patterns to evaluate the loss of form vision following early abnormal visual experience in humans. Anderson and Swettenham (2006) measured thresholds for the detection of dynamic Glass patterns of 3 different configurations in one strabismic amblyopic human. Lewis et al. measured sensitivity to coherence in concentric Glass patterns following early monocular and binocular visual deprivation due to dense congenital cataracts (Lewis et al., 2002). Our findings that the extent of the deficit on a global form task varies substantially with the stimulus conditions are the first such report. It is important to note, though, that we represent the extent of the amblyopic loss as measured

against the performance of the fellow eye. Many prior studies have noted that the fellow eye of amblyopes is not necessarily “normal” (e.g., Ho et al., 2005; Kiorpes & Kozma, 2003; see Simons, 2005). Given the wide range of thresholds reported for visually normal observers (see Results section), it would be difficult to define with confidence what was and was not normal for Glass pattern discrimination. The fellow eye thresholds of our amblyopes were not substantially different from the performance of our control subjects, and our control subjects were well within the range found in other studies of typical observers. Thus, we are confident that the range of deficits that we found is an accurate reflection of the loss of global form perception in strabismic amblyopia.

It is interesting to note that the participants with the most dramatic losses in Glass pattern perception were also the oldest (GH, SP, NK). One might therefore wonder whether age is an important factor in Glass pattern perception. We think this is unlikely since one of our control participants (CT) was in the same age range as these subjects at the time of testing (54 years) and his thresholds were among the lowest that we measured. In addition, participant SK showed quite a large amblyopic deficit, especially for translational patterns, and he was among the youngest participants.

Although a number of studies have investigated global form vision in strabismic amblyopia (e.g., Hess et al., 1997; Kovacs et al., 2000; Levi et al., 2007; Simmers et al., 2005; Wang et al., 2007), most of these studies used stimuli of a single spatial scale, often one for which low-level visual function in amblyopic eyes is relatively well preserved, so those results are not necessarily general. Indeed, since amblyopic eye deficits found in assessments of basic visual functions such as contrast sensitivity vary considerably with spatial scale (see McKee et al., 2003), it is reasonable to suppose that higher order form processing deficits would also show some kind of variation with spatial scale. Our data support this notion: amblyopic eye deficits when tested using concentric patterns were minimal for patterns of coarse spatial scale and substantial for patterns of the finest spatial scale we tested. Additionally, when tested using translational patterns, some amblyopic observers were unable to do the task at all with their amblyopic eyes, and those who could typically showed much larger deficits at the finest spatial scale we tested. These results are in good agreement with findings of Levi et al. (2007), who found that increasing the spatial frequency of pattern elements coupled with decreasing display and target size resulted in larger deficits in contour processing. Our data are also consistent with results from amblyopic monkeys showing variation in the size of the perceptual deficit with the underlying spatial scale of Glass patterns (Kiorpes, 2006). This pattern is also reminiscent of that found for coherent motion detection in amblyopic monkeys (Kiorpes et al., 2006).

Although we found variation in the extent of the amblyopic deficit with the underlying spatial scale of the Glass pattern discrimination, we were unable to directly

compare this effect with the loss in contrast sensitivity due to the large number of subjects who were unable to perform the discrimination at fine scale or with translational patterns. However, it is worth noting that Glass pattern detection is relatively immune to the contrast of the elements (Alliston, 2004; Wilson et al., 2004), so there may not be a close relationship to contrast sensitivity in any case. Furthermore, other studies have reported that amblyopes show higher order form vision losses that cannot be predicted from losses in acuity or contrast sensitivity (e.g., Kovacs et al., 2000; Kozma & Kiorpes, 2003; Levi et al., 2007; Simmers et al., 2005). We were surprised to find that participant ER, who was aggressively treated as a child with good CS results, shows a clear deficit in her formerly amblyopic eye when tested using translational Glass patterns although she had no deficit with concentric patterns. Similarly, observer NK, with Snellen acuity of 20/30 for the amblyopic eye, was unable to detect the structure in translational Glass patterns consistently enough to provide a threshold at any spatial scale with that eye; he was only able to perform reliably above 80% correct at the highest coherence level (90%) at the largest dot displacement. These results highlight the growing evidence that higher order perceptual losses can exist in apparently successfully treated amblyopes.

It is not unreasonable to find that amblyopes show greater losses in sensitivity to patterns of fine spatial scale than to patterns of coarse spatial scale given that sensitivity of amblyopic eyes is often relatively well preserved for low, but not high, spatial frequencies (e.g., Hess, 1979; Levi & Harwerth, 1977). Such psychophysical findings, together with physiological data showing a reduction in the number of neurons tuned to high spatial frequencies in strabismic amblyopic monkeys (Kiorpes et al., 1998), suggest that there are fewer detectors available at the first cortical stage of Glass pattern processing for fine compared to coarser patterns. Presuming that these detectors are necessary for subsequent recognition of the global structure in these patterns (Barlow & Olshausen, 2004; Smith et al., 2002, 2007; Wilson et al., 2004), it is therefore not surprising that strabismic amblyopes would show a particular weakness for detection of fine scale patterns.

Various mechanisms have been suggested to account for the higher order perceptual deficits observed in amblyopia. Sharma, Levi, and Klein (2000) provide evidence for a high-level deficit in strabismic amblyopia characterized by undercounting features in a way that cannot be emulated in normal observers through alterations to the stimulus, such as jittering the positions of pattern elements or reducing stimulus contrast and therefore visibility. They ruled out a number of low-level processing explanations for their data (Sharma et al., 2000). Other studies show that strabismic amblyopes appear to be less efficient than controls at using information contained within the features of a pattern, needing many more samples than normal for position discrimination (Wang, Levi, & Klein, 1998) and pattern recognition (Levi, Klein, & Sharma, 1999; for review see

Kiorpes & McKee, 1999). These authors suggested that higher form vision deficits in amblyopia were due largely to undersampling of a stimulus or using information from a stimulus in a highly inefficient manner. Inefficient processing might result from sparse sampling at the level of the early visual cortex, spatial scrambling or increased positional uncertainty, alternative hypotheses for amblyopic mechanisms (Hess et al., 1997; Levi, Klein, & Yap, 1987; Watt & Hess, 1987), or other higher order deficiencies.

We wondered whether local mechanisms like undersampling or increased positional uncertainty could explain the pattern of our results. Although there is likely to be sparse sampling of the image structure at the level of the cortex—due to reduced numbers of neurons driven by the amblyopic eye at fine spatial scales—local orientation information is likely diminished equally for both pattern types. Using coarse scale detectors to process fine scale patterns could result in inappropriate dot pairings that would decrease the percentage of coherent dipoles, perhaps disrupt orientation coherence, and increase the apparent proportion of noise dots/dipoles in a given pattern. This scenario is consistent with our observation of greater losses in sensitivity to patterns of fine spatial scale but again would not distinguish between pattern types.

The question remains, how might we account for the particular loss of sensitivity to translational over concentric patterns? The answer may lie in differential integration properties of the mechanisms detecting the different pattern types. Wilson et al. (1997), and subsequently others (Kurki & Saarinen, 2006; Wilson & Wilkinson, 1998; Wilson et al., 2004), have shown that translational Glass patterns are detected by a mechanism that integrates over a much smaller area than the mechanism that integrates concentric patterns. Undersampling or spatial scrambling may have greater impact on a mechanism that pools over a smaller area, since there would be fewer samples of the signal available to the second-stage integrator and signal-to-noise ratio would then be reduced. A mechanism that pools over a larger area may be less affected by a small reduction in the proportion of signal samples. It is also possible that concentric patterns are more easily detected and less susceptible to disruption in amblyopia because they contain signals at effectively all orientations. Early-stage pooling mechanisms are orientation specific, so that translational patterns are detected and integrated by only a subset of the possible detectors, those that match the orientation of the linear pattern (Smith et al., 2002, 2007), while concentric ones may be pooled over a broad range of oriented detectors.

Conclusion

In conclusion, we found that for adults with strabismic amblyopia, deficits in sensitivity to global form in Glass patterns are largest for patterns of fine spatial scale and that impairment is more profound for discrimination of

translational patterns from noise than for discrimination of concentric patterns from noise. Our data are consistent with earlier studies of normal vision suggesting that the structure in concentric and translational patterns may be detected by different mechanisms or at different levels of the visual system. We found deficits even in participants with quite good Snellen acuity, emphasizing that perceptual losses can persist even in “successfully treated” amblyopes. Our data also show that, even with “high-level” global stimuli, it is important to explore a range of stimulus parameters to fully characterize the nature of the amblyopic loss.

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