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The representation of global spatial structure in amblyopia

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Abstract

Visual processing is thought to involve initial local analyses that are subsequently integrated globally to derive functional representations of structure that extends over large areas of visual space. Amblyopia is a common deficit in spatial vision that could be based on either unreliable local estimates of image structure, irregularities in global image integration or a combination of errors at both these stages. The purpose of this study was to quantify the integration of local spatial information in amblyopia with global orientation discrimination and inter-ocular matching tasks. Stimuli were composed of pseudo-random arrays of highly visible and resolvable features (Gabor patches) whose local orientation and position were drawn from global distributions whose mean and variance statistics were systemically varied. Global orientation discrimination thresholds in both the amblyopic *and* fellow eye were elevated. The orientational and positional variances perceived by the amblyopic eye were matched by stimuli with higher variances perceived in the fellow eye. It would appear that amblyopes are able to integrate orientation information across visual space but the global representation of local structure shows greater variability compared to normal. It is this increased spatial uncertainty that underlies the spatial deficit in amblyopia.

1. Introduction

Amblyopia is a developmental condition that is characterised by reduced visual acuity in one eye due to strabismus (ocular misalignment) or anisometropia (unequal refractive error), occurring in early visual development. Although it is known that the site of the processing deficit in amblyopia is cortical in both humans and animals, little is known about its extent within the cortex.

Physiological and behavioural studies show that the receptive fields of early visual detection mechanisms are spatially limited and highly selective for a limited range of stimulus attributes—such as spatial frequency, orientation and direction of motion (Anderson & Burr, 1987; Henry, Bishop, & Dreher, 1974; Hubel & Wiesel, 1968; Schiller, Finlay, & Volman, 1976; Wurtz, 1969). It is here, in the early stages of visual processing that the neural deficit for amblyopia is thought to originate: sensory deficits at the single cell level (Chino, Shansky, Jankowski, & Banser, 1983; Crewther & Crewther, 1990; Eggers & Blakemore, 1978; Kiorpes, Kiper, O'Keefe, Cavanaugh, & Movshon, 1998; Movshon, Hendrickson, Kiopres, & Boothe, 1987) have revealed reduced spatial resolution, reduced contrast sensitivity and a reduced numbers of binocular cells.

However, it has become increasingly apparent in recent years that the perceptual difficulties experienced by amblyopes when using their amblyopic eye are due to spatial rather than contrast disturbances. Much of the recent work on amblyopia has centred on this perceptual deficit, in particular the positional uncertainty amblyopes demonstrate in judging the relative position of a target with respect to a nearby reference. Amblyopes consistently show marked losses in the accuracy of spatial localisation uncorrelated to either their contrast or acuity loss (Hess, 1982; Hess & Field, 1994; Hess & Holliday, 1992; Levi & Klein, 1986; Levi, Klein, & Yap, 1987) see also Hess (2001) for a review.

Animal models have also consistently shown that the physiological deficits in V1 are not sufficient to explain the full range of perceptual deficits in amblyopia (Kiorpes et al., 1998). While the advent of neuroimaging studies may have confirmed early cortical deficits (Barnes, Hess, Dumoulin, Achtman, & Pike, 2001; Goodyear, Nicolle, Humphrey, & Menon, 2000) they too have shown additional cortical deficits associated with amblyopia within visual areas beyond V1

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(Imamura et al., 1997; Sireteanu, Tonhausen, Muckili, Zanella, & Singer, 1998). Following these early losses, how then is visual information (initially extracted from the image by the early quasi-linear filtering operations of the retina and V1) combined to reveal basic information about image structure in amblyopia?

In visual space it is often necessary to integrate information over an extended area to determine a useful global percept. This means that information about image structure over extended areas of visual space must be based on the combined responses of a number of independent, local inputs. Studies of the integration of motion (Newsome & Pare, 1988; Verghese, Watamaniuk, McKee, & Grzywacz, 1999) and orientation (Dakin, 2001; Dakin & Watt, 1997) have shown that global estimates of mean direction and orientation can be obtained with great accuracy in the absence of spatial structure. These results are consistent with both psychophysical (Burr, Morrone, & Vaina, 1998) and anatomical (Essen & Orbach, 1986) evidence showing an increase in receptive field size at higher stages of visual processing. Neurons in early visual processing are more likely to be activated by spatially local events; neurons in the later stages of visual processing are more likely to be activated by more global events.

Amblyopia is characterised by distorted representations of spatial form, but it is not clear whether the deficit is based on unreliable local estimates of spatial structure or on irregularities in processes of global integration, or a combination of error at both these stages. Although contrast sensitivity is attenuated at high spatial frequencies in amblyopia, there is little or no contrast sensitivity loss at lower spatial frequencies (Gstalder & Green, 1971; Hess & Howell, 1977). Furthermore, when stimuli are equated for visibility by appropriate scaling of spatial frequency or contrast, amblyopic vision is equivalent to that of normal vision observers in judgements of supra-threshold apparent contrast (Goodyear et al., 2000; Hess & Bradley, 1980; Hess, Burr, & Campbell, 1980; Loshin & Levi, 1983), orientation discrimination (Demanins, Hess, Williams, & Keeble, 1999; Skottun, Bradley, & Freeman, 1986) blur discrimination (Simmers, Bex, & Hess, 2002) and texture discrimination (Mussap & Levi, 1999). These results argue that local coding in amblyopia is equally accurate as local coding in normal vision and therefore suggest that perceptual distortions arise from anomalous grouping processes. Indeed, a recent report has confirmed that amblyopes show deficits in detecting global motion for both luminance and contrast defined stimuli, that are unrelated to (independent of) the contrast sensitivity deficit (Simmers, Ledgeway, Hess, & McGraw, 2003).

The purpose of this study was to quantify such perceptual distortions by means of an orientation discrimination and an inter-ocular matching task. We adapted stimuli from previous studies (Dakin, 2001; Dakin & Watt, 1997) in which observers are required to make judgements of the global statistics (in this case the mean orientation) of a stimulus composed of a large number of pseudo-randomly positioned features (Gabor elements, see Fig. 1 for illustrations). Orientation discrimination thresholds for this noisy stimulus are equivalent to that for comparable noise-free single-grating stimuli (Dakin & Watt, 1997) and increase with the orientation variance applied to the individual elements. Although a local mechanism can encode the orientation of any single element in the stimulus, performance in this task is ultimately limited by a global mechanism that requires integration or pooling of a series of local estimates over the stimulus. As orientation discrimination thresholds for single gratings are not impaired, as long as the target visibility is equated (in terms of spatial frequency or contrast compensation), this task allows us to quantify noise in global integration processes. Unlike previous studies that have examined form perception in amblyopia (Hess, McIlhagga, & Field, 1997; Hess, Wang, Demanins, Wilkinson, & Wilson, 1999; Levi, Klein, & Sharma, 1999; Mussap & Levi, 1999) performance in this task is not contingent on the precise locations of target elements, which is already known to be impaired in amblyopia. Orientation discrimination thresholds with this stimulus can therefore provide an objective measure of the internal noise in the pooling of local orientation by the visual system. Inter-ocular matches with this stimulus can provide a subjective measure of the apparent structure perceived between fellow and amblyopic eyes.

2. Methods

2.1. Observers

Four strabismic, two anisometropic and two strabismic/anisometropic amblyopes (mean age 29.4 ± 5.8 years) were recruited for the study (see Table 1 for clinical details). A control group of 3 naïve observers (mean age 27 ± 4.4 years) were selected with normal visual acuity and binocular vision. All observers were similarly practised on the task before formal data collection. Viewing was monocular in all cases with the appropriate refractive correction. All experimental procedures followed the institutional guidelines, and informed consent was obtained once the nature and possible consequences of the experiment had been explained.

2.2. Apparatus and stimuli

Stimuli were generated on a Macintosh G4 computer using software adapted from the VideoToolbox routines

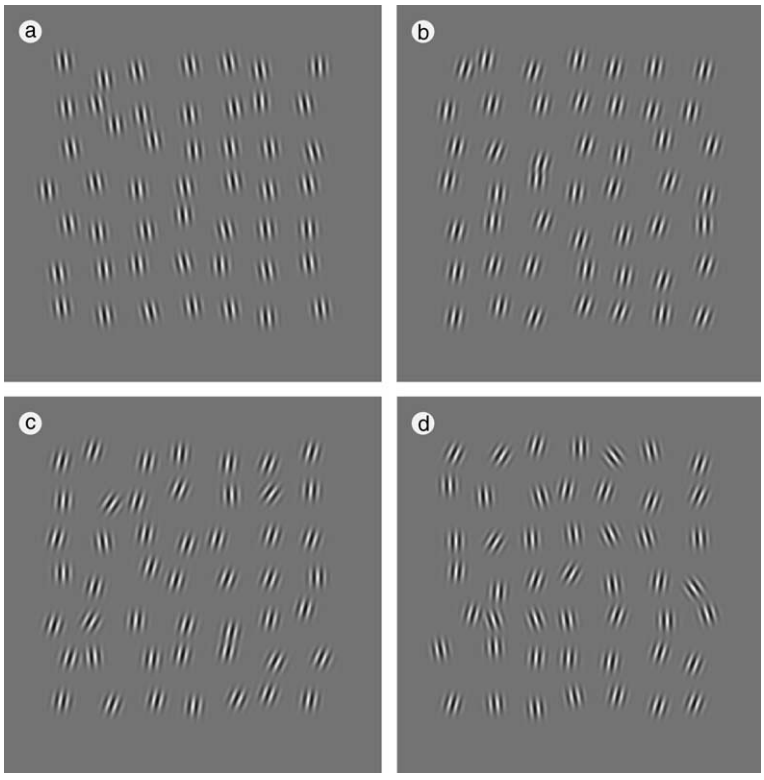

Fig. 1. Examples of the stimuli from the discrimination task composed of 49 high contrast elements. The orientation of each element is randomly selected from the same Gaussian distribution, whose mean (μ) and standard deviation (σ) is systematically varied. (a) μ is 2° with an σ of 7.06°, (b) μ is 4° with σ of 11.19°, (c) μ is 8° with σ of 14.09°, (d) μ is 16° with σ of 3.54°. See text for detailed explanation.

Table 1
Clinical characteristics of the amblyopic subjects. Red symbols correspond to individual strabismic, green symbols to strabismic anisometropes and blue symbols to anisometropic amblyopes

Subject	Visual acuity	Spectacle prescription	Ocular alignment
●	RE 6/5 LE 6/5	Nil	L SOT 10Δ
▲	RE 6/30 LE 6/5	Nil	L XOT 15Δ
■	RE 6/60 LE 6/6	Nil	R SOT 20Δ
◆	RE 6/6 LE 6/38	Nil	L SOT 20Δ
■	RE 6/6 LE 6/38	RE + 4.00/−1.00 × 170 LE + 6.00/−1.75 × 177	L XOT 14Δ
●	RE 6/6 LE 6/15	RE plano LE + 3.25 × 90	L XOT 8Δ
◆	RE 6/5 LE 6/24	RE plano LE + 2.50DS	Straight
▲	RE 6/5 LE 6/24	RE plano LE + 3.25/+1.00 × 90	Straight

(Pelli, 1997). Images were displayed on a LaCie Electron22 monitor in greyscale at a frame rate of 75 Hz and a mean luminance of 50 cd m^{-2} with a contrast of 75%. Stimuli were presented in a raised cosine temporal envelope (1 s with 40 ms on- and off-set). The luminance of the display was linearised to a pseudo-12 bit resolution with an ISR Video Attenuator (Pelli & Zhang, 1991) and calibrated with a Minolta photometer.

Pseudo-12 bit resolution in this case will allow the presentation of 2^8 monochrome levels from a possible 2^{12} levels. Images were presented in grey-scale by amplifying the monochrome signal and driving R–G and B guns equally. The display was 36° horizontally (1152 pixels) by 27.2° vertically (870 pixels) and was viewed in a dark room from a distance of 57 cm.

Stimuli were composed of multiple Gabor elements pseudo-randomly positioned in a 12.6×12.6 square region in the centre of the display. The display was divided into a 7×7 grid of equal sized cells. Each cell contained a Gabor element that was the product of a circular Gaussian envelope and an oriented sinusoid:

$$G(x,y) = e^{-(x^2+y^2)/2\sigma^2} * \cos[2\pi * (\cos\theta * x + \sin\theta * y)/\rho + \phi],$$

where θ controls orientation, ρ spatial frequency and ϕ the phase of the sinusoid, which was random. The spatial frequency of the elements was 3.2 cycles per degree (c/deg) and the standard deviation of the Gaussian envelope was 0.5° with a Michelson contrast of 75%. The low spatial frequency and high contrast of the Gabor patches in our study ensured that the micro-patterns were highly visible and resolvable for all observers. The orientation and x–y placement of each Gabor micro-pattern within its cell was randomly drawn from the same Gaussian distribution whose peak and standard deviation determined the global statistics of the stimulus and were under experimental control.

2.3. Experiment 1: orientation discrimination

In Experiment 1 we measured orientation discrimination thresholds for the global mean of the Gabor micro-patterns as a function of the standard deviation of the orientation distribution. Illustrations of the stimuli are shown in Fig. 1.

As a pre-experiment control, local orientation discrimination thresholds were measured for an isolated Gabor element in a single interval 2-alternative force choice (AFC) procedure. The stimuli subtended 4° and was presented in a raised cosine temporal envelope (1 s with 40 ms on- and off-set). Spatial frequencies were interleaved at either 1 or 3 c/deg and Michelson contrast was fixed at 75%. Observers were required to fixate a central cross and to indicate by pressing one of two mouse buttons whether the stimulus (horizontally or vertically orientated) was titled clockwise or anti-clockwise. Auditory feedback was provided following incorrect responses. Stimulus levels were varied from trial to trial according to an adaptive staircase QUEST procedure designed to concentrate observations near threshold level (Watson & Pelli, 1983). The raw data across a minimum of four runs for each condition for each observer, were combined and were fitted with cumulative normal psychometric functions by a least χ^2 fit. From this fit, the thresholds and 95% confidence limits were estimated at the 75% correct point with standard methods (Press, Teukolsky, Vetterling, & Flannery, 1992).

Global orientation discrimination thresholds were then measured in a single interval 2-AFC procedure. The interval lasted one second and contained pseudo-random Gabor stimulus. One Gabor element was placed at the centre of each cell (mean separation = 1.8°) at a position randomly drawn from a Gaussian distribution with a standard deviation (σ_{position}) of 0.25° to avoid periodicity in the stimulus. The orientation of the element was randomly selected from a Guassian distribution with a standard deviation ($\sigma_{\text{orientation}}$, which controlled the orientational variability of the display) fixed at 2°, 4°, 8° or 16°, randomly interleaved within a run. The mean of the Gaussian distribution ($\mu_{\text{orientation}}$, which specified the overall mean orientation of the display) was under the control of a staircase procedure (QUEST) designed to concentrate observations at the 75% correct point. Observers were required to fixate a central cross and to indicate by pressing one of two mouse buttons whether the mean orientation of the elements was titled to the right or left of vertical. Auditory feedback was provided following incorrect responses. Each run contained 32 trials randomly interleaved for each of the four levels of orientational variance and was repeated a minimum of four times by each observer, randomly interleaved with the matching conditions described below. The raw data across all runs for each condition for each observer were combined and were fitted with cumulative normal psychometric functions by a least χ^2 fit. From this fit, the thresholds and 95% confidence limits were estimated at the 75% correct point. In a further series of control experiments the contrast of individual elements and the number of elements present were also varied (Fig. 2).

In those observers with amblyopia measurements were repeated with both the amblyopic eye and non-amblyopic eye in random order (see Table 1 for clinical details).

2.4. Experiment 2: inter-ocular matching

To assess the subjective distortions represented by the amblyopic visual system, we asked observers to match both the orientational variability and spatial position variability with equivalent stimuli. Stimuli were similar to those employed in orientation discrimination tasks, with the exception they were viewed dichoptically at all times. An illustration of the stimuli is shown in Fig. 3. A pseudo-random Gabor stimulus with $\mu_{\text{orientation}}$ fixed at ±45°, $\sigma_{\text{orientation}}$ fixed at 5°, 10°, 15°, 20° (randomly interleaved within a run and σ_{position}, as before) was presented to the amblyopic eye. A similar stimulus was

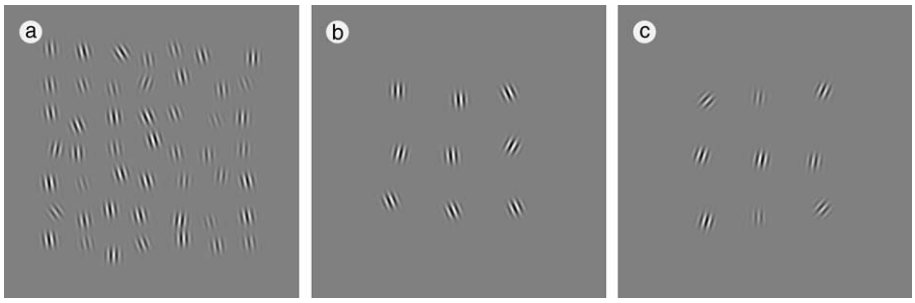

Fig. 2. Examples of discrimination stimuli from the control experiments. (a) Forty-nine elements with a contrast range across individual elements of $50 \pm 40\%$, (b) high contrast stimuli comprising nine elements, (c) nine elements with a contrast range across individual elements of $50 \pm 40\%$.

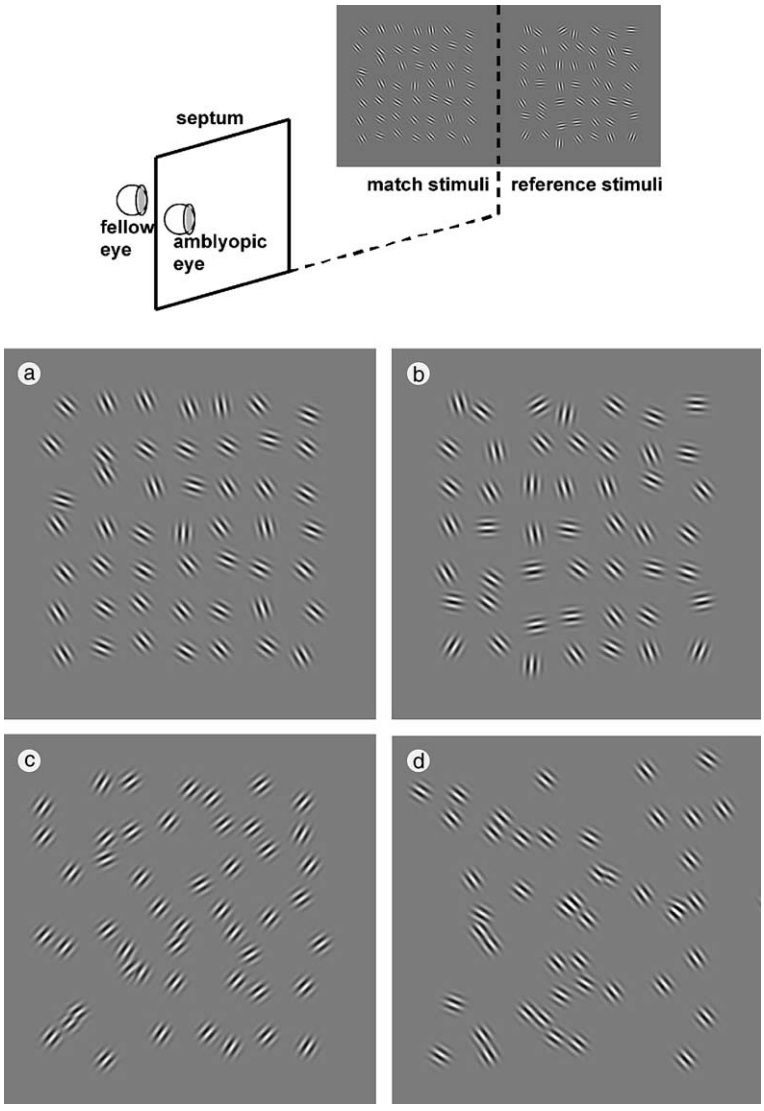

Fig. 3. Inter-ocular matching set-up and example stimuli. Arrays are composed of 49 elements examples at high contrast, (a) local orientational Stdv of 5°, (b) local orientational Stdv of 10°, (c) positional Stdv of 8°, (d) positional Stdv of 16°.

presented to the normal eye with a mean orientation of ±45° but whose orientational variability was initialised with a random value between 0° and 90° and was then adjusted by the observer to obtain a perceptual match. The observer pressed one of two mouse buttons to increase or decrease the variability, which caused the computer to generate a new random standard and match stimulus, pressing a third mouse button indicated

that a satisfactory match had been obtained and advanced the next trial. The changes in the appearance of the stimuli are illustrated in a QuickTime movie at the following web site: http://www.ucl.ac.uk/~smgxpbe/amblyopia.html. The reader is encouraged to move the frame-slider by hand to adjust the orientational and positional variability of the stimuli.

We used the same procedure to characterise positional distortions in amblyopia. Stimuli and procedure were the same as for orientation variability matching except the positional standard deviation ($\sigma_{position}$, the standard deviation of the distribution controlling the random placement of each Gabor in its cell) of the stimulus presented to the amblyopic eye was fixed at 4°, 8°, 16°, 32°, and the positional standard deviation of stimulus presented to the fellow eye was under the observer's control. The orientation of the elements was random.

Constant across all trials, the reference array was presented to the amblyopic eye or randomly assigned to the left or right eye of normal-vision observers (pilot data showed no significant difference in threshold between either eye of normal vision observers). Adjustment time was unrestricted but was not usually more than 2 s. All observers matched each baseline level at least fifteen times.

3. Results

3.1. Experiment 1: orientation discrimination

In the orientation discrimination control experiment for a single Gabor element (Fig. 4), a mixed analysis of variance revealed no significant difference between normal vision and amblyopic observers ($F_{(1,32)} = 1.78$; NS) there was also no significant effect of spatial frequency ($F_{(1,32)} = 0.01$; NS) and more importantly the interaction between these two subject factors was also not significant ($F_{(1,32)} = 1.02$; NS). These results confirm the absence of any low-level deficit in orientation discrimination (at the spatial frequencies tested) in our amblyopic subject group.

Fig. 5a shows orientation discrimination thresholds as a function of orientation variability for the mean of three normal vision observers (filled black symbols) and the amblyopic eyes of eight amblyopic observers (filled coloured symbols). Global orientation discrimination

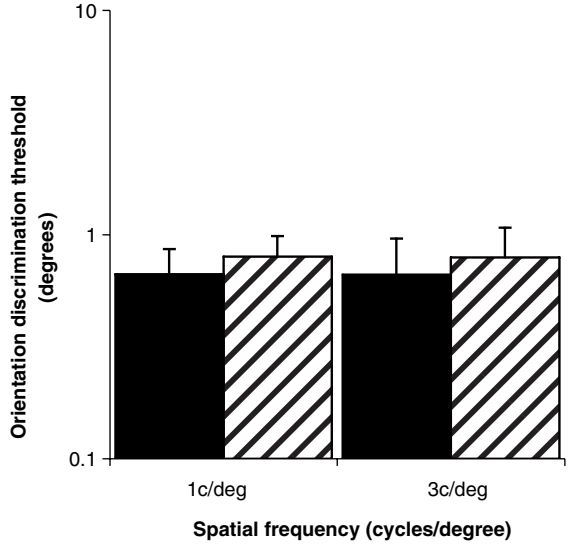

Fig. 4. Mean orientation discrimination thresholds for a single Gabor patch. Solid bars represent normal observers and shaded bars represent amblyopic observers. Error bars represent ±1 standard deviation.

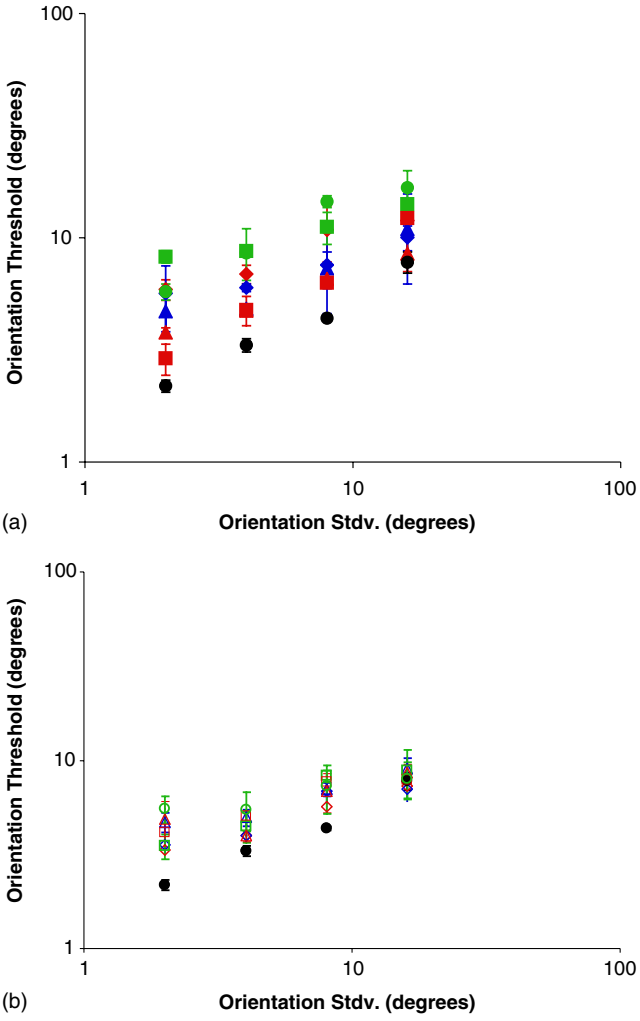

Fig. 5. (a) Global orientation discrimination thresholds as a function of orientation variability in an array of 49 elements. Individual amblyopic observers are shown by the coloured symbols, and the mean of the normal observers by the filled black symbols. Each estimate of threshold was based on at least four separate QUEST determinations (128 observations per point). Error bars show ±1 s.e.m. (b) As (a) for the fellow eye of amblyopic observers. Data for the normal vision observers are replotted (filled black symbols). Note: Figure reproduced in colour on the web; See: www.sciencedirect.com.

thresholds increase with local orientation variability for all observers. This trend is in close agreement with previous studies (Dakin, 2001) over the same range as are threshold values under similar conditions for normal-vision observers. Thresholds for amblyopic eyes of amblyopic observers are uniformly higher than those for normal-vision observers and the difference is greatest at low levels of orientation variability. Fig. 5b shows thresholds for the fellow eye of amblyopic observers (open coloured symbols) with thresholds of normal observers re-plotted (filled black symbols). It can be seen that global orientation discrimination thresholds are elevated in the fellow eye as well as the amblyopic eye of amblyopic observers. Fig. 6 further compares performance in the amblyopic and fellow eye for individual observers, illustrating a greater deficit in the amblyopic eye.

A leading explanation of the spatial deficit in amblyopia (Levi & Klein, 1986) posits that the reduced performance of the amblyopic eyes is due to early abnormalities such as undersampling of low-level receptive fields [such as those observed in area in V1 of other primates (Hubel & Wiesel, 1968; Schiller et al., 1976)] or poor stimulus visibility. This explanation predicts that potentially fewer micro-patches are represented by the amblyopic eye which might account for the present results. The low spatial frequency and high contrast of the Gabor patches in our study ensured that the micro-patches were highly visible and resolvable, but to test the undersampling hypothesis, we conducted a control experiment in which the contrast range of the individual elements and their number was varied (Fig. 2). To simulate the effects of reduced contrast sensitivity, the contrast of the Gabor elements was randomly assigned a value in the uniform interval $50 \pm 40\%$, and to stimulate the effects of undersampling, 9 Gabor elements were pseudo-randomly positioned this time in a 9.6×9.6 square region divided into a 3×3 grid of equal sized cells. Fig. 7 shows the results of the normal observers with no significant effect on performance being found for either the reduced number of elements ($p > 0.05$) or the contrast variation ($p > 0.05$). The graphs inset to the right represent orientation thresholds of the individual amblyopic observers in these control conditions respectively. Not only can it be seen that the increase in global orientation discrimination thresholds in amblyopia cannot be mimicked in normal eyes (reducing the contrast or presenting fewer elements failed to increase thresholds to levels comparable to the amblyopic eye with no change in the mean estimates) it is also evident that the thresholds in the individual amblyopic observers are proportional to those losses seen in Fig. 5. So although the stimulus had been further degraded this had no discernable effect on the amblyopic thresholds therefore ruling out a simple low-level explanation for the present results. Recently, Dakin (2001) reported small reductions for two out of three observers in orientation discrimination thresholds as the number of elements was reduced from 64, 16 then to 4. Our results show no significant reduction in sensitivity over a slightly smaller range.

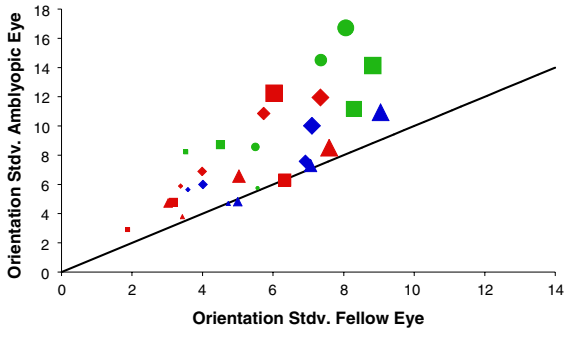

Fig. 6. Correlogram of the orientation discrimination thresholds illustrated in Fig. 5 for the amblyopic v's the fellow eye in individual amblyopic subjects. The increasing size of the symbols for each individual amblyope corresponds to the increasing degree of orientation variability in the stimulus array (e.g. 2° = ▪, 4° = ■, 8° = ■, 16° = ■). Note: Figure reproduced in colour on the web; See: www.sciencedirect.com.

These results indicate that the representation of global orientation is much noisier in amblyopic than normal observers. The increased variability present in the non-amblyopic fellow eyes as well as the amblyopic eye would indicate that elevated noise levels at 'late' or higher levels of processing exists in the amblyopic visual system.

3.2. Experiment 2: orientation and positional matching

Fig. 8 shows the local orientational variability viewed with the normal eye that matched that of a reference array viewed with the amblyopic eye as a function of the local orientation variability of the reference array. Fig. 9 shows the local positional variability viewed with the normal eye that matched that of a reference array viewed with the amblyopic eye as a function of the local positional variability of the reference array. For normal observers the reference and match stimuli were viewed with either the left or right eye at random.

In normal vision observers (filled black symbols) all matches lie close to the line of equality demonstrating that representation of both orientational and positional structure is approximately the same for stimuli viewed with either eye. For amblyopic observers, all matches were above the line of equality (slope >1) demonstrating that they matched the orientation and position variability of images viewed with their amblyopic eye with a *noisier* image viewed with their fellow eye. Recall that Experiment 1 showed that orientation discrimination thresholds were elevated in both amblyopic and fellow eyes of amblyopic observers, although less so the fellow

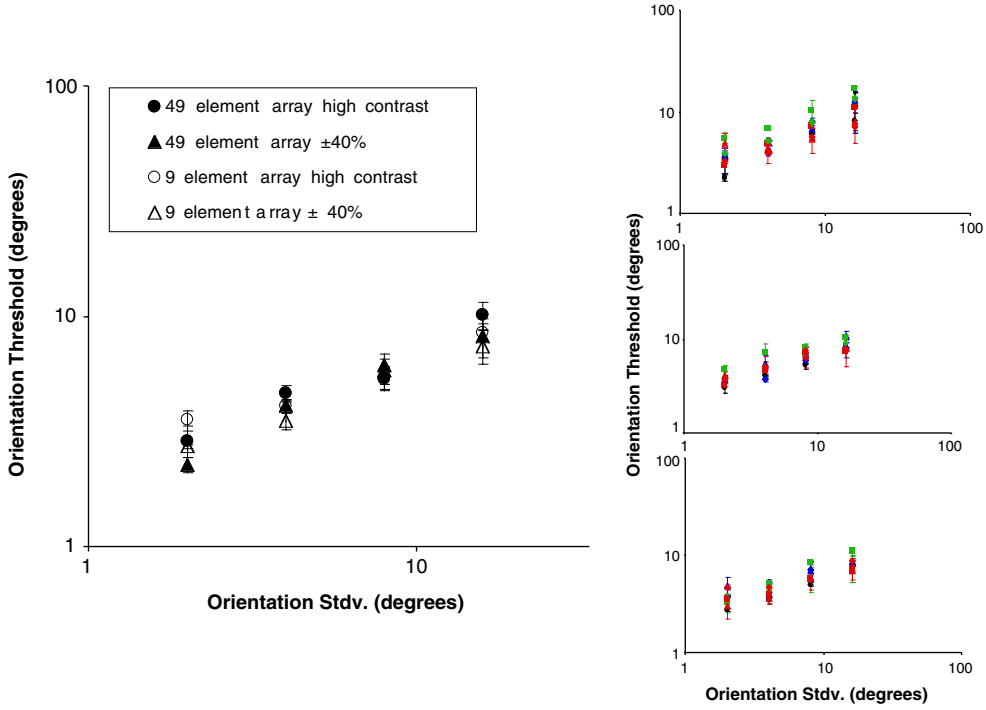

Fig. 7. In a series of control experiments the contrast range of the individual elements (50 ± 40%) and the number of elements (3×3 grid) presented were also varied. The main graph shows the mean orientation thresholds for the normal observers in these extra conditions. The graphs inset to the right represent orientation thresholds for individual amblyopic observers (coloured symbols) in these control conditions respectively: 49 element array ±40%, nine element array high contrast and nine element array ±40% (top to bottom) and the mean of the normal observers (filled black symbols). Each estimate of threshold was based on at least four separate QUEST determinations (128 observations per point). Error bars show ±1 s.e.m. Note: Figure reproduced in colour on the web; See: www.sciencedirect.com.

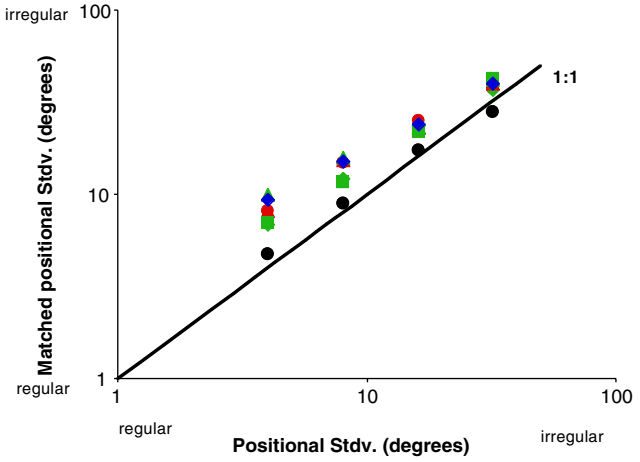

Fig. 8. Matched orientation variability as a function of reference orientation variability. Individual amblyopic observers (coloured symbols) and the mean of the normal observers (black symbols) are plotted. The diagonal line shows veridical matches. The mean slope of performance was found to be 0.87 ± 0.02 for the normal observers and 1.27 ± 0.3 for the amblyopic observers. Note: Figure reproduced in colour on the web; See: www.sciencedirect.com.

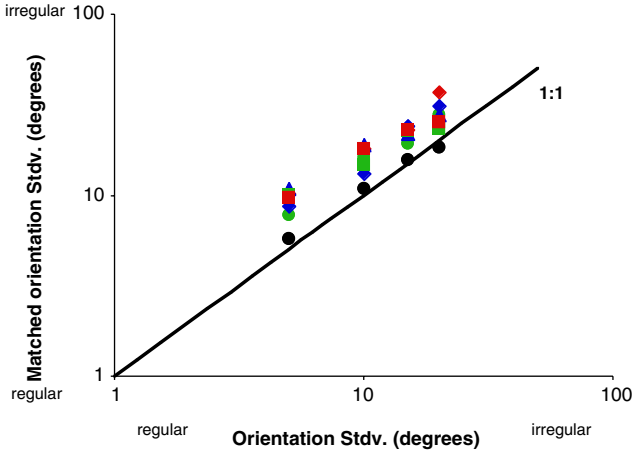

Fig. 9. Matched positional variability as a function of reference positional variability. Individual amblyopic observers (coloured symbols) and the mean of the normal observers (black symbols) are plotted. The diagonal line shows veridical matches. The mean slope of performance was found to be 0.82 ± 0.01 for the normal observers and 1.1 ± 0.08 for the amblyopic observers. Note: Figure reproduced in colour on the web; See: www.sciencedirect.com.

eye. This means that the representation of orientation is noisy in both eyes of amblyopic observers, relative to normal vision observers. This alone cannot account for the matching data showing greater noise in the amblyopic eye (matches would otherwise tend towards equality but with larger error bars), but it prevents us from comparing matches between normal vision eyes and either fellow or amblyopic eyes in amblyopic observers.

Overall, this suggests that the representation of orientation and positional structure in amblyopia shows a greater variability compared to normal. Again these results suggest the visual deficit in amblyopia involves elevated unreliability in the global representation of local structure.

4. Discussion

Normal vision subjects are able to discriminate the mean orientation of arrays of orientated Gabors, even when there is considerable orientation variability in the array (Dakin & Watt, 1997). Orientation discrimination thresholds with this noisy stimulus are approximately equal to discrimination thresholds with noise-free single grating stimuli, suggesting that the human visual system is able to integrate large numbers of local estimates of spatial structure to derive a meaningful global representation of object shape and texture. This global pooling mechanism is useful in situations where there may be uncertainty in the low-level visual code. Such a noisy visual input characterises the introspective reports of perceptual experience in amblyopic observers (Barrett, Pacey, Bradley, Thibos, & Morrill, 2003) and raises the possibility of using judgements of the global statistics of an image to understand the nature of the spatial deficit in amblyopia.

Spatial frequency and orientation discrimination thresholds have been studied in amblyopia (Demanins, Hess, & Keeble, 1996; Hess, 1980; Hess et al., 1980; Skottun et al., 1986). Both have previously been found to show selective losses at the high spatial frequencies, which are described well by individual acuity and contrast losses. However previous studies using isolated stimuli have failed to identify deficits at lower spatial frequencies, we have replicated this result (Fig. 4). Our experiments use stimuli whose spatial frequency and contrast are comfortably within the acuity limit of amblyopic observers and are composed of highly visible and resolvable elements. In Experiment 1, we show that with a stimulus that requires observers to integrate across large areas of visual space, orientation discrimination thresholds are elevated relative to those for normal vision observers. However, whether this reflects a smaller or perhaps more 'patchy' pooling/integrative region in amblyopia or indeed if amblyopes indiscriminantly integrate both signal and noise within a stimulus, cannot be answered with the present data. This result is substantiated by the inter-ocular matching tasks in Experiment 2, which show that the apparent orientation and positional uncertainty of stimuli perceived by the amblyopic eye is much greater than that perceived with the fellow eye.

In principle an orientation discrimination deficit could be due to any number of the presently accepted low-level explanations for the neural deficit in amblyopia, such as visibility, an undersampling of receptive fields in V1. However our stimuli were highly resolvable and visible and control manipulations of either the contrast or number of elements had no discernable effect on the results. A further low-level explanation of amblyopia proposes neural/spatial disarray in the location of initial filter mechanisms. This account is also ruled out by our results because the precise location of each element in our stimulus is unimportant; performance is limited by the observer's ability to integrate information across the stimulus. Taken together, these factors rule out any of the well-known sensitivity losses that are present in amblyopia.

Much less however is known about how local stimulus attributes are integrated into the coherent perception of visual objects. Using psychophysical techniques several studies have investigated the mechanisms that mediate the integration of local elements into a global pattern in amblyopia. Hess, Wang, and Dakin (1999) compared the ability of normal vision observers and strabismic amblyopes to detect permutations in a large circle, formed by a narrow band of spatial frequencies. Strabismic amblyopes were more impaired on this shape discrimination task even for targets composed of spatial frequencies well within their acuity range. Modelling of the results showed that both neural disarray and undersampling could account for the results. The authors favoured the disarray hypothesis because undersampling would need to be scale invariant to completely capture the deficit. Unlike our task, the relative locations of the elements in this stimulus must be veridically encoded for good performance. We show that even when the precise locations of the elements are rendered unimportant, visual integration is impaired in amblyopia.

Levi et al. (1999) attempted to resolve this dichotomy by employing a pattern recognition task that required observers to integrate information over both foveal and peripheral viewing areas. They jittered the position of individual Gabor elements that comprised an E pattern and measured thresholds for the global discrimination of E orientation. Tolerance for positional jitter was identical for normal and strabismic amblyopes over a wide range of contrast levels. At threshold identification however, strabismic amblyopes were less efficient than normals needing more individual elements to be present in the pattern to perform the task especially at fine spatial scales. These results suggest that for strabismic amblyopes the stimulus is underrepresented at the stage of feature integration providing further support for the undersampling hypothesis. If this hypothesis were correct, we would expect the performance of normal vision observers to approach that of amblyopes if the number of elements in the stimulus were reduced. However we found that this manipulation did not reliably affect orientation discrimination thresholds for any observers.

It has also been suggested that contour integration is disrupted in amblyopia with contour detection tasks in which observers are required to detect a path defined by a series of co-aligned Gabors in a background of randomly orientated, noise Gabors (Chandna, Pennefather, Kovacs, & Norcia, 2001; Hess et al., 1997; Kovacs, Polat, Pennefather, Chandna, & Norcia, 2000; Kovacs, Polat, & Norcia, 1996). In anisometropic amblyopes, however it has been argued that performance in these type of tasks are equivalent to normal observers provided that the contrast and spatial frequency of the patches are chosen with equal visibility to either eye (Hess & Demanins, 1998). In normal vision observers, the visibility of such embedded contours is reduced by orientational or positional perturbations (Field, Hayes, & Hess, 1993). Our results suggest that the representation of orientation and position is noisy in both anisometropic and strabismic amblyopes and it would therefore follow that contour integration should be affected in amblyopia; whether this is necessarily due to anomalous integration or the established anomaly in positional coding remains open to question.

We cannot definitively state whether the orientation deficit we report is based on uncertainty at initial stages of visual coding or at later stages at which such local estimates of orientation are combined to form a representation of the global image. The critical difference between the stimuli employed in previous studies that have failed to show an orientation discrimination deficit with resolvable stimuli and our study is our use of micro-pattern stimuli. While orientation discrimination can be based on the response of any single unit that responds to any part of a large uniform stimulus, our task forces the observer to integrate across the image to derive an estimate of the global image statistics. In this way performance is limited by the mean orientation noise across detectors instead of that of the most sensitive local detector.

Performance in such a global integration task, could, in principle be reduced because of an early deficit to orientation-selective detectors, such as those reported in area V1 of monkey brains, for reasons that have nothing to do with contrast sensitivity. However, this seems unlikely for a number of reasons. Firstly, in human amblyopes, orientation thresholds for simple grating stimuli are normal provided that the contrast and spatial frequency are equally visible to either eye (Skottun et al., 1986). Secondly, in amblyopic animals, the number and orientation and directional selectivity of neurons in V1 driven by the amblyopic eye has also been shown to be normal (Kiorpes et al., 1998). Finally, the fact that the fellow eye in amblyopia is also affected suggests that the abnormality must at least in part affect the pathway at a point where the majority of the neurons are increasingly indifferent to the eye of stimulation (e.g. extra-striate cortex). A recent study (Sharma, Levi, & Klein, 2000) has shown that amblyopes underestimate the number of elements or blank spaces present in a stimulus similar to ours (for an alternative explanation see Simmers & Bex, in press). This finding implicates a high-level deficit in amblyopia, but it is surprising that no equivalent deficit was observed with the fellow eye, even although higher stages of visual processing are indifferent to the eye of stimulation and should therefore show equivalent effects. Our task does however, show modest orientation discrimination deficit effects in both the amblyopic and fellow eye, taken together with previously reported deficits in global motion processing for both the amblyopic and fellow eye (Simmers et al., 2003) the results of this present study suggest that visual integration is impaired and therefore consistent with a deficit at global stages of visual processing in amblyopia.

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