



Impaired spatial and binocular summation for motion direction discrimination in strabismic amblyopia

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ABSTRACT

Amblyopia is characterised by visual deficits in both spatial vision and motion perception. While the spatial deficits are thought to result from deficient processing at both low and higher level stages of visual processing, the deficits in motion perception appear to result primarily from deficits involving higher level processing. Specifically, it has been argued that the motion deficit in amblyopia occurs when local motion information is pooled spatially and that this process is abnormally susceptible to the presence of noise elements in the stimulus. Here we investigated motion direction discrimination for abruptly presented two-frame Gabor stimuli in a group of five strabismic amblyopes and five control observers. Motion direction discrimination for this stimulus is inherently noisy and relies on the signal/noise processing of motion detectors. We varied viewing condition (monocular vs. binocular), stimulus size (5.3–18.5°) and stimulus contrast (high vs. low) in order to assess the effects of binocular summation, spatial summation and contrast on task performance. No differences were found for the high contrast stimuli; however the low contrast stimuli revealed differences between the control and amblyopic groups and between fellow fixing and amblyopic eyes. Control participants exhibited pronounced binocular summation for this task (on average a factor of 3.7), whereas amblyopes showed no such effect. In addition, the spatial summation that occurred for control eyes and the fellow eye of amblyopes was significantly attenuated for the amblyopic eyes relative to fellow eyes. Our results support the hypothesis that pooling of local motion information from amblyopic eyes is abnormal and highly sensitive to noise.

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1. Introduction

Amblyopia is a developmental visual disorder caused by a discrepancy in the images falling on each retina during early development. Under such conditions the visual system develops abnormally resulting in a loss of visual function, typically in one eye (Holmes & Clarke, 2006). Importantly, once amblyopia has developed, correcting the original amblyogenic factor will not fully restore vision to the amblyopic eye, as the visual deficit is cortical in nature (Anderson & Swettenham, 2006; Barnes, Hess, Dumoulin, Achtman, & Pike, 2001; Barrett, Bradley, & McGraw, 2004; Kiorpes, 2006; Kiorpes & McKee, 1999). While amblyopia is primarily thought of as a disorder of spatial vision (Barrett, Pacey, Bradley, Thibos, & Morrill, 2003; Levi, 2006), amblyopes do also exhibit anomalous motion perception (Aaen-Stockdale & Hess, 2008;

Aaen-Stockdale, Ledgeway, & Hess, 2007; Buckingham, Watkins, Bansal, & Bamford, 1991; Constantinescu, Schmidt, Watson, & Hess, 2005; Ellemberg, Lewis, Maurer, Brar, & Brent, 2002; Hess, Demanins, & Bex, 1997; Ho & Giaschi, 2006, 2009; Ho et al., 2005; Kelly & Buckingham, 1998; Kiorpes, Tang, & Movshon, 2006; Levi, Klein, & Aitsebaomo, 1984; Schor & Levi, 1980; Simmers, Ledgeway, Hess, & McGraw, 2003; Simmers, Ledgeway, Mansouri, Hutchinson, & Hess, 2006; Steinman, Levi, & McKee, 1988; Thompson, Aaen-Stockdale, Mansouri, & Hess, 2008). However there is an interesting difference between the spatial and temporal visual deficits that occur in amblyopia. The spatial deficit is known to affect low level visual functions, such as contrast sensitivity and visual acuity (Bradley & Freeman, 1981; Hess, 1979; Hess & Howell, 1977; Levi & Harwerth, 1980), as well as higher level visual functions that require global processing such as contour integration (Chandna, Pennefather, Kovacs, & Norcia, 2001; Hess & Demanins, 1998; Kozma & Kiorpes, 2003). However, based on the current evidence described below, the motion deficit appears to primarily affect tasks that require global integration of

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motion information with local motion perception remaining largely intact.

There is increasing evidence that amblyopia is associated with a deficit in the perception of global motion (Aaen-Stockdale & Hess, 2008; Aaen-Stockdale et al., 2007; Constantinescu et al., 2005; Elleberg et al., 2002; Ho et al., 2005; Kiorpes et al., 2006; Simmers et al., 2003, 2006) and that this deficit is not limited to the amblyopic eye but also affects the fellow fixing eye (Elleberg et al., 2002; Giaschi, Regan, Kraft, & Hong, 1992; Ho & Giaschi, 2006; Ho et al., 2005; Simmers et al., 2003, 2006). Global motion perception typically requires the integration of distributed signal elements and the segregation of these signal elements from noise elements. Therefore it is likely that global motion tasks rely upon processing in extrastriate dorsal stream visual areas such as V5/MT (Britten, Shadlen, Newsome, & Movshon, 1992; Newsome & Pare, 1988). Further psychophysical evidence implicating an extrastriate motion processing deficit in amblyopia includes abnormalities in the motion after-effect (Hess et al., 1997), impaired perception of motion defined form (Giaschi et al., 1992) and elevated D_{\max} thresholds (Ho & Giaschi, 2006, 2007) that persist when the stimuli are high pass filtered (Ho & Giaschi, 2007), therefore implicating abnormal function of high-level, possibly feature tracking mechanisms in amblyopia (Cavanagh & Alvarez, 2005; Ho et al., 2006).

In contrast to the pronounced deficits found for higher level motion perception, local motion perception appears to be largely unaffected by amblyopia (Hess & Anderson, 1993; Hess, Howell, & Kitchin, 1978; Hess, Mansouri, Dakin, & Allen, 2006; Thompson, Hansen, Hess, & Troje, 2007). In addition, the local motion deficits that have been found mainly concern the detection of stimuli with high spatial frequencies (Hess & Anderson, 1993) or low temporal frequencies (Schor & Levi, 1980), therefore implicating low level losses in acuity and contrast sensitivity rather than motion perception per se (Hess & Anderson, 1993). There is also evidence to suggest that in the absence of noise elements, integration of motion information is normal (Hess et al., 2006) or even excessive (Thompson et al., 2008) in the amblyopic visual system and that the motion processing deficit is associated with poor segregation of signal elements from noise elements (Mansouri & Hess, 2006; Thompson et al., 2007). It would appear therefore that while that the spatial impairments in amblyopia extend from low level processing within the primary visual cortex through to extrastriate visual areas, motion impairments may be primarily due to abnormal pooling of visual information within the extrastriate visual cortex (Kiorpes et al., 2006; Simmers et al., 2003).

Consistent with this distinction, neurophysiological investigations have demonstrated that neurons within the primary visual cortex of amblyopic monkeys show abnormalities in their spatial but not their temporal responses when driven by the amblyopic eye (Kiorpes, Kiper, O'Keefe, Cavanaugh & Movshon, 1998). In contrast, extrastriate visual areas appear to demonstrate deficits in both spatial (Movshon et al., 1987) and motion processing (El-Shamayleh, Kiorpes, Kohn, & Movshon, 2010), with motion deficits being most evident for stimuli that require global processing (El-Shamayleh et al., 2010). Human neuroimaging has also indicated both striate and extrastriate deficits for amblyopic eye viewing of grating stimuli (Barnes et al., 2001; Hess, Li, Lu, Thompson, & Hansen, 2010; Hess, Li, Mansouri, Thompson, & Hansen, 2009; Muckli et al., 2006), whereas motion specific deficits appear to be most pronounced in extrastriate visual areas (Bonhomme et al., 2006; Ho & Giaschi, 2009; Thompson, Villeneuve, Casanova, & Hess, 2010).

In order to further investigate the nature of the motion processing deficit in amblyopia we employed a motion direction discrimination task for two-frame motion sequences in which an abruptly presented Gabor patch of suprathreshold contrast was offset by a

variable phase step from the first frame to the second (Nakayama & Silverman, 1985). This paradigm was chosen because task performance is limited by noise that is inherent in the stimulus itself rather than due to the addition of noise elements to which amblyopic vision is known to be highly sensitive (as described above). Specifically, the abrupt presentation of the stimulus generates motion energy in multiple directions (Churan, Richard, & Pack, 2009; Maunsell, Nealey, & DePriest, 1990). Therefore in order identify the direction of motion presented in the stimulus, the visual system must detect the directional signal generated by the small phase displacement against the noise generated by the stimulus onset. In other words the task is limited by the signal/noise ratio of the motion stimulus (Churan et al., 2009; Nakayama & Silverman, 1985).

We quantified motion discrimination thresholds in terms of phase step size (Churan et al., 2009; Nakayama & Silverman, 1985; Tadin, Lappin, Gilroy, & Blake, 2003) for both normal observers and a group of strabismic amblyopes. We measured thresholds at a range of stimulus sizes (5.3–18.5°), under both monocular and binocular viewing conditions and at a fixed high and suprathreshold low contrast in order to assess the effects of spatial summation, binocular summation and contrast on motion discrimination. The spatial frequency of our stimuli was fixed at 0.5 cpd to minimise spatial contrast sensitivity differences between amblyopic and non-amblyopic eyes (Hess, 1979) and to optimize the effects of binocular summation on motion perception (Rose, 1978, 1980). We found that for high contrast stimuli, task performance was equivalent for the amblyopic observers and the control observers confirming that local motion measurements are normal in amblyopia. However for the low contrast stimuli we observed a pronounced binocular summation effect for normal observers that was absent for the amblyopic observers. In addition we found a strong spatial summation effect for the normal eyes of controls and the fellow fixing eyes of amblyopes. However the effect of spatial summation was significantly attenuated for amblyopic eyes relative to fellow fixing eyes, and this loss of spatial summation was independent of any reduction in task performance due to impaired contrast sensitivity. Given that sensitivity to spatial displacement is similar between V1 and MT (Pack, Conway, Born, & Livingstone, 2006), we suggest that our results are due to a specific impairment in the extrastriate mechanisms responsible for spatial summation.

2. Methods

2.1. Participants

Five observers with strabismic amblyopia and five control observers with normal or corrected to normal vision took part in this study. Details of the amblyopic observers can be found in Table 1. Acuity in the amblyopic eye ranged from 20/40 to 20/70, thus our amblyopic sample can be characterised as mild to moderate in terms of their acuity loss. All amblyopic and control participants were experienced psychophysical observers and all were naive to the purpose of the study. All study protocols were approved by the institutional ethics committee and were in accordance with the Declaration of Helsinki.

2.2. Apparatus and procedure

Stimulus design, apparatus and general procedural details were that same as those used by Churan et al. (2009). Stimuli were generated using a standard Pentium 3 PC computer using Matlab v7.0 and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and displayed using a CRT Electrohome 8000 projector with a spatial

Table 1

Details of the five amblyopic observers that took part in this study. Obs for observers, M for male, F for female, RE for right eye, LE for left eye, strab for strabismus, ET for exotropia and DS for diopter sphere. The term mixed refers to the presence of both a strabismus and anisometropia. Low contrast refers to the contrast of the low contrast test patch used for all conditions in % Michelson contrast.

Obs	Age/gender	Type	Refraction	Axis	Letter acuity	Squint	History	Low contrast (%)
AA	29/F	RE strab	+1.00	90°	20/40	ET	Detected age 8, intermittent patching, no surgery, stereo of 70 s of arc	3.4
AR	48/M	LE	∅	DS	20/20	1°	Detected age 6 no patching no surgery, no stereo	5.1
		RE	∅	DS	20/20	ET		
GH	45/M	LE strab	∅	DS	20/50	1°	Detected at 11y, no surgery, no patching, eye exercise 1–2y, glasses since 12y, no stereo.	3.4
		RE	−1.75 + 0.5	90°	20/20	ET		
GN	30/M	LE mixed	+1.25	DS	20/63	6°	Detected age 5y, patching for 3 m, no glasses tolerated, 2 strabismus surgeries RE age 10–12y, no stereo.	1.7
		RE mixed	+5.00 – 2.00	120°	20/70	ET		
VD	23/F	LE	+3.50 – 1.00	75°	20/20	8°	Detected age 5–6y, patching for 6 m, no surgery, no stereo.	1.7
		RE	+0.25	DS	20/20	ET		
		LE mixed	+2.75 – 1.25	175°	20/40	3°		

resolution of 1024×768 pixels and a presentation frame rate of 85 Hz.

The Gabor-gratings had a spatial frequency of 0.5 cpd, and the diameters (as determined by two standard deviations of the Gaussian envelope) were always 5.3°, 7.9°, 10.5°, 13.2°, 15.8°, and 18.5°. The gratings were presented on a gray background with a luminance of 6 cd/m². The Michelson contrast of the high contrast gratings was fixed at 98%. The contrast of the low contrast gratings was fixed at 1.7% for the control participants. For the amblyopes the low contrast values varied from 1.7% to 5% depending on each individual participant (see Table 1).

2.3. Procedure

The experiments were conducted in a darkened room (luminance <0.2 cd/m²). Participants were seated 56 cm behind a semi-transparent screen subtending a visual angle of $90 \times 40^\circ$ with their head fixed using a forehead support. A single trial is shown schematically in Fig. 1. Participants were required to report the direction (up or down) of a single motion step of a Gabor-grating. Task performance was quantified as the size of the phase step (0–90°) between the two successive grating presentations that was required for successful discrimination of the motion direction. Thresholds were obtained using a weighted up-down staircase procedure (Kaernbach, 1991). The initial phase step was 90° and the staircase terminated after 16 reversals. Initial step sizes were 10° up and 5° down for the first five reversals after which the steps were reduced to 2° up and 1° down. The final three reversals were averaged to provide an estimate of the threshold phase step required for 66% correct performance. Trials for each contrast/stimulus size combination staircase were randomly interleaved during each set of threshold measurements.

Participants completed at least three threshold measurements for each contrast/stimulus size combination for each of three viewing conditions; binocular, amblyopic/non-dominant eye and fellow/dominant eye. Eye dominance was assessed using a standard sighting test (Rosenbach, 1903). During monocular viewing conditions a tight-fitting eye patch was worn over one eye. The sequence of viewing conditions was randomized across participants. Prior to the first threshold measurements, participants were familiarized with the task under binocular viewing conditions. For amblyopic participants measurements were then made for the amblyopic eye for the 1.7% contrast stimuli in order to ensure that the low contrast stimulus was suprathreshold for the amblyopic eye. If the participant reported that they were unable to detect the presence of the 1.7% contrast target and their task performance was at chance (a phase offset greater than 80° for all stimulus sizes), then

the contrast of the target was increased in steps of 1.7% contrast until the target was reported to be visible and task performance confirmed this. Once set, the same low contrast was used for all viewing conditions (i.e. the amblyopic eye, the fellow eye and the binocular conditions).

During the staircase measurements the start of each trial was signaled with a visual cue positioned 20° in the periphery. The motion stimulus, consisting of two sequentially presented gratings with a particular phase offset between them, was then presented foveally 500 ms later. Each grating was presented for 35 ms. Participants responded by pressing one of two mouse buttons to indicate upwards or downwards motion. Trialwise feedback was provided and the next trial was shown after a 300 ms inter-trial interval. Group data were analyzed using within-subjects ANOVAs (degrees of freedom corrected for sphericity using the Greenhouse–Geisser correction).

3. Results

A mixed omnibus ANOVA with factors of group (amblyopic vs. control), viewing condition (amblyopic/non-dominant eye vs. fellow/dominant eye vs. binocular), contrast (low vs. high) and stimulus size (6 levels) revealed a significant 4-way interaction ($F[10, 80] = 103.46, p = 0.04$), indicating that the relative effects of these factors varied significantly between the control group and the amblyopic group.

Since the contrast values for the low contrast stimuli varied between the control and the amblyopic groups, we first conducted

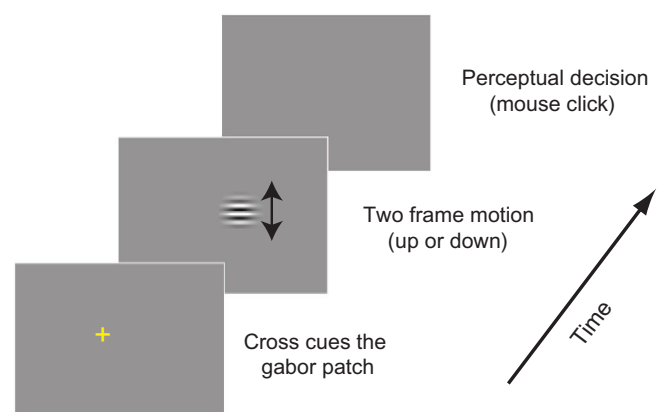


Fig. 1. A schematic of a single trial in the staircase procedure.

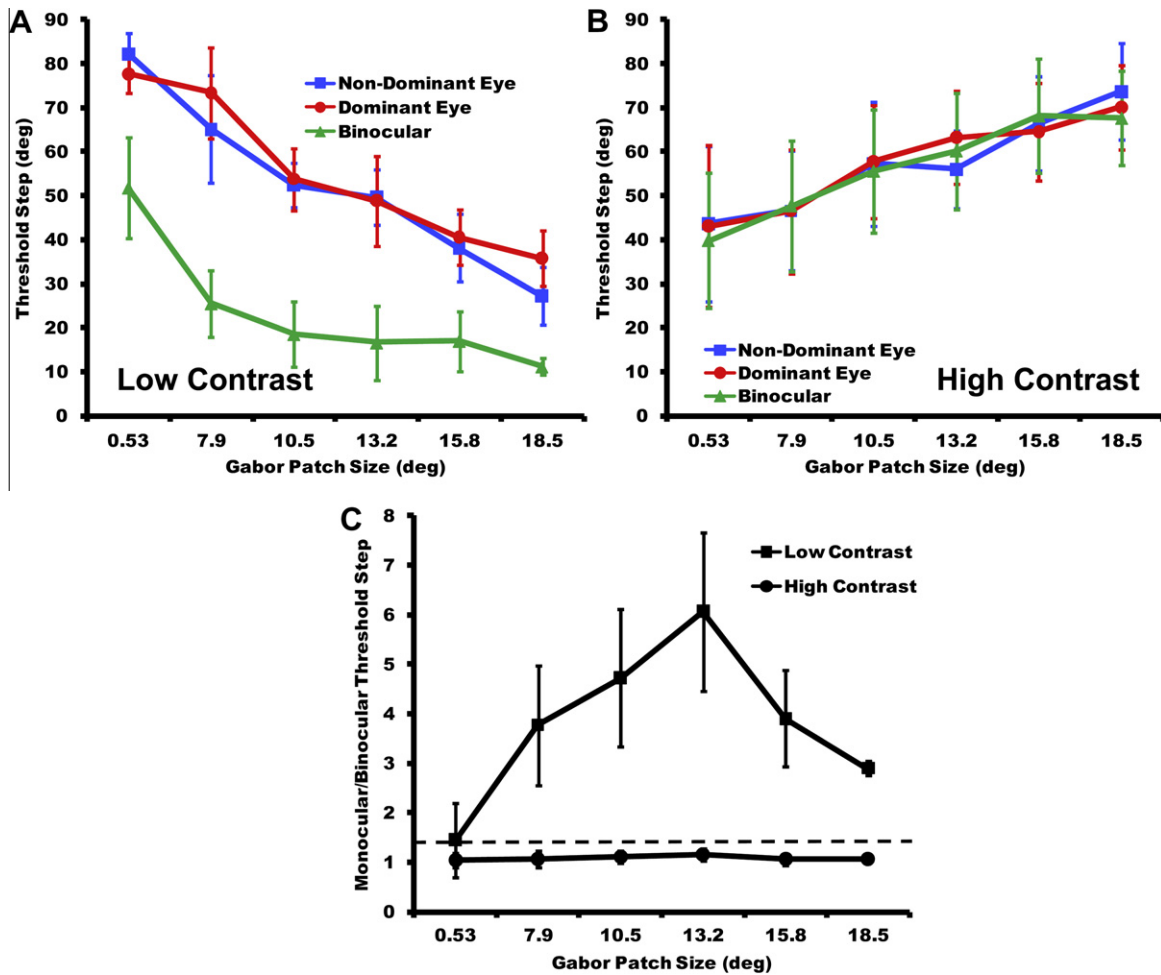


Fig. 2. Motion direction discrimination thresholds (A and B) and monocular/binocular threshold ratios (C) for the participants with normal vision. Thresholds for the low contrast stimuli are shown in A and those for the high contrast stimuli are shown in B for each of the three different viewing conditions; non-dominant eye (squares), dominant eye (circles) and binocular viewing (triangles). These data are re-plotted as threshold ratios in C to highlight the effect of binocular summation. The ratios were calculated for each participant as the average of the dominant and non-dominant eye thresholds divided by the binocular threshold. A ratio of 1 indicates no binocular summation and a ratio of 1.4 (dashed line) indicates the predicted level of summation based on probability summation. There is a pronounced effect of binocular summation for the low contrast stimuli only. Error bars show ± 1 standard error of the mean.

separate analyses for each group. Participants with normal vision demonstrated a pronounced effect of binocular summation for the low contrast stimuli (Fig. 2A). This was confirmed by a significant main effect of viewing condition (dominant eye vs. non-dominant eye vs. binocular viewing, $F[1, 4] = 10.1$, $p = 0.03$) which was driven by a significant reduction in threshold under binocular viewing conditions compared to both dominant eye viewing ($F[1, 4] = 20.9$, $p = 0.01$) and non-dominant eye viewing ($F[1, 4] = 33.7$, $p = 0.004$). There was also a significant effect of spatial summation for all viewing conditions whereby thresholds decreased as stimulus size increased ($F[2, 7] = 31.1$, $p < 0.001$). It is notable that although binocular viewing improved task performance, it did not significantly alter the gain of spatial summation. In other words, the relative advantage of increasing the stimulus size was constant across monocular and binocular viewing conditions (no interactions between viewing condition and size, $p > 0.05$). A different pattern of results was evident for the high contrast stimuli where there were no differences between binocular viewing and either of the two monocular viewing conditions ($p > 0.05$). Although there was a trend for task performance to deteriorate with increasing stimulus size for stimuli presented at a high fixed contrast, this did not reach significance ($F[1, 5] = 4.6$, $p = 0.08$).

The results from Fig. 2A and B are re-plotted in Fig. 2C to highlight the effects of binocular summation on task performance for the participants with normal vision. A monocular to binocular threshold ratio of 1 indicates an absence of binocular summation whereas a ratio of 1.4 ($\sqrt{2}$, dashed line) indicates the usual extent of binocular summation for spatial contrast (Meese, Georgeson, & Hess, 2004). For the low contrast stimuli the average binocular threshold ratio (across all stimulus sizes) was 3.7 (SE = 1.1). As can be seen from Fig. 2C the effect peaked at the Gabor patch size of 13.2° and then decreased with further increases in stimulus size. It is also evident that there was considerable variability between participants (although all showed strong binocular summation). Fig. 2C also highlights the lack of binocular summation for the high contrast stimuli with all ratios lying close to 1.

For the amblyopic observers a comparison between the non-amblyopic eye viewing condition and the binocular viewing condition demonstrated that there was no effect of binocular summation for either the low (Fig. 3A) or high (Fig. 3B) contrast stimuli ($p > 0.05$). This suggests that under binocular viewing conditions the amblyopic eye does not contribute to the performance of this task. It is clear from Fig. 3A, however, that not all viewing conditions were equivalent. For the low contrast stimuli, there was a significant interaction between viewing condition (amblyopic eye vs.

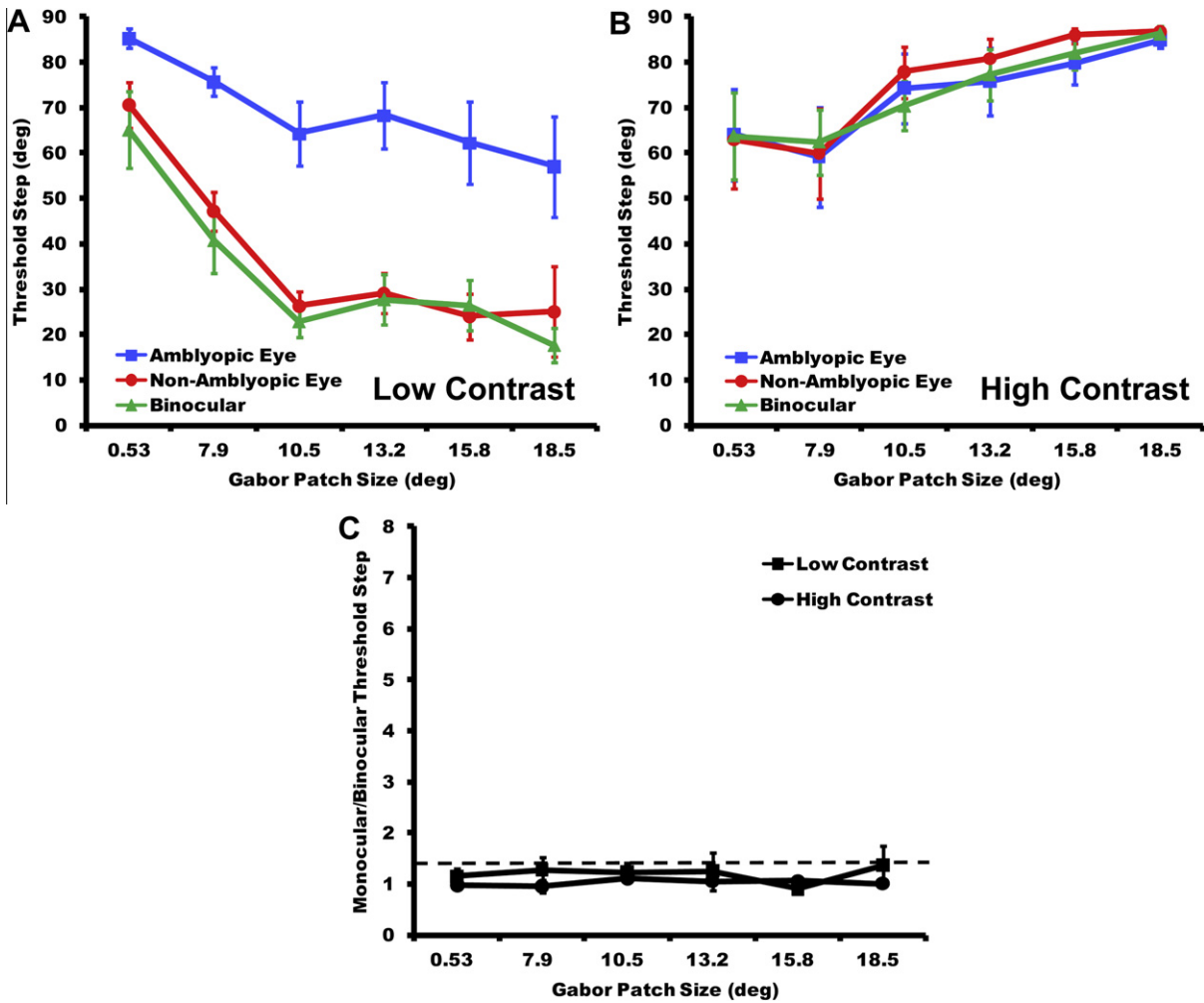


Fig. 3. Motion direction discrimination thresholds (A and B) and monocular/binocular threshold ratios (C) for amblyopic participants. Thresholds for the low contrast stimuli are shown in A and those for the high contrast are shown in B for each of the three different viewing conditions; amblyopic eye (squares), non-amblyopic eye (circles) and binocular viewing (triangles). These data are re-plotted as thresholds ratios in C to highlight any effects of binocular summation. The ratios were calculated for each participant as the non-amblyopic eye threshold divided by the binocular threshold. As in Fig. 2, a ratio of 1 indicates no binocular summation and a ratio of 1.4 (dashed line) indicates probability summation. There is no evidence of any binocular summation. Error bars show ± 1 standard error of the mean.

fellow eye) and stimulus size (6 levels), $F[8, 9] = 5.4, p = 0.03$, as well as a pronounced elevation in motion direction discrimination threshold for amblyopic eye viewing relative to both non-amblyopic eye viewing ($F[1, 4] = 26.2, p = 0.007$) and binocular viewing ($F[1, 4] = 29.6, p = 0.006$) conditions. This indicates an impairment in amblyopic eye performance with two distinct components; a general threshold elevation and impaired spatial summation whereby amblyopic eyes showed significantly less benefit in task performance than fellow eyes with increasing stimulus size. This deficit for the amblyopic eye was limited to the low contrast stimuli, as there were no differences between any of the viewing conditions for the high contrast stimuli (Fig. 3B).

In order to determine the source of the differences between the control group and the amblyopic group indicated by the omnibus analysis, we first conducted a separate analysis for the high contrast stimuli as this contrast was constant across the two groups. This analysis revealed a significant main effect of stimulus size ($F[2, 14] = 11.5, p = 0.001$) with no other significant main effects or interactions. This indicated that there were no reliable between-group differences for the high contrast condition. This was also the case if only the monocular conditions were included in the analysis. An analysis of the low contrast data revealed a significant difference between the two groups (significant group by

viewing condition interaction, $F[2, 16] = 11.4, p = 0.01$) as well as reliable effects of viewing condition ($F[2, 16] = 35.8, p < 0.0001$) and stimulus size ($F[2, 16] = 35.7, p < 0.0001$). To further investigate the between-group differences, separate analyses were conducted for each viewing condition. There were no reliable differences for binocular viewing ($p > 0.05$). For monocular viewing the fellow eye of amblyopes showed significantly lower thresholds than either eye of controls (dominant eye; $F[1, 8] = 5.4, p = 0.049$, non-dominant eye; $F[1, 8] = 6.8, p = 0.03$). However the sensitivity of the fellow eyes of amblyopes was still significantly less than the binocular performance of controls ($F[1, 8] = 8.1, p = 0.021$). Amblyopic eye performance showed a trend for reduced sensitivity relative to the non-dominant eye of controls. This effect was not significant when all stimulus sizes were included in the analysis ($F[1, 8] = 4.6, p = 0.065$), but became significant if only the three largest stimulus sizes were considered ($F[1, 8] = 5.6, p = 0.046$), consistent with the reduction of spatial summation identified by the differences in thresholds between the amblyopic eye and fellow eye. Amblyopic eye performance was not reliably different from the dominant eye of controls ($p > 0.05$). It should be noted that the absolute contrast used for the low contrast conditions varied between the groups to ensure that the stimulus was visible to amblyopic eyes and therefore

contrast differences may have contributed to these between-group effects.

4. Discussion

We found two main differences between amblyopic observers and control observers for motion direction discrimination, both of which were only apparent for the low contrast stimuli. Firstly we observed a substantial effect of binocular summation for the control participants that was entirely absent for the amblyopic observers. Secondly we found that the pronounced effect of spatial summation that was present for both eyes of controls was greatly reduced in amblyopic eyes compared to fellow fixing eyes. Importantly this reduction of spatial summation was independent of the generally increased thresholds found for the amblyopic eye relative to the fellow fixing eye for the low contrast stimuli.

The finding that binocular summation was entirely absent for low contrast motion direction discrimination in our sample of strabismic amblyopes is consistent with a number of previous studies demonstrating a lack of binocular summation for static stimuli of the same interocular contrast in amblyopia (Holopigian, Blake, & Greenwald, 1988; Hood & Morrison, 2002; Lema & Blake, 1977; Levi, Harwerth, & Manny, 1979; Levi, Harwerth, & Smith, 1980; Levi, Pass, & Manny, 1982; Pardhan & Whitaker, 2000). This however should not be interpreted as evidence that amblyopes lack binocular mechanisms as there is good support for normal binocular combination of stimuli at (Baker, Meese, & Hess, 2008) and above (Mansouri, Thompson, & Hess, 2008) threshold if the contrast is suitably adjusted between the two eyes. This suggests that the lack of binocular function under normal viewing conditions is due to active suppression of the amblyopic eye (Mansouri et al., 2008). It is worth noting that there was no binocular summation even for the largest stimulus (18.5°) that we tested. Therefore the suppression of the amblyopic eye was not limited only to central vision in the observers with strabismic amblyopia that we tested.

In contrast to the observers with strabismic amblyopia, our sample of observers with normal binocular vision demonstrated a pronounced effect of binocular summation for this task, with the binocular threshold across all sizes being on average a factor of 3.7 lower than the equivalent monocular thresholds. Binocular summation above that expected based on a signal/noise argument (Campbell & Green, 1965) has previously been shown by Rose (1978, 1980) for both counterphasing and drifting stimuli. Rose reported summation indices approaching 2, though this can be pushed to around 3 for stimuli of sufficiently low spatial frequency and large spatial extents (Hess, unpublished observation). Our estimate of 3.7 for stimuli of 0.5 cpd across a range of field sizes, while not being unexpected, does challenge current explanations for binocular summation (Georgeson & Meese, 2005; Meese, Georgeson, & Baker, 2006; Meese et al., 2004). We also found that spatial summation did not interact with binocular summation, indicating that while binocular summation lowered motion direction discrimination thresholds, the effect of spatial summation remained constant. This is consistent with the binocular stimulus being detected by binocular motion detectors of the AND type that have higher contrast gains than their monocular counterparts. It is clear from a comparison of Figs. 2 and 3 that the difference in binocular summation between the controls and amblyopes is driven by monocular differences, since there were no reliable differences in binocular performance between the two groups. Specifically, the fellow eye of amblyopes showed greater sensitivity than either eye of controls and accounts almost entirely for the binocular performance of the amblyopes. This suggests a greater than normal task performance for the fellow fixing eye. However a direct comparison between

the two groups must be made with caution as the absolute contrasts used for the low contrast conditions varied between the groups for some amblyopic observers who required slightly higher contrasts (see Table 1).

Our use of the two-frame Gabor motion stimulus (Nakayama & Silverman, 1985) did reveal a motion direction discrimination deficit for amblyopic eyes relative to fellow eyes when the stimulus was presented at a low contrast whereby thresholds for the amblyopic eye were elevated relative to the fellow eye. This is consistent with a previous report of poor direction discrimination in amblyopic eyes for small, abruptly displaced stimuli at low spatial frequencies (Levi et al., 1984). It seems unlikely that this effect is due to the spatial properties of the stimuli which were of low spatial frequency. Rather, the deficit is consistent with motion detectors having a poorer signal/noise ratio when driven by the amblyopic eye. The reduced spatial summation for motion direction detection in the amblyopic visual system is also likely to be related to the signal/noise nature of the task, whereby the brief and abrupt presentation of the stimulus generates motion energy in many directions with only a small offset in the direction of the phase displacement (Churan et al., 2009; Nakayama & Silverman, 1985). This deficit could therefore lie within V1 and be characterised by an abnormally broad directional bandwidth for motion detectors with high contrast gains. Alternatively the locus of the deficit could be extrastriate dorsal stream visual areas such as V3A and V5 where spatial summation is more pronounced due to larger receptive field sizes. In this case the deficit could be characterised by a poor signal/noise ratio within the motion pathway meaning that summation is less effective. Due to the finding that the spatial summation deficit was independent from the threshold elevation, we favor the latter explanation which implicates extrastriate pooling mechanisms that are more sensitive to noise (i.e. reduced signal/noise properties) when driven by the amblyopic eye. This interpretation is consistent with previous reports of deficient global motion processing and signal/noise segregation of motion stimuli in amblyopia (Aaen-Stockdale & Hess, 2008; Aaen-Stockdale et al., 2007; Constantinescu et al., 2005; Ellemberg et al., 2002; Ho et al., 2005; Kiorpes et al., 2006; Simmers et al., 2003, 2006; Thompson et al., 2007).

As described above, the contrasts at which the low contrast stimuli were presented to the observers with amblyopia were selected based on visibility of the stimuli to the amblyopic eye. This means that the stimuli were likely to have been presented at greater multiples of detection threshold for the fellow eye than for the amblyopic eye for each stimulus size/phase offset combination. However, if effective contrast was the main factor driving our results, we would anticipate that the effect of spatial summation would be more pronounced for the amblyopic eye since spatial summation diminishes with increasing contrast (e.g. Tadin et al., 2003). The fact that we find the opposite result suggests that the impaired spatial summation we report is sufficiently strong to overcome any effect of these contrast differences.

Here we report differences in spatial summation between the amblyopic eye and fellow eyes, whereas previous studies have reported deficits in both eyes of amblyopes for global motion (Ellemberg et al., 2002; Giaschi et al., 1992; Ho & Giaschi, 2006; Ho et al., 2005; Simmers et al., 2003, 2006) and coherent motion (Ho & Giaschi, 2006) stimuli. Our results are not necessarily inconsistent with these previous studies however, as fellow eye deficits have tended to be found for high contrast stimuli in anisometric patients with residual stereopsis (Ho & Giaschi, 2006; Ho et al., 2005) whereas the deficits we report here are for strabismic amblyopes viewing low contrast stimuli.

We did not find any effects of viewing condition or group for the high contrast stimulus, indicating that the amblyopic eye behaved normally for this task. Performance for the high contrast stimulus

was poor for all observers, and when the data were collapsed across group, thresholds reliably increased with increasing stimulus size. This is an established effect that has been attributed to center surround interactions in area V5 (Churan, Khawaja, Tsui, & Pack, 2008; Glasser & Tadin, 2010; Pack, Hunter, & Born, 2005; Tadin et al., 2003). However this interpretation is controversial (Aaen-Stockdale, Thompson, Huang, & Hess, 2009; Churan et al., 2009; Wallisch & Kumbhani, 2009). For example, the brief nature of the stimulus may introduce directional ambiguities even for mechanisms that lack surround suppression. Specifically, briefly displayed motion stimuli contain motion energy in many different directions, such that the true direction of motion can only be discerned by comparing the relative responses of different detectors. This problem is made more difficult by the saturating nonlinearities typically found in cortical neurons (Albrecht & Hamilton, 1982), which may diminish the differences between responses to the various motion directions. Indeed a previous study (Derrington & Goddard, 1989) has shown that performance on a similar task can be predicted on the basis of a saturating contrast nonlinearity and the frequency content of the stimulus.

We suggest that for the particular stimulus we use in this study the two interpretations are likely to be different ways of looking at the same phenomenon. Surround suppression at the single-cell level is likely to reflect, at least in part, the activity of normalization mechanisms, which are also thought to be responsible for the aforementioned saturating nonlinearities (Heeger, 1992). In both cases the single-cell observation is likely due to inhibitory influences from within the local network, which would also drive the perceptual effects by blurring the differences between responses to motion signals in opposite directions (Derrington & Goddard, 1989).

Overall our results extend previous reports of abnormal motion perception in amblyopia by demonstrating impaired spatial summation of motion information for stimuli that contain motion noise due to their abrupt and brief presentation rather than due to the presence of noise elements. This finding is consistent with the current hypothesis that motion processing deficits in amblyopes occur for stimuli that require pooling of local motion signals and the segregation of signal from noise (Aaen-Stockdale & Hess, 2008; Aaen-Stockdale et al., 2007; Kiorpes et al., 2006; Mansouri & Hess, 2006; Simmers et al., 2003; Thompson et al., 2007, 2008).

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