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Plaid perception is only subtly impaired in strabismic amblyopia

Benjamin Thompson *, Craig R. Aaen-Stockdale, Behzad Mansouri, Robert F. Hess

McGill Vision Research, Department of Ophthalmology, McGill University, Royal Victoria Hospital, Room H4.14, 687 Pine Avenue West, Montreal, Que., Canada H3A 1A1

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ABSTRACT

Amblyopes exhibit a global motion anomaly that implicates processing beyond the local motion analysis of V1 possibly involving areas MT and MST in the extra-striate cortex. Here, we sought to further investigate this deficit by measuring the perception of moving plaid stimuli by amblyopic observers, since there is good physiological evidence that the motion of such stimuli is determined by processes beyond V1. The conditions under which the two moving components constituting the plaids were seen to cohere or move transparently over one another were investigated by manipulating their relative spatial frequencies. Percepts were measured using both short presentation durations, where both the percept and the direction of motion were reported, and long presentation durations where the bi-stability of the stimulus was directly measured. In addition, we measured the ability of amblyopic eyes to perceive globally coherent motion in a multiple aperture stimulus. We found a small increased tendency for both amblyopic and fellow-fixing eyes to perceive short duration plaid stimuli as coherent relative to control eyes, but no difference for long duration plaids. In addition, amblyopic eyes saw less coherence in multiple aperture stimuli than fellow-fixing eyes but were not reliably different from control eyes. We therefore conclude that the neural mechanisms underlying plaid perception are only subtly abnormal in amblyopia.

1. Introduction

Amblyopia is characterised by a loss of visual function that cannot be corrected by surgery or spectacles and is due to a loss of neural function. The site of this dysfunction is not retinal but cortical. Although it is clear that there are striate deficits in strabismic animals from single cell studies (Kiorpes, Kiper, O'Keefe, Cavanaugh, & Movshon, 1998; Kiorpes, Tang, & Movshon, 1999; Movshon et al., 1987), and in strabismic humans from neuroimaging studies (Barnes, Hess, Dumoulin, Achtman, & Pike, 2001; Goodyear, Nicolle, Humphrey, & Menon, 2000), it is also generally recognised that striate cortex abnormalities alone cannot explain the range of perceptual problems found in amblyopia (Kiorpes et al., 1998; Kiorpes, Tang, & Movshon, 2006; Simmers, Ledgeway, & Hess, 2005; Simmers, Ledgeway, Hess, & McGraw, 2003; Simmers, Ledgeway, Mansouri, Hutchinson, & Hess, 2006).

Few neurophysiological studies have examined extra-striate visual areas in amblyopic animals but those that have show that the amblyopic eye drives fewer cells than its fellow-fixing counterpart (Schroder, Fries, Roelfsema, Singer, & Engel, 2002; Sireteanu & Best, 1992). In addition, psychophysical measurements of performance designed to target areas responsible for motion integration, specifically MT (Newsome & Pare, 1988), have revealed that both amblyopic eyes (Constantinescu, Schmidt, Watson, & Hess, 2005; Simmers et al., 2003, 2006) and fellow-fixing eyes (Aaen-Stockdale, Ledgeway, & Hess, 2007; Ho et al., 2005) are impaired at perceiving global motion. However the extent and the nature of the processing deficit in area MT in human strabismic amblyopes remains unclear since it has been shown that amblyopes can integrate motion direction signals normally (Hess, Mansouri, Dakin, & Allen, 2006) and that it is only when noise is introduced that amblyopic performance falls below normal (Mansouri & Hess, 2006). Thus one possibility is that the extra-striate processing deficit in amblyopia is confined to tasks requiring signal/noise integration/segregation. An alternate hypothesis is that the loss of function in MT is of a general nature and can be revealed by a variety of global motion tasks. What is needed is a different type of global motion stimulus that does not involve noise but that is effective in targeting MT function. The plaid stimulus satisfies such requirements as it has been shown to target specific cell types in MT that respond not to component directions but to the pattern direction (Movshon, Adelson, Gizzi, & Newsome, 1985). Our understanding of the cellular computations underlying plaid perception is relatively advanced compared with other visual functions (Rust, Mante, Simoncelli, & Movshon, 2006) as is the role MT cells themselves play in the component integration (Majaj, Carandini, & Movshon, 2007). On the basis of what we already know of the MT motion deficit in amblyopia from coherence motion tasks (Aaen-Stockdale et al., 2007; Constantinescu et al., 2005; Simmers et al., 2003, 2006), we would hypothesise that plaids will be perceived as less coherent (impaired MT function) and that a similar deficit will be

* Corresponding author. Fax: +1 514 843 161.
E-mail address: ben.thompson@mcgill.ca (B. Thompson).

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seen in the normal fixing eye. Such a prediction is supported by a number of computational models (Rust et al., 2006; Simoncelli & Heeger, 1998; Wilson, Ferrera, & Yo, 1992) and by patient lesion studies (Clifford & Vaina, 1999). However, if the deficit is selective for particular aspects of global motion processing at MT (i.e. those targeted by motion coherence tasks) we would expect to find normal plaid perception.

Here, we undertook three experiments that were designed to measure the perception of plaid stimuli by amblyopic observers. The veridical direction of a coherently moving plaid is given by the IOC or *intersection of constraints* (Adelson & Movshon, 1982). The IOC is a geometric solution, not a neural model, and fails to predict perceived plaid direction at short durations, low contrast or eccentric presentations (Yo & Wilson, 1992), although a Baysian version of the IOC has had some success in modelling these psychophysical results (Weiss, Simoncelli, & Adelson, 2002). It is unlikely that the visual system computes the IOC explicitly, although it could do so by pooling the outputs of local V1 neurons of different orientations tuned to spatial and temporal frequencies consistent with contour motion of a given speed and direction (Simoncelli & Heeger, 1998). Vector averaging of the first- and second-order components of plaid stimuli approximates the IOC direction (Wilson et al., 1992) and can account for psychophysical data if the second-order pathway component is extracted slower than the first-order, for which there is some evidence (Derrington, Badcock, & Henning, 1993).

One way of manipulating whether a plaid is perceived as being coherent or transparent is to alter the relative spatial frequencies of the two components, the greater the difference in the spatial frequencies, the greater the probability that transparent motion will be perceived (Adelson & Movshon, 1982; Smith, 1992). We employed such a technique using short duration plaids (Clifford & Vaina, 1999) and found a subtle trend for both the amblyopic and fellow-fixing eyes of amblyopic observers to perceive plaids as being more coherent than control eyes. To further investigate this effect, a different technique was used to measure the way in which the plaid stimuli were perceived. This technique was originally described by Hupe and Rubin (2003) and entailed presenting a single plaid stimulus for a long duration and asking the observer to continuously report whether they perceived coherent or transparent motion. Using this technique no difference was found between amblyopic and control observers suggesting that the small effect found for experiment 1 may be due to the short presentation interval.

A final experiment was conducted to assess motion integration in amblyopic eyes using a different type of stimulus closely related to plaids. This stimulus was constructed from multiple circular apertures each containing a drifting sinusoidal grating following previous studies which used multiple aperture stimuli to study motion integration processes (Alais, van der Smagt, van den Berg, & van de Grind, 1998; Mingolla, Todd, & Norman, 1992; Takeuchi, 1998). Using the continuous report technique with this multiple aperture stimulus, we found that amblyopic eyes showed a decreased level of motion integration compared to fellow-fixing eyes. This result suggests a subtle but specific abnormality for amblyopes when processing spatially distributed motion signals not unlike that previously reported using motion coherence stimuli (Aaen-Stockdale et al., 2007; Constantinescu et al., 2005; Simmers et al., 2003, 2006).

2. Methods

2.1. Participants

All amblyopic observers had strabismic or strabismic-anisometropic amblyopia with a best visual acuity of 20/40 in the amblyopic eye and normal acuity in the fellow-fixing eye. Three amblyopic observers completed all three experiments, five completed only experiments 1 and 2 and seven completed only experiment 3 (see Table 1 for details). Twelve control observers with normal acuity and binocularity participated in experiment 1, 11 of the same observers participated in exper-

Table 1
Details of amblyopic observers

Obs	Age (years)/sex	Type	Refraction	Acuity	Squint	History	Experiment
BH	27/M	RE	Ø	20/20		Detected age 2 years, patching and glasses for	3
		LE	Ø	20/50	XT 2°	2 years, no surgery, 1/10 local stereopsis	
ED	43/F	RE	+0.5 DS	20/16		Detected age 6 years, patching for 1 year, normal	1, 2 and 3
		LE strab	+0.5 DS	20/63	ET 5°	local stereovision	
GAC	20/F	RE	Ø	20/20		Detected age 7 years, patching for 1 year and	3
		LE strab	+0.5 DS	20/50	ET 1°	glasses for 3 years, 2, no stereopsis	
GN	30/M	RE mixed	+5.00 – 2.00 120°	20/70	ET 8°	Detected age 5 years, patching for 3 months, no	3
		LE	+3.50 – 1.00 75°	20/20		glasses tolerated, 2 strabismus surgery RE age 10–12 years, no stereopsis	
JD	21/M	RE	+4 DS	20/63	ET 5°	Detected age 5 years, patching for 3 years, no	3
		LE	+1.5 DS	20/16		surgery, 2/10 local stereopsis	
JL	29/M	RE	Ø	20/20		Detected age 4 years, no patching, no surgery, no	1 and 2
		LE mixed	+2.5 DS	20/40	XT 20°	stereopsis	
ML	20/F	RE mixed	+1.0 – 0.75 90°	20/80	ET 6°	Detected age 5 years, patching for 2 years, no	3
		LE	−3.25 DS	20/25		stereopsis	
PH	33/M	RE	−2.0 + 0.50 DS	20/25		Detected age 4 years, patching for 6 months,	1, 2 and 3
		LE strab	+0.50 DS	20/63	ET 5°	Surgery age 5 years, no stereopsis	
RDB	49/F	RE	+3.25 DS	20/15		Detected age 6 years, glasses, near normal local	1 and 2
		LE strab	+4.75 – 0.75 45°	20/40	XT 5°	stereo vision	
RB	31/F	RE mixed	−3.00 – 2.00 90°	20/40	ET 1°	Detected age 7 years, patching 6 months, glasses	1 and 2
		LE	−1.75 – 2.25 80°	20/20		since 10 years, no surgery, 7/10 local stereopsis	
SDP	35/M	RE strab	−0.75 DS	20/40	ET 1°	Detected at birth, surgery at 3 years, glasses since	1,2 and 3
		LE	Ø	20/20		3 years, patching 3–9 years, 1/10 local stereopsis	
SH	24/F	RE	−0.5 90°	20/32		Detected at birth, no patching, no surgery, glasses	1 and 2
		LE mixed	+2.5 + 2 180°	20/63	XT 6°	6–7 years, no stereopsis	
VD	23/F	RE	+0.25 DS	20/20	ET 3°	Detected age 5–6 years, patching for 6 months, no	3
		LE mixed	+2.75 – 1.25 175°	20/40		surgery, normal local stereovision	
WM	20/M	RE	Ø	20/20		Detected age 12 years, no patching, no surgery, no	3
		LE strab	+1.75 – 0.5 180°	20/63	ET 1°	stereopsis	
XL	31/F	RE	−2.50 DS	20/20		Detected age 13 years, no treatment, no stereopsis	1 and 2
		LE strab	−2.75 + 0.75 110°	20/400	ET 15°		

iment 2 and five completed experiment 3. Control participants all had normal or corrected to normal vision. All experimental procedures conformed to institutional guidelines for ethical research and accordingly all participants gave informed consent to participate in the study.

2.2. Stimuli

2.2.1. Plaids

Plaid stimuli were presented within a circular aperture with a diameter of 8° surrounded by mean luminance grey (51.3 cd/m^2, Sony Trinitron monitor, 53.2 cd/m^2, Iiyama Vision Master pro monitor). A circular region in the centre of the of the aperture was also set to mean luminance grey to assist stable fixation on a black fixation point located in the very centre of the display. The blank region in the centre of the aperture had a diameter of 0.5° of visual angle for the short duration plaids and 1.5° for the long duration plaids. Long duration plaids required a larger blank central region as stable fixation was more difficult to maintain over the extended viewing time.

Plaids were constructed from two sinusoidal gratings oriented 60° either side of vertical. Both gratings drifted diagonally upwards at 3° per second and had a contrast of 30%. Within every plaid one component was always held constant at a spatial frequency of 1 cpd and the second component had a spatial frequency ranging from 0.25 to 2.5 cpd in steps of 0.25 cpd. All contrasts and spatial frequency combinations were supra-threshold and clearly visible for all observers. As depicted in Fig. 1, the veridical direction of a coherent plaid under these presentation conditions is vertical (Fig. 1B). A transparent percept would consist of two motion directions 60° either side of vertical (Fig. 1A and C).

Short duration plaids were created offline by generating the two components individually (at 15% contrast) and then summing them together. The stimuli were then presented as a sequence of frames using the psychophysics toolbox (Brainard, 1997; Pelli, 1997). Long duration plaids were generated using a ViSaGe VSG (Cambridge Research Systems) and were presented using frame interleaving and CLUT cycling functions.

2.2.2. Multiple aperture stimuli

The spatial arrangement of the multiple aperture stimulus was a direct replication of the stimulus described by Alais et al. (1998). This particular stimulus however was scaled up in size to allow for a reasonable comparison to the plaid stimuli and also to ensure it was easily visible to amblyopic eyes. The stimulus consisted of 16 sinusoidal grating stimuli, each with a diameter of 1.3°, a contrast of 30% and a speed of 3° per second (the same parameters as the plaid stimuli). The gratings were alternately oriented + or −60° from vertical (Fig. 2) and were equally spaced within a 7.3° × 7.3° region with a fixation point at the center. The spatial frequencies of all component gratings were always identical, as using different spatial frequencies within the stimulus removed the coherent percept.

2.3. Procedure

Participants completed both the short and long duration plaid experiments once under binocular viewing conditions, and twice under monocular viewing conditions, once for the fellow-fixing eye (or dominant eye in controls) and once for the amblyopic eye (or non-dominant eye). For monocular viewing one eye was covered with an eye patch. The order of viewing conditions was randomised over subjects. Participants viewed the multiple aperture stimuli monocularly.

2.3.1. Short duration plaids

Before starting the experiment, participants were shown a range of plaid stimuli and the experimenter ensured that they had a clear understanding of the concept of transparent (“slidy”) vs. coherent (“sticky”) motion. Stimuli were presented on a 22 inch Sony Trinitron monitor at a resolution of 1024 × 768 pixels and a 60 Hz refresh rate. Participants sat 1 metre from the display and were asked to fixate on a dot in the centre of the screen. Plaid stimuli were presented for 1 s and there was a minimum of 4 s between each stimulus presentation in order to prevent a build up of adaptation. Each spatial frequency combination was presented 22 times, with the constant spatial frequency component (1 cpd) oriented clockwise from vertical for 11 of these trials and counter-clockwise from vertical for the remaining 11 trials.

Participants were asked to perform two tasks. Firstly they were asked to indicate, using a button press, whether they perceived the plaid as transparent or coherent. If the plaid was perceived as transparent the next trial was presented after a 4 s inter-trial interval. However, if the plaid was perceived as coherent, participants were then required to indicate in which direction they saw the plaid move. A vertical line was presented on the screen running from the fixation point to the edge of the presentation aperture. Participants used two keys to pivot the line around the fixation point until it lay along the motion direction they had perceived. There was no time limit for this process. A key press confirmed the direction selection and the next stimulus was displayed.

2.3.2. Long duration plaids

The design of this experiment was based on that used by Hupe and Rubin (2003) to exploit the inherent bi-stability of plaids. Stimuli were presented on a 22 inch Iiyama Vision Master pro 513 monitor via a CRS Visage VSG unit at a resolution of 1024x768 and a refresh rate of 120hz (60 Hz per component due to the frame interleaving). The viewing distance was 1 m. Plaid stimuli were presented for an extended amount of time and participants were asked to report their current percept, either coherent or transparent, by holding down one of two mouse buttons. If no button was depressed for a period of 1 s, a buzzer sounded to instruct the participant to make a response. If the percept did not switch (i.e. the plaid was constantly perceived as coherent or transparent) the plaid would be displayed for 2 min. Otherwise the plaid was displayed for 1 min after the first switch. To avoid the motion after-effect generated by each trial interfering with the subsequent trial, an interstimulus interval of twice the square root of the adaptation period (Hershenson, 1989) plus 3 s was enforced between each stimulus presentation. During this time a countdown was presented on the screen so that participants knew how long they had to wait before they could begin the next trial. Observers were instructed that if they still perceived a motion after-effect when the inter-trial interval had expired, they were not to trigger the next trial until they were confident that it had passed.

Following Hupe and Rubin (2003), two measures of the perception of long duration plaids were made. The first was the proportion of the viewing time during which a coherent plaid was perceived (proportion coherent). The second was the time it took for the first percept to switch, i.e. from coherent to transparent or visa versa (RTswitch). Each plaid was always presented for 60 s after the first switch and it was only after the first switch that the proportion coherent measure was calculated. This way of measuring proportion coherent allowed for this measure to be kept independent of the RTswitch measure. If no switch occurred the plaid was presented for 120 s and accordingly the proportion coherence measure was set to 1 or 0 depending on whether the plaid was perceived as always being coherent or transparent. In this situation the RTswitch measure was set to 120 s. Each spatial frequency combination was presented twice, once with the constant component (1 cpd) orientated clockwise of vertical and once counter-clockwise from vertical.

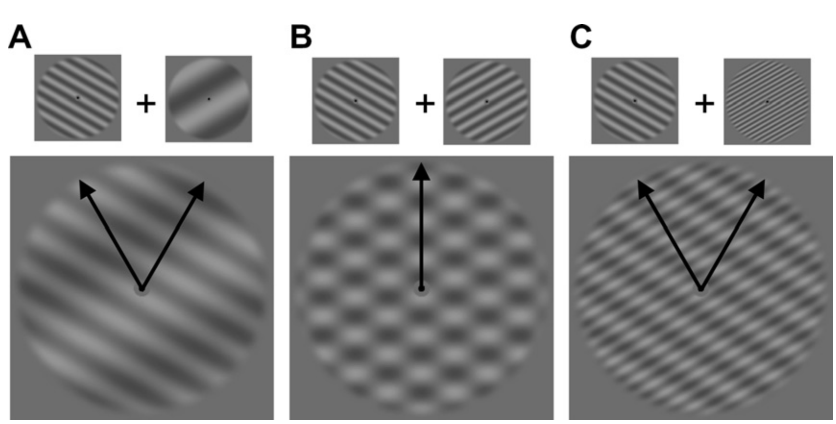

Fig. 1. Examples of the plaid stimuli and the components used to create them. Plaids were created by combining two component gratings oriented 60° either side of vertical (top row). Solid arrows depict the most likely perceived motion directions within each stimulus. One component always had a spatial frequency of 1 cpd, depicted oriented counter-clockwise in this figure, with the second having a spatial frequency ranging from 0.25 cpd (A) through 1 cpd (B, both spatial frequencies the same) up to 2.5 cpd (C) in steps of 0.25 cpd. This gave 10 individual plaid combinations.

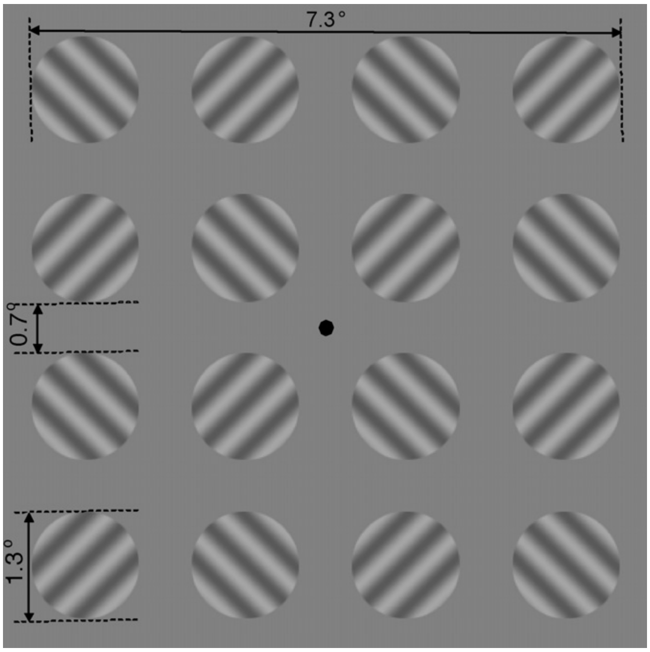

Fig. 2. The multiple aperture stimulus. The stimulus was constructed from 16 gratings each oriented + or −60° from vertical. The stimulus gave a bi-stable percept of either independently drifting gratings or a coherent pattern drifting upwards behind apertures.

2.3.3. Multiple apertures

Perception of the multiple aperture stimuli was measured in the same way as the long duration plaids. The stimulus was shown for an extended period of time and participants indicated their perceptual state continuously throughout the presentation interval. Initially the spatial frequency of the gratings making up the multiple aperture stimulus was kept constant at 1 cpd. This condition was repeated five times per eye for amblyopic subjects and five times for just the dominant eye for control subjects, since the earlier experiments had indicated no effect of eye dominance for controls. For two participants (GC and VD) trials were also run at spatial frequencies of 2, 3 and 4 cpd with each spatial frequency measured at least five times per eye.

3. Results

3.1. Short duration plaids

The results from the first, short duration, experiment are shown in Fig. 3. The left portion of Fig. 3 shows the proportion of trials where the plaid was perceived as being coherent as a function of the spatial frequency of the varied plaid component. In order to not be solely reliant on subjective reports of coherence and transparency, any coherent responses were checked against the reported *direction* of coherent motion for those specific trials. Any coherent trials associated with a reported motion direction of 20° or more away from vertical were counted as transparent, as the two components were considered to have not been fully combined to give a veridical, vertical, motion direction percept. A significant 3-way interaction between group (controls vs. amblyopes), viewing condition (binocular viewing vs. dominant/fellow-fixing eye vs. no-dominant/amblyopic eye) and spatial frequency was found $F(16) = 2.28$, $p < 0.02$. As can be seen from Fig. 1 this effect was characterised by increased coherence judgements by amblyopic observers, for plaids containing a spatial frequency at the higher end of the range used, only when viewing the stimuli with either their amblyopic or fellow-fixing eye. A significant 2-way interaction was found between group and viewing condition further supporting this interpretation of the data ($F(2) = 9.58$, $p < 0.001$). Finally a significant main effect of viewing condition was also found ($F(2) = 3.42$, $p < 0.05$) along with the expected main effect of spatial frequency ($F(9) = 60.13$, $p < 0.001$). In order to further explore the 3-way interaction, two 2-way ANOVAs were conducted, one for the control data and the one for amblyopic observer data. The control group ANOVA showed only the expected main effect of spatial frequency ($F(9) = 43.08$, $p < 0.001$) indicating that there were no differences between the viewing conditions. The amblyopic observer ANOVA on the other hand showed significant main effects of both spatial frequency ($F(9) = 22.81$, $p < 0.001$) and viewing condition ($F(2) = 7.85$, $p = 0.007$. Fig. 2 shows that this main effect of viewing condition is characterised by an increased reporting of a coherent percept at higher spatial frequencies for both fellow-fixing and amblyopic eyes relative to binocular viewing. Finally, in or-

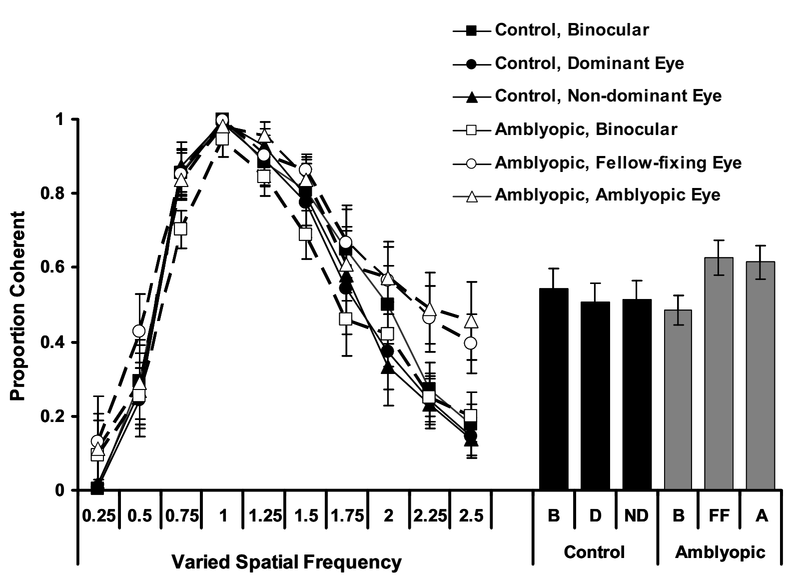

Fig. 3. Proportion of coherent responses as a function of the spatial frequency of the altered component in cycles per degree (one component was always shown at 1 cpd). The left side of figure shows the psychometric functions for the control observers and the amblyopic observers for each viewing condition (2 monocular, 1 binocular). The right side of the figure shows the average proportion of coherent responses across all spatial frequencies for each viewing condition for controls and amblyopes. For the control observers B denotes binocular, D dominant eye and ND non-dominant eye. For amblyopes FF denotes fellow fixing and A amblyopic. Error bars show ±1 SEM.

der to test where the monocular data of the amblyopic observers differed from control eyes, fellow-fixing eye data and the amblyopic eye data were compared the with the monocular data from control eyes (the dominant and non-dominant data for each control subject was pooled as these eyes did not differ). Guided by the pattern of data shown in Fig. 2, the analysis targeted the high spatial frequencies. Independent measures 2-tailed t-tests showed significant differences when the varied plaid component was presented at 2.5 cpd (fellow-fixing eye vs. control eyes, $t(18) = 12.16$, $p = 0.02$; amblyopic eye vs. control eyes, $t(18) = 10.04$, $p = 0.02$)), and marginal differences at 2.25 cpd (fellow-fixing eye vs. control eyes, $t(18) = 13.83$, $p = 0.05$; amblyopic eye vs. control eyes, $t(18) = 14.61$, $p = 0.07$).

3.2. Long duration plaids

The use of long duration plaids to measure the perception of coherence and transparency generated data that was strikingly similar to that found for short duration plaids (compare Figs. 3 and 4) suggesting that these two methods are comparable in the way in which they measure the perception of plaids. Fig. 4 shows both the proportion coherent (A) and RTswitch (B) data as a function of varied spatial frequency. Transparent initial percepts are plotted as negative values in plot B whereas positive values indicate a coherent initial percept. Inspection of Fig. 4 reveals that the increased coherence found for amblyopic observers for the short duration experiment is no longer evident at longer presentation durations. An analyses of the proportion coherent dataset showed the expected main effect of spatial frequency ($F(9) = 84.23$, $p < 0.001$) but no other main effects or interactions ($p > 0.05$). The same analysis applied to the RTswitch data also revealed a main effect of spatial frequency $F(9) = 76.73$, $p < 0.001$) with no other meaningful main effects or interactions ($p > 0.05$).

3.3. Multiple apertures

The multiple aperture stimulus was measured using the same technique as the long duration plaids and therefore also produced

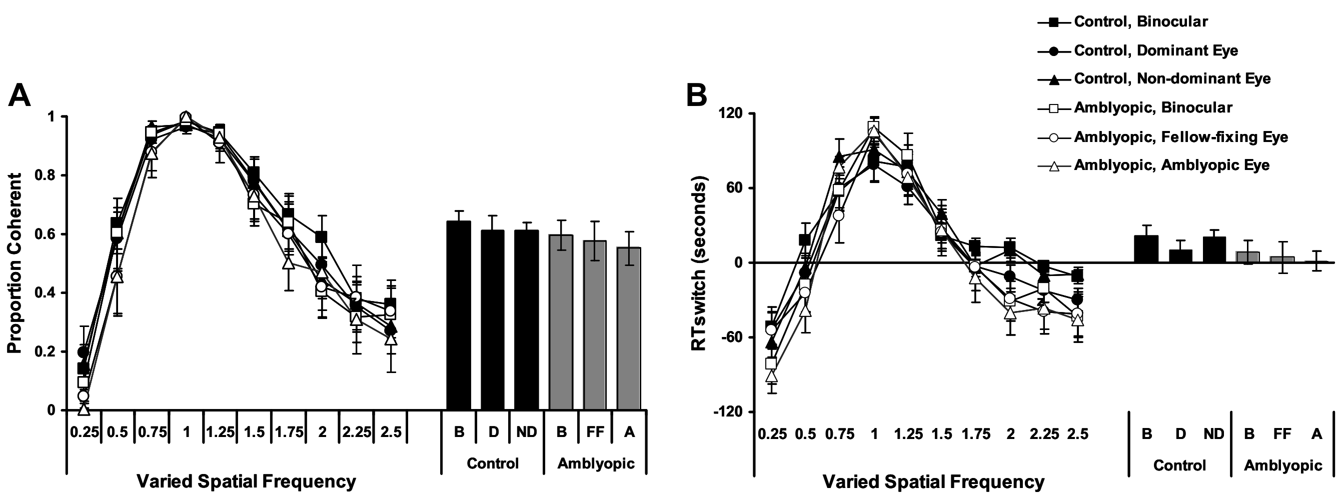

Fig. 4. The perception of long duration plaids measured by both the proportion of time a coherent percept was reported (A) and the duration of the initial percept (B). The left portion of A shows the proportion of time that a coherent percept was reported for the final 60 s of the presentation, i.e. excluding the initial percept, as a function of the varied spatial frequency. If there was no switch in percept this value was set to 1 or 0 accordingly. The left portion of B shows the duration of the initial percept in seconds as a function of spatial frequency. The maximum duration of the initial percept (i.e. no switch in percept reported for the whole presentation interval) was 120 s. Negative values indicate a transparent initial percept and positive values a coherent first percept. The right portion of both A and B shows the mean across all spatial frequencies for each viewing condition for controls and amblyopes. For the control observers B denotes binocular, D dominant eye and ND non-dominant eye. For amblyopes FF denotes fellow fixing and A amblyopic. Error bars show ± SEM.

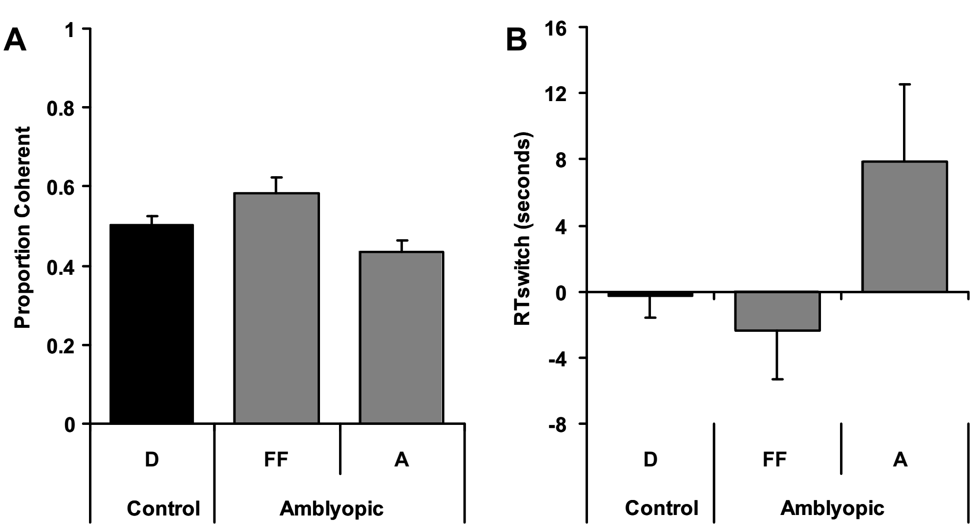

Fig. 5. Mean proportion coherent (A) and RTswitch (B) data for control, fellow fixing and amblyopic eyes using the multiple aperture stimulus. Error bars show ± SEM.

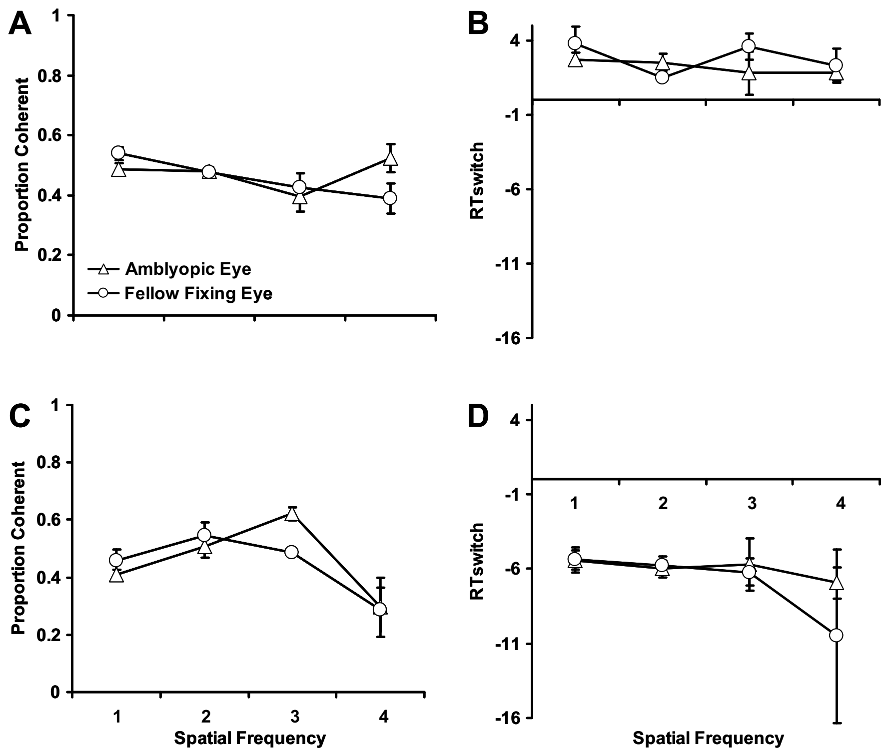

Fig. 6. Mean proportion correct (A and C) and RTswitch (B and D) data for participant GAC (A and B) and VD (C and D). Data are shown as a function of the spatial frequency of the constituent gratings for the multiple aperture stimulus. Error bars show ± SEM.

measures of proportion coherent and RTswitch. Fig. 5 shows the mean data for 10 amblyopic participants and 5 control subjects for a spatial frequency of 1 cpd. Amblyopic eyes saw a coherent pattern of motion for significantly less of the viewing time than fellow-fixing eyes ($t(9) = 2.93$, $p = 0.02$) however neither eye deviated significantly from control eyes ($p > 0.05$), which on average saw coherent motion exactly half of the time for this stimulus (mean proportion coherent = 0.50, standard deviation = 0.12). There were no reliable differences between eyes for the RTswitch measure ($p > 0.05$).

Two participants, one strabismic (GAC) and one strabismic anisometrope (VD) who showed little difference in proportion coherent between their amblyopic and fellow-fixing eyes for multiple aperture stimuli of 1 cpd were tested on a range of spatial frequencies to assess whether the difference between their eyes would be exacerbated by higher spatial frequencies. Fig. 6 shows the proportion coherent and RTswitch results for these two participants as a function of spatial frequency. For participant GAC a Greenhouse–Geisser corrected ANOVA conducted on proportion coherent scores showed no main effect of eye (amblyopic vs. fellow fixing), no main effect of spatial frequency and no interaction ($p > 0.05$). The same analysis of the RTswitch data also revealed no significant main effects or interactions ($p < 0.05$). For participant VD a Greenhouse–Geisser corrected ANOVA conducted on the proportion coherent data showed a significant main effect of spatial frequency ($F(2,6) = 16.5$, $p = 0.004$), no main effect of eye (amblyopic vs. fellow fixing) ($p > 0.05$), and no interaction ($p > 0.05$). The same analysis conducted on the RTswitch data revealed no significant main effects or interactions ($p > 0.05$).

4. Discussion

Plaid stimuli provide an important additional tool with which to assess MT function in amblyopia. Such an approach is valuable because currently there is evidence for a global motion processing deficit in MT using motion coherence stimuli in which noise plays a vital role. We wanted to know whether the previously described deficit for global motion processing could be generalised to other global motion stimuli and in particular those that were not of a signal/noise type. By manipulating the relative spatial frequencies of the two components making up a plaid, it is possible to explore how much deviation in spatial frequency the visual system can tolerate before the coherent percept breaks down and the stimulus is perceived as two independent components moving over one another (Kim & Wilson, 1993; Movshon et al., 1985; Smith, 1992). When used in a clinical population, this manipulation can provide some useful information about specific deficits in the visual system (Clifford & Vaina, 1999), since plaid stimuli are often thought to rely on early stages of visual processing for segregation of the two component motion signals and extra-striate areas, particularly area MT, for re-integration of the component motion directions to form a coherently moving plaid (Movshon et al., 1985; Simoncelli & Heeger, 1998; Wilson et al., 1992).

The results from experiment 1 using short duration (1 s) plaids indicated that amblyopic observers have a subtle abnormality in their perception of these stimuli, specifically an increased level of coherence when one component was presented at the highest spatial frequency used in this experiment (2.5 cpd). This finding cannot easily be explained by either decreased acuity or contrast sensitivity in amblyopic eyes as firstly all stimuli were suprathreshold for all eyes and secondly, the increased coherence was observed for both amblyopic and fellow-fixing eyes. In addition, perceiving the stimuli as being lower in contrast than they really were would have increased the tendency for a transparent percept to be reported (Delicato & Derrington, 2005), whereas the opposite effect was found here. Finally, if one of the higher frequency components had not been clearly visible to the observer, a coherent percept may have been reported as only one component was seen, however the reported direction of motion would necessarily have been close to that of the single visible component. To control for this eventuality, any coherent percept with a reported motion direction that deviated 20°or more from vertical was reclassified as transparent. A further benefit of this design was that it put the inherently subjective coherent/transparent response options on a more objective footing, as the reported percept and the reported direction had to match before the two components were considered to have reliably cohered. This conservative approach to accepting a coherent judgment increases the probability that plaids truly cohered when they fulfilled both perceptual and motion direction criteria.

The increased coherence found for amblyopic eyes is consistent with a subtle abnormality at a stage prior to signal integration, currently thought to be MT (Clifford & Vaina, 1999). A similar abnormality was found for the fellow-fixing eyes but not for binocular viewing. Coherence motion tasks have also demonstrated that the fellow-fixing eye of amblyopes is impaired (Aaen-Stockdale et al., 2007; Ho et al., 2005). Therefore the finding that fellow-fixing eyes show an increase in coherence judgments along with the amblyopic eyes is not unexpected. The finding that binocular viewing of the stimuli yielded results that did not differ from control observers however, cannot easily be explained in this way. One may speculate that MT neurons receiving a residual binocular input in the amblyopic visual system develop more normally than those that do not. However further investigation into visual perception under binocular viewing conditions in amblyopia is required to investigate this idea further.

Given that the difference between controls and amblyopes in experiment 1 was subtle, a second experiment was conducted using a different measurement technique to test the reliability of the effect. In experiment 2 plaid stimuli were presented for long durations (a minimum of 1 min) and the inherent bi-stability of the coherent/transparent percept was measured (Hupe & Rubin, 2003). Under these measurement conditions amblyopic perception of plaid stimuli was the same as controls for all viewing conditions, suggesting that the effect found in experiment 1 was dependant on the time given for integration to take place.

A final experiment was conducted to test whether the largely normal plaid perception of amblyopic eyes would translate to conditions when the motion components to be integrated were separated in space, in this case using a multiple aperture approach (Alais et al., 1998; Mingolla et al., 1992; Takeuchi, 1998). Here we found that, on average, amblyopic eyes were less likely to see coherent motion than fellow-fixing eyes suggesting that the ability to integrate motion information that is not spatially coincident may be impaired in amblyopic vision. This effect was subtle however, and the performance of amblyopic and fellow-fixing eyes was bisected by control eyes' performance (amblyopic eyes saw less coherent motion than controls and fellow-fixing eyes saw more coherent motion than controls) with neither amblyopic nor fellow-fixing eyes deviating significantly from control performance. Two participants who showed little difference between their amblyopic and fellow-fixing eyes on the initial multiple apertures task were tested at higher spatial frequencies to test for any increased difference between the eyes as a function of spatial frequency. No consentient differences between eyes were found, suggesting that in those participants who showed normal motion integration across space, this ability was not dependent on the particular parameters chosen (i.e. a low spatial frequency).

Unlike previous reports of a robust global motion deficit in amblyopia for coherence motion stimuli, the abnormalities reported here for plaid stimuli are less pronounced and exhibit duration and spatial dependency. In general we were surprised by the relative lack of motion processing deficit using this particular stimulus, particularly at long durations (experiment 2) highlighting the specificity of the deficit previously found for motion coherence stimuli. These results are unexpected and provide important constraints on the interpretation of previous studies that have reported reliable extra-striate processing deficits (Constantinescu et al., 2005; Simmers et al., 2003, 2006). Specifically, global motion deficits can not be directly extrapolated to other stimuli such as the plaids used here. We show that over a considerable part of the parameter space, the perception of plaids is normal in amblyopia and this extends to the processing of spatially distributed plaid motion. Having said that, we do show that under limited conditions subtle motion anomalies can be revealed and these need to be explained. The perception of increased coherence at short duration could have a number of explanations. It could reflect a deficit to motion processing before component integration in MT, similar to that found in patients with striate lesions (Clifford & Vaina, 1999). On the other hand, it may reflect an over-integration of local component motion in extra-striate cortex at or beyond MT, an explanation not inconsistent with the global motion abnormality revealed with motion coherence stimuli (Aaen-Stockdale et al., 2007; Constantinescu et al., 2005; Simmers et al., 2003, 2006). Interestingly, amblyopes perceive spatially distributed plaids (experiment 3) as being less coherent with their amblyopic eye. This effect is subtle but does suggest integration of motion signals over space may not be entirely normal in amblyopia.

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