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Visual deficits in amblyopia constrain normal models of second-order motion processing

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ABSTRACT

It is well established that amblyopes exhibit deficits in processing first-order (luminance-defined) patterns. This is readily manifest by measuring spatiotemporal sensitivity (i.e. the “window of visibility”) to moving luminance gratings. However the window of visibility to moving second-order (texture-defined) patterns has not been systematically studied in amblyopia. To address this issue monocular modulation sensitivity (1/threshold) to first-order motion and four different varieties of second-order motion (modulations of either the contrast, flicker, size or orientation of visual noise) was measured over a five-octave range of spatial and temporal frequencies. Compared to normals amblyopes are not only impaired in the processing of first-order motion, but overall they exhibit both higher thresholds and a much narrower window of visibility to second-order images. However amblyopia can differentially impair the perception of some types of second-order motion much more than others and crucially the precise pattern of deficits varies markedly between individuals (even for those with the same conventional visual acuity measures). For the most severely impaired amblyopes certain second-order (texture) cues to movement in the environment are effectively invisible. These results place important constraints on the possible architecture of models of second-order motion perception in human vision.

1. Introduction

The ability to perceive motion is invaluable. It not only conveys the presence and intentions of other potentially important organisms (e.g. predators, prey and mates), but can break camouflage and facilitate navigation through the world by providing cues (e.g. motion parallax) to the three-dimensional (3-d) layout of the environment. Visual motion can also drive and control many other biologically-important functions such as eye movements to stabilise the retinal image and in maintaining posture and balance (for reviews see Burr & Thompson, 2011; Smith & Snowden, 1994; Zanker & Zeil, 2001). Thus elucidating the mechanisms that encode motion is central to our understanding of sensory processing in general and this is reflected in the breadth of disciplines that are involved in its study ranging from psychology, neurology, neurophysiology, engineering and computer science.

What types of visual input drive motion perception? Objects principally differ from each other, and their surroundings, in terms of reflected light intensity and consequently luminance variations within a visual scene correspond to object boundaries, edges and contours. Whenever an object moves these luminance variations are displaced and give rise to “first-order motion” (Cavanagh & Mather, 1989). However in the last 20 yrs or so it has become evident that motion perception is possible in the absence of first-order cues. Impressions of movement can arise from a range of more complex image properties, such as contrast, orientation, flicker and size (Chubb & Sperling, 1988). This originates in the natural world when moving objects differ from their surroundings in terms of their textural attributes and has been termed “second-order motion” (Cavanagh & Mather, 1989).

First-order and second-order motion perception have been substantially investigated in the laboratory using a range of techniques including single-cell recording, neuroimaging and psychophysics. Although a single mechanism could in principle encode both (e.g. Benton & Johnston, 2001; Benton et al., 2001; Johnston, McOwan, & Buxton, 1992), most of the available evidence points to the notion that the two varieties of motion are detected by distinct (separate) but parallel visual mechanisms. This is evidenced by the presence of uncorrelated deficits for first-order and second-order motion following brain damage (Greenlee & Smith, 1997; Vaina & Cowey, 1996; Vaina, Cowey, & Kennedy, 1999; Vaina & Soloviev, 2004), in the elderly (e.g. Habak & Faubert, 2000) as well as in normal (Ellemberg et al., 2004, 2010) and abnormal visual development (e.g. Ellemberg et al., 2005).

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The “Filter-Rectify-Filter” (FRF) class of models has been shown to be consistent with the processing of these two stimulus types and can accommodate a broad range of results from both motion and form perception studies (Sutter, Beck, & Graham, 1989; Wilson, Ferrera, & Yo, 1992; Zhou & Baker, 1993). It consists of a first stage composed of an oriented, linear, spatiotemporal filter bank (the operation of which is thought to be akin to that of V1 simple cells). The output from this first filtering stage undergoes a gross nonlinearity before being processed by a second filtering stage: convolution with a filter-bank tuned to proportionally lower spatial frequencies and perhaps different orientations. In this way the second stage is capable of detecting and making explicit the second-order image structure for further analysis (see Fig. 7, left-most column).

Although the mechanism(s) underlying the perception of second-order motion have been extensively probed using psychophysical methods, almost all studies have employed a single class of second-order image (contrast modulation) to investigate this issue. Given the complexity of real world patterns, it may seem naïve to assume that all second-order information, at least with respect to the visual system and indeed individuals, are processed in a similar manner. Indeed there is growing evidence pointing to heterogeneity in the encoding of different varieties of second-order motion (Hutchinson & Ledgeway, 2006; Lu & Sperling, 2001a; Petersik, 1995) and spatial patterns (e.g. Kingdom, Prins, & Hayes, 2003), with high-level attentive, feature-based strategies also having been implicated (e.g. Ledgeway & Hutchinson, 2008; Lu & Sperling, 1995).

It is well established that amblyopes exhibit deficits in processing first-order, luminance-defined patterns. Amblyopia is widely characterised by low-level sensory deficits including reduced spatial resolution, reduced contrast sensitivity and marked losses in spatial accuracy. Psychophysical studies suggest that these perceptual deficits appear to be either alterations in the density (e.g. Levi & Klein, 1983) or position (Hess, 1982) of visual receptive fields i.e. a sparsely coded or topographically jittered image representation, that can be characterised by under sampling or increased orientation and positional variability/noise in the visual system. Furthermore there is also now firm evidence that global-motion processing is anomalous in amblyopia and that these losses may be more extensive for second-order, contrast-defined, stimuli and independent of any first-order spatial input (Simmers, Ledgeway, & Hess, 2005; Simmers et al., 2003, 2006).

However the processing of different types of second-order motion patterns (e.g. those defined by sinusoidal variation in either the contrast, orientation, flicker or spatial length of a visual texture) has not been studied in amblyopic observers. To address this issue we systematically measured spatiotemporal modulation sensitivity functions to first-order and several different varieties of second order motion, see if these are also impaired in amblyopia relative to normal observers. Furthermore this establishes the “window of visibility” for motion and defines what types of visual information in the world can be seen, and thus potentially acted upon, by amblyopic observers and hence is crucial to our understanding of this complex visual deficit.

2. Methods

2.1. Subjects

Three adult amblyopes (LN, PC and PK) with strabismus (mean age 40.30 yrs; SD ± 9.60 yrs) were recruited for the study (see Table 1 for clinical details). Observer PK was one of the authors and the other two amblyopes were naïve volunteers. For the purposes of this study amblyopia was defined as a visual acuity of 20/30 or worse in the amblyopic eye and anisometropia was defined as an interocular difference of greater than 1.00 dioptre sphere or 1.0 dioptres of cylinder. A control group of three observers (authors AS, CH and TL) were selected with normal visual acuity and normal binocular vision (mean age 37 yrs; SD ± 6.08 yrs). Viewing was monocular in all cases with the appropriate and full refractive correction. All experimental procedures followed the institutional guidelines, and informed consent was obtained after the nature and possible consequences of the experiment had been explained. All subjects were experienced in psychophysical testing.

Table 1
Clinical characteristics of the amblyopic observers.

Observer	Visual acuity	Spectacle prescription	Ocular alignment
LN	RE 20/30 LE 20/17	RE +0.50DS LE +0.75DS	L XOT 10Δ
PC	RE 20/120 LE 20/17	RE +5.00/−1.00 × 165° LE +5.00/−2.00 × 5°DS	R SOT 25Δ
PK	RE 20/17 LE 20/30	RE −1.00DS LE −0.25DS	R SOT 10Δ

2.2. Apparatus and stimuli

Stimuli were generated using an *Apple Macintosh* computer and presented on a *P1220 Compaq* CRT monitor at a frame rate of 75 Hz and a mean luminance of 50 cd/m^2 using custom software written in C. The luminance of the display was controlled with pseudo 12-bit resolution using a custom-built video attenuator (Pelli & Zhang, 1991), allowing intensity levels to be chosen from a set of 4096 possible values. Images were presented in grey-scale by amplifying the monochrome signal and driving the three colour guns of the monitor equally. The monitor was carefully gamma-corrected using a photometer and look-up tables and checked psychophysically (Ledgeway & Smith, 1994) to confirm that any residual luminance nonlinearities were imperceptible (cf Gurnsey, Fleet, & Potechin, 1998; Ledgeway & Smith, 1994; Lu & Sperling, 2001b; Scott-Samuel & Georgeson, 1999). Images were viewed monocularly in darkness at a distance of 137 cm. One screen pixel subtended 0.94 arc min of visual angle, resulting in a display that subtended 6° both vertically and horizontally.

Motion stimuli were periodic grating patterns in which a drifting, vertically-oriented, sinusoidal waveform was used to modulate either a first-order or a second-order property of a dynamic visual noise carrier. For all motion patterns the noise had a (mean) Michelson contrast of 0.30 and was replaced with a new random sample (or its elements were subjected to luminance reversal in the case of polarity-modulated dynamic noise, as described below) each time the position of the drifting waveform was updated. Five different varieties of motion stimuli were used and their construction has been described in detail elsewhere (e.g. Hutchinson & Ledgeway, 2006; Ledgeway & Hutchinson, 2008; Schofield, Ledgeway, & Hutchinson, 2007). First-order motion stimuli were composed of luminance-modulated, spatially two-dimensional (2-d), dynamic noise. In the case of the second-order motion patterns, the sinusoidal waveform modulated either the local contrast, polarity, orientation or spatial length of a field of dynamic noise. Stimulus examples are shown in Fig. 1.

In all cases the motion stimulus was presented for a total duration of 853 ms, but the sinusoidal modulation was ramped on and off by a raised cosine window both temporally (half cycle 170 ms) and horizontally (half cycle 1.2°). This was done to minimise the presence of temporal and spatial transients, respectively.

The amplitude of the sinusoidal modulation (i.e. the modulation depth of each stimulus) could be varied in the range from 0 to 1, to

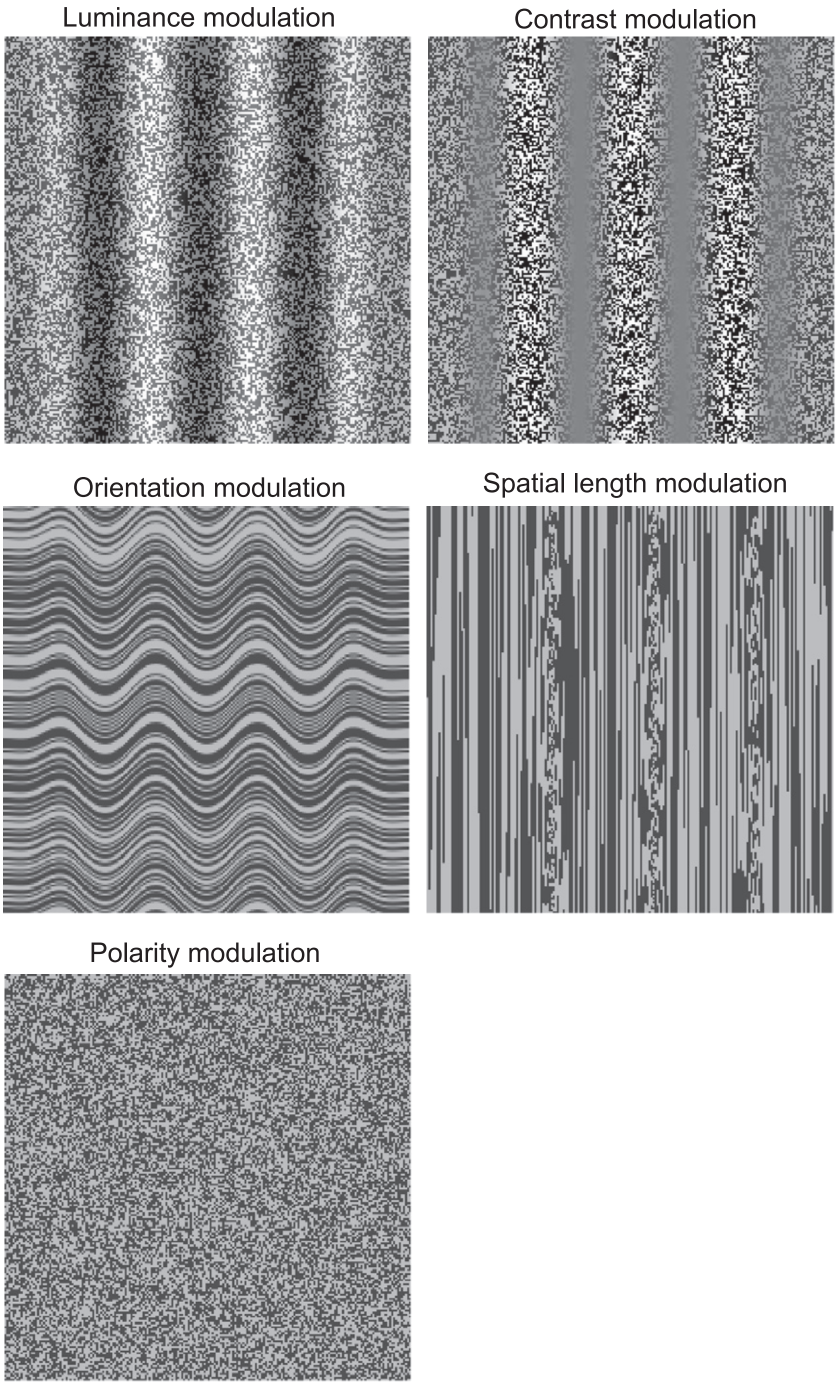

Fig. 1. Space (x)–space (y) plots showing examples of the types of first-order and second-order motion stimuli used in the experiments. In each case a drifting sinusoidal waveform (windowed both spatially and temporally by a raised cosine envelope) modulates either a first-order (luminance) or second-order (contrast, orientation, polarity or spatial length) property of a dynamic, random noise carrier. Note that for the polarity modulation the sinusoidal waveform determines the probability that a given noise element in the image will reverse its luminance polarity (i.e. dark pixels become light and vice versa) and thus it cannot be depicted in this figure.

measure a motion threshold, according to the following equation (with the exception of orientation-modulated dynamic noise):

$$\text{Modulation depth} = (A_{\max} - A_{\min})/(A_{\max} + A_{\min})$$

where $A_{\min}$ and $A_{\max}$ represent the minimum and maximum values of the first-order or second-order property of the dynamic visual noise carrier that was being modulated. For luminance-modulated dynamic noise $A_{\min}$ and $A_{\max}$ are the minimum and maximum local luminance values in the image, averaged over neighbouring noise elements with opposite polarity. For contrast-modulated noise $A_{\min}$ and $A_{\max}$ are the minimum and maximum local contrasts of the noise, calculated over neighbouring elements with opposite polarity. For polarity-modulated noise $A_{\min}$ and $A_{\max}$ are the minimum and maximum probabilities that the noise elements will reverse (flip) their luminance polarity. For spatial length-modulated dynamic noise $A_{\min}$ and $A_{\max}$ refer to the minimum and maximum heights of the noise elements, expressed as a percentage of the full image height. For orientation-modulated dynamic noise the modulation depth could be varied in the range from 0 to 1 according to following equation:

Table 2
Summary metrics characterising the modulation sensitivity surface for each stimulus type and observer. Amblyopic observers are denoted by italics.

Stimulus type	Obs.	Peak sensitivity (±1 SEM)	Volume of log–log sensitivity plot	Spatial cut-off (c/deg)	Temporal cut-off (Hz)	Number visible stimuli
Luminance	TL	522.90 (±51.98)	6709.20	>16	>16	36/36
	AS	441.00 (±73.15)	6812.70	>16	>16	36/36
	CH	350.17 (±161.84)	4141.80	>16	>16	36/36
	PK	330.47 (±29.86)	3854.30	16	>16	30/36
	PC	681.74 (±179.31)	4039.70	16	>16	23/36
	LN	263.04 (±109.55)	1676.50	16	>16	24/36
Orientation	TL	15.80 (±1.27)	86.86	8	>16	24/36
	AS	13.99 (±1.90)	98.15	8	>16	24/36
	CH	19.99 (±3.48)	120.74	8	16	19/36
	PK	5.96 (±0.09)	50.02	4	16	15/36
	PC	2.74 (±0.54)	3.86	2	8	7/36
	LN	1.00 (±0.00)	0.00	0.5	0.5	0/36
Contrast	TL	9.10 (±0.67)	54.61	8	16	19/36
	AS	9.13 (±0.80)	60.20	8	16	19/36
	CH	11.09 (±0.87)	70.84	8	16	19/36
	PK	6.43 (±0.71)	36.97	4	16	14/36
	PC	5.41 (±1.11)	29.36	4	>16	16/36
	LN	3.20 (±0.51)	8.26	4	16	12/36
Polarity	TL	4.82 (±0.15)	25.15	8	8	13/36
	AS	5.13 (±0.16)	27.29	8	8	13/36
	CH	7.81 (±0.03)	38.08	8	8	15/36
	PK	4.00 (±0.05)	19.25	4	8	12/36
	PC	1.08 (±0.01)	0.20	1	8	4/36
	LN	1.17 (±0.17)	0.33	2	2	3/36
Spatial length	TL	1.66 (±0.15)	3.65	4	8	10/36
	AS	1.60 (±0.06)	1.87	4	8	10/36
	CH	2.02 (±0.44)	4.45	4	8	11/36
	PK	1.46 (±0.05)	1.65	4	8	10/36
	PC	1.04 (±0.01)	0.05	1	1	1/36
	LN	1.00 (±0.00)	0.00	0.5	0.5	0/36

$$\text{Modulation depth} = (O_{\max} - O_{\min})/90$$

where $O_{\min}$ and $O_{\max}$ refer to the minimum and maximum local orientations in the image, computed relative to a reference of 90° (corresponding to vertical).

Sensitivity to the drift direction of each the motion patterns described above was measured (visual acuity permitting) over a five-octave range of spatial frequency and temporal frequency. Spatial sensitivity was measured from 0.5 to 16 c/deg and temporal sensitivity was measured from 0.5 to 16 Hz in one-octave steps.

2.3. Procedure

Monocular thresholds for identifying the direction of image motion (amblyopic eye or a randomly assigned eye in the visually normal observers) were measured using a single-interval, binary, forced-choice task. On each trial observers were presented with a central fixation cross, on an otherwise homogenous field, for 1000 ms followed by a motion stimulus for 853 ms that drifted either leftwards or rightwards (randomly chosen with equal probability on each presentation). After the offset of the motion stimulus, the observer was required to respond with a key press to indicate the direction in which they perceived the stimulus to move. Feedback was given after trials in which the observer responded incorrectly. The fixation cross was then presented on screen again and following a 1000 ms inter-trial interval another motion stimulus was presented, and so on.

An adaptive staircase routine selected the modulation depth of the motion stimulus on each trial, according to the observer's recent response history. The staircase implemented a simple 3-down, 1-up decision rule designed to converge on the 79.4% correct response level (e.g. Levitt, 1971; Wetherill & Levitt, 1965). At the beginning of each staircase the modulation depth was set to a suprathreshold level (typically 6 dB above threshold based on pilot studies) and the initial step size was half this value. After each reversal the step size was halved and the staircase terminated after 12 reversals. The mean of the last four reversals was taken as the threshold. Each observer completed a minimum of four runs of trials (i.e. staircases) for each of the 36 spatiotemporal frequency combinations tested for each type of motion stimulus and the order of testing was randomised. A staircase typically took about 2 min (60 trials) to converge, so the entire experiment required 20 or more hours of observing time for each participant and took several months to complete.

3. Results

To express the results of each observer in terms of absolute sensitivity, the reciprocal of the threshold estimated from each staircase, that converged, was calculated. The mean modulation sensitivity and standard error of the mean (SEM) were then computed separately for each spatial frequency, temporal frequency and stimulus type. From these data a spatiotemporal modulation sensitivity surface was constructed, for each of the five types of motion pattern, to illustrate the overall window of visibility for first-order and second-order motion in our six observers. This took the form of a 3-d plot in which modulation sensitivity is plotted as a function of both spatial frequency and temporal frequency on log–log frequency axes. For the current purposes when sensitivity could no longer be measured (e.g. the acuity limit was exceeded), it was set to unity in each case. In addition a number of summary metrics characterising the shape of each plotted surface were derived (see Table 2). These were the peak sensitivity (and SEM),

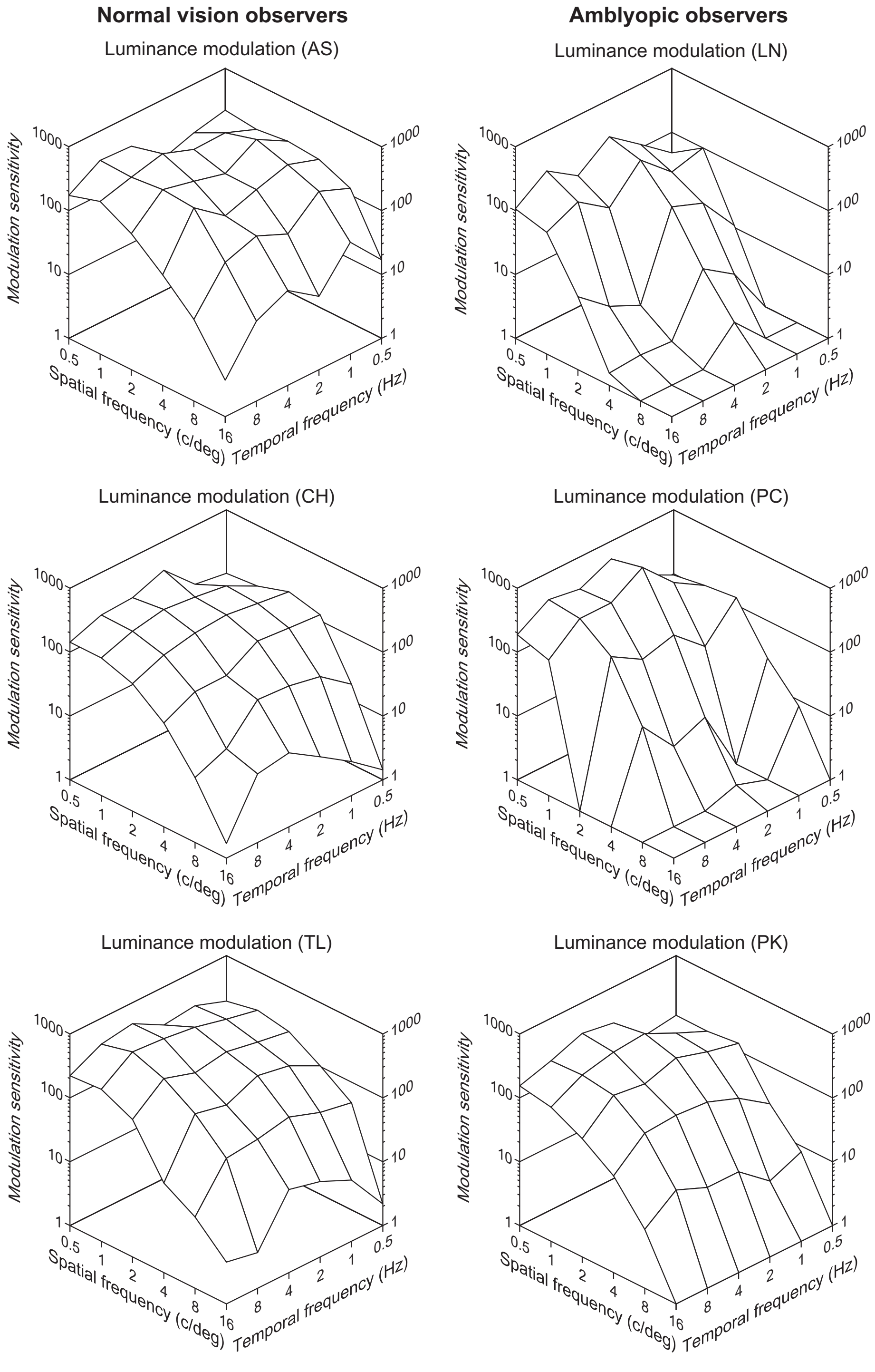

Fig. 2. Spatiotemporal sensitivity surfaces (1/modulation depth threshold) for luminance-modulated (first-order) dynamic noise patterns. The left-hand column shows individual plots for three normal vision observers and the right-hand column depicts the amblyopic (strabismic) observers. In general all observers exhibit bandpass tuning characteristics for first-order motion, with the amblyopes showing reduced sensitivity at the highest spatial frequencies.

the upper spatial cut-off frequency (for which sensitivity is unity at all temporal frequencies tested), the upper temporal cut-off frequency (for which sensitivity is unity at all spatial frequencies tested) and the number of visible stimuli (sensitivity greater than unity) for the 36 spatiotemporal frequency combinations tested. Furthermore the volume under the log–log sensitivity plot provides a useful broad sensitivity metric and is analogous to similar measures such as the area under the log contrast sensitivity function (CSF) used previously in clinical studies of spatial vision (e.g. Applegate et al., 1998, 2000; Oshika et al., 1999, 2006). This was estimated by simply summing all sensitivity values (after subtracting 1 from each value) in each surface plot.

For luminance-modulated (first-order) dynamic noise patterns (Fig. 2) sensitivity covered the largest range. In terms of the shapes of the surfaces, sensitivity was greatest at lower spatial and temporal frequencies. Specifically, the data were temporally bandpass and the surfaces were generally quite flat at the lowest spatial frequencies tested. Spatially, sensitivity was also modestly bandpass but

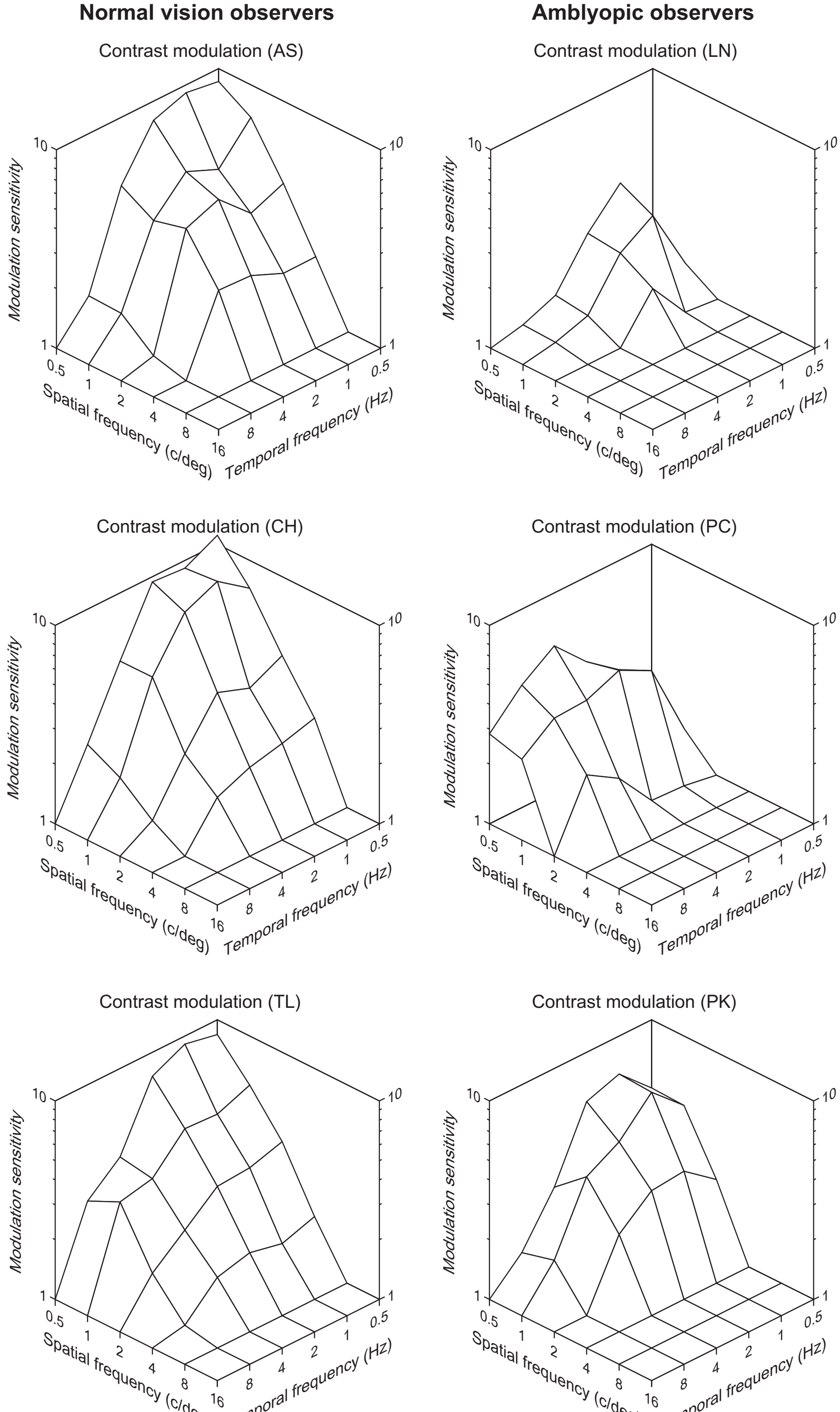

Fig. 3. Spatiotemporal sensitivity surfaces for contrast-modulated (second-order) dynamic noise patterns. The left-hand column shows individual plots for three normal vision observers and the right-hand column depicts the amblyopic (strabismic) observers. Note the change in scale of the sensitivity axes compared to Fig. 1. Sensitivity to this variety of second-order motion is predominantly lowpass in nature (both spatially and temporally) and is uniformly lower in amblyopia.

exhibited a much more rapid fall-off with increasing spatial frequency, a pattern that was accentuated in the amblyopic observers. There was little difference in the magnitude of peak sensitivity between the normal vision and amblyopic observers (see Table 2) but the volume under the surfaces was approximately a factor of 2 less in the amblyopes, due to the much more limited range of visible spatial frequencies.

For contrast-modulated (second-order) dynamic noise patterns (Fig. 3) spatiotemporal sensitivity covered a much smaller range than for the luminance-defined patterns. Surfaces were generally

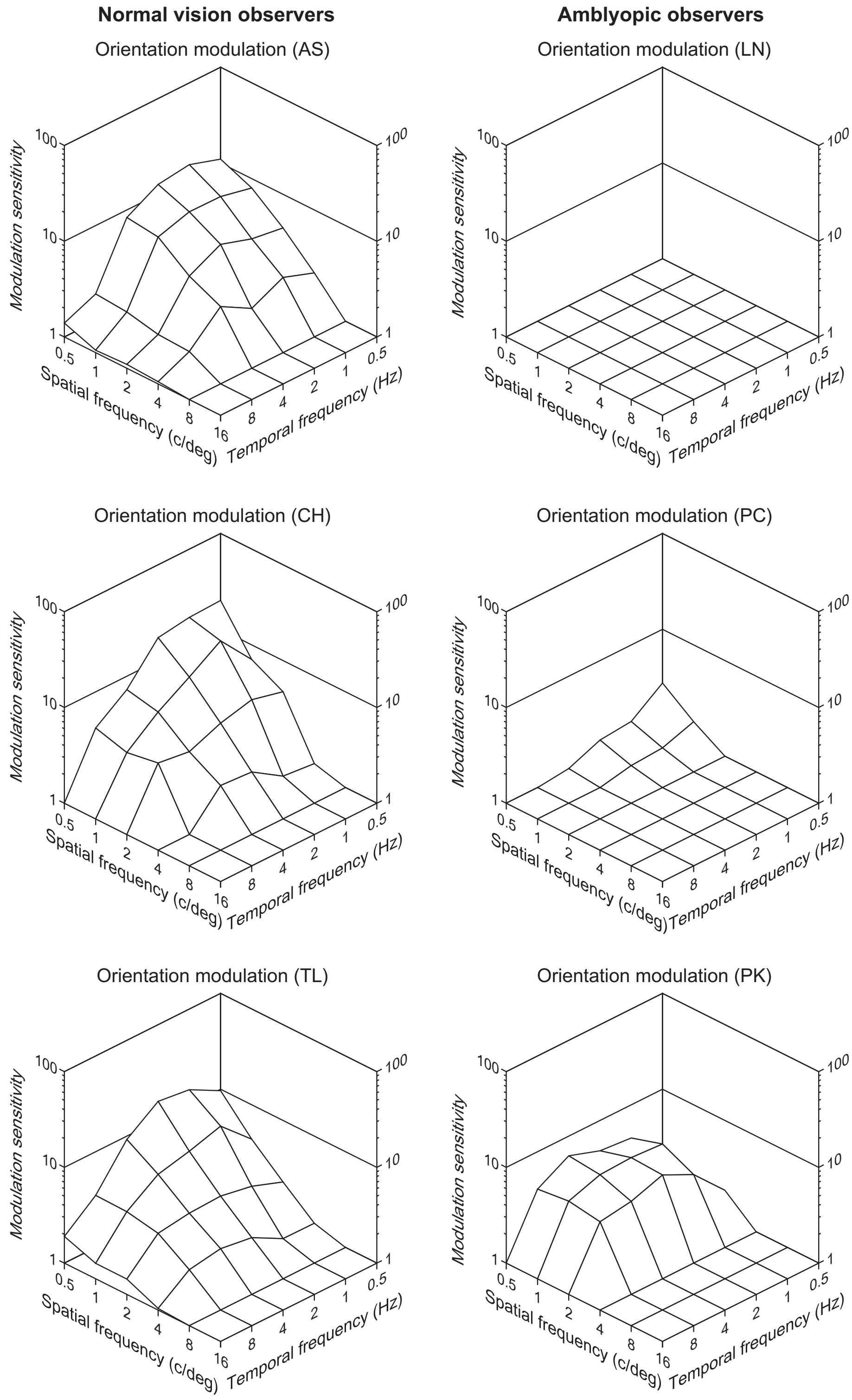

Fig. 4. Spatiotemporal sensitivity surfaces for orientation-modulated (second-order) dynamic noise patterns. The left-hand column shows individual plots for three normal vision observers and the right-hand column depicts the amblyopic (strabismic) observers. Sensitivity to this variety of second-order motion is for the most part lowpass (both spatially and temporally) and is uniformly lower, or indeed absent in some cases, in amblyopia. Note that amblyopes LN and PK have the same level of visual acuity in their amblyopic eye, so it is clear that this comparable loss in resolution cannot account for their marked differences in sensitivity to orientation modulations.

lowpass both spatially and temporally. In comparison to the normal observers the overall shape of the modulation sensitivity functions in amblyopia showed an overall marked reduction in peak sensitivity, volume and number of visible stimuli. This is quantified in Table 2. However all three amblyopes were able to discern reliably the direction of contrast modulations over many of the frequencies tested.

Fig. 4 shows the spatiotemporal sensitivity surfaces for orientation-modulated (second-order) dynamic noise patterns. Sensitivity to this type of second-order motion is predominantly lowpass (both spatially and temporally) in nature and uniformly lower, or indeed absent in some cases, in amblyopia. As amblyopes LN and PK have the same level of visual acuity in their amblyopic eye (see Table 1), it can therefore be seen that this comparable

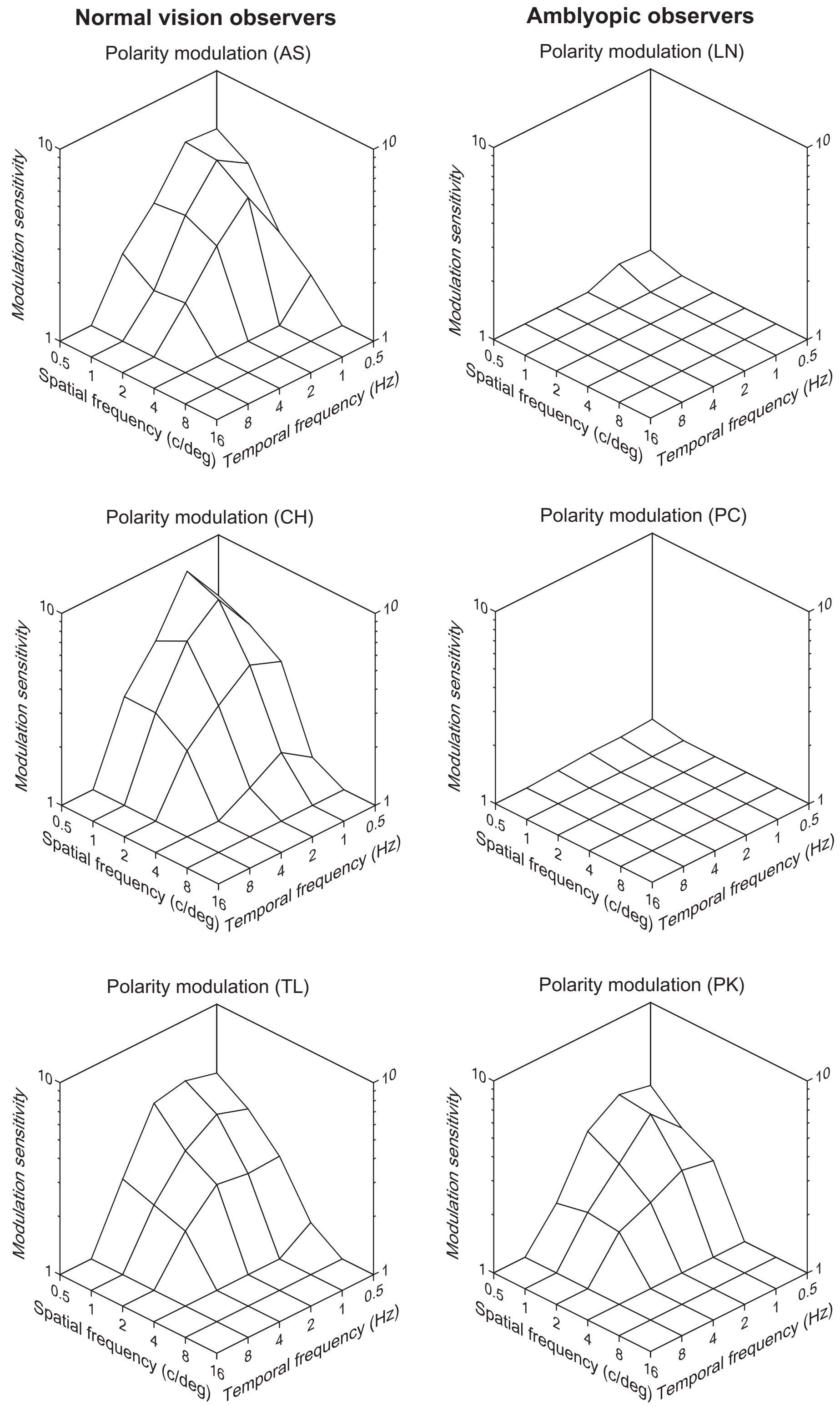

Fig. 5. Spatiotemporal sensitivity surfaces for polarity-modulated (second-order) dynamic noise patterns. The left-hand column shows individual plots for three normal vision observers and the right-hand column depicts the amblyopic (strabismic) observers. Sensitivity to this variety of second-order motion is again spatially and temporally lowpass in normal vision observers. Amblyopic observer PK exhibits a similar profile to the normals, but LN and PC show little or no sensitivity to these stimuli.

low-level loss in resolution cannot account for the substantial differences in their windows of visibility for these orientation-modulated motion patterns.

For polarity-modulated (second-order) dynamic noise (Fig. 5), sensitivity is again spatially and temporally lowpass in normal vision observers and covers a very similar range to that found for contrast modulations, with the exception that the upper temporal cut-off is about an octave lower in this case (see Table 2). Interestingly amblyopic observer PK shows a similar sensitivity profile to the normal controls, but the other two amblyopes appear relatively insensitive to this variety of second-order motion.

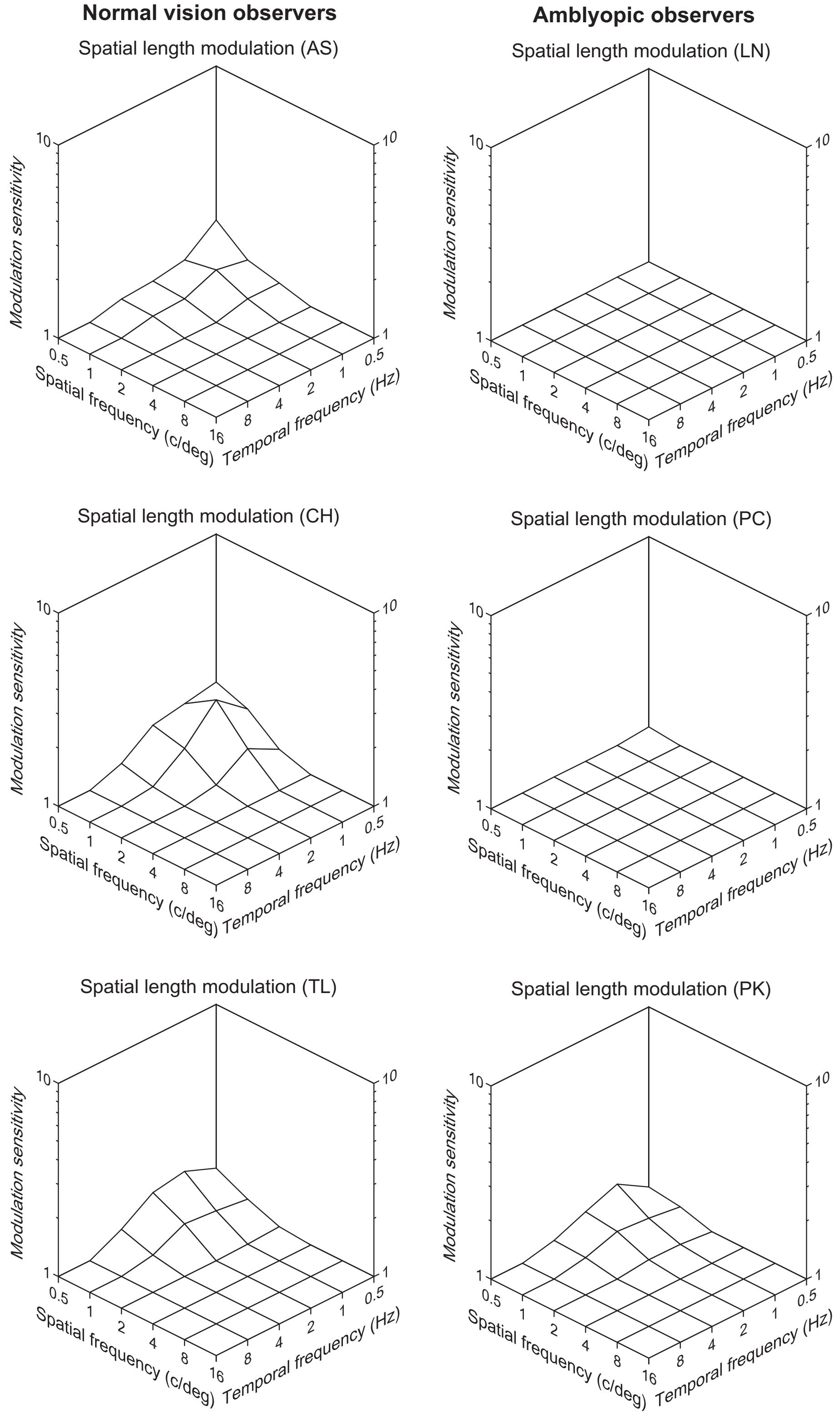

Fig. 6. Spatiotemporal sensitivity surfaces for spatial length-modulated (second-order) dynamic noise patterns. The left-hand column shows individual plots for three normal vision observers and the right-hand column depicts the amblyopic (strabismic) observers. Sensitivity to this variety of second-order motion is relatively poor (and the window of visibility is restricted to a very narrow range of frequencies) in normal vision observers and this pattern is exacerbated in the amblyopes.

Finally, for spatial length-modulated (second-order) motion patterns (Fig. 6), peak sensitivity is relatively poor and the window of visibility is restricted to a very narrow range of frequencies (about 1/3 of those tested) in normal vision observers (Table 2). The surfaces were clearly lowpass both spatially and temporally, although sensitivity declined most rapidly with increasing spatial (rather than temporal) frequency. Overall the amblyopic performance was markedly degraded for this variety of second-order motion stimulus, especially for observers LN and PC.

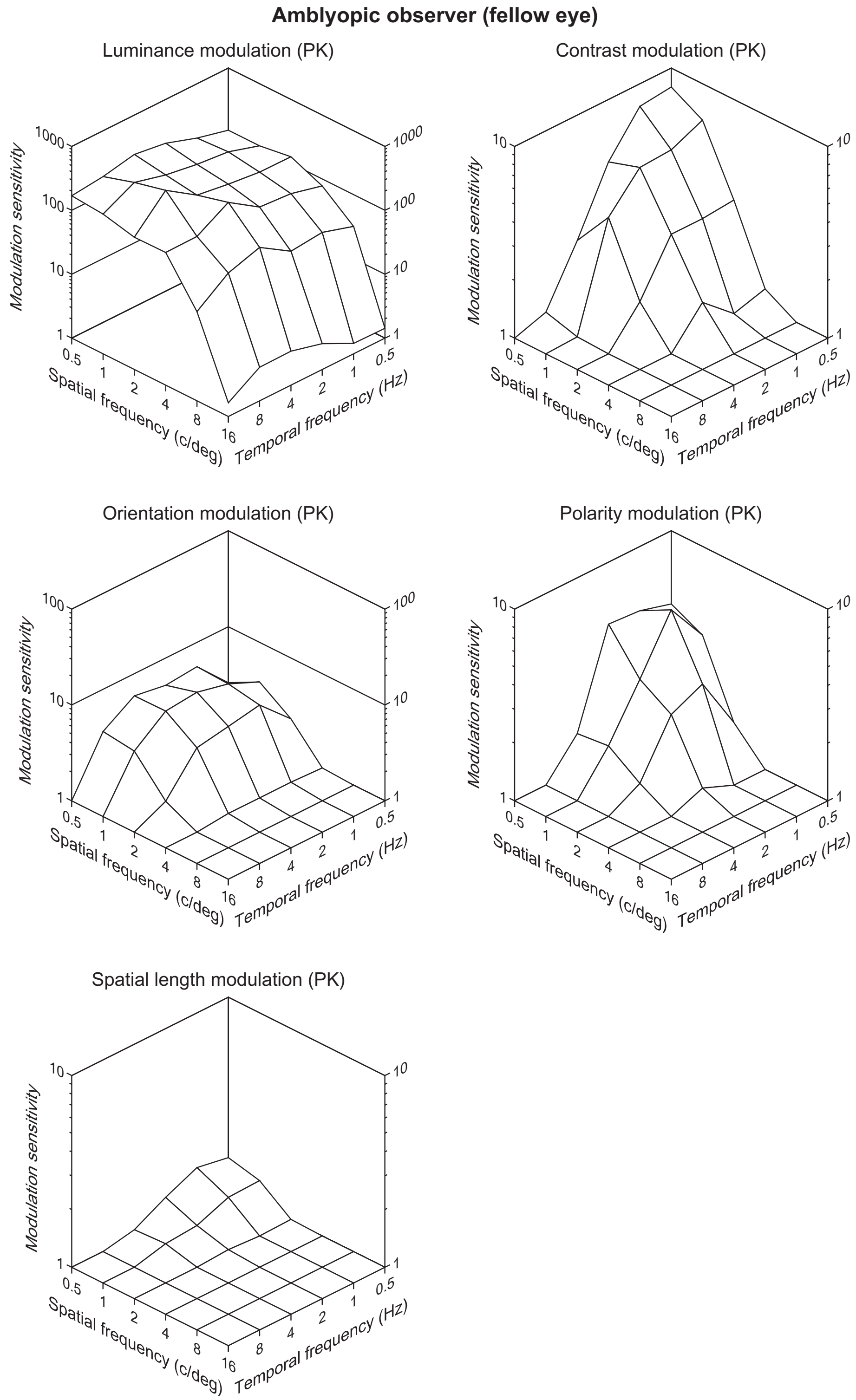

Fig. 7. Spatiotemporal sensitivity surfaces for the luminance-modulated and second-order dynamic noise patterns in the fellow eye of amblyopic observer PK. On average performance across all stimulus types is poorer than the normal subject group. Summary metrics can be found in Table 3.

Deficits in second-order motion processing may well occur at a late (binocular) stage of processing and this can be reflected as processing deficits in the fellow eye of amblyopia. The spatiotemporal sensitivity modulation surfaces for each stimulus type for the fellow eye of amblyopic observer PK is shown in Fig. 7 with summary metrics further detailed in Table 3. In the present study it can be seen that performance in the fellow eye is on average poorer than that of the normal observers, despite excellent visual acuity measures (20/17).[1]

It could be argued that the reduced performance of the amblyopic eyes for second-order motion patterns may be due, in part, to

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[1] Unfortunately at time of review observers LN and PC were no longer available for extensive testing of their fellow eye.

Table 3
Summary metrics characterising the modulation sensitivity surface for each stimulus type for the fellow eye of amblyopic observer PK.

Stimulus type	Obs.	Peak sensitivity (±1 SEM)	Volume of log–log sensitivity plot	Spatial cut-off (c/deg)	Temporal cut-off (Hz)	Number visible stimuli
Luminance	PK	359.81 (±194.30)	4187.10	>16	>16	36/36
Orientation	PK	6.40 (±0.22)	49.08	8	16	19/36
Contrast	PK	7.96 (±0.60)	42.64	8	16	17/36
Polarity	PK	4.75 (±1.26)	24.67	8	8	13/36
Spatial length	PK	1.56 (±0.12)	2.33	4	8	10/36

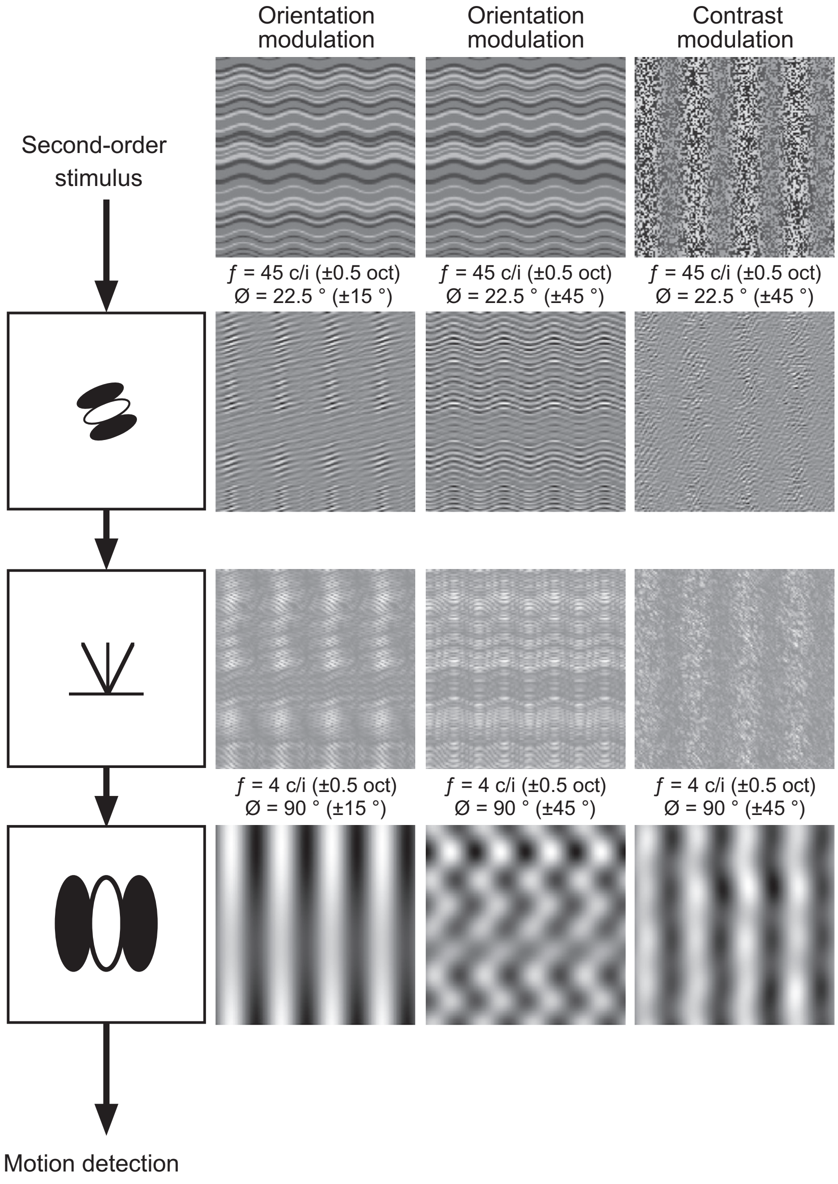

Fig. 8. Schematic depiction of the "Filter-Rectify-Filter" (FRF) cascade model of second-order motion processing (first column). The image is initially filtered at a given orientation and spatial (and/or temporal) scale, subjected to a pointwise nonlinearity such as rectification and then secondary filtering at a coarser spatial scale (and perhaps different orientation). The degree of selectivity (tuning bandwidth) of the two filtering stages in the FRF model determines the fidelity of the final output. Applying a pair of narrowly-tuned, oriented filters (for simplicity ±15° bandwidth ideal filters), readily extracts the sinusoidal structure of a second-order, orientation-modulated noise image (second column). Applying filters that are less selective (±45° orientation bandwidth), to mimic the net effect of additional noise/uncertainty in the amblyopic visual system, to the same image fails to reveal its sinusoidal structure (third column). However the same pair of broadly-tuned filters successfully demodulate a contrast-modulated noise image (fourth column). For clarity the intensity values of the filtered images are scaled to cover the available range of brightness.

the poor visibility of the noise carrier in these individuals. After all there are well-established, low-level deficits in the processing of luminance information in amblyopia that could ultimately limit the ability to extract the sinusoidal image structure from the carrier. To rule-out this explanation a control experiment was undertaken to confirm that overall carrier visibility was not the limiting factor in second-order motion perception in this study. A series of temporal two-alternative-forced-choice (2AFC) detection tasks were performed, whereby observers had to judge which of two temporal intervals (order randomised on each trial) contained an *unmodulated* dynamic noise field. For the normal vision observers the mean contrast threshold for detecting the noise (corresponding to 79.4% correct) in each of the *unmodulated* noise carriers was as follows; 2-d noise (used with luminance, contrast and flicker-defined motion stimulus) = 0.043 (SEM ± 0.007); horizontal noise (used with the orientation-defined motion stimulus) = 0.013 (SEM ± 0.001) and vertical noise (used with the spatial length-defined motion pattern) = 0.011 (SEM ± 0.007). The corresponding value for the amblyopic observers (AE) was 2-d noise 0.065 (SEM ± 0.008); horizontal noise 0.016 (SEM ± 0.001) and vertical noise 0.022 (SEM ± 0.002). It is clearly evident that the noise carrier in the main experiment was over four times the monocular threshold for both the normal and the amblyopic observers and therefore was readily visible in all conditions.

4. Discussion

The results of the current study are important in that they clearly demonstrate that the window of visibility for motion is much more restricted for amblyopic than normal vision observers for both first-order and second-order stimuli. However it would appear that amblyopia can differentially impair the perception of some types of second-order motion much more than others (see Figs. 3–7), but crucially the precise pattern of deficits varies markedly from individual to individual (even for those with the same conventional visual acuity measures). For the most severely impaired strabismic amblyopes certain second-order (texture) cues to movement in the environment are effectively outside the window of visibility and hence invisible to those individuals.

A particularly informative result in this regard concerns the processing of contrast-modulated dynamic noise patterns. Despite the fact that amblyopic observer LN was insensitive to second-order motion defined by modulations of either image orientation or spatial length, she nonetheless was able to accurately encode the direction of contrast modulations over a substantial range of frequencies. Similarly although PC was effectively blind to the motion of polarity and spatial length modulations, his sensitivity to contrast modulations was relatively intact (albeit over a more restricted range and with uniformly lower sensitivity than normals). This has important implications for the architecture of theoretical models of second-order motion processing in the human visual system.

The most popular models of motion assume that first-order and second-order motion are detected independently in parallel pathways. In Wilson, Ferrera, and Yo's (1992) model, for example, first-order (luminance-based) motion is encoded by a pathway that uses low-level motion sensors to extract the motion energy in the stimulus. To demodulate a second-order image and encode its motion a more complex FRF pathway is required: the image is subjected to an initial stage of linear filtering, a gross nonlinearity (e.g. rectification or squaring) then secondary filtering at a coarser spatial scale, prior to conventional motion energy detection. This general FRF principle could potentially encode a diverse range of second-order motion stimuli. All that is required is for the first stage linear filters to respond in a differential manner (i.e. to be selectively sensitive or tuned) to the local texture differences (e.g. orientation, flicker rate or spatial length) carrying that motion.

There is still much uncertainty concerning the precise mappings between the initial and secondary filtering stages within this scheme, as applied to both motion and spatial vision (e.g. Schofield, 2000). Nonetheless the most parsimonious explanation of the finding that some amblyopes can perceive certain varieties of second-order motion but not others, is that separate first-stage filters must exist for different varieties of second-order motion (e.g. variations in orientation versus flicker rate) and these may be differentially compromised in clinical anomalies such as amblyopia. If this is the case then one might still expect the processing of contrast modulations, of a spatiotemporally broadband and orientation isotropic noise carrier (like the one used in the present study), to be relatively preserved in these individuals. This is because the response of any linear filter will always be proportional to the local contrast of the image, even if its response selectivity (tuning bandwidth) is, say, deleteriously affected by the presence of additional intrinsic noise or orientation uncertainty in amblyopia (Simmers & Bex, 2004). This is depicted schematically in Fig. 8, in which the ability to demodulate a contrast-varying image is relatively immune to the orientation bandwidths of the filters used in the FRF pathway, unlike the case for an orientation-modulated noise image. Consequently the pattern of results found in amblyopia, place important constraints on possible models of second-order motion processing in human vision.

In summary amblyopes are not only impaired in the processing of first-order motion, they also exhibit both higher thresholds and a much more restricted window of visibility to most varieties of second-order motion. Therefore the visual deficit in amblyopia extends to the processing of a diverse range of complex, higher-order cues to movement. Indeed some amblyopes are effectively “blind” to certain kinds of second-order motion textures, but the precise pattern of impairments present depends critically upon the individual and is not predicted on the basis of their low-level, first-order perceptual deficits.

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