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Border distinctness in amblyopia

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Abstract

On the basis of the contrast sensitivity loss in amblyopia which mainly affects higher spatial frequencies, one would expect amblyopes to perceive sharp edges as blurred. We show that they perceive sharp edges as sharp and have veridical edge blur perception. Contrary to the currently accepted view, this suggests that the amblyopic visual system is not characterized by a blurred visual representation.

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1. Introduction

Our view of amblyopia is still in a state of flux. In the early 70s when contrast sensitivity measurements were first used to quantify the vision in human amblyopes, we learnt that the deficit, in terms of contrast sensitivity, affected mainly higher spatial frequencies (Gstalder & Green, 1971; Hess & Howell, 1977; Levi & Harwerth, 1977). Though it was true that some amblyopes exhibited up to a factor of 3 loss at low spatial frequencies (Hess & Howell, 1977), the loss of contrast sensitivity was far greater at higher spatial frequencies, sometimes up to two orders of magnitude. These losses of contrast sensitivity can be modelled by optical defocus and it would not have been unreasonable to think of amblyopic perception in terms of that experienced by a normal observer with optical defocus.

More recently research in this area has focussed on another unrelated anomaly in amblyopia, that of positional uncertainty (Bedell & Flom, 1981, 1983; Bedell, Flom, & Barbeito, 1985; Hess & Holliday, 1992; Lagreze & Sireteanu, 1991, 1992; Levi & Klein, 1982). The fact that amblyopes are so uncertain of the relative position of objects and the fact that this anomaly is scale invariant means that amblyopic perception must be more than simply neurally “blurred”. On the contrary there is a possibility that amblyopes don’t perceive objects blurred at all because informally they insist

that the world does not appear blurred when using their amblyopic eye. In the light of their contrast sensitivity deficit, this is not at all expected and if true could help us understand the nature of the underlying deficit.

In the present study, we measured border distinctness or what has previously been referred to as “edge-sharpness” in a group of normal and amblyopic subjects using a dichoptic edge matching paradigm. We used edges with sinusoidal edge profiles and asked amblyopes to match the edge sharpness of a standard seen by the amblyopic eye with a similar but variable stimulus seen by the fellow fixing eye. The results for normals with optical blur were predictable but results for amblyopes were unexpected. For both strabismic and non-strabismic amblyopes, edges that should have appeared blurred on the basis of their contrast sensitivity losses did not.

2. Methods

2.1. Apparatus

A vertically-oriented sinusoidal “edge” was displayed near the centre of each of two identically-constructed high resolution cathode-ray oscilloscopes (external tube face dimensions 23×30 cm, P4 white phosphor: Joyce Electronics Ltd., Cambridge, UK). The CROs were positioned side-by-side with their long axes horizontal at a height such that the vertical centre of both screens was aligned at eye level. The mean luminance of the two

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Table 1
Clinical details for the group of amblyopes tested

Subject	Class	Age	Prescription	Fixation	Clinical history
N.N.	Anisometropic	29	R: plano; L: -2.00/-3.00×10	Central	First Rx at age 25
P.M.	Anisometropic	30	R: -5.00; L: -1.00/-1.00×50	Central	First Rx at 5 patching
L.C.	Strabismic	38	R: -1.50; L: -1.50	1° temp	15° LXT no therapy
C.F.	Strabismic	31	R: +4.50; L: +4.25	10° temp	20° LXT surgery
S.T.	Strabismic	52	R: -0.25; L: +0.50	10° nasal	5° LET patching
C.G.	Strabismic/an-isometric	18	R: plano; L: +3.00/-0.50×5	0.5° nasal	6° LET patching
J.S.	Strabismic/an-isometric	42	R: -5.00; L: -0.50/-0.50×15	Central	1° RXT

Rx refers to optical prescription, LXT to left exotropia, RXT to right exotropia, LET to left esotropia and RET to right esotropia.

screens was matched and set to an absolute level of 500 cd/m²; the contrast linearity of both screens was checked and found to extend up to 98% contrast (light meter: United Detector Technology, Santa Monica, CA). The frame rate was set to 100 Hz.

The display window of each screen was masked down by black card to a rectangular aperture subtending 4 × 5.5 deg at the usual viewing distance of 2.85 m. To expand the test range to lower spatial frequencies for some of the amblyopic subjects, the viewing distance was reduced to 0.57 m on certain occasions, in which case the viewing aperture was scaled such that the vertical height of the edge remained 4 deg. To remove any sources of distraction all data collection took place in a completely darkened room. To prevent the subject using any alignment cues associated with the viewing apertures, one or both of the two masks were randomly re-positioned in the horizontal plane during formal data collection sessions (Table 1).

A large (1.5 m²) black wooden screen with a brow and nose rest at its proximal end was moved up to the subject along the midline between his nose and the abutting inner edges of the two display screens. In this way the two eyes of the subject were physically dissociated, the left eye seeing only the left-hand display, and vice versa.

2.2. Stimuli

The vertically-oriented luminance edges on the two screens were generated independently. The fixed or “comparison” edge, arbitrarily placed on the right-hand screen for all normally-sighted subjects or before the amblyopic eye of the other subjects, was digitally generated using a PDP 11/34 A laboratory computer connected to the screen via a Cambridge Electronic Design 502 interface system. The variable or “match” edge was generated via a specially-constructed interface board linked to a Tektronix TM515 Function Generator. In each case the edge displayed was half (i.e. 180 deg extent) of one cycle of a sinusoid, between the peak (90 deg) and trough (270 deg) of the waveform. The subject could adjust the sharpness of this edge, i.e. the spatial

frequency (c/deg) of the parent sinusoid, over a continuous scale by turning a potentiometer which controlled the voltage signal to the z-input of the “match” CRO. While such a stimulus has a broad spectrum containing frequencies both higher and lower than the nominal sinusoid from which the edge is derived (see Hess, Pointer, & Watt, 1989 for the Fourier transform of this stimulus), we plot our results in terms of the parent sinusoid because operationally this is what was varied to obtain a perceptual match. Although the stimulus has a broad spectrum, the low spatial frequency components are not of any use in the task because all stimuli to be matched have equivalent low spatial frequencies. This is best demonstrated in the bandpass nature of the difference spectrum between two edges made from different parent sinusoids (see Fig. 1 in Hess et al., 1989).

Both edges were displayed continuously, via independent attenuators, and could be precisely equated in Michelson contrast terms. The majority of the data was collected at high (90%) contrast. At the usual test distance of 2.85 m a five octave range of edge frequencies could be tested (0.5, 1, 2, 4, 8, 16 c/deg); at a reduced distance of 0.57 m these could be interlaced with test edges of 0.1, 0.2, 0.4, 0.8, 1.6, 3.2 c/deg.

2.3. Procedure

After a short interval to allow the subject to adapt to the darkened room and to ensure that his two eyes were correctly dissociated by the septum, a standard luminance edge (usually chosen to be of a medium spatial frequency) was continuously presented on the computer-controlled screen. The experimenter turned the potentiometer control linked to the matching screen such that the luminance edge which it presented was at a lower spatial frequency (i.e. appeared more blurred) than the standard edge. The subject’s preferred hand then adjusted the potentiometer until he felt that he had set a satisfactory match in edge sharpness, given that an anti-clockwise turn of the control produced an increase in spatial frequency i.e. edge “sharpness”. The scale of the potentiometer had previously been calibrated directly in

'c/deg' units, so that the experimenter could readily note the subject's matched setting. A blurred edge was then re-set on the matching screen and the procedure repeated. After ample trial settings to acquaint the subject with the task, matches over the range of standard edges were obtained on a randomized basis (the fixed standard edges were presented in random order and the potentiometer setting of the matching edge relative to the fixed standard edge was also initially random). The mean of five settings constituted a datum point in the formal experiments reported here. The range of standard deviations for the match for normal eyes ranged between 2% and 11% of the mean match whereas for amblyopic eyes this range was 5–18%. Contrast sensitivity measurements were made using a standard 2 AFC psychophysical procedure with a 1 up/2 down staircase procedure using the same apparatus. Thresholds were estimated as the mean of the final 10 reversals. The range of standard deviations for the normal eye was between 0.5 and 1.5 dB. The range for the amblyopic eye was 0.5–2 dB. The stimuli were presented in a Gaussian temporal window whose sigma was 250 ms (field size 10 deg \times 10 deg, mean luminance 500 cd/m²).

2.4. Subjects

The normally-sighted subjects were two of the authors (RFH and JSP), plus one other (RMC) who was naïve to the aims of the experiment. The amblyopic subject group consisted of three strabismic, two anisometric and two strabismic anisometropes drawn from a roster of individuals screened for vision experiments in the laboratory. All refractive errors were fully corrected prior to data collection, and natural pupils were used in all experiments.

3. Results

Dichoptic "edge-blur" matching results on two normal observers are shown in Fig. 1A–C. A sinusoidal edge constructed from a preset comparison parent sinusoid was shown to one eye and this was matched with a similar sinusoidal edge shown to the other eye. The parent sinusoid of the matching stimulus was variable. Since transitions constructed from high frequency parent sinusoids appear sharp and those from low spatial frequency sinusoids appear blurred, we have referred to this task as an edge-blur matching task. Here we plot the comparison edge sharpness in terms of the parent sinusoid comprising the edge against the matched test sinusoid. Each are plotted on logarithmic axes in cycles/degree of the parent half-cycle sinusoid used to construct the edge (see Section 2). Under normal circumstances a certain edge-sharpness seen by one eye is matched veridically by the other eye (Fig. 1A), this is

true regardless of the contrast of the edge (Fig. 1B). When one eye is optically blurred as in Fig. 1C, unsurprisingly, the perception, as reflected in the non-veridical matches for the sharpest comparison edges, becomes less sharp. The greater the blur, the less is the perceived sharpness; results are illustrated for 1, 2 and 3 dioptres of blur resulting in acuities of 6/12, 6/36 and 6/60 respectively. Fig. 1D shows how optical blur affected the contrast sensitivity function in this subject; the higher the spatial frequency the more contrast is attenuated by a given amount of optical blur (Campbell & Green, 1965).

Similar measurements in two anisometric amblyopes did not yield the expected result. The contrast sensitivity functions for these anisometric amblyopes are shown in Fig. 2C and D. They show the now familiar loss of sensitivity especially at high spatial frequencies (Levi & Harwerth, 1977). For all subsequent edge-matching experiments, the comparison edge was presented to the amblyopic eye and the variable matching edge to the fellow fixing eye. For the anisometric amblyopes, although the matches were not veridical for the sharpest edges (Fig. 2A and B), they were surprisingly closer to veridicality than one would expect on the basis of their acuity in light of the results obtained from optically blurred normals (Fig. 1C and D).

The degree to which sharp edges are seen as blurred is slight compared with normals optically defocused to the same acuity level (compare unfilled symbols in Fig. 1C with filled symbols in Fig. 2A and B). Also, small degrees of defocus of the amblyopic eye result in the expected perception of blur for a normal observer (compare unfilled symbols in Figs. 1C, 2A and B). Since there is good quantitative agreement between how optical defocus affects normal and amblyopic eyes, it would seem that amblyopic eyes are just as sensitive to defocus.

Contrast sensitivity losses are seen in Fig. 3 for a group of three strabismic amblyopes. These range from a mild loss of high spatial frequencies to much more severe losses of both high and low spatial frequencies, typical of those seen in strabismic amblyopia (Hess & Howell, 1977). Surprisingly, the edge matching measurements on this group of strabismic individuals produced veridical matches over the whole range (Fig. 4). To show that these amblyopes were not using either the luminance gradient or the width of the edge transition to indirectly gauge the degree of blur, we compared matches for edges of different contrasts and viewing distances. This varied both the absolute and relative edge transitions. Under all conditions, the matching of edge-blur by the amblyopic eye was veridical.

The contrast sensitivity losses for two individuals with mixed strabismic/anisometric amblyopia are shown in Fig. 5C and D. These amblyopic deficits are severe. Measurements of edge matching on these individuals

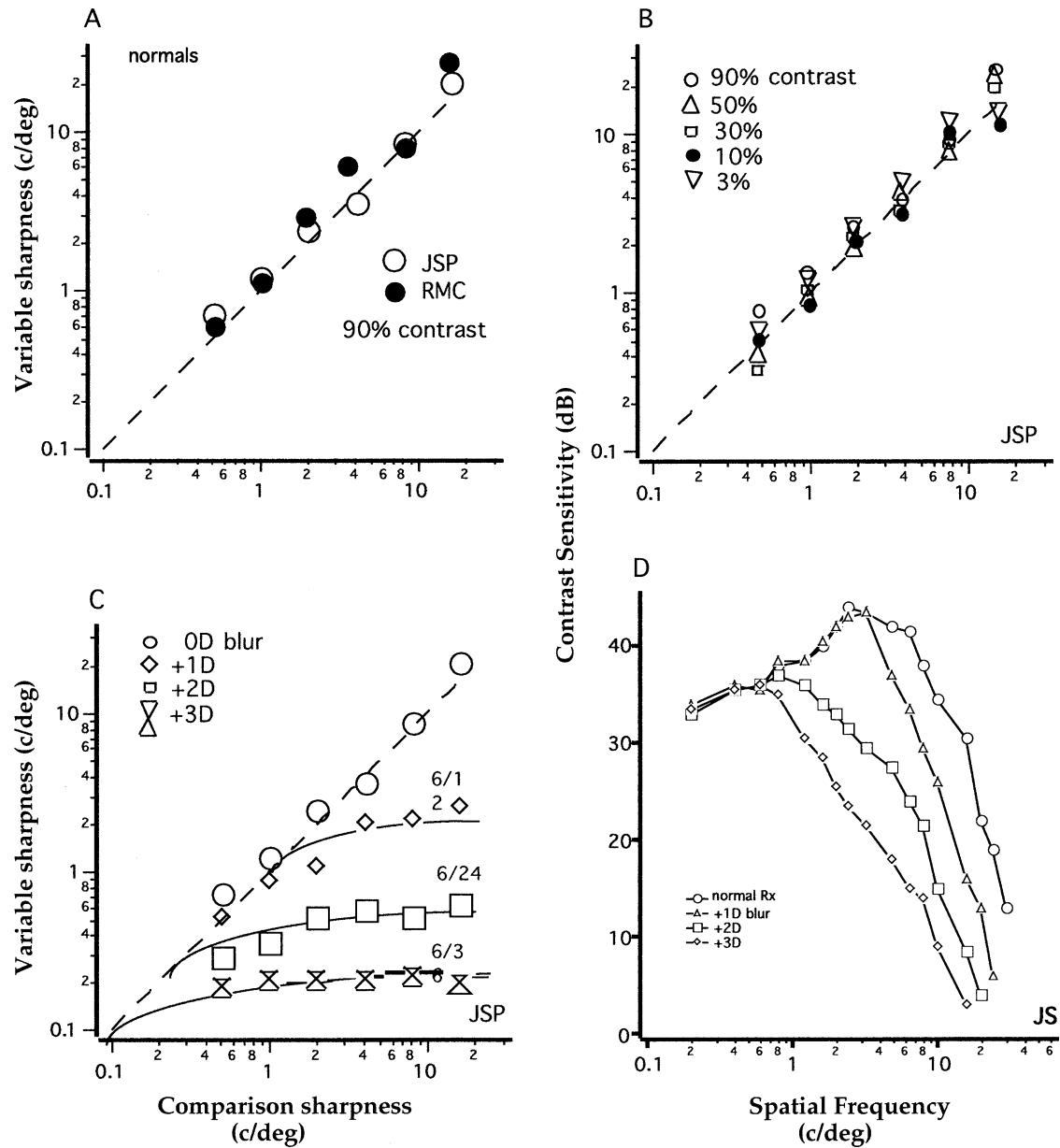


Fig. 1. The perceptual matching of edges with variable amount of edge-blur for normal observers and the influence of defocus on contrast sensitivity. In (A), veridical matches for two normal subjects. In (B), veridical matches for edges of a range of different contrasts. In (C), the effect of unocular optical blur of three different levels; 1, 2 and 3 dioptres. In (D), the normal contrast sensitivity function for in-focus and defocus (1, 2 and 3 dioptres of unocular defocus). Contrast sensitivity is plotted against spatial frequency for a 1D sinusoidal grating stimulus. The standard deviation for the mean matches for the normal eye ranged between 2% and 11% and for the amblyopic eye between 5% and 18%. For the contrast sensitivity measurements, the standard deviations for the normal eye ranged between 0.5–1.5 and 0.5–2 dB for the amblyopic eye.

with both anisometropia and strabismus (Fig. 5A and B) resulted in veridical matches along the lines previously observed for subjects with a pure strabismic deficit.

4. Discussion

Amblyopes perceive sharp edges as sharp and not blurred even though their acuity and contrast sensitivity is dramatically reduced. This is the inescapable conclu-

sion from their veridical matches for our edge-blur task. This is true for amblyopes with a strabismus regardless of whether they also have an associated anisometropia. Anisometropes without a strabismus are different in that they do exhibit a mild degree of perceived blur, however one that is much less than would be predicted from their reduced acuity. Amblyopia which means “blunt sight” should not be thought of as “blurred sight” or indeed “reduced contrast sight” (Hess & Bradley, 1980). The veridicality of the matches in amblyopes did not

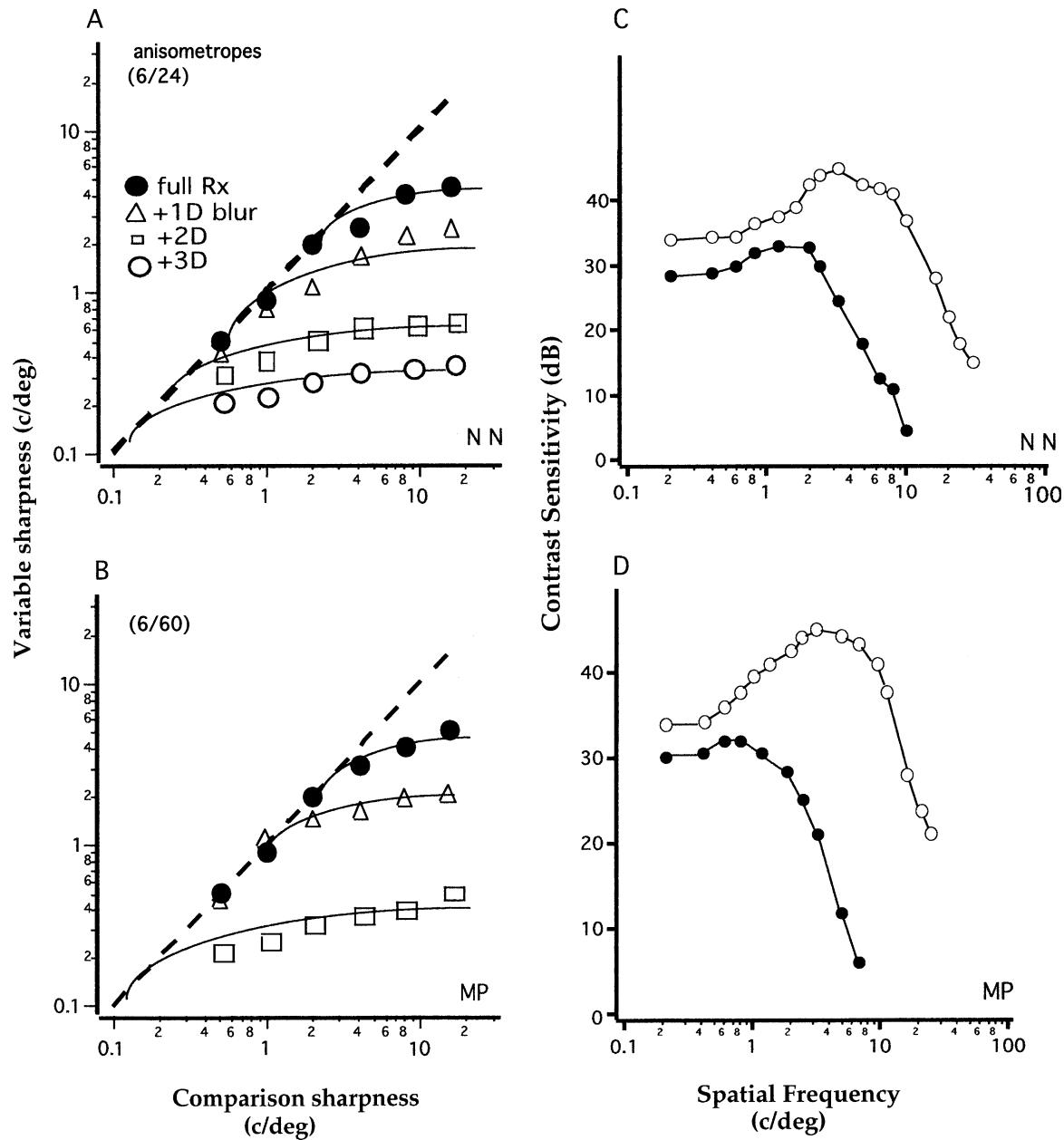


Fig. 2. The contrast sensitivity losses and edge-matching results for two anisometropes. In (A) and (B), edge-matching results for the anisometropic amblyopes are shown. In focus results (filled symbols) are compared with different levels of optical defocus of the amblyopic eye (unfilled symbols). In (C) and (D), the contrast sensitivity of the amblyopic and fellow fixing eyes are compared. The standard deviation for the mean matches for the normal eye ranged between 2% and 11% and for the amblyopic eye between 5% and 18%. For the contrast sensitivity measurements, the standard deviations for the normal eye ranged between 0.5–1.5 and 0.5–2 dB for the amblyopic eye.

depend on edge contrast over the range tested (10–90%), suggesting that the luminance gradient per se does not correlate with perceived blur (e.g. the luminance gradient has changed by a factor of 9 in this case). The contrast invariance of perceived blur is a well documented feature of normal vision (Georges, 1994). This also suggests that the perceived width of the edge was not being used as a secondary cue to perceived sharpness since perceived width depends on the contrast.

These results are intriguing because the relationship between the contrast sensitivity loss and the non-veridical edge matching of normals with optical defocus appears to be violated in amblyopia. In normals, optical defocus results in a spatial frequency-dependent loss of contrast sensitivity and a concurrent perception that sharp edges are blurred. Such a relationship is not present for amblyopes; they exhibit similar spatial frequency-dependent losses of contrast sensitivity but no perception of blur for even the sharpest edge.

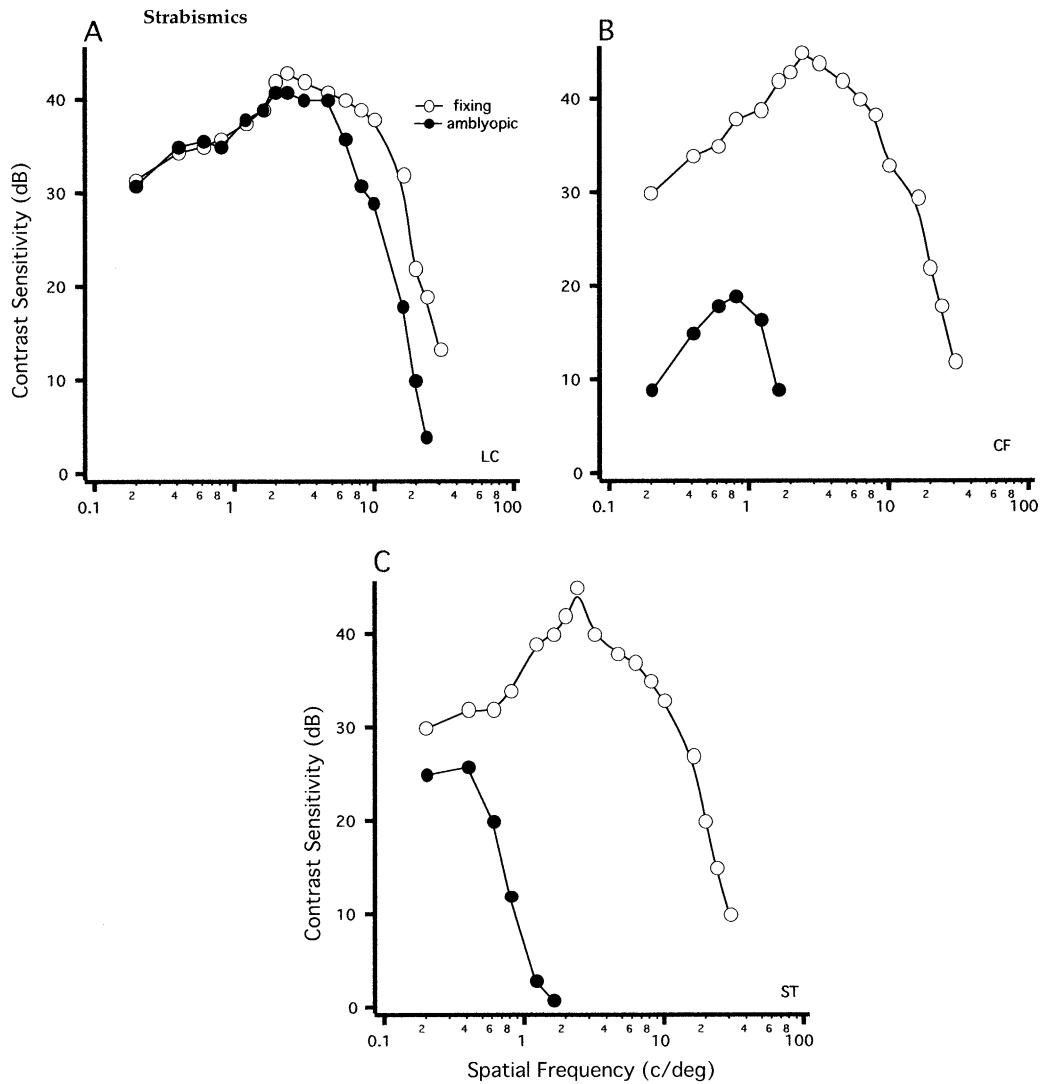


Fig. 3. The contrast sensitivity losses for three strabismic amblyopes. The contrast sensitivity of the amblyopic (filled symbols) and fellow fixing eyes (unfilled symbols) are compared. The standard deviations for the normal eye ranged between 0.5–1.5 and 0.5–2 dB for the amblyopic eye.

4.1. "Blurred" perception versus veridical matches

These experiments were aimed at assessing how distinct edges are represented by the amblyopic visual system. We did not ask amblyopes to tell us whether the edges looked blurred but merely to match edges presented to the amblyopic eye of different degrees of distinctness with edges of variable distinctness seen by the fellow fixing eye. Amblyopes always report that their visual world is not "blurred". This is not surprising for neither do normals report that objects seen in peripheral view are blurred. In normal vision, peripherally located edges are matched veridically with their foveal counterparts, even though the high spatial frequencies that represent them are attenuated in the periphery (Galvin, O'Shea, Squire, & Govan, 1997). This is simply a case of not being aware of what is missing. Being unaware of

image structure because one lacks detectors is different from having a set of detectors that should be stimulated but are not. The former represents strabismic amblyopia or the normal peripheral field, the latter, optical defocus. What we do find surprising is not that amblyopes do not report blurred perceptions but that edges that are subtly different in their distinctness are accurately encoded even in the severely amblyopic visual system. Amblyopia and normal peripheral function share this feature in common.

None of our current models of blur perception in normal vision offer a solution. While it is now accepted that blur is not necessarily signaled exclusively by neurones operating at the finest spatial scale (Watt & Morgan, 1983), all of the current models be they global (Field & Bradly, 1997; Mather, 1997) or local template models involving the 2nd (Elder & Zucker, 1998; Watt

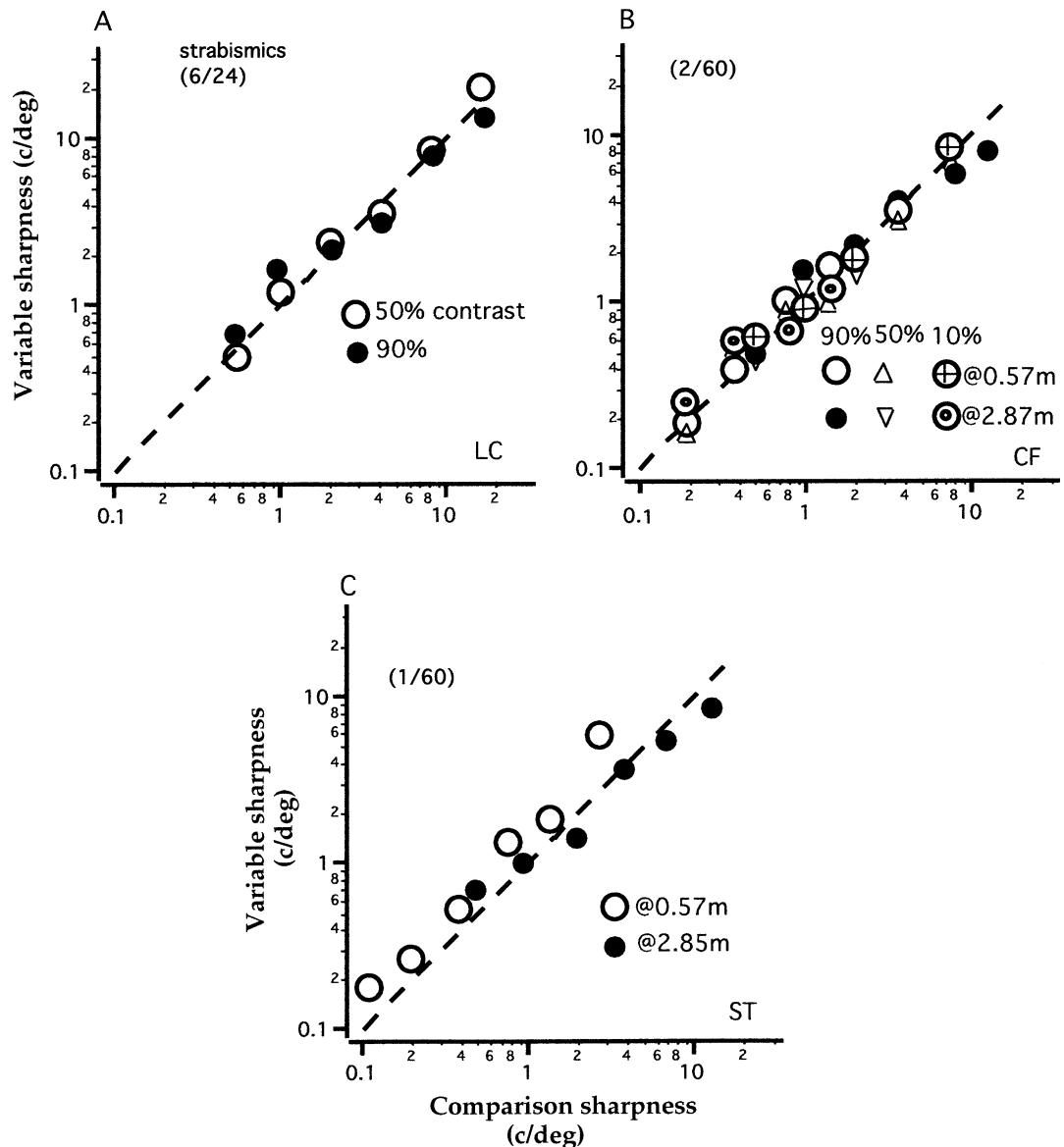


Fig. 4. Edge-matching results for three strabismic amblyopes. Results are shown for three contrast levels (10%, 50% and 90%) and two different viewing distances (0.57 and 2.87 m). The standard deviation for the mean matches for the normal eye ranged between 2% and 11% and for the amblyopic eye between 5% and 18%.

& Morgan, 1983) or 3rd (Georgeson, 1994; Kayargadde & Martens, 1996) derivatives, would all predict that the scale of the filter changes in proportion to the sharpness of the edge being processed. Simply put, sharp edges that are transformed by filters of a much lower scale will result in an additional intrinsic blur. The present matching results and more recent discrimination results (Simmers, Bex, & Hess, 2003) do not support a raised level of intrinsic blur within the amblyopic visual system. Three possible explanations for the present results are considered; a high level compensation, restricted filter access and a population code for blur that is normalized to the highest spatial frequency filters available.

4.2. High-level compensation

It is possible that amblyopes perceive sharp edges as sharp even though their early visual representation is neurally blurred due to filtering losses because of a high-level compensation. There is evidence that such compensation routinely occurs in normal vision for moving targets (Bex, Edgar, & Smith, 1995; Burr, 1980; Hammett, 1997; Ramachandran, Madhusudhan, & Vidyasagar, 1974), briefly presented targets (Galvin, O'Shea, Squire, & Hailstone, 1999) and for peripherally located targets (Galvin et al., 1997). Just how this could be achieved in amblyopia without a corresponding overcompensation at moderate to large edge-blurs is a

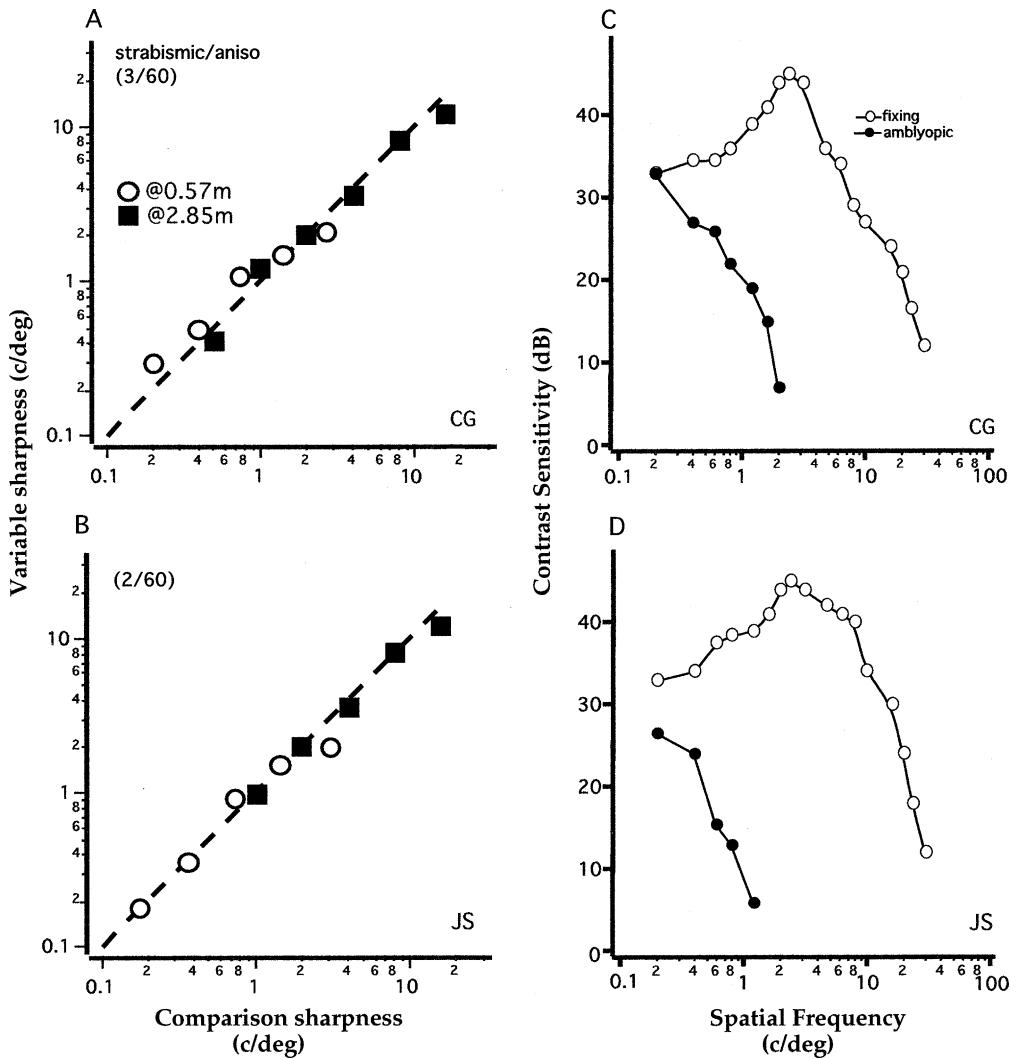


Fig. 5. The contrast sensitivity losses and edge-matching results for two mixed strabismic/anisotropic amblyopes. In (A) and (B), edge-matching results for the mixed strabismic/anisotropic amblyopes are displayed. Matches are shown for two different viewing distances (0.57 and 2.87 m). In (C) and (D), the contrast sensitivity of the amblyopic (filled symbols) and fellow fixing eyes (unfilled symbols) are compared. The standard deviation for the mean matches for the normal eye ranged between 2% and 11% and for the amblyopic eye between 5% and 18%. For the contrast sensitivity measurements, the standard deviations for the normal eye ranged between 0.5–1.5 and 0.5–2 dB for the amblyopic eye.

mystery. To explain the present matching results, the compensation mechanism must have exact knowledge of the degree to which the lower visual processes are amblyopic. If this occurs at a binocular site then such information may be available by way of a comparison of normal and amblyopic eye responses.

4.3. Restricted filter access

Imagine that high spatial frequency filters were unable to be independently accessed by higher levels of processing for contrast sensitivity measurements but their combined output was available for edge-blur comparisons. This would provide a satisfactory explanation for the dissociation observed contrast sensitivity and the perception of edge blur. There is some

evidence that in both animals (Crewther & Crewther, 1990) and humans (Barnes, Hess, Dumoulin, Achtman, & Pike, 2001; Imamura et al., 1997; Sireteanu, Tonhausen, Mickli, Zanella, & Singer, 1998) the striate cortex may be able to respond at spatial frequencies well beyond the behaviourally measured limit. Having said this, there is also evidence from animal neurophysiology (Chino, Shansky, Jankowski, & Banser, 1983; Crewther & Crewther, 1990; Kiorpes, Kiper, O'Keefe, Cavanaugh, & Movshon, 1998; Kiorpes & McKee, 1999), human electrophysiology (Arden, Barnard, & Mushin, 1974; Kubova, Kuba, Juran, & Blakemore, 1996; Levi & Nanny, 1982) and human brain imaging (Anderson, Holliday, & Harding, 1999; Barnes et al., 2001; Demer, von Noorden, Volkow, & Gould, 1988; Kabasakal et al., 1995) that the ambly-

opic cortex exhibits a loss of neurones responding to high spatial frequencies.

4.4. A different way of looking at blur

Following on from what has been said above for peripheral vision and in particular its similarity to amblyopia for blur matching, imagine if our encoding of edge distinctness is directly related to the lack of stimulation of high frequency filters. If all high frequency detectors are stimulated then, regardless of their absolute peak tuning, edge transitions are perceived to be maximally distinct. The extent to which the highest spatial frequency detectors are under-stimulated relates to the extent to which edges appear less distinct. Hence in the normal periphery and in amblyopia, regardless of its severity, edges that adequately stimulate the highest spatial frequency filters available will be seen as maximally distinct. This proposal is just a special case of the one put forward by Field and Bradley (1997). Their proposal relied in the differential activity of mid-high spatial frequency filters. This suggestion which relies on relative rather than the absolute levels of stimulation is akin to the adaptational control that we know operate in luminance or colour domains and receives recent support from the finding that perceived blur can be affected by prior adaptation to blurred or sharpened stimuli or by simultaneous contrast from blurred or sharpened surrounds (Sevec, Reiner, & Webster, 2002).

4.5. Differences in the neural basis of amblyopia

A number of studies have argued that the neural basis of amblyopia differs depending on whether there is a strabismus present or not. Differences have been shown between strabismic (whether there be an anisometropia present or not) and non-strabismic, anisometropic amblyopia in the way the anomaly is distributed across the visual field (Hess & Pointer, 1985), the way the anomaly varies with mean luminance (Hess, Campbell, & Zimmern, 1980), the way the anomaly varies with suprathreshold contrast (Hess & Bradley, 1980) and the extent of positional uncertainty (Hess & Holliday, 1992). One more difference can now be added to this list, namely the perception of edge-blur. Non-strabismic anisometropes experience mild perceptual blur while strabismics (be they also anisometropic or not) do not. It is possible that the reason why anisometropes perceive only a mild degree of blur is due to the fact that contrast constancy helps to reduce the suprathreshold consequences of the threshold filtering loss. Optical defocus results in a multiplicative loss of suprathreshold contrast at a particular spatial frequency where as in anisometropic amblyopia, the loss is additive in nature (Hess & Bradley, 1980). This would result in neural blur having a

reduced impact for stimuli within the resolution range of the amblyopic eye.

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References

- Anderson, S. A., Holliday, I. E., & Harding, G. F. (1999). Assessment of cortical dysfunction in human strabismic amblyopia using magnetoencephalography. *Vision Research*, 39, 1723–1738.
- Arden, G. B., Barnard, W. M., & Mushin, A. S. (1974). Visually evoked responses in amblyopia. *British Journal of Ophthalmology*, 58, 183–192.
- Barnes, G. R., Hess, R. F., Dumoulin, S. O., Achtman, R. L., & Pike, G. B. (2001). The cortical deficit in humans with strabismic amblyopia. *Journal of Physiology (London)*, 533, 281–297.
- Bedell, H. D., & Flom, M. C. (1981). Monocular spatial distortion in strabismic amblyopia. *Investigative Ophthalmology & Visual Science*, 20, 263–268.
- Bedell, H. E., & Flom, M. C. (1983). Normal and abnormal space perception. *American Journal of Optometry & Physiological Optics*, 60, 426–435.
- Bedell, H. E., Flom, M. C., & Barbeito, R. (1985). Spatial aberrations and acuity in strabismus and amblyopia. *Investigative Ophthalmology & Visual Science*, 26, 909–916.
- Bex, P. J., Edgar, G. K., & Smith, A. T. (1995). Sharpening of drifting blurred images. *Vision Research*, 35, 2539–2546.
- Burr, D. C. (1980). Motion smear. *Nature*, 284, 164–165.
- Campbell, F. W., & Green, D. G. (1965). Optical and retinal factors affecting visual resolution. *Journal of Physiology (London)*, 181, 576–593.
- Chino, Y. M., Shanks, M. S., Jankowski, W. L., & Banser, F. A. (1983). Effects of rearing kittens with convergent strabismus on development of receptive-field properties in striate cortex neurons. *Journal of Neurophysiology*, 50, 265–286.
- Crewther, D. P., & Crewther, S. G. (1990). Neural site of strabismic amblyopia in cats: spatial frequency deficit in primary cortical neurons. *Experimental Brain Research*, 79, 615–622.
- Demer, J. L., von Noorden, G. K., Volkow, N. D., & Gould, K. L. (1988). Imaging of cerebral flow and metabolism in amblyopia by positron emission tomography. *American Journal of Ophthalmology*, 105, 337–347.
- Elder, J. H., & Zucker, S. W. (1998). Local scale control for edge detection and blur estimation. *IEEE Transactions on Pattern Analysis & Machine Intelligence*, 20, 699–716.
- Field, D. J., & Bradley, N. (1997). Visual sensitivity, blur and the sources of variability in the amplitude spectra of natural scenes. *Vision Research*, 37, 3367–3383.
- Galvin, S. J., O'Shea, R. P., Squire, A. M., & Govan, D. G. (1997). Sharpness overconstancy in peripheral vision. *Vision Research*, 37, 2649–2657.
- Galvin, S. J., O'Shea, R. P., Squire, A. M., & Hailstone, D. S. (1999). Sharpness constancy; the roles of visibility and current context. *Vision Research*, 39, 2649–2657.
- Georgeson, M. A. (1994). From filters to features location orientation contrast and blur. In M. J. Morgan (Ed.), *Higher-order processing in the visual system: CIBA foundation symposium 184*. Chichester, UK: John Wiley and Sons.

Gstalder, R. J., & Green, D. G. (1971). Laser interferometric acuity in amblyopia. *Journal of Pediatric Ophthalmology*, 8, 251–256.

Hammett, S. T. (1997). Motion blur and motion sharpening in the human visual system. *Vision Research*, 37, 2505–2510.

Hess, R. F., & Bradley, A. (1980). Contrast coding in amblyopia is only minimally impaired above threshold. *Nature*, 287, 463–464.

Hess, R. F., Campbell, F. W., & Zimmern, R. (1980). Differences in the neural basis of human amblyopias: effect of mean luminance. *Vision Research*, 20, 295–305.

Hess, R. F., & Holliday, I. E. (1992). The spatial localization deficit in amblyopia. *Vision Research*, 32, 1319–1339.

Hess, R. F., & Howell, E. R. (1977). The threshold contrast sensitivity function in strabismic amblyopia: evidence for a two type classification. *Vision Research*, 17, 1049–1055.

Hess, R. F., & Pointer, J. S. (1985). Differences in the neural basis of human amblyopias: the distribution of the anomaly across the visual field. *Vision Research*, 25, 1577–1594.

Hess, R. F., Pointer, J. S., & Watt, R. J. (1989). How are spatial filters used in fovea and parafovea. *Journal of the Optical Society of America A*, 6, 329–339.

Imamura, K., Richter, H., Lennerstrand, G., Rydberg, A., Andersson, J., Schneider, H., Watanabe, Y., & Langstrom, B. (1997). Reduced activity in the extra-striate visual cortex of individuals with strabismic amblyopia. *Neuroscience Letters*, 225, 173–176.

Kabasakal, L., Devranoglu, K., Arslan, O., Erdil, T. Y., Sonmezoglu, K., Uslu, I., Tolum, H., Isitman, A. T., Ozker, K., & Onsel, C. (1995). Brain SPECT evaluation of the visual cortex in amblyopia. *Journal of Nuclear Medicine*, 36, 1170–1174.

Kayargadde, V., & Martens, J. B. (1996). Perceptual characterization of images degraded by blur and noise: experiments. *Journal of the Optical Society of America A—Optics & Image Science*, 13, 1166–1177.

Kiorpis, L., Kiper, D. C., O'Keefe, L. P., Cavanaugh, J. R., & Movshon, J. A. (1998). Neuronal correlates of amblyopia in the visual cortex of macaque monkeys with experimental strabismus and anisometropia. *Journal of Neuroscience*, 18, 6411–6424.

Kiorpis, L., & McKee, S. P. (1999). Neural mechanisms underlying amblyopia. *Current Opinion in Neurobiology*, 9, 480–486.

Kubova, Z., Kuba, M., Juran, J., & Blakemore, C. (1996). Is the motion system relatively spared in amblyopia? Evidence from cortical evoked potentials. *Vision Research*, 36, 181–190.

Lagreze, W. D., & Sireteanu, R. (1991). Two-dimensional spatial distortions in human strabismic amblyopia. *Vision Research*, 31, 1271–1288.

Lagreze, W. D., & Sireteanu, R. (1992). Errors of monocular localization in strabismic amblyopia. Two-dimensional distortion. *Klinische Monatsblätter für Augenheilkunde*, 201, 92–96.

Levi, D. M., & Klein, S. (1982). Hyperacuity and amblyopia. *Nature*, 298, 268–270.

Levi, D. M., & Nanny, R. S. (1982). The pathophysiology of amblyopia: electrophysiological studies. *Annals of the New York Academy of Science*, 388, 243–263.

Levi, M., & Harwerth, R. S. (1977). Spatio-temporal interactions in anisometropic and strabismic amblyopia. *Investigative Ophthalmology & Visual Science*, 16, 90–95.

Mather, G. (1997). The use of image blur as a depth cue. *Perception*, 26, 1147–1158.

Ramachandran, V. S., Madhusudhan, V., & Vidyasagar, T. R. (1974). Sharpness constancy during movement perception. *Perception*, 3, 97–98.

Sevec, L. A., Reiner, T., & Webster, M. A. (2002). Vision Sciences Society, Sarasota, Florida, S53, abstract # 141.

Simmers, A. J., Bex, P. J., & Hess, R. F. (2003). Perceived blur in amblyopia. *Investigative Ophthalmology & Visual Science*, 44, 1395–1400.

Sireteanu, R., Tonhausen, N., Mickli, L., Zanella, F. F., & Singer, W. (1998). Cortical site of amblyopic deficit in strabismic and anisometropic subjects. *Investigative Ophthalmology & Visual Science*, 39(Suppl.), s909.

Watt, R. J., & Morgan, M. J. (1983). The recognition and representation of edge blur: evidence for spatial primitives in human vision. *Vision Research*, 23, 1465–1477.