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Interactions between luminance and contrast signals in global form detection

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Abstract

The human visual system is adept at detecting global structure, or form, within a scene. The initial stage of post-retinal processing for all aspects of vision is fed by On- and Off-centre cells sensitive to centred luminance increments and decrements respectively. These cells provide input to two parallel pathways that process variations in local luminance (first-order pathway) and local contrast (second-order pathway). Here, we investigate the contribution of luminance and contrast information to global form detection, a stage between the extraction of local orientation and the recognition of objects. The underlying processes involve two stages. We find that signals in the On-, Off- and second-order pathways are segregated at both stages of processing. Surprisingly, the non-linear stage in the second-order form pathway is different from that in motion processing: the second-order form detectors show an asymmetry in sensitivity to increments and decrements that is not apparent in motion. A functional architecture for global form detection is proposed along with its possible neural substrates.

Keywords: Global form; Local form; On-centre cells; Off-centre cells; Second-order pattern

1. Introduction

The visual system subdivides its task into operations working on different stimulus dimensions (Schiller, Logothetis, & Charles, 1990; Van Essen & DeYoe, 1995). An understanding of the functional consequences of these divisions is needed for a full account of visual performance. The early stages of the visual pathways segregate signals on some visual dimensions and convey them to the cortex in anatomically segregated pathways (Van Essen, Anderson, & Felleman, 1992). The pathways diverge in the cortex with a distinction between form (ventral cortical areas) and motion (more dorsal cortical areas) processing being helpful in understanding cases with brain damage (Gallant, Shoup, & Mazer, 2000; Zihl, von Cramon, & Mai, 1983) as well as normal visual processing (Lennie, 1998). An equally important distinction has been demonstrated in motion perception between detectors that are sensitive to variations in local luminance (first-order detectors) and some sensitive to variations in local contrast (second-order detectors) (Badcock & Derrington, 1985; Chubb & Sperling, 1988; Derrington & Badcock, 1985; Wilson, Ferrera, & Yo, 1992). Since these stimulus characteristics are salient for pattern definition more broadly, it is important to determine whether these two processes form a common first-stage of processing for all visual tasks or whether they are restricted to motion processing.

Some steps have already been taken towards determining the answer to this question. It has been shown that both first- and second-order stimulus characteristics can be used to localize stimuli (McGraw, Whitaker,

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Badcock, & Skillen, 2003) and to detect both their presence (Graham & Sutter, 1996; Langley, Fleet, & Hibbard, 1996) and their orientation (Smith, Clifford, & Wenderoth, 2001; Thomas & Olzak, 1996; Wenderoth, Clifford, & Ma-Wyatt, 2001). However, the properties of the detectors are less well understood in pattern vision, so it is not possible to determine whether the early processes are the same as are employed in motion processing. Neither is it known whether the signals from these detectors remain separate from each other at the higher levels of the cortical pathway that process form just as they are in higher-level motion processing (Badcock & Khuu, 2001) or whether they are effortlessly combined as in spatial localization tasks (McGraw et al., 2003).

To explore these questions Glass patterns have been employed as stimuli (depicted in Fig. 1). The stimuli have properties that allow exploration of the processing characteristics of both early and late stages in the cortical form pathway (Earle, 1999). These patterns are produced by randomly placing dot pairs within an image. Orienting the dot-pair in a consistent manner, e.g. on a line projecting through the centre of the pattern or lines orthogonal to such a projection creates a radial or rotary global structure respectively (Glass, 1969; Glass & Perez, 1973). The structure of such patterns is readily apparent (see Fig. 1) and an understanding of the processes that underlie the detection of such structure is likely to be a useful step towards understanding global form perception (Dakin & Bex, 2001; Earle, 1999; Gallant et al., 2000; Smith, Bair, & Movshon, 2002; Wilson & Wilkinson, 1998; Wilson, Wilkinson, & Asaad, 1997).

It is likely that such detection is a two-stage process because classical receptive fields of cells early in the visual pathways are small and therefore only capable of detecting local properties in the image (e.g. the orientation of a dot-pair in Fig. 1). A later stage is needed to integrate these local image descriptors into a global representation. A case for such two-stage models has been made for global motion perception (Burr, Morrone, & Vaina, 1998; Edwards & Badcock, 1994) and explicit models have been presented (Nishida & Ashida, 2000; Wilson et al., 1992).

Recently, Wilson and colleagues (Wilson & Wilkinson, 1998; Wilson et al., 1997) have presented a two-stage model for the detection of radial and rotary global form. This model could explain many aspects of human detection of Glass patterns, such as the lower sensitivity to translational than rotary or radial patterns reported in several studies (Wilson & Wilkinson, 1998; Wilson et al., 1997), although disputed by Dakin and Bex (2001). In the current report we examine the properties of the two proposed stages in order to cha-

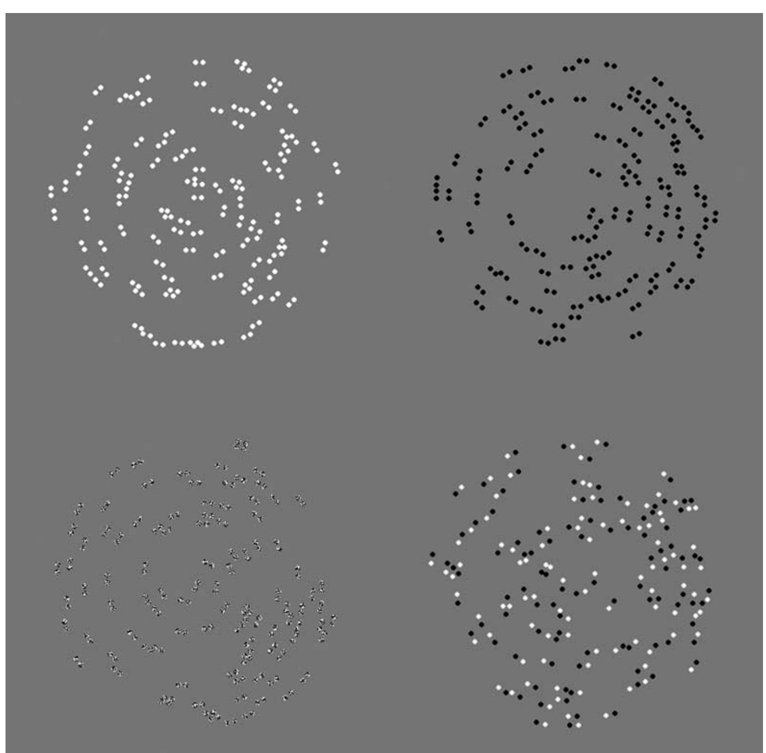

Fig. 1. Glass patterns constructed to show circular structure composed of either incremental, decremental, mixed increment and decrement or textured dot pairs. The texture pairs may not remain balanced following the printing process but in the research reported those dots had the same average luminance as the background.

racterise the manner in which signals are processed at each stage. In particular, the experiments address the interaction between signals carried by luminance variation (increments and decrements) and contrast variation at both the first and the second stage of processing.

2. Method

2.1. Observers

Four observers participated in the present study. All had normal or corrected to normal visual acuity. SKK and CC were co-authors of the paper while JAM and AMW were experienced observers, but unaware of the purpose of the experiments.

2.2. Apparatus

Five experiments are described. The same equipment was used in each study. The stimuli were generated by a custom produced C programme which generated image arrays and loaded them onto the framestore section of a Cambridge Research Systems (CRS) VSG 2/3 Graphics card housed in a Pentium II 400 MHz computer. The stimuli were displayed on a Hitachi 4721 colour monitor (29.7 cm H × 27.6 cm V) that had been gamma corrected using a CRS Optical (Head #265) and associated software. The monitor was capable of 1600 × 1200 pixel resolution but was run at a resolution of 752 × 752 pixels; this reduction minimizing any luminance uncertainties produced by adjacent pixel non-linearities (Klein, Hu, & Carney, 1996). The refresh rate of the monitor was 100 Hz.

Observers viewed the screen with their head in a chin and forehead rest at a distance of 89 cm from the screen. They signalled their responses using a two-button mouse.

2.3. Stimuli

The Glass patterns were produced by placing dot-pairs at random locations within a circular aperture set to a background luminance of 46.3 cd/m^2. The orientation of the dot-pair relative to a radial line projecting from the centre of the aperture was varied to produce the different types of Glass patterns. An angle of 0° produces a pair that is aligned with this radial line and thus produces a radial Glass pattern. An angle of 90° produces a circular pattern. The stimuli consisted of either 50 or 100 approximately round dots-pairs (dots were approximately round with a 3 pixel radius of 0.09° and pairs had a centre-to-centre separation of 12 pixels or 0.36°) with a proportion being placed according to the specified angle. These signal dots carry the global structure. The remainder of the dots (noise) were assigned random orientations. The dots did not overlap.

The dots were either uniform luminance increments (92.6 cd/m^2), uniform luminance decrements (0 cd/m^2) or textured dots composed of equal numbers of pixels that were increments and decrements. The assignment of a pixel as an increment or decrement was randomly determined for each textured dot in the first experiment but in subsequent experiments, an additional constraint was introduced; dots had to contain equal numbers of increments and decrements.

2.4. Procedure

The observer's task in all of the experiments was to indicate which of two briefly displayed patterns contained a global structure. The other pattern contained the same number and types of dots but the pairs were randomly oriented. The target structure had a proportion of pairs oriented according to a global rule and the remainder of the dot-pairs randomly oriented. The sensitivity measure employed was the number of dot-pairs that had to be placed according to the rule for the observers to be able to reliably identify the pattern that contained the structure.

Sensitivity to global structure was measured using a temporal two alternative forced choice procedure. The task of the observer was to indicate the interval containing global structure, the other interval contained the same number of dot pairs, but each dot pair was randomly oriented. Each interval was displayed for 1 s and separated by a 500 ms period in which a blank screen was displayed at the background luminance. An adaptive staircase that converged on the 79% correct performance level (three correct responses to step down, one incorrect response to step up) was used to modify the coherence level. Staircases began at a signal level of 25 dot pairs, and with an initial step size of eight dot pairs. On the first and subsequent reversals, the step size was halved. After three reversals the step size was one dot pair and remained at this value until the end of the trial. Staircases lasted for eight reversals and the threshold estimate was the average of the last four reversals.

Each observer performed the conditions in a randomized order, one staircase at a time, and then the reverse of that order. This procedure ensured that any order effects were minimized and was repeated until 10 independent threshold estimates were obtained. These estimates were averaged for each observer to provide an indication of the final threshold for each condition.

Experiment 1: *First-stage processing*. In order to detect the local orientation of the dot-pairs it is necessary for a common unit to detect both dots in the pair. Later these local orientations can be compared to determine the global structure. The first experiment investigated the local stage of processing by producing dot-pairs in which the dot-types may be independently defined. Three types of dots were used; light increments, light decrements and textured dots having the same average luminance as the background. All three dot-types present a 50% contrast step relative to the background and thus all three should drive a second-order system sensitive to local contrast (Edwards & Badcock, 1995). However, a first-order system sensitive to changes in local average luminance at the scale of the dot will not respond to the textured dots because they are constructed so as to match the background in average luminance. In order to render signals from first-order detectors operating at other scales irrelevant, the texture of the dot is randomly reallocated for each dot in order to add random variation to the signals.

The simple cells in primary visual cortex (area V1) represent the earliest stage of orientation detectors in the human visual system (Ferster & Miller, 2000). These cells are sensitive to the signed luminance deviations from the local average falling within their elongated excitatory and inhibitory zones. If these units are responsible for detecting the orientation of the dot-pair (Glass, 1969; Smith et al., 2002; Wilson & Wilkinson, 1998; Zucker, 1985) then for optimal performance the first-order system would require dots to be either both increments or both decrements. When mixed, the matched increment and decrement will cancel each other out if aligned with a neurone's preferred orientation resulting in a weaker response than obtained with randomly placed light and dark individual dots (Smith et al., 2002). Cells at other orientations will also be weakly stimulated if the bright dot falls in an excitatory region and a dark dot falls in an inhibitory region (Dakin, 1997; Smith et al., 2002; Wilson, Switkes, & De Valois, 2004). This will prevent clear orientation signals being passed to the global stage and make it very difficult to detect the global structure.

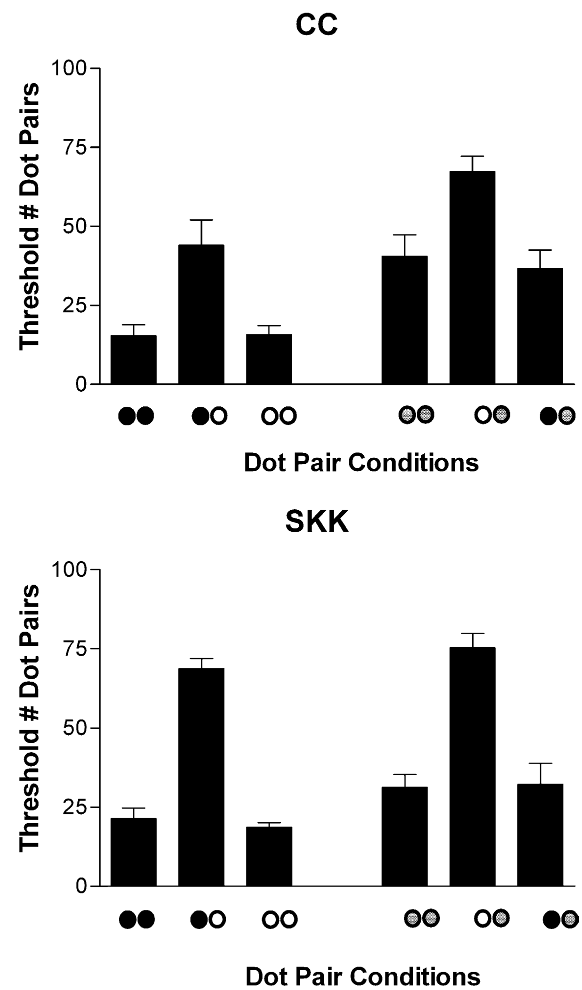

Fig. 2. First-stage processing. Coherence thresholds for the detection of concentric Glass patterns composed of 100 dot pairs for subjects CC and SKK. Data from six conditions are shown for each subject, corresponding to all possible pairings of three types of dot: light increments (open circle), light decrements (black circle) and textured dots (grey circle) having the same average luminance as the background. Error bars represent the standard error of the mean.

2.5. Results and discussion

Fig. 2 presents the performance of two observers showing the mean number of coherently oriented dot-pairs at the threshold (+1 sem). On the left hand side the dots were uniform in texture and either light increments (indicated by white circle) or decrements (indicated by black circle). On the right hand side at least one dot of each pair was textured (indicated by the grey circle) containing both increments and decrements so that the mean luminance would be equivalent to the background.

Fig. 2 shows that when increments and decrements are mixed within a pair the threshold rises from 15–20 pairs, with matched dots, to 50–60 pairs out of the hundred.

When textured dots are combined with increments performance also deteriorates but it does not do so when they are paired with decrements. The Glass pattern data suggest that the form mechanisms responsible for detecting the contrast variation include an asymmetric rectification in the process so that contrast signalled by decrements can be as effective as that signalled by balanced textured dots. A system acting as an asymmetric rectifier with greater sensitivity to decrements could be sensitive only to decrements in the stimulus and be blind to increments. While some previous evidence points to the existence of a negative half-wave rectifier in the second-order form processing pathway (Chubb & Nam, 2000; Van der Zwan, Badcock, & Parkin, 1999), full-wave rectification is used to characterise the non-linear stage in the second-order motion pathway (Ledgeway & Smith, 1994; Wilson et al., 1992).

Experiment 2: *Second stage processing:* In order to look at the second stage of processing we exploited a previously established property of performance with these patterns: adding extra, randomly-oriented pairs of the same dot-type to the pattern increases the number of pairs that must be appropriately oriented in order to detect the structure (Edwards & Badcock, 1994; Van der Zwan et al., 1999). However, the thresholds only change if the added dots are processed by the same mechanism as the one detecting the signal dots. Thus, by adding different types of dots to the pattern, it is possible to determine which are combined in the processes at the global pattern detection stage.

2.6. Results and discussion

Fig. 3A–C shows the number of dot-pairs that need to be appropriately oriented to detect the structure. The sections (A–C) show performance with different dot-types carrying the structure for each of four observers. When the dot-pairs are defined by either luminance increments or decrements (A & B), only extra randomly-oriented dot-pairs of the same type make it harder to see the structure (see also Wilson et al. (2004)). The exception was for Observer SK where decrements and increments interacted in a radial Glass pattern. However, SK showed the same pattern as others with concentric patterns.

This result can be readily explained if neurones early in the visual system with 'on-centre' and 'off-centre' receptive fields were to generate separate signals from the dot-pairs and those signals remained separate at all stages of global form detection. This however implies a greater separation than has been seen in other tasks, including global motion perception where the signals interact at the global stage of processing (Edwards & Badcock, 1994).

Adding extra randomly oriented textured dot pairs to Glass patterns defined by either increment or decrement dot pairs did not change the thresholds (Fig. 3A and B). This was to be expected, since these dots present no change of the local average luminance on the scale of the dot. However, this lack of interaction indicates that first- and second-order systems are separate in global form processing at the second stage of processing, as well as at the first.

Fig. 3C represents performance when the textured dots carried the global form signal. In this case adding dots of any type interfered with performance. Thus any contrast change relative to the background is sufficient for the second-order system. The pattern of results does differ a little between observers. Observer SK

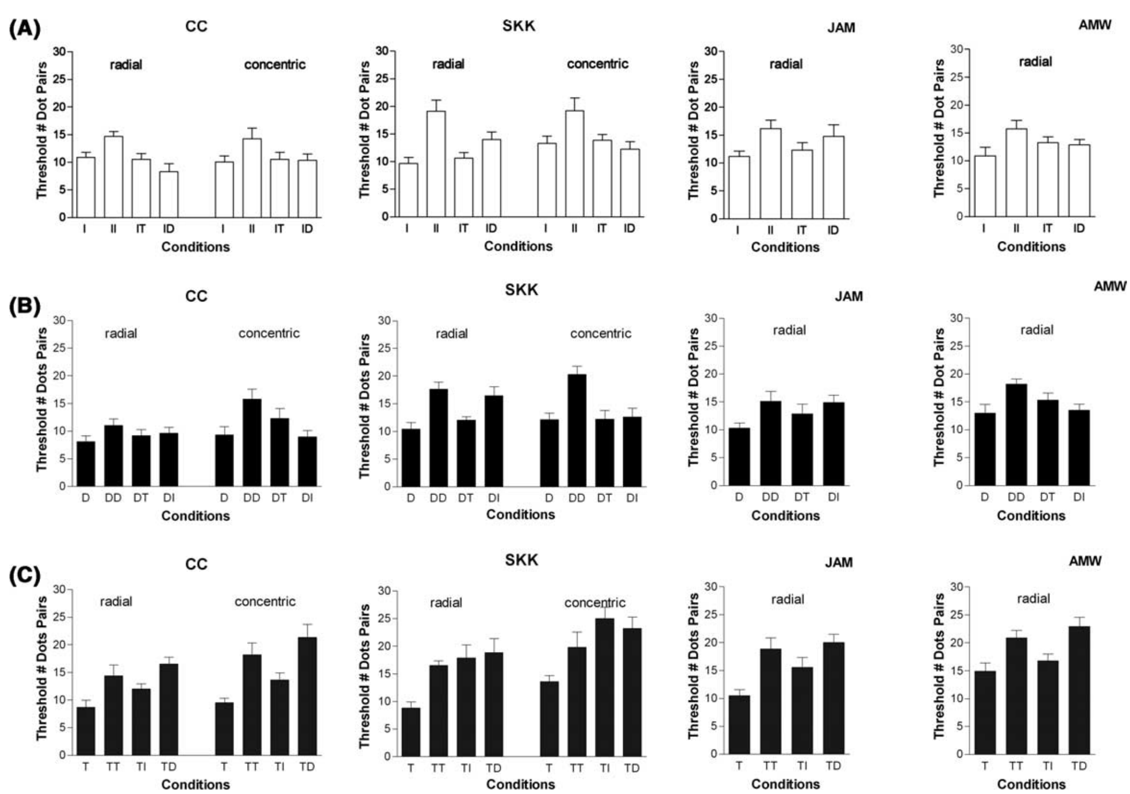

Fig. 3. (A) Second-stage processing. Coherence thresholds for the detection of Glass patterns composed of two sets of 50 dot pairs for four subjects. The first set contained a variable proportion of signal pairs while the second contained only noise. The set of dots containing the signal was defined by light increments (I) from the background. The additional noise dots consisted of a single type of dot, either light increments (I), light decrements (D), or textured (T). (B) Second-stage processing for decrement signal dots. (C) Second-stage processing for textured signal dots.

shows approximately equal threshold elevations with extra dots of any of the three types while the other three observers showed a smaller threshold elevation with incremental dots than with the other two types.

Experiment 3: *Responses to increments and decrements:* One reason why the results might differ would be if the increments and decrements constituting the texture in the textured dots were not an exact perceptual match. The response of the visual system to increments and decrements need not be symmetrical with respect to contrast (Burton, Nagshineh, & Ruddock, 1977; Schiller, 1992). An imbalance of this sort could produce an effective shift in the average luminance of the textured dot relative to background and thus produce a first-order (luminance modulation) signal. To investigate this possibility we examined the effect of the contrast of noise dot-pairs on the detection of Glass patterns defined by balanced textured dot-pairs. The noise dots were themselves textured such that half the pixels were at the luminance of the background and half were systematically varied in contrast.

2.7. Results and discussion

Fig. 4 shows coherence thresholds for four observers plotted as a function of the contrast of the variable pixels in the noise dot-pairs. Data points to the left of centre of each graph show coherence thresholds for decrement noise, and those to the right for increment noise. A contrast of zero corresponds to the absence of additional noise dots (i.e. a pattern composed of only 50 dot-pairs). For each subject the data have been fitted by a pair of straight lines sharing a common *y*-intercept. The slopes of these lines are a metric of the effective gain of the On and Off inputs into the global stage of the second-order pathway mediating Glass pattern detection. For full-wave rectification, the two slopes should be of approximately equal magnitude. For (positive) half-wave rectification, the gain of the Off inputs should be zero, corresponding to a flat line on the left of the graph. For negative half-wave rectification, the gain of the On inputs should be zero, corresponding to a flat line on the right.

On analysis neither pure full-wave, nor pure half-wave rectification is found. For subjects CC, AMW and JM, the ratio of the slopes is 0.44, 0.29 and 0.48, corresponding to a much higher gain for the Off than On inputs, producing an asymmetric rectifier. For subject SK, the contrast dependence function is more symmetrical (slope ratio = 0.80), showing that the gains of the On and Off inputs are almost equal, as would be expected from a full-wave rectifier. Differences between

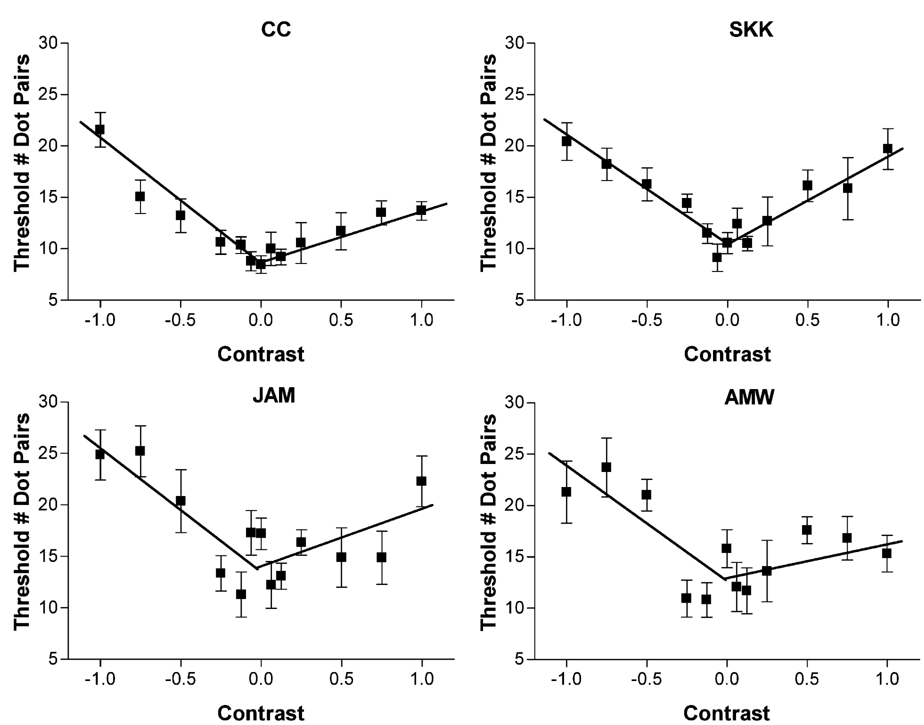

Fig. 4. Rectification in the processing of textured dots. Coherence thresholds for the detection of Glass patterns carried by textured signal dots as a function of the contrast of the additional noise dots. The additional noise dots were themselves textured such that half the pixels were at the luminance of the background and half were systematically varied in contrast. Data points to the left of centre of each graph show coherence thresholds for decrement noise, and those to the right for increment noise. A contrast of zero corresponds to the complete absence of noise dots. For each subject the data have been fitted by a pair of straight lines sharing a common y-intercept. The two slopes and the intercept are −11.77, 5.19 and 8.55 for subject CC; −10.71, 8.52 and 10.48 for SKK; −11.63, 5.55 and 13.88 for JAM; and −11.26, 3.28 and 12.88 for AMW.

observer responses to texture contrast and second-order motion have been noted previously (Graham, 1994) and emphasise the need to measure these functions for individual observers in order to determine whether their system employs an asymmetric or full-wave rectification prior to investigating second-order processing. This is best assessed by considering the gains of the two inputs independently.

3. Discussion

The results of these experiments allow us to characterise the functional architecture of global form detection in the human visual system. The underlying processes can be described in two stages. The first experiment characterises the initial local stage of processing by manipulating the composition of dots within each pair of a Glass pattern. For luminance-defined dots, it was found that coherence thresholds for global pattern detection were considerably lower when the two dots within each pair were of the same type (increment–increment, decrement–decrement) than for increment–decrement pairings (Glass & Switkes, 1976). This is consistent with the detection of local structure by oriented linear filters (Dakin, 1997; Smith et al., 2002; Wilson & Wilkinson, 1998). When increment and decrement dots are paired together, they will very weakly stimulate a broad range of oriented linear filters that provide input to the second stage global form detectors, thereby elevating detection thresholds for coherent structure.

For textured dots, coherence thresholds were lower for the texture-texture condition or when decrement and texture dots were paired together than for increment-texture pairings. This supports the view that the pre-processing stage in the second-order form detection pathway approximates a negative half-wave rectifier that is sensitive to decrement dots and the contrast decrements in texture elements but less so to contrast increments (Chubb & Nam, 2000; Van der Zwan et al., 1999).

The subsequent experiments measured coherence thresholds for different combinations of signal and noise dot pairs. All of the signal dots in a given pattern were always of the same type, as were all of the noise dots. The results showed that overall, the luminance-defined signals were only affected by luminance-defined noise of the same contrast polarity. The exception was for Observer SK where decrements and increments interacted in a radial Glass pattern. However, SK showed the same pattern as others with concentric patterns. For texture-defined signals, all noise dot types showed a degree of interference, although this was generally much weaker for increment noise dots than for decrement or textured dots. Thus, the results paralleled those in the first experiment, suggesting that the selectivity observed at the second stage is simply a consequence of the first stage architecture. Signals at the first stage are segregated into three separate pathways (first-order increment and decrement and second-order) and these pathways remain separate at the second stage of processing.

The recent two-stage model of global form perception proposed by Wilson and colleagues (Wilson & Wilkinson, 1998; Wilson et al., 1997) accounts for many aspects of human detection of Glass patterns (Seu & Ferrera, 2001). According to this model, a stage of oriented linear filtering putatively identified with cortical area V1 is followed by full-wave rectification and second stage filtering, occurring in V2, before pooling of signals in area V4 to detect global structure. The full-wave rectification stage in this model renders the global pooling mechanisms insensitive to the characteristics of the dot-pairs carrying the signal.

While the results presented here show that global form detection in the visual system is selective for contrast polarity and texture, the Wilson model in its current form is unable to account for the differential effects of different noise types on the detection of global form. In order to explain these data, we propose an alternative model in which three parallel pathways process increment, decrement and texture information independently (Fig. 5). The first stage of the On pathway is an array of oriented linear filters excited by contrast increments (Smith et al., 2002). The output of these oriented linear filters is then combined spatially to produce global form detectors sensitive only to contrast increments. A similar pathway processes contrast decrements. The second-order pathway performs an initial spatial-frequency-selective filtering of the stimuli and then a rectification on the incoming signals in which decrements are processed with higher gain than increments. This pre-processed signal is then fed into an array of oriented linear filters similar to those in the other two pathways, and thence into a global form detector. The initial filtering stage is required because earlier research has shown that behaviour of the second-order pattern detection system is inconsistent with an early non-linearity (Henning, Hertz, & Broadbent, 1975; Nachmias, 1989; Nachmias & Rogowitz, 1983), just as in motion processing (Badcock & Derrington, 1989; Langley et al., 1996; Scott-Samuel & Georgeson, 1995).

The first stage of oriented filtering in the linear pathways could be implemented by simple cells in primary visual cortex (V1). The rectification stage of the non-linear pathway must come after relatively narrow band spatial frequency filtering (Henning et al., 1975) suggesting a cortical origin (Mareschal & Baker, 1998; Smith et al., 2002), which then feeds into oriented linear filters in V1 or V2 (Wilson et al., 1992). The outputs of these oriented linear filters must then be pooled by global form detectors (Wilson & Wilkinson, 1998; Wilson et al., 1997) of the type identified in area V4 of macaque

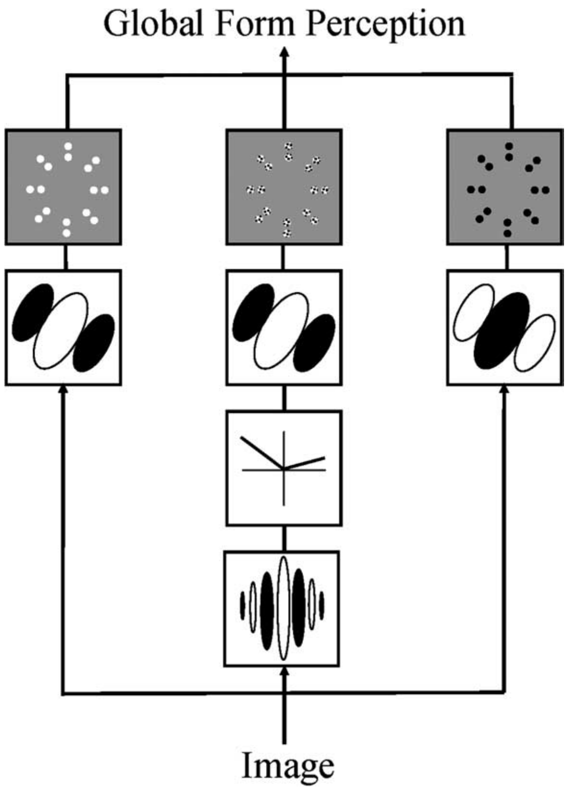

Fig. 5. Schematic diagram of the functional architecture of global form detection inferred from the present experiments, consisting of three parallel pathways. The first stage of the 'On' pathway (left) is an array of oriented linear filters excited by contrast increments. The output of these oriented linear filters is then combined spatially to produce global form detectors sensitive only to contrast increments. A similar pathway (right) processes contrast decrements. The second-order pathway (middle) pre-filters the incoming signals at a high spatial frequency and then performs a rectification, the gain of which is higher for decrements than for increments. This pre-processed signal is then fed into an array of oriented linear filters similar to those in the other two pathways, and thence into a global form detector.

visual cortex (Gallant, Braun, & Van Essen, 1993; Gallant, Connor, Rakshit, Lewis, & VanEssen, 1996).

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References

Badcock, D. R., & Derrington, A. M. (1985). Detecting the displacement of periodic patterns. *Vision Research, 25*(9), 1253–1258.

Badcock, D. R., & Derrington, A. M. (1989). Detecting the displacements of spatial beats: no role for distortion products. *Vision Research, 29*(6), 731–739.

Badcock, D. R., & Khuu, S. K. (2001). Independent first- and second-order motion energy analyses of optic flow. *Psychological Research, 65*, 50–56.

Burr, D. C., Morrone, M. C., & Vaina, L. M. (1998). Large receptive fields for optic flow detection in humans. *Vision Research, 38*, 1731–1743.

Burton, G. J., Nagshineh, S., & Ruddock, K. H. (1977). Processing by the human visual system of the light and dark contrast components of the retinal image. *Biological Cybernetics, 27*(4), 189–197.

Chubb, C., & Nam, J. H. (2000). Variance of high contrast textures is sensed using negative half-wave rectification. *Vision Research, 40*(13), 1677–1694.

Chubb, C., & Sperling, G. (1988). Drift-balanced random stimuli: a general basis for studying non-Fourier motion perception. *Journal of the Optical Society of America, A5*(11), 1986–2006.

Dakin, S. C. (1997). Glass patterns: some contrast effects re-evaluated. *Perception, 26*, 253–268.

Dakin, S. C., & Bex, P. J. (2001). Local and global visual grouping: tuning for spatial frequency and contrast. *Journal of Vision, 1*, 99–111.

Derrington, A. M., & Badcock, D. R. (1985). Separate detectors for simple and complex grating patterns? *Vision Research, 25*(12), 1869–1878.

Earle, D. C. (1999). Glass patterns: grouping by contrast similarity. *Perception, 28*, 1373–1382.

Edwards, M., & Badcock, D. R. (1994). Global motion perception: interaction of the on and off pathways. *Vision Research, 34*, 2849–2858.

Edwards, M., & Badcock, D. R. (1995). Global motion perception: no interaction between the first- and second-order motion pathways. *Vision Research, 35*(18), 2589–2602.

Ferster, D., & Miller, K. D. (2000). Neural mechanisms of orientation selectivity in the visual cortex. *Annual Review of Neuroscience, 23*, 441–471.

Gallant, J. L., Braun, J., & Van Essen, D. C. (1993). Selectivity for polar, hyperbolic, and Cartesian gratings in macaque visual cortex. *Science, 259*(5091), 100–103.

Gallant, J. L., Connor, C. E., Rakshit, S., Lewis, J. W., & VanEssen, D. C. (1996). Neural responses to polar, hyperbolic and cartesian gratings in area V4 of the macaque monkey. *Journal of Neurophysiology, 76*, 2718–2739.

Gallant, J. L., Shoup, R. E., & Mazer, J. A. (2000). A human extrastriate area functionally homologous to macaque V4. *Neuron, 27*, 227–235.

Glass, L. (1969). Moire effect from random dots. *Nature, 223*, 578–580.

Glass, L., & Perez, R. (1973). Perception of random dot interference patterns. *Nature, 246*, 360–362.

Glass, L., & Switkes, E. (1976). Pattern recognition in humans: correlations which cannot be preceived. *Perception, 5*, 67–72.

Graham, N. (1994). Non-linearities in texture segregation. In G. R. Bock & J. A. Good (Eds.), *Higher-order processing in the visual system* (pp. 309–322). Chichester: John Wiley & Sons.

Graham, N., & Sutter, A. (1996). Effect of spatial scale and background luminance on the intensive and spatial nonlinearities in texture segregation. *Vision Research, 36*(10), 1371–1390.

Henning, G. B., Hertz, B. G., & Broadbent, D. E. (1975). Some experiments bearing on the hypothesis that the visual system analyses spatial patterns in independent bands of spatial frequency. *Vision Research, 15*, 887–897.

Klein, S. A., Hu, Q. J., & Carney, T. (1996). The adjacent pixel nonlinearity: problems and solutions. *Vision Research, 36*(19), 3167–3181.

Langley, K., Fleet, D. J., & Hibbard, P. B. (1996). Linear filtering precedes nonlinear processing in early vision. *Current Biology, 6*, 891–896.

Ledgeway, T., & Smith, A. T. (1994). Evidence for separate motion-detecting mechanisms for first- and second-order motion in human vision. *Vision Research, 34*(20), 2727–2740.

Lennie, P. (1998). Single units and visual cortical organization. *Perception, 27*, 1–44.

Mareschal, I., & Baker, C. L. J. (1998). A cortical locus for the processing of contrast-defined contours. *Nature Neuroscience, 1*, 150–154.

McGraw, P. V., Whitaker, D., Badcock, D. R., & Skillen, J. (2003). Neither here nor there: localising conflicting visual attributes. *Journal of Vision, 3*, 265–273.

Nachmias, J. (1989). Contrast modulated maskers: test of a late nonlinearity hypothesis. *Vision Research, 29*(1), 137–142.

Nachmias, J., & Rogowitz, B. E. (1983). Masking by spatially-modulated gratings. *Vision Research, 23*(12), 1621–1629.

Nishida, S., & Ashida, H. (2000). A hierarchical structure of motion system revealed by interocular transfer of flicker motion aftereffects. *Vision Research, 40*(3), 265–278.

Schiller, P. H. (1992). The ON and OFF channels of the visual system. *Trends In Neurosciences, 15*(3), 86–92.

Schiller, P. H., Logothetis, N. K., & Charles, E. R. (1990). Role of the color-opponent and broad-band channels in vision. *Visual Neuroscience, 5*, 321–346.

Scott-Samuel, N., & Georgeson, M. A. (1995). Does early non-linearity account for second-order motion. *Perception, 24*, 104.

Seu, L., & Ferrera, V. P. (2001). Detection thresholds for spiral Glass patterns. *Vision Research, 41*, 3785–3790.

Smith, M. A., Bair, W., & Movshon, J. A. (2002). Signals in macaque striate cortical neurons that support the perception of Glass patterns. *The Journal of Neuroscience, 22*(18), 8334–8345.

Smith, S., Clifford, C. W., & Wenderoth, P. (2001). Interaction between first- and second-order orientation channels revealed by the tilt illusion: psychophysics and computational modelling. *Vision Research, 41*(8), 1057–1071.

Thomas, J. P., & Olzak, L. A. (1996). Uncertainty experiments support the roles of second-order mechanisms in spatial frequency and orientation discriminations. *Journal of the Optical Society of America. A., 13*(4), 689–696.

Van der Zwan, R., Badcock, D. R., & Parkin, B. (1999). Global form perception: interactions between luminance and texture information. *Australian and New Zealand Journal of Ophthalmology, 27*(3–4), 268–270.

Van Essen, D. C., Anderson, C. H., & Felleman, D. J. (1992). Information processing in the primate visual system: an integrated systems perspective. *Science, 255*(5043), 419–423.

Van Essen, D. C., & DeYoe, E. A. (1995). Concurrent processing in the primate visual cortex. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 383–400). Cambridge, MA: MIT press.

Wenderoth, P., Clifford, C. W., & Ma-Wyatt, A. M. (2001). Hierarchy of spatial interactions in the processing of contrast-defined contours. *Journal of the Optical Society of America A, 18*(9), 2190–2196.

Wilson, H. R., Ferrera, V. P., & Yo, C. (1992). A psychophysically motivated model for two-dimensional motion perception. *Visual Neuroscience, 9*, 79–97.

Wilson, H. R., & Wilkinson, F. (1998). Detection of global structure in Glass patterns: implications for form vision. *Vision Research, 38*, 2933–2948.

Wilson, H. R., Wilkinson, F., & Asaad, W. (1997). Concentric orientation summation in human form vision. *Vision Research, 37*, 2325–2330.

Wilson, J. A., Switkes, E., & De Valois, R. L. (2004). Glass pattern studies of local and global processing of contrast variations. *Vision Research, 44*, 2629–2641.

Zihl, J., von Cramon, D., & Mai, N. (1983). Selective disturbance of movement vision after bilateral brain damage. *Brain, 106*, 313–340.

Zucker, S. W. (1985). Early orientation selection: Tangent fields and the dimensionality of their support. *Computer Vision, graphics and image processing, 8*, 71–77.