

Available online at www.sciencedirect.com

SCIENCE @ DIRECT®

Vision Research 46 (2006) 925–931

**Vision
Research**

www.elsevier.com/locate/visres

Motion-detection thresholds for first- and second-order gratings and plaids

Craig Aaen-Stockdale*, Linda Bowns

School of Psychology, University of Nottingham, University Park, Nottingham NG7 2RD, UK

Received 25 July 2005; received in revised form 11 October 2005

Abstract

The two-stage decomposition–recombination model of 2D motion perception has been criticised on the basis that the direction of plaid stimuli can be accurately discriminated at speeds so low that the direction of their Fourier components is not discriminable. The nature of this gap in performance between gratings and plaids was investigated across a range of spatial frequencies and durations for first- and second-order stimuli. Motion-detection thresholds were obtained using a 2AFC, constant stimuli procedure and it was found that although thresholds for detection of plaid motion were often lower than those for gratings, the gap in performance between first-order plaids and gratings was unreliable, varying in magnitude and occasionally direction with the spatial frequency of the stimulus, presentation duration and observer. Curiously, an analogous gap found between purely second-order gratings and second-order plaids was more reliable and stable. It has been suggested that the gap is the result of ‘local motion detectors’ or broadly tuned V1 cells. The data presented here suggest that second-order mechanisms are responsible for the gap and that first-order information may even disrupt it.

© 2005 Elsevier Ltd. All rights reserved.

Keywords: Plaid; Spatial; Second-order; Motion

1. Introduction

Some models of 2D (pattern) motion detection emphasise two stages of visual analysis: the first stage being decomposition of a stimulus into its constituent 1D components followed by the subsequent recombination of these separate motion vectors via an integration computation at the second stage (Adelson & Movshon, 1982; Movshon, Adelson, Gizzi, & Newsome, 1985; Simoncelli & Heeger, 1998; Wilson, Ferrera, & Yo, 1992). The standard conception of the two-stage model is that the retinal image undergoes a Fourier-like decomposition via component-selective neurons such as those in V1, and then the 1D motion vectors are recombined at a higher stage (probably MT/V5), where many neurons show pattern-selective responses (Movshon et al., 1985). This two-stage model has much

support in the literature, and has generated a debate regarding the precise form of the second-stage integration computation (Bowns, 2002; Ferrera & Wilson, 1990; Simoncelli & Heeger, 1998; Wilson et al., 1992).

The two-stage model has, however, been criticised on the basis that motion of a spatially 2D plaid pattern is still detectable at velocities so low that the motion of the components, were they presented individually, would not be detectable (Derrington & Badcock, 1992; Wright & Gurney, 1992). It is suggested by Derrington and Badcock that this gap in performance may be bridged by “localised motion detectors” (LMDs). Georgeson and Scott-Samuel (2000) have hypothesised that motion sensors with receptive fields that possess broad orientation-tuning could directly detect the motion of local blob features in the plaid stimulus. This ties in well with published accounts of wide orientation-tuning for local motion (Anderson & Burr, 1991; Anderson, Burr, & Morrone, 1991; Georgeson & Scott-Samuel, 2000; Snowden, 1992; van den Berg, van de Grind, & van Doorn, 1990) and evidence that the size,

* Corresponding author.

E-mail address: crs@psychology.nottingham.ac.uk (C. Aaen-Stockdale).

number, and ‘optimality’ of 2D ‘blob’ features present within plaid stimuli bias their perceived direction (Alais, Burke, & Wenderoth, 1996; Alais, Wenderoth, & Burke, 1994, 1997; Bowns, 1996).

Physiological evidence for these proposed LMD units was provided recently by Tinsley et al. (2003). Using single-cell recording, Tinsley et al. found V1 simple cells in the marmoset monkey that responded to the pattern-motion, rather than the component-motion, of a plaid. They found that these pattern-selective neurons had receptive fields that were short and wide, therefore were broadly tuned for orientation and could directly detect the motion of ‘blob’ features within the plaid if their receptive field spatial tuning matched the spatial frequency (SF) of the blobs. Fig. 1 shows how V1 neurons with differing receptive field shapes could function to detect either the components or blobs of a plaid pattern.

Support for the findings of Tinsley et al. comes from Pack, Livingstone, Duffy, and Born (2003) who used a reverse correlation technique to map the receptive field of individual V1 neurons. They showed that a subpopulation of cells in V1 responded to the direction of motion of a bar regardless of its orientation. Further analysis showed that these same cells were end-stopped and as such were detecting only the motion of the terminators of the bar. If these cells were simply responding to the Fourier energy in the stimulus, they should signal a direction of motion perpendicular to the orientation of the bar.

The findings of Tinsley et al. and Pack et al. challenge the standard view of 2D motion perception. If information about the direction of features, like the blobs of a plaid, is accessible directly to neurons in V1, then 2D motion perception may not be a two-stage, decomposition–recombination process after all.

The primary aim of this experiment was to investigate whether motion-discrimination thresholds for first-order (FO) luminance-defined plaids were always better than that

predicted by the thresholds for their FO component gratings, across a range of SFs. So far, the only investigation of the effects of spatial frequency on the gap in performance between components and plaids was limited to only two different frequencies (Cox & Derrington, 1994). The second aim was to investigate whether FO or second-order (SO) features in the stimulus were responsible for the gap in performance. Because the ‘blobs’ formed by areas of maximum and minimum luminance and SO contrast modulations present in plaid stimuli move in the same direction at the same speed, it is difficult to conclude that one rather than the other is causing a particular effect. Plaids were constructed of contrast-modulated static noise gratings, the 2D profile of which contained the same SO contours as those present in the FO plaid. It was hypothesised that if the gap was caused by broadly orientation-tuned V1 neurons detecting the motion of FO luminance ‘blobs’ in the stimulus, then no gap should be present for these purely SO stimuli. Finally, the duration of the stimulus was varied in order to investigate how the performance gap varied over time.

2. Method

A 2AFC design and the method of constant stimuli were adopted for this experiment. After a period of fixation the observer was shown a test stimulus. The test stimulus could be a first- or second-order grating or plaid. The observer was asked to respond whether they perceived the stimulus to be moving upward or downward. The motion-detection threshold was defined as the minimum temporal frequency (TF) at which the observer could correctly detect the motion of the stimulus on 75% of the trials.

The experimenter (CAS) and two observers naïve with respect to the hypothesis (FM and YH) took part in this experiment. All participants were practiced psychophysical observers.

2.1. Apparatus and stimuli

Stimuli were generated on an *Apple Macintosh G4* computer with a 17-in. gamma-corrected *Apple ColorSync Studio Display* CRT monitor with a screen resolution of 1024×768 pixels and a frame rate of 99 Hz. The screen subtended 31° of visual angle when viewed from 57 cm, therefore each pixel subtended 1.81 arcmin. The experiment was programmed and run in Matlab version 5 incorporating the Psychophysics Toolbox routines (Brainard, 1997; Pelli, 1997). The screen background was maintained at a constant level corresponding to the mean luminance of the stimuli (22.03 cd/m^2).

The test stimulus was presented in a 5 cm diameter circular aperture, which at a viewing distance of 57 cm subtended 5° of visual angle. The FO stimuli (see Fig. 2) were a horizontally oriented sinusoidal luminance grating or a plaid pattern composed of two sinusoidal luminance gratings of the same spatial frequency, oriented $\pm 30^\circ$ from

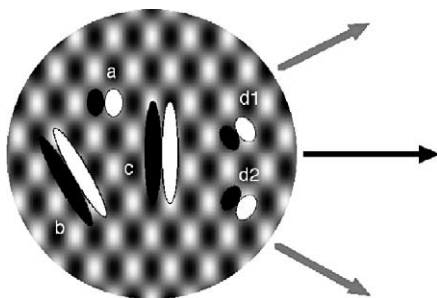


Fig. 1. Double ellipses schematically represent V1 receptive fields. Black ellipses are inhibitory regions of the receptive field whilst white ellipses are excitatory regions. The single black arrow shows the direction of pattern motion whilst the two grey arrows show the directions of the component gratings. A neuron with a broadly tuned receptive field like **a** would respond to the motion of the plaid blobs. A neuron with a narrowly tuned receptive field like **b** would respond to the motion of the component grating oriented at 120° . Neuron **c** demonstrates that a narrowly tuned neuron would not respond to the pattern direction (as the mean luminance is the same in each region). Broadly tuned neurons would also respond to the components (demonstrated by **d1** and **d2**).

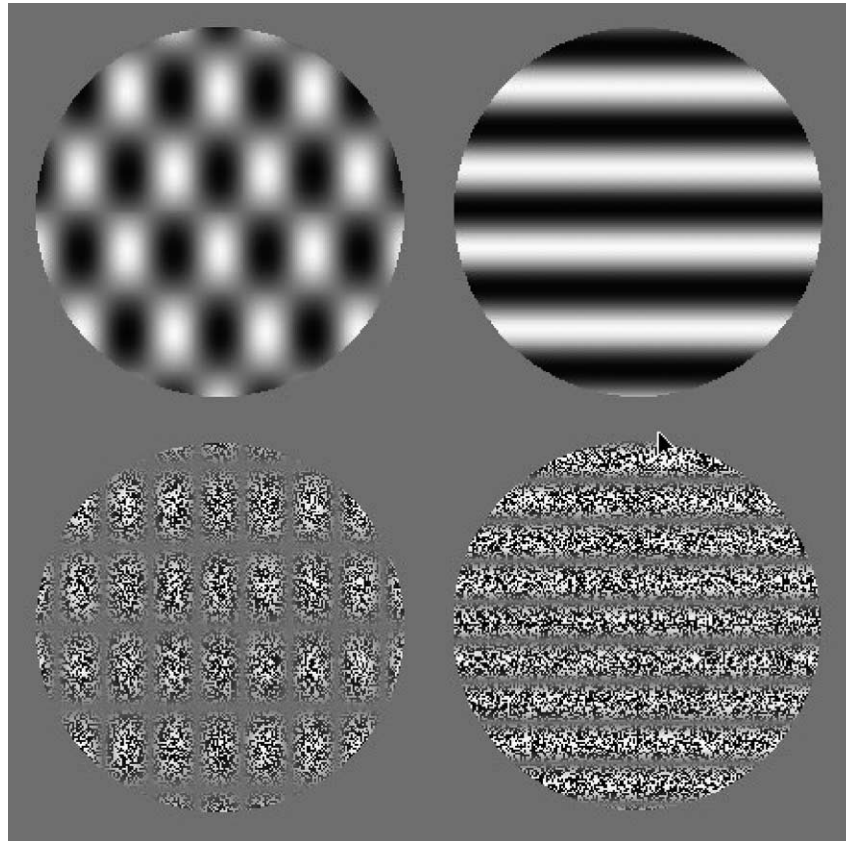


Fig. 2. Stimuli used in the study. The top row shows the first-order (luminance-defined) stimuli and the bottom row shows the second-order (contrast-defined) stimuli. Plaids are on the left and gratings on the right. As can be seen from the figure, the SO plaids contained the same 2D SO structure as the FO plaids, but without luminance features that might be detected by 'blob' detectors.

vertical. The SO stimuli were a field of static random noise whose contrast was sinusoidally modulated by a horizontally oriented grating or by a plaid composed of two gratings of the same spatial frequency, oriented $\pm 30^\circ$ from vertical. This produced a pattern with the same vertical and horizontal contrast-modulations as the FO plaid but without the luminance features. The stimuli can be compared in Fig. 2. The contrast of the FO stimuli was 0.2, which is above saturation for both gratings and plaids (Wright & Gurney, 1992). The contrast of the noise pixels in the SO stimuli was 0.2 and the modulation depth of the envelope was 100%. The grating moved upwards or downwards and the components of the plaid moved at the same speed in directions separated by 120° around vertical, causing the plaid to move vertically upwards or downwards.

2.2. Procedure

Observations were carried out in a dimly lit room over several sessions, which typically lasted between 1 and 2 h each. Observers used a chinrest to ensure correct viewing distance (57 cm).

Within a block the stimulus could be a grating or a plaid and the TF of the stimulus was varied logarithmically from 0.0125 to 0.4 Hz in order to derive a complete psychometric function, except at the two highest SF values when they

were increased to 0.025–0.8 Hz to cover the increasing thresholds. There were equal numbers of data points collected for each condition and these were established in a pilot study.

The type of stimulus could be either FO (luminance-defined) or SO (contrast-defined) and this was varied between blocks. The spatial frequency of the stimulus was also varied between blocks. Spatial frequency varied between 0.25 and 6 c/deg for FO stimuli and between 0.25 and 2 c/deg for SO stimuli. Beyond a SF of 2 c/deg, the motion in the SO stimuli became incoherent, in line with previous research (Smith, Hess, & Baker, 1994). Duration of the stimulus was either 400 or 1000 ms. Fifteen observations were collected per point. The order of presentation within a block, the direction of stimulus motion (upward or downward), and the starting phase of the stimuli were randomised.

A trial would begin with a fixation cross in the centre of the screen, for a period of 1 s. This would be followed by the presentation of the test stimulus in the centre of the screen for a duration of either 400 or 1000 ms. Immediately after disappearance of the test stimulus, the fixation cross reappeared. The observer was required to answer with a keypress whether they perceived the grating or plaid to be moving upwards or downwards. Responding initiated a waiting period of 1 s followed by the next trial. The

observer could take a break at any point by not responding.

3. Results

The direction (up or down) of the test stimulus did not appear to influence motion detection, so the data were collapsed over direction and analysed only in terms of which type of stimulus (grating or plaid, FO or SO) was presented. This doubled the number of observations per point to 30.

Weibull psychometric functions were fitted to the psychophysical data using the `psignifit` toolbox version 2.5.41 for Matlab (see <http://bootstrap-software.org/psignifit/>). These toolbox functions implement the maximum-likelihood method described by Wichmann and Hill (2001a). Seventy-five percent correct thresholds were extracted from the fitted functions.

Error bars on the psychophysical summary charts show the standard deviation, which was determined by the BCa bootstrap method implemented by `psignifit`, based on 1999 simulations (Wichmann & Hill, 2001b).

Fig. 3 shows the motion-detection thresholds plotted by temporal frequency (Hz) as a function of SF. Data for short duration stimuli are presented in the left-hand column and data for long duration stimuli plotted in the right-hand column. Unsurprisingly, thresholds for the motion of FO gratings and plaids are much lower than those for SO stimuli. This supports much research, which suggests that the visual system is far less sensitive to SO motion (e.g., Smith et al., 1994), although it should be pointed out that this decrease in sensitivity could be the result of the presence of a carrier in the SO stimuli. Of more interest is the difference in thresholds between gratings and plaids. The psychophysical functions are plotted by the SF of the grating or the SF of the *components*, in the case of plaid stimuli. This means that when thresholds for gratings and plaids are the same, as they appear to be most of the time, then a two-stage model such as the IOC is still feasible.

3.1. First-order stimuli

At short durations (Fig. 3, left column, circular symbols), plaid thresholds are lower than grating thresholds only very occasionally, and the particular SF at which this occurs varies by observer. CAS shows an effect at 0.5–1 c/deg and again at a very high SF. FM shows a plaid-advantage only at 2 c/deg and actually shows a grating-advantage at very low SF. YH shows a plaid-advantage at 1 and 4 c/deg and also shows a reversed effect at very low SF.

At long durations (Fig. 3, right column, circular symbols), the situation has become much more stable, with performance gaps eliminated except at a SF of 4 c/deg for all observers.

3.2. Second-order stimuli

At short durations (Fig. 3, left column, square symbols), SO plaids exhibit a consistent advantage over SO gratings at intermediate SFs. At long durations (Fig. 3, right column, square symbols), this gap has been eliminated except for observer CAS. Observer YH shows a pronounced reversed effect at a SF of 1 c/deg.

4. Discussion

Fig. 4 shows those data points from Fig. 3 that actually demonstrated a gap between plaids and gratings. The details of each condition are included above each column. The data shown in Fig. 4 are normalised to the threshold for the relevant grating for comparison with different models and each other. Bear in mind that this constitutes only 17 cases out of a possible 66, which suggests that this effect is not as robust as may have previously been suggested. Of the 17 cases in which a difference was found between gratings and plaids, three show a reversed effect, where plaid thresholds are *higher* than gratings. This tends to occur at low spatial frequencies. Reversals have not been noted in previous investigations of this effect.

4.1. Probability summation

Amongst the possible explanations that have been advanced to account for the gap in performance between gratings and plaids, probability summation is the most intuitive. A plaid pattern is composed of two gratings, which means that the motion-detection system will have two opportunities to detect the motion, so comparing plaid thresholds to thresholds for components in isolation is not a valid comparison. Probability summation (Ferrera & Wilson, 1987; Graham, 1989; Graham, Robson, & Nachmias, 1978; Quick, 1974) predicts that thresholds for plaids (p) would be better than thresholds for gratings (g) according to the following formula:

$$p = g/\sqrt{2}.$$

Of the 14 remaining cases where a gap *does* exist between gratings and plaids in the expected direction, in four cases the magnitude of the gap is within the range predicted by probability summation (shown as the shaded area in Fig. 4). For the remaining 10 cases, the gap is greater than that predicted by probability summation. Interestingly, all of the remaining SO gaps are beyond that predicted by probability summation, whilst the FO gaps are much more variable.

4.2. Intersection-of-constraints

A two-stage computation such as the IOC has been criticised on the basis that plaid motion is detectable at speeds

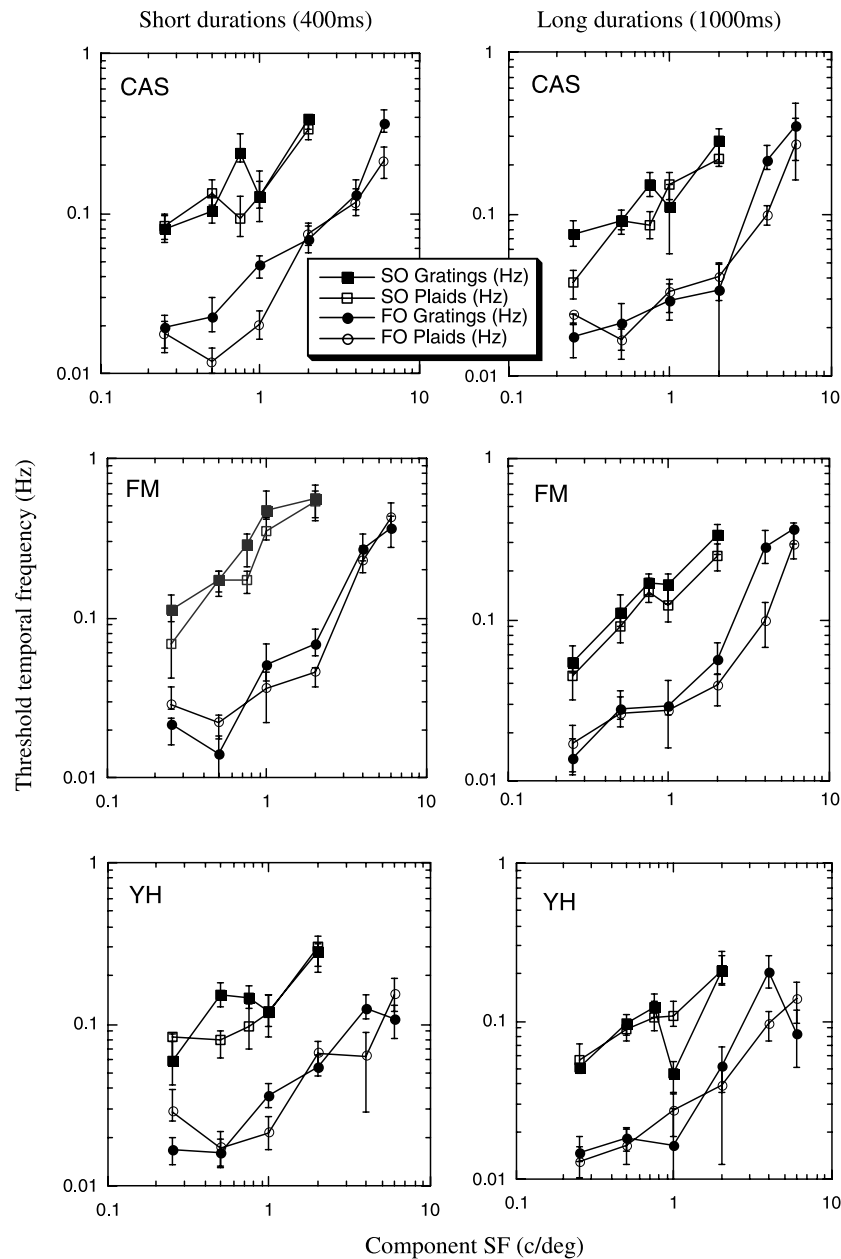


Fig. 3. Temporal frequency thresholds for grating and plaid motion detection. Data from short presentations are shown on the left and long presentations on the right. Circles represent first-order stimuli, whilst squares represent second-order stimuli. Solid symbols are grating thresholds and open symbols are plaid thresholds. Error bars represent one standard deviation. Plaid thresholds are often lower than grating thresholds, but this gap is not constant across SF.

too low to detect the motion of the components. The data presented here show that for 74% of cases, thresholds for components within a plaid are equivalent to thresholds for components in isolation, making a two-stage model entirely plausible. In a further 4.5% of cases, a reversed effect from that previously reported was found and 6% of the gaps could be explained by probability summation. This leaves only 15% in which a reliable gap was found.

Fig. 4 includes a prediction from the IOC calculation (see Appendix of Bowns (1996) or Bowns (in press) for the IOC computation) as a dotted line on the plot. Where

a reliable gap *does* exist between gratings and plaids, for both FO and SO, the magnitude of the gap is predicted with a reasonable level of accuracy by the IOC calculation. This suggests either that an IOC computation could be carried out with sub-threshold components or that the motion of some local feature in the stimulus is being detected (as the IOC and features predict the same result).

4.3. Local motion detectors

It would be more satisfying to postulate local motion detectors (LMDs) than a sub-optimal calculation of the

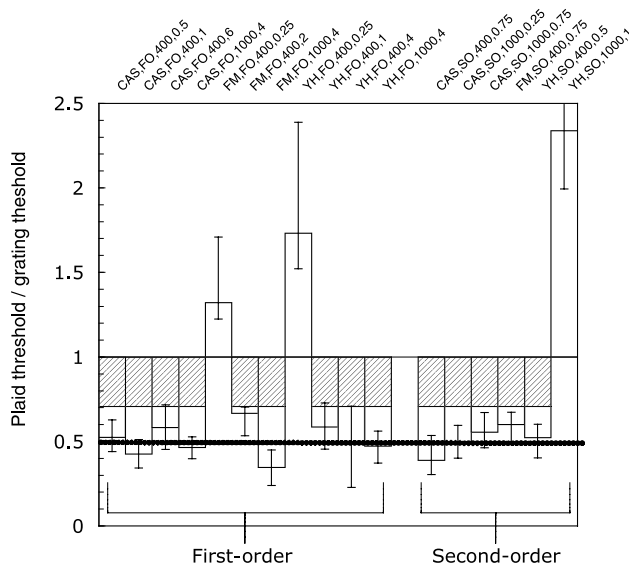


Fig. 4. Direction-discrimination thresholds for conditions in which a gap was found. The thresholds for plaid detection are plotted as a ratio of the grating thresholds. The hatched area of the plot shows the prediction from probability summation. The dotted line shows the prediction from the speed of the blobs/SO features. The details of each condition are included above each column (subject, stimulus type, duration, and SF). Error bars represent one standard deviation.

IOC, but which features could be detected, and by what sort of mechanism? The results of this experiment have shown that the presence of a gap between FO gratings and FO plaids in direction-discrimination thresholds varies inconsistently with SF and that, in half of those cases in which a gap is found, the difference can be explained by probability summation. This is interesting as it means that the performance gap between plaids and gratings reported by Derrington and Badcock (1992) and Wright and Gurney (1992) may not be as reliable as has been previously suggested.

4.4. Second-order stimuli

In SO plaids the effect is much more consistent, being found at intermediate SFs and of a magnitude beyond that predicted by probability summation. It is interesting that the gap can still be found with plaids in which luminance blobs have been removed, as recent work (Tinsley et al., 2003) has explained the effect purely in terms of FO blob detectors. Perhaps SO mechanisms, which detect the SO contrast modulations present in luminance plaids, are responsible for the advantage when detecting plaid stimuli, but interference from FO blob detecting mechanisms disrupts this effect, leading to the inconsistencies for FO stimuli remarked upon here.

5. Conclusions

It has been found that the gap in performance between plaids over gratings is very unreliable, occurring

very rarely and varying with the SF of the stimulus, presentation duration and observer. Most (80%) of the data collected here is consistent with a two-stage model of plaid perception, with the addition of probability summation. A relatively consistent gap, greater than that predicted by probability summation, was found between SO gratings and SO plaids at intermediate SFs, an important finding that suggests that SO mechanisms rather than luminance blob detectors are causing reported differences between plaid and grating thresholds and FO information may, in fact, disguise this effect in luminance plaids.

References

- Adelson, E. H., & Movshon, J. A. (1982). Phenomenal coherence of moving visual patterns. *Nature*, 300(5892), 523–525.
- Alais, D., Burke, D., & Wenderoth, P. (1996). Further evidence for monocular determinants of perceived plaid direction. *Vision Research*, 36(9), 1247–1253.
- Alais, D., Wenderoth, P., & Burke, D. (1994). The contribution of one-dimensional motion mechanisms to the perceived direction of drifting plaids and their after effects. *Vision Research*, 34(14), 1823–1834.
- Alais, D., Wenderoth, P., & Burke, D. (1997). The size and number of plaid blobs mediate the misperception of type-II plaid direction. *Vision Research*, 37(1), 143–150.
- Anderson, S. J., & Burr, D. C. (1991). Spatial summation properties of directionally selective mechanisms in human vision. *Journal of the Optical Society of America A*, 8(8), 1330–1339.
- Anderson, S. J., Burr, D. C., & Morrone, M. C. (1991). Two-dimensional spatial and spatial-frequency selectivity of motion-sensitive mechanisms in human vision. *Journal of the Optical Society of America A*, 8(8), 1340–1351.
- Bowns, L. (1996). Evidence for a feature tracking explanation of why type II plaids move in the vector sum direction at short durations. *Vision Research*, 36(22), 3685–3694.
- Bowns, L. (2002). Can spatio-temporal energy models of motion predict feature motion? *Vision Research*, 42(13), 1671–1681.
- Bowns, L. (in press). “Squaring” is better at predicting plaid motion than vector-averaging or IOC. *Perception*.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10(4), 433–436.
- Cox, M. J., & Derrington, A. M. (1994). The analysis of motion of two-dimensional patterns: Do Fourier components provide the first stage? *Vision Research*, 34(1), 59–72.
- Derrington, A. M., & Badcock, D. R. (1992). Two-stage analysis of the motion of 2-dimensional patterns, what is the first stage? *Vision Research*, 32(4), 691–698.
- Ferrera, V. P., & Wilson, H. R. (1987). Direction specific masking and the analysis of motion in two dimensions. *Vision Research*, 27(10), 1783–1796.
- Ferrera, V. P., & Wilson, H. R. (1990). Perceived direction of moving two-dimensional patterns. *Vision Research*, 30(2), 273–287.
- Georgeson, M. A., & Scott-Samuel, N. E. (2000). Spatial resolution and receptive field height of motion sensors in human vision. *Vision Research*, 40(7), 745–758.
- Graham, N. (1989). *Visual pattern analyzers*. Oxford: Oxford University Press.
- Graham, N., Robson, J. G., & Nachmias, J. (1978). Grating summation in fovea and periphery. *Vision Research*, 18(7), 815–825.
- Movshon, J. A., Adelson, E. H., Gizzi, M. S., & Newsome, W. T. (1985). The analysis of moving visual patterns. In C. Chagass, R. Gattass, & C. Gross (Eds.), *Pattern recognition mechanisms* (pp. 117–151). Rome: Vatican Press.

- Pack, C. C., Livingstone, M. S., Duffy, K. R., & Born, R. T. (2003). End-stopping and the aperture problem: Two-dimensional motion signals in macaque V1. *Neuron*, 39(4), 671–680.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10(4), 437–442.
- Quick, R. F. Jr., (1974). A vector-magnitude model of contrast detection. *Kybernetik*, 16(2), 65–67.
- Simoncelli, E. P., & Heeger, D. J. (1998). A model of neuronal responses in visual area MT. *Vision Research*, 38(5), 743–761.
- Smith, A. T., Hess, R. F., & Baker, C. L. Jr., (1994). Direction identification thresholds for second-order motion in central and peripheral vision. *Journal of the Optical Society of America. A, Optics, image science, and vision*, 11(2), 506–514.
- Snowden, R. J. (1992). Orientation bandwidth: The effect of spatial and temporal frequency. *Vision Research*, 32(10), 1965–1974.
- Tinsley, C. J., Webb, B. S., Barraclough, N. E., Vincent, C. J., Parker, A., & Derrington, A. M. (2003). The nature of V1 neural responses to 2D moving patterns depends on receptive-field structure in the marmoset monkey. *Journal of Neurophysiology*, 90(2), 930–937.
- van den Berg, A. V., van de Grind, W. A., & van Doorn, A. J. (1990). Motion detection in the presence of local orientation changes. *Journal of the Optical Society of America A*, 7(5), 933–939.
- Wichmann, F. A., & Hill, N. J. (2001a). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics*, 63(8), 1293–1313.
- Wichmann, F. A., & Hill, N. J. (2001b). The psychometric function: II. Bootstrap-based confidence intervals and sampling. *Perception & Psychophysics*, 63(8), 1314–1329.
- Wilson, H. R., Ferrera, V. P., & Yo, C. (1992). A psychophysically motivated model for two-dimensional motion perception. *Visual Neuroscience*, 9(1), 79–97.
- Wright, M. J., & Gurney, K. N. (1992). Lower threshold of motion for one and two dimensional patterns in central and peripheral vision. *Vision Research*, 32(1), 121–134.