Stereoscopic and contrast-defined motion in human vision

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There is considerable evidence for the existence of a specialized mechanism in human vision for detecting moving contrast modulations and some evidence for a mechanism for detecting moving stereoscopic depth modulations. It is unclear whether a single second-order motion mechanism detects both types of stimulus or whether they are detected separately. We show that sensitivity to stereo-defined motion resembles that to contrast-defined motion in two important ways. First, when a missing-fundamental disparity waveform is moved in steps of 0.25 cycles, its perceived direction tends to reverse. This is a property of both luminance-defined and contrast-defined motion and is consistent with independent detection of motion at different spatial scales. Second, thresholds for detecting the direction of a smoothly drifting sinusoidal disparity modulation are much higher than those for detecting its orientation. This is a property of contrast-modulated gratings but not luminance-modulated gratings, for which the two thresholds are normally identical. The results suggest that stereo-defined and contrast-defined motion stimuli are detected either by a common mechanism or by separate mechanisms sharing a common principle of operation.

Keywords: vision; motion perception; stereoscopic depth; missing fundamental

1. INTRODUCTION

Movement within a visual image may be defined in any of several ways. Normally it takes the form of a moving luminance modulation, but it can also take the form of a moving colour modulation, contrast modulation, flicker frequency modulation or disparity modulation. Considerable debate has taken place concerning (i) whether these various types of motion are detected by separate mechanisms, and (ii) if so, which types are detected by special-purpose low-level mechanisms and which can be detected only by tracking the positions of spatial features (e.g. Anstis 1980; Braddick 1980; Cavanagh 1991).

In the case of stereoscopic motion (motion defined purely by spatiotemporal modulations of the local horizontal disparity between the images of the two eyes), both questions remain controversial. Some studies suggest that stereo-defined motion is weak (Chang 1990) and does not give rise to adaptation (e.g. Anstis 1980), leading some to the view that there is no specialized stereoscopic motion mechanism. However, several recent studies suggest that stereoscopic motion is detected by a specialpurpose motion-sensitive mechanism. For example Patterson et al. (1997) found that speed discrimination of stereoscopic motion stimuli is possible under conditions (dense dot patterns) where displacement discrimination is not, suggesting that motion perception does not rely on tracking features. Moreover, speed discrimination performance is, at least in some circumstances, as good for stereoscopic as for luminance-defined motion (Portfors & Regan 1997). These studies suggest that a mechanism

exists for encoding not only the direction, but also the speed, of stereoscopic motion. But the evidence is indirect, controversial (Harris & Watamaniuk 1996) and open to other interpretations.

If we accept the existence of a special-purpose stereoscopic motion mechanism, the second question arises: whether that mechanism is the same as that which detects luminance-defined motion. Patterson and colleagues (Patterson et al. 1994, 1996; Bowd et al. 1996) showed that, contrary to earlier studies, motion adaptation can result from prolonged viewing of stereoscopic motion. Moreover, they found that adaptation transfers between the luminance- and stereo-defined motion domains, suggesting that the two types of motion are detected by a common neural substrate. However, although such transfer indicates a common substrate at some level, it does not necessarily imply a common detection stage. In addition, there are various important differences between the sensitivity to stereoscopic motion and that to luminance motion. The most striking, perhaps, is that sensitivity to stereoscopic motion is limited to much lower temporal frequencies than luminance motion (Patterson et al. 1992; Lankheet & Lennie 1996), frequencies above about 8 Hz being undetectable. Spatial frequency resolution is also poor, the maximum resolvable frequency being around $5 \text{ cycles deg}^{-1}$ (Lankheet & Lennie 1996). These differences leave the notion of common detection far from certain. In addition, the prevailing computational models of luminance motion (e.g. Adelson & Bergen 1985) are blind to stereoscopic motion. If stereoscopic and luminance-defined motion are detected by a common mechanism then these models, for which there is much empirical evidence, are rendered inadequate.

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In the case of the detection of moving contrast modulations, the literature is larger and the answers are clearer, although not uncontroversial. That moving contrast modulations are normally detected by a motion mechanism that does not rely on feature matching is suggested by the experiments of Smith (1994). He showed that when a contrast modulation with a missingfundamental waveform is moved in steps of 0.25 cycles, the direction perceived is that of the (aliased) third harmonic of the contrast envelope, not the true motion direction of the waveform. This also occurs for luminance-defined stimuli (Adelson 1982; Georgeson & Shackleton 1989). It is consistent with the notion that contrast modulations are passed through multiple, local spatial filters prior to motion analysis. More specifically, it is consistent with models in which standard motion energy detection is preceded by a nonlinear luminance transformation such as rectification (Chubb & Sperling 1988). It is not consistent with tracking the positions of the spatial features of the image. A similar conclusion was reached in Smith's (1994) second experiment, in which the spatial features of a drifting sinusoidal contrast modulation were masked with little resultant change in the detectability of the direction of motion. Other studies have also produced results that are consistent with this interpretation (e.g. Nishida 1993; Werkhoven et al. 1993; Lu & Sperling 1995).

As in the case of stereoscopic motion, if the detection of moving contrast modulations is performed by a lowlevel mechanism then it is necessary to ask whether that mechanism is the same as the one that detects luminance-defined motion. Again, several important differences between the two image types suggest not. First, temporal resolution is much lower for contrastdefined than luminance-defined motion (Derrington & Badcock 1985; Smith & Ledgeway 1998). Second, the threshold for detecting the direction of motion of a sinusoidal contrast modulation is much higher than that for detecting its orientation (Smith & Ledgeway 1997). This is not the case for luminance-defined motion, in which direction identification thresholds are identical to absolute detection thresholds for most spatial and temporal frequencies (Watson et al. 1980; Green 1983). Third, the two types of stimulus cause independent threshold elevation (Nishida et al. 1997). Direct evidence for separate detection of contrast-defined and luminancedefined motion comes from the fact that alternate frames of the two types cannot be combined to produce a motion percept (Mather & West 1993; Ledgeway & Smith 1994).

Thus, a clear picture is emerging in the case of moving contrast modulations, but important uncertainties remain concerning the mechanisms of detection of stereoscopic motion. We have sought to resolve these uncertainties, using similar methods to those we have used for contrastdefined motion (Smith 1994; Smith & Ledgeway 1997). In experiment 1, we use the missing-fundamental paradigm to seek direct evidence that stereoscopic motion is encoded by a mechanism which analyses components at different spatial scales. In experiment 2, we examine whether direction thresholds for stereoscopic motion exceed those for orientation, as they do for contrast modulations but not luminance modulations.



Figure 1. A stereo-pair (top) typical of those used in experiment 1. When fused, the images give rise to a depth modulation with a form similar to that shown diagrammatically beneath. The modulation moved upwards or downwards as indicated by the arrows.

2. GENERAL METHODS

The stimuli were generated by an Apple Macintosh 7500 computer fitted with two identical video cards. These were used to drive two identical monochrome monitors. Mirrors were used to present one image to each eye. The video cards were modified so that the on-board crystal in one provided line/frame timing for both, so that video timing was synchronized in the two monitors. This made it possible to update the images on every frame without losing correspondence between the eyes.

All images consisted of a circular patch of high-contrast, dynamic, two-dimensional binary noise. The diameter of the patch was 3.7° at the viewing distance of 2.5 m and the noise element size was 0.45 min arc. The noise patch was surrounded by a dark ring whose purpose was to assist fusion of the two images. The ring had gaps designed to aid cyclotorsional fusion. Figure 1 illustrates the images used. The images presented to the two eyes were identical except for a horizontal displacement of the noise. The magnitude of the displacement varied with position to provide spatial variation in stereoscopic depth. Disparity varied periodically, in one dimension only, with either a missing-fundamental (experiment 1) or a squarewave (experiment 2) profile. This produced a cyclopean grating pattern. The phase of the disparity waveform was incremented over time to produce motion (frontoparallel translation). To eliminate monocular motion cues, the noise sample was replaced every time the phase was updated, so that each monocular image consisted only of dynamic noise with no spatial structure and no consistent motion. A central fixation spot was provided in the same depth plane as the dark ring. The mean disparity of the cyclopean grating was zero (i.e. it extended both in front of and behind the fixation plane) and the disparity amplitude of the waveform could be varied symmetrically about zero.

3. EXPERIMENT 1: MISSING FUNDAMENTAL

A missing-fundamental waveform is a squarewave from which the fundamental component has been removed (see figure 1). When a missing-fundamental luminance grating drifts smoothly, it is seen veridically. But Georgeson & Shackleton (1989) showed that if, instead of updating its spatial phase frequently in small steps, its phase is updated in 90° steps (0.25 spatial cycles) with a correspondingly lower frequency (to give the same drift speed), it appears to move in the opposite direction. They interpreted this as evidence for a motion-sensing mechanism based on temporal changes in spatially filtered representations of the image. A missingfundamental grating has, by definition, no energy at the fundamental frequency (f). The lowest and most visible component is at three times that frequency (3f). When the waveform is moved 0.25 cycles of f(0.75 cycles of 3f), the 3f component will alias, i.e. it will appear to move 0.25 cycles backwards rather than 0.75 cycles forward. If reversed motion is perceived, it suggests that motion detection is based on spatial frequency components. If perception is based on tracking the spatial features, which repeat with a period of f, then aliasing will not occur and veridical motion perception is expected. The perception of reversed motion is therefore a signature of motion energy (or other spatial-scale-specific) mechanisms.

The same logic holds in any domain. As already stated, the same result is obtained if the waveform is a contrast modulation instead of a luminance modulation (Smith 1994), suggesting that contrast modulations are also detected within spatial frequency channels by a process akin to detection of motion energy, this time in the contrast domain. In experiment 1, we sought to establish whether the same result obtains for a stereoscopically defined missing-fundamental grating. There is some evidence for multiple spatial frequency channels in stereoscopic vision (Glennerster & Parker 1997). If these exist, they might in principle be used to generate stereoscopic motion energy signals, in which case perceived direction reversal of a stereoscopic missing-fundamental grating of the type described is expected.

(a) Methods

The stimulus was a horizontally oriented missingfundamental grating defined only by binocular disparity modulation of dynamic noise (see figure 1). The spatial frequency was 0.25 cycles deg⁻¹. Thus the frequency of the 3f component was 0.75 cycles deg⁻¹. The low spatial frequency was chosen to ensure that several spatial harmonics were visible despite the limited spatial resolution of the human stereoscopic depth system. An explicit test of their visibility was also conducted (see § 3b). The disparity amplitude of the missing-fundamental waveform varied from trial to trial in the range 3.5-21.4 min arc (peak-to-peak). The spatial phase was updated in 90° steps at a frequency of 16.7 Hz, to give a drift speed of 16.7 deg s⁻¹ (4.17 Hz). The direction of motion could be either upward or downward.

Initially the screen was blank except for the fixation spot and the surrounding ring. The luminance of the blank field was the same as the mean luminance of the binary noise (38 cd m^{-2}) . On each trial, the subject was presented with an animation sequence lasting for 0.5 s, the direction of motion being chosen at random. The subject reported, by pressing one of two buttons, the perceived direction of motion. Each subject conducted two runs of 120 trials. One run comprised 20 presentations of each of six disparity amplitudes. Trials were separated by 1s during which time the screen was blank apart from the fixation spot and ring. Four subjects were used. All had normal or corrected acuity and normal stereoacuity. All but one (A.S.) were unaware of the purpose of the experiment. All subjects found the task difficult. Several other subjects were tested who, despite good stereoacuity for stationary images, were unable to do the task.

(b) *Results*

For each subject, the percentage of 'correct' responses (i.e. motion perceived in the direction of the displacement) was calculated for each disparity value. The results are shown in figure 2. Performance tended to be below 50%, i.e. motion tended to be perceived in the direction opposite the drift direction. But it varied considerably among the subjects. One subject (A.S.) consistently reported motion in the 'reverse' direction for all disparity values. The other three all tended to see reversed motion, but less consistently than A.S. The mean performance level, averaged across all disparities used, was 4.4% for A.S., 27.5% for S.A., 35.8% for K.S. and 26.9% for S.D.

In an additional (control) experiment, the 3f and 5f components of the missing-fundamental waveform used in the main experiment were presented separately, again drifting at 16.7 deg s⁻¹. This was to control for the possibility that detection of motion of the missing fundamental was based on feature tracking, but that reversed motion was nonetheless seen because motion led to the cyclopean image being blurred to leave something resembling a 3fmodulation (whose features repeat at 3f) when in motion. The two components were found to be about equally visible, indicating that low-pass filtering (blurring) was not responsible for the reversed motion observed in the main experiment.

Subjects K.S. and S.A. both spontaneously commented that they frequently saw both directions simultaneously, in which case they reported the stronger percept. Although this does not normally happen with luminance-defined missing fundamentals, Hammett et al. (1993) reported that it invariably happens when the missing fundamental is replaced by the sum of two sine components with frequencies in the ratio 3:4 (termed a 3f+4f grating), which is updated in steps of 0.25 cycles of the fundamental. This stimulus is related to the missing fundamental in that the 4f component is stationary when sampled at this frequency, whereas the 3f component aliases in the same way as in the missing-fundamental case, so reversed motion is expected if detection is based on motion energy. The observed transparent motion was interpreted by Hammett et al. (1993) as reflecting simultaneous perception of motion energy in the reverse direction and displacement of spatial features in the forward direction. In view of the comments of subjects K.S. and S.A., it seems likely that the same phenomenon occurred here in the stereoscopic motion domain and that the explanation is the same, although in the missing-fundamental case it is conceivable that



forward motion reflects independent detection of the 5f component.

(c) Discussion

The results of experiment l suggest that there is indeed a special-purpose motion-detection mechanism for stereoscopic motion. Moreover, that mechanism appears to decompose disparity modulations into components at different spatial scales and then detects motion within each of these restricted scales (spatial frequencies). The subjective reports of the observers suggest that feature tracking may also sometimes be used, leading to transparent motion percepts if the two cues give conflicting information. Thus, the pattern of results and conclusions for stereoscopic motion are similar to those previously obtained for luminance-defined (Georgeson & Shackleton 1989; Hammett *et al.* 1993) and contrast-defined (Smith 1994) motion.

4. EXPERIMENT 2: THRESHOLDS FOR ORIENTATION AND DIRECTION

The results of experiment 1 lead us to concur with Patterson *et al.* (1997) and Portfors & Regan (1997) in their view that a special-purpose mechanism exists for the detection of stereoscopic motion. This being so, we now wish to ask whether or not that mechanism is the same as the standard motion-detection mechanism used for luminance-based motion. One criterion that we have used previously in the case of contrast-defined motion is the similarity or otherwise of the thresholds (in terms of contrast modulation depth) for detecting the orientation and direction of motion of a drifting one-dimensional contrast modulation. The threshold for detecting direction of contrast-defined motion is much higher than that for detecting orientation (Smith & Ledgeway 1997), whereas for luminance-defined motion, direction can be seen at the absolute detection threshold, except for very low drift speeds (Watson *et al.* 1980; Green 1983). The purpose of experiment 2 is to make the same comparison of thresholds in the case of a drifting one-dimensional disparity modulation.

(a) Methods

The stimuli and methods were similar to those used in experiment 1. This time the stimulus was a squarewave grating, but it was again defined by spatial modulation of binocular disparity. The carrier was again dynamic noise and the stimuli contained no monocular cues to the spatial or temporal structure of the grating. The spatial frequency of the grating was fixed at $0.5 \text{ cycles } \text{deg}^{-1}$. The gratings were obliquely oriented and had one of two orthogonal orientations: $+45^{\circ}$ and -45° from horizontal. The reason for this choice is as follows. In any stereopair, some of the noise pixels in one image do not have corresponding points in the other image. In the case of gratings, the effect that this has on visibility varies with orientation, being least for horizontal and greatest for vertical gratings. The use of two orientations that are symmetrical about either the horizontal or vertical ensures that neither grating is more visible than the other. The grating phase and the noise sample were both





(c) $8.3 \deg s^{-1}$; (d) $11.7 \deg s^{-1}$;

(e) 16.7 deg s⁻¹.

updated at a rate of 33 Hz and the grating drifted smoothly at one of several drift speeds ranging from 4.2–16.7 deg s⁻¹. Higher speeds were not tested as it is known that stereoscopic motion is not detectable above about 8 Hz (16 deg s^{-1} at 0.5 cycles deg⁻¹) (Lankheet & Lennie 1996). The grating could drift in either of the directions orthogonal to its orientation.

Sensitivity to the orientation and the direction of motion of a drifting grating was estimated using the method of constant stimuli. Sensitivity was measured in terms of the disparity modulation amplitude required for correct identification of orientation or direction. This approach was used (in preference to adding disparity noise to a fixed signal disparity) because it is analogous to varying contrast modulation depth in the contrast-defined motion case (Smith & Ledgeway 1997). Three subjects were used. All had normal or corrected acuity and normal stereoacuity. One (A.S.) was aware of the purpose of the experiment; the other two (S.D. and R.W.) were not. A.S. and S.D. also participated in experiment 1.

Initially the screen was blank except for the fixation spot and the ring surrounding the stimulus. On each trial, the subject was presented with an animation sequence lasting for 0.5 s. The orientation and direction of motion were chosen independently and at random. The subject made two responses to each trial: (i) orientation (tilted clockwise or counter-clockwise from vertical); and (ii) direction of motion (vertical component of motion upward or downward). The different drift speeds were tested in separate runs. Each run contained 100 trials,



separated by 1 s during which time the screen was blank apart from the fixation spot and ring. The disparity of the grating varied from trial to trial, in the range 0.9– 14.6 min arc peak-to-trough, centred on zero disparity (i.e. symmetrical in depth about the fixation plane). For each drift speed, each subject conducted three runs of trials to give a total of 300 trials (60 per disparity value). Performance levels for orientation and direction were established separately by fitting a sigmoid curve to the psychometric function relating performance (per cent correct) to disparity amplitude in each case.

(b) *Results*

Psychometric functions for the three subjects are shown in figures 3–5. In the case of subject A.S., orientation could be detected perfectly for all drift speeds, provided the disparity was above about 5 min arc. Drift speed had little effect on sensitivity in the range investigated. Performance on the direction task was substantially worse than for orientation. At all speeds, a greater disparity was needed to identify direction, and at the highest speed (16.7 deg s⁻¹) direction performance was at chance levels for all disparities. The results for S.D. are similar, except that she was unable to see even orientation reliably at the highest speed. At all other drift speeds, there is a clear difference between orientation and direction thresholds. For subject R.W., performance on the orientation task was near-perfect for all disparities, at all but the highest speed. At the highest speed, it was near-perfect at medium disparities only. In the case of direction of



motion, performance was also near-perfect at all disparities for the two slowest speeds. In these cases, to establish whether thresholds for direction are higher than those for orientation would require the use of smaller disparities than was possible under our viewing conditions. However, the next two speeds (8.3 and 11.8 deg s⁻¹) show clearly that direction-identification performance was inferior to orientation-identification performance. At the highest speed, performance on the direction task was at chance levels, as for the other two subjects.

(c) **Discussion**

The results of experiment 2 show that thresholds, in terms of disparity magnitude, for identifying the direction

of motion of a smoothly drifting, periodic, stereoscopically defined pattern are substantially higher than those for identifying the orientation of the same pattern.

5. GENERAL DISCUSSION

The results presented here suggest that stereoscopic motion is detected by a low-level motion-detection mechanism (as opposed to relying on high-level tracking of spatial features). Orientation and direction of motion appear to be detected either by different mechanisms or by a single mechanism that requires a greater disparity amplitude for detecting direction than it does for orientation. In this respect, stereoscopic motion differs from standard, luminance-defined motion. These conclusions are identical to those reached in the case of motion of contrast modulations in the absence of luminance cues (Smith 1994; Smith & Ledgeway 1997).

(a) A single non-luminance motion system?

Superficially, we are threatened with an alarming proliferation of motion-detection mechanisms. However, several of the features that distinguish luminance-defined motion from stereoscopic motion are the same as those that distinguish it from contrast-defined motion. One is the difference between orientation and direction thresholds demonstrated here. Another is that the temporal contrast sensitivity function is low-pass and limited to 8-10 Hz in both cases, whereas for luminance motion it is band-pass and extends to about 50 Hz (e.g. Kelly 1979). A third class of motion stimulus, colour-defined motion, shows similar temporal tuning (Derrington & Henning 1993) to contrast-defined and stereoscopic motion and also shows differences between the thresholds for orientation and direction (Lindsey & Teller 1990). In the past, chromatic and contrast-defined motion have tended to be given separate treatments. But similarities have already been noted (e.g. Cropper & Derrington 1994). The apparent 'jerkiness' of the motion percept in the case of stereoscopic motion (Chang 1990) and chromatic motion (Mullen & Boulton 1992), but not luminance-defined motion, provides another parallel between these two nonluminance motion types.

These similarities in motion sensitivity among stereoscopic, chromatic and contrast-defined motion raise the possibility that a single mechanism exists which detects all three types of motion. An alternative interpretation is that they are detected by separate mechanisms that are very similar apart from having quite different front-end filters. Various phenomena suggest that each of these motion types is detected by multiple mechanisms operating at different spatial scales. Experiment 1 demonstrates that a missing-fundamental grating defined stereoscopically and moved in steps of 0.25 cycles appears to move in the opposite of its true direction, suggesting that motion analysis is based on analysis at restricted spatial scales. The same is true for contrast-defined (Smith 1994) as well as luminance-defined (Georgeson & Shackleton 1989) motion. Another similarity is that reversed-phi motion occurs with contrast-defined, as well as luminance-defined, motion (Nishida 1993), consistent with the use of a process akin to motion energy detection. The same is true of chromatic motion, although only in certain circumstances (Dobkins & Albright 1993).

In the case of contrast modulations, it has been suggested that a simple transformation renders secondorder motion visible to a system that operates in the same way as the first-order motion system (Chubb & Sperling 1988). This would explain many of the similarities with luminance-based motion. Likewise, it is theoretically straightforward and plausible to construct motion energy detectors whose inputs are chrominance, rather than luminance, modulations. In the case of motion of disparity modulations, however, there is no simple transformation that will render the motion amenable to standard motion analysis. Presumably, local retinal disparities must be detected at a fine spatial scale and then spatial disparity modulations detected at a coarser scale by a subsequent process involving integration over space. This requires two processing stages, both at a binocular level. Only then would a disparity-modulation signal exist that could be fed into a motion energy detection system. Whether this is indeed the mechanism used, and if so whether disparity modulation signals feed into the same motion energy mechanism as that used for contrast modulations and colour modulations, remains speculative.

Perhaps, then, it may be appropriate to revise our current model of second-order motion detection to accommodate (i) motion defined by other second-order characteristics, including retinal disparity, and (ii) motion defined by colour. It is possible that we possess two low-level motion-detection systems (in addition to a capacity to track features, however defined, at a high level). The first (for convenience, the first-order motion system) detects luminance-defined motion. It has good temporal acuity and motion is encoded on the basis of the same low-level information that is used separately to determine spatial structure, and so orientation and direction thresholds are similar. The second mechanism (for convenience, the second-order system, even though strictly speaking colour is a first-order image characteristic) detects motion defined by colour, contrast and disparity. It has inferior temporal resolution and its sensitivity is less than that of the mechanism that detects spatial structure defined by these characteristics. Hence, the direction of motion of such stimuli is not detectable at the threshold for detecting spatial orientation.

The alternative is to invoke one mechanism for each motion type. This option seems inefficient. It is often dismissed as unparsimonious, although this remains to be proved. For these reasons the simpler scheme proposed above seems to warrant consideration.

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REFERENCES

- Adelson, E. H. 1982 Some new motion illusions, and some old ones, analysed in terms of their Fourier components. *Invest. Ophthal. Vis. Sci. Suppl.* 34, 144.
- Adelson, E. H. & Bergen, J. R. 1985 Spatiotemporal energy models for the perception of motion. *J. Opt. Soc. Am.* A 2, 284–299.
- Anstis, S. M. 1980 The perception of apparent movement. *Phil. Trans. R. Soc. Lond.* B **290**, 153–168.
- Bowd, C., Rose, D., Phinney, R. E. & Patterson, R. 1996 Enduring stereoscopic motion aftereffects induced by prolonged adaptation. *Vision Res.* 36, 3655–3660.
- Braddick, O. J. 1980 Low-level and high-level processes in apparent motion. *Phil. Trans. R. Soc. Lond.* B 290, 137–151.
- Cavanagh, P. 1991 Short-range vs long-range motion: not a valid distinction. *Spatial Vision* 5, 303–309.
- Chang, J. J. 1990 New phenomena linking depth and luminance in stereoscopic motion. *Vision Res.* **30**, 137–147.
- Chubb, C. & Sperling, G. 1988 Drift-balanced random stimuli: a general basis for studying non-Fourier motion perception. *J. Opt. Soc. Am.* A **5**, 1986–2006.
- Cropper, S. J. & Derrington, A. M. 1994 Motion of chromatic stimuli: first-order or second-order? *Vision Res.* 34, 49–58.

- Derrington, A. M. & Badcock, D. R. 1985 Separate detectors for simple and complex patterns? Vision Res. 25, 1869–1878.
- Derrington, A. M. & Henning, G. B. 1993 Detecting and discriminating the direction of motion of luminance and colour gratings. *Vision Res.* 33, 799–812.
- Dobkins, K. R. & Albright, T. D. 1993 What happens if it changes color when it moves? Psychophysical experiments on the nature of chromatic input to motion detectors. *Vision Res.* 33, 1019–1036.
- Georgeson, M. A. & Shackleton, T. M. 1989 Monocular motion sensing, binocular motion perception. *Vision Res.* 29, 1511–1523.
- Glennerster, A. & Parker, A. J. 1997 Computing stereo channels from masking data. Vision Res. 37, 2143–2152.
- Green, M. 1983 Contrast detection and direction discrimination of drifting gratings. *Vision Res.* 23, 281–289.
- Hammett, S. T., Ledgeway, T. & Smith, A. T. 1993 Transparent motion from feature- and luminance-based processes. *Vision Res.* 33, 1119–1122.
- Harris, J. M. & Watamaniuk, S. N. J. 1996 Poor speed discrimination suggests that there is no specialized speed mechanism for cyclopean motion. *Vision Res.* 36, 2149–2157.
- Kelly, D. H. 1979 Motion and vision. II. Stabilized spatiotemporal threshold surface. *J. Opt. Soc. Am.* A 69, 1340–1349.
- Lankheet, M. J. M. & Lennie, P. 1996 Spatio-temporal requirements for binocular correlation in stereopsis. *Vision Res.* 36, 527–538.
- Ledgeway, T. & Smith, A. T. 1994 Evidence for separate motiondetecting mechanisms for first- and second-order motion in human vision. *Vision Res.* 34, 2727–2740.
- Lindsey, D. T. & Teller, D. Y. 1990 Motion at isoluminance: discrimination/detection ratios for moving isoluminant gratings. *Vision Res.* **30**, 1751–1761.
- Lu, Z.-L. & Sperling, G. 1995 The functional architecture of human visual motion perception. *Vision Res.* 35, 2697–2722.
- Mather, G. & West, S. 1993 Evidence for second-order motion detectors. *Vision Res.* 33, 1109–1112.
- Mullen, K. T. & Boulton, J. C. 1992 Absence of smooth motion perception in color vision. *Vision Res.* 32, 483–488.
- Nishida, S. 1993 Spatiotemporal properties of motion perception for random-check contrast modulations. *Vision Res.* 33, 633–646.

- Nishida, S., Ledgeway, T. & Edwards, M. 1997 Dual multiplescale processing for motion in the human visual system. *Vision Res.* 37, 2685–2698.
- Patterson, R., Ricker, C., McGary, J. & Rose, D. 1992 Properties of cyclopean motion perception. *Vision Res.* 32, 149–156.
- Patterson, R., Bowd, C., Phinney, R., Pohndorf, R., Barton-Howard, W. J. & Angilletta, M. 1994 Properties of the stereoscopic (cyclopean) motion aftereffect. *Vision Res.* 34, 1139–1147.
- Patterson, R., Bowd, C., Phinney, R., Fox, R. & Lehmkuhle, S. 1996 Disparity tuning of the stereoscopic (cyclopean) motion aftereffect. *Vision Res.* 36, 975–983.
- Patterson, R., Donnelly, M., Phinney, R. E., Nawrot, M., Whiting, A. & Eyle, T. 1997 Speed discrimination of stereoscopic (cyclopean) motion. *Vision Res.* 37, 871–878.
- Portfors, C. V. & Regan, D. 1997 Just-noticeable difference in the speed of cyclopean motion in depth and the speed of cyclopean motion within a frontoparallel plane. *J. Exp. Psychol.*, *Hum. Percept. Perform.* 23, 1074–1086.
- Scott-Samuel, N. E. & Smith, A. T. 1998 Out of our depth: cyclopean motion energy mechanisms? *Invest. Ophthal. Vis. Sci.* 39, S1081.
- Smith, A. T. 1994 Correspondence-based and energy-based detection of second-order motion in human vision. *J. Opt. Soc. Am.* A 11, 1940–1948.
- Smith, A. T. & Ledgeway, T. 1997 Separate detection of moving luminance and contrast modulations: fact or artifact? *Vision Res.* 37, 45–62.
- Smith, A. T. & Ledgeway, T. 1998 Sensitivity to second-order motion as a function of temporal frequency and eccentricity. *Vision Res.* 38, 403–410.
- Watson, A. B., Thompson, P. G., Murphy, B. J. & Nachmias, J. 1980 Summation and discrimination of gratings moving in opposite directions. *Vision Res.* 20, 341–347.
- Werkhoven, P., Sperling, G. & Chubb, C. 1993 The dimensionality of texture-defined motion: a single channel theory. *Vision Res.* 33, 463–486.

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