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Second-order processing of four-stroke apparent motion

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Abstract

In four-stroke apparent motion displays, pattern elements oscillate between two adjacent positions and synchronously reverse in contrast, but appear to move unidirectionally. For example, if rightward shifts preserve contrast but leftward shifts reverse contrast, consistent rightward motion is seen. In conventional first-order displays, elements reverse in luminance contrast (e.g. light elements become dark, and vice-versa). The resulting perception can be explained by responses in elementary motion detectors tuned to spatio–temporal orientation. Second-order motion displays contain texture-defined elements, and there is some evidence that they excite second-order motion detectors that extract spatio–temporal orientation following the application of a non-linear 'texture-grabbing' transform by the visual system. We generated a variety of second-order four-stroke displays, containing texture-contrast reversals instead of luminance contrast reversals, and used their effectiveness as a diagnostic test for the presence of various forms of non-linear transform in the second-order motion system. Displays containing only forward or only reversed phi motion sequences were also tested. Displays defined by variation in luminance, contrast, orientation, and size were effective. Displays defined by variation in motion, dynamism, and stereo were partially or wholly ineffective. Results obtained with contrast-reversing and four-stroke displays indicate that only relatively simple non-linear transforms (involving spatial filtering and rectification) are available during second-order energy-based motion analysis.

Keywords: Four-stroke apparent motion display; Phi motion sequence; Spatial filtering

1. Introduction

Reversed phi apparent motion was first reported by Anstis (1970). Anstis and Rogers (1975) described the effect as follows:

> When a black-and-white pattern was followed, via a fade or dissolve, by its own photographic negative, overlapping but slightly displaced, the perceived apparent motion was in the opposite direction to the image displacement.

Anstis and Rogers (1986) later elaborated the stimulus sequence as a repetitive 'four-stroke' cycle of oscillating forward apparent motion (i.e. no contrast reversal) and reversed apparent motion, which gave a strong illusion of unidirectional apparent motion in the forward direction. A simple example is shown in Fig. 1 (left). One dimension of space (x) is represented on the horizontal axis, and time on the vertical axis (we assume that the display is extended in the y-axis). A dark bar is present during the first time frame (1). In the second time frame (2) the bar displaces to the right. The bar shifts back to its initial position, and reverses in contrast, in the third frame (3). In the fourth frame (4) the bar again shifts to the right. The temporal cycle then repeats itself. Note that there is a quarter-cycle offset in the temporal modulations of the two bars' contrasts. Four-stroke displays are thus related to quadrature motion displays described by Carney and Shadlen (1993), in which each bar's contrast varies sinusoidally, but the modulation in one bar lags behind that in the other by a quarter-cycle (middle-left display in Fig. 1). Both of kinds of display depicted in Fig. 1 should lead to an impression of unidirectional rightward motion.

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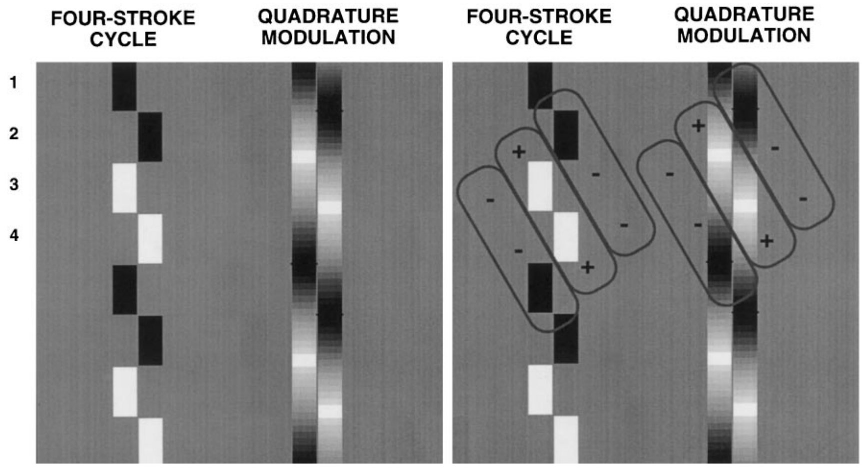

Fig. 1. Four-stroke and quadrature motion sequences. The lefthand *xt* strip in the lefthand panel shows a dark bar at time (1) that shifts rightward (2), shifts back and reverses contrast (3), shifts rightwards again (4), and then shifts back with a contrast reversal to repeat the sequence. The adjacent strip shows two abutting bars that repeatedly fade between bright and dark; the righthand bar's modulation is delayed relative to that on the left by one quarter of a temporal cycle (as in the lefthand strip). Both strips create an impression of unidirectional rightward motion. The strips in the righthand panel are identical to those in the lefthand panel, but a spatio–temporally oriented receptive field is superimposed on them to demonstrate how such a field is well matched to the pattern of spatio–temporal modulation.

Reichardt (1961) reported that the optomotor response of the beetle can be reversed by stimulus contrast reversals. Marr and Ullman (1981), Adelson and Bergen (1985), and Sato (1989) showed that models of early motion energy detection in the human visual system can successfully predict reversed phi and four-stroke apparent motion, as follows. Psychophysical and electrophysiological data indicate that motion detecting receptive fields are elongated in space–time (Burr, Ross & Morrone, 1986; Emerson, Bergen & Adelson, 1992). Each detector collects energy along a particular orientation in space–time, corresponding to a particular preferred velocity. Such detectors are often called 'motion energy' detectors, because their response depends on coherent, oriented spatio–temporal energy in the stimulus. The displays in Fig. 1 may lead to unidirectional motion perception because the pattern of coherent stimulation aligns with the spatio–temporal receptive field of rightward detectors, while providing no consistent signal for leftward detectors (righthand *xt* plots in Fig. 1).

What is the value of studying the full four-stroke cycle, rather than just forward and reversed phi transitions in isolation? It is important to consider possible contributions from a feature-based motion detection mechanism. We assume that such a mechanism would rely on tracking segmented contours, defined by the intensity edges in the four-stroke display in Fig. 1 (left). In forward transitions (e.g. frame 1 to frame 2) both energy-based and feature-based mechanisms would signal rightward motion. In reversed phi transitions (e.g. frame 2 to frame 3) the energy-based mechanism would again signal rightward motion, but the feature-based mechanism would signal leftward motion. Thus, over the full four-stroke cycle (and multiples of it), the response of the feature-based mechanism is 'drift-balanced' (no net directional signal), whereas the response of the energy-based mechanism is highly directional. The four-stroke cycle is thus a powerful method of isolating any energy-based directional signals generated by the display. Of course, we cannot assume that the forward and reversed phi transitions are equally effective in generating energy-based responses, so in the experiments below observations were made on these components separately as well as on the full four-stroke cycle.

Motion energy detectors with receptive fields such as those in Fig. 1 are now classified as first-order motion detectors, because they rely on movement of intensity defined contours (Cavanagh & Mather, 1989). Many motion displays do not contain coherent spatiotemporal energy, yet do support motion perception (e.g. moving texture boundaries). Recent research indicates that (at least some) such displays are processed by motion detecting receptive fields (second-order motion detectors) that are oriented in space–time, but a non-linear 'texture-grabbing' transformation (e.g. rectification, either full-wave or half-wave) precedes motion energy detection (Chubb & Sperling, 1988). A strong prediction of such a theory is that it should be possible to generate second-order four-stroke displays analogous to the first-order displays shown in Fig. 1, containing reversals in 'texture contrast polarity' instead of reversals in luminance contrast polarity. This prediction was tested in a series of experiments. Stimuli contained random block arrays, rather than isolated bars such as those in Fig. 1. Fig. 2 shows examples of first-order and second-order displays.

The upper plot is a space–time diagram of a first-order display—a row of random bright/dark elements shifts to the right from frame 1 to frame 2 by one quarter of an element width. In frame 3 all elements return to their original position, but reverse in contrast, and so on to create a four-stroke cycle. The lower plot is a space–time diagram of an equivalent second-order display. This display is identical to the first-order display, except that previously dark elements are now filled with random black/white texture at the same mean intensity as the uniform grey elements (texture is uncorrelated from frame to frame). Does the second-order display support unidirectional motion perception?

There are many ways to generate second-order motion, but only some forms of second-order attribute may be supported by a texture-grabbing transform preceding energy analysis, as indicated earlier. To investigate the varieties of second-order attribute that are supported by energy analysis, we generated six different second-order displays, as well as a first-order display.

Fig. 3 illustrates the kinds of display we used:

- *Intensity*—Black versus grey (i.e. first-order)
- *Contrast*—Static texture versus grey (isoluminant)
- *Tilt*—cw tilted texture versus ccw tilted texture
- *Size*—Fine texture versus coarse texture

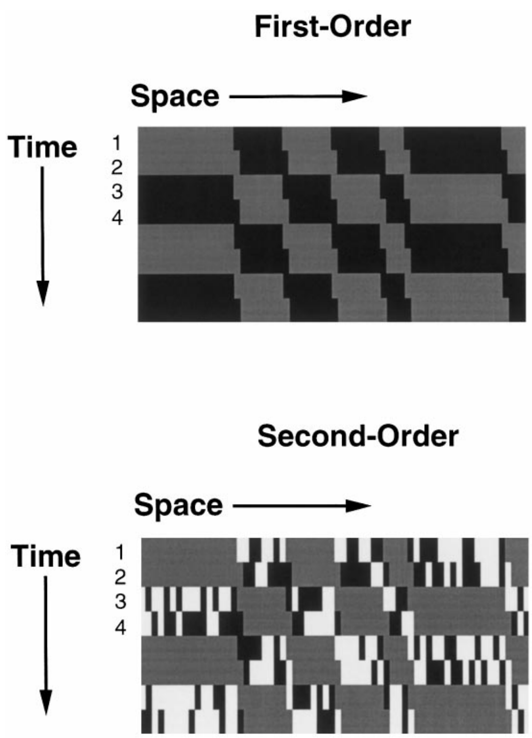

Fig. 2. First-order and second-order four-stroke displays of the kind used in the experiments. The top xt plot shows a row of random black-grey elements (time 1) that shift rightward (2), shift back and reverse contrast (3), shift rightward again (4), and then shift back with a contrast reversal to repeat the cycle. The bottom xt plot is identical except that black elements have been filled with random black-white microtexture that is uncorrelated across time frames.

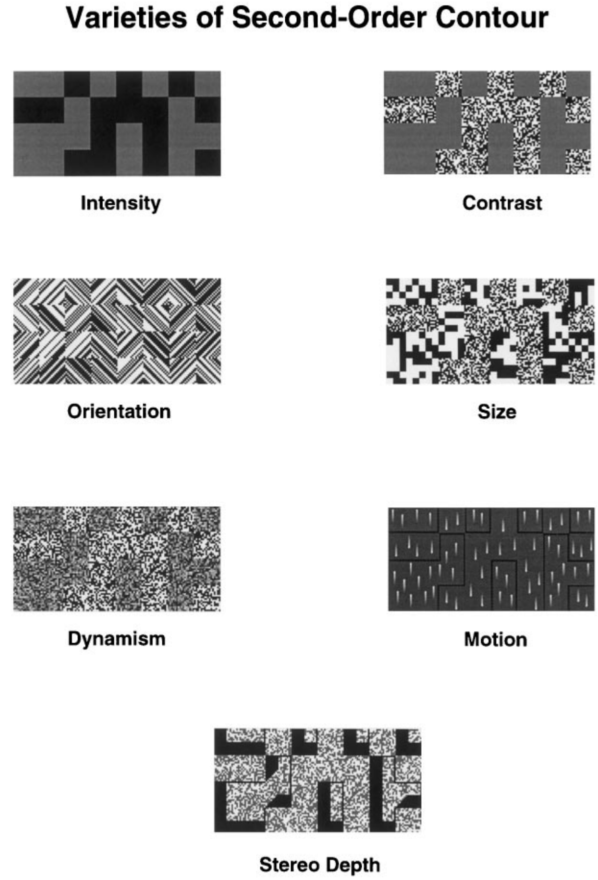

Fig. 3. Random block displays defined by seven different attributes as used in the experiments. In each case, half of the blocks (selected at random) were defined by one attribute (e.g. dark, fine black-white texture, $-45°$ tilt) and the other half were defined by the alternate attribute (e.g. grey, $+45°$ tilt, coarse black-white texture). In actual experimental stimuli, texture attributes were always re-randomised between frames of the motion sequence.

- *Dynamism*—Static texture versus dynamic texture
- *Motion*—Upward moving texture versus downward moving texture
- *Depth*—zero disparity texture versus near or far disparity texture

Different kinds of texture-grabbing transformation would be required for each before motion energy analysis, so our experiments tested which of these transforms are actually implemented in the visual system. Contrast-, tilt-, and size-defined displays would require only spatial transformations to make them amenable to energy analysis (e.g. spatial frequency and/or orientation selective filtering followed by rectification). Dynamism-, motion-, and depth-defined displays would require more complex operations (e.g. spatio–temporal filtering or stereo analysis).

The full four-stroke cycle involves both forward and reversed transitions. In principle, unidirectional motion could be perceived even if only one of these transitions led to a directional signal. For example, if simple half-wave rectification preceded motion analysis, then only forward (same contrast polarity) transitions of intensity-defined patterns would generate motion signals. We already know that both transitions are effective for first-order stimuli, and for second-order stimuli defined by contrast. Nishida (1993), Morgan and Ingle (1994), and Benton, Johnston and McOwan (1997) obtained reports of reversed phi for a range of stimuli, including intensity defined, intensity and colour defined, and texture defined patterns. Morgan and Ingle (1994) reported that in some conditions colour reversal without luminance reversal can wipe out the forward motion signal. However, nothing is known about the relative effectiveness of the two transitions for the other five displays. We therefore tested three different variants of each display: a full four-stroke cycle (upper plot, Fig. 4), forward transitions alone (middle plot), and reverse transitions alone (lower plot).

2. Method

2.1. Subjects

Five subjects participated in all observations, four naive observers and one of the authors (LM in some observations, GM in others).

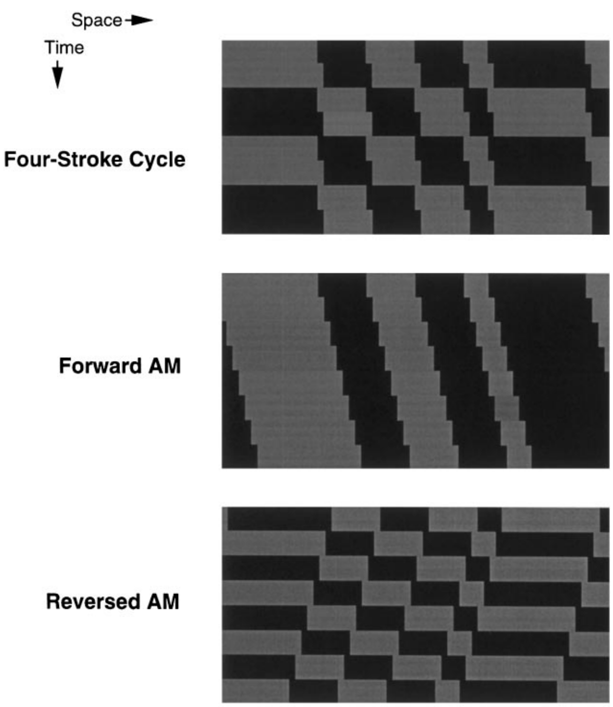

Fig. 4. Three different motion sequences used in experimental stimuli. Top: the full four-stroke cycle. Middle: repeated forward transitions from the four-stroke cycle. Bottom: repeated reversed transitions from four-stroke cycle. (In each case, only five successive frames were actually shown in each trial, though eight are depicted).

2.2. Apparatus

Stimuli were generated by a PC-compatible computer equipped with a high resolution graphics board (Imaging Technology), and displayed on a NEC Multisynch Plus monitor (84 Hz refresh rate).

2.3. Stimuli

All patterns were random block arrays at 50% density (16×16 block array; 6.8×6.8 arc deg). Half of the blocks contained one kind of texture, and the rest contained the other texture. A single presentation comprised a single five-frame apparent motion sequence containing one of the three motion displays shown in Fig. 4. (five frames gave two forward and two reverse transitions in the four-stroke cycle). Two different frame durations were used in different presentations: 71 ms and 155 ms. All displacements were one quarter of a block width. Parameters for different displays were as follows.

2.3.1. Intensity defined patterns

Half of the blocks were light (30 cd/m^2), and half were dark (20 cd/m^2). In luminance contrast reversals, all light blocks became dark, and vice versa.

2.3.2. Contrast defined patterns

Half of the blocks were uniform grey, and half were textured. Each textured block was filled with an array of random 50% black/white microtexture (12×12 pixel elements per block, 0 and 61 cd/m^2). Microtexture was uncorrelated from frame to frame of the motion sequence. It is important to remove residual intensity differences between the grey blocks and the textured blocks. We matched the apparent brightness of the two using a flicker photometry task. A flickering pattern alternated repeatedly between grey and textured, and the subject adjusted the intensity of the grey field to arrive at a minimum-flicker setting. Isoluminance settings provided by this technique agree closely with those provided by a motion-reversal technique (Mather & Murdoch, 1997). In texture contrast reversals, all uniform blocks became textured, and vice-versa.

2.3.3. Size defined patterns

All blocks were filled with random 50% black/white microtexture (0 and 61 cd/m^2). Half of the blocks contained small microtexture (12×12 elements per block), and the rest contained large random microtexture (4×4 elements per block, as depicted in Fig. 3). In texture contrast reversals, all small microtexture was replaced with large microtexture, and vice-versa.

2.3.4. Dynamism defined patterns

All blocks were filled with random 50% black/white microtexture (12×12 elements per block, 0 and 61 cd/m^2), but the texture in half of the blocks remained static during each frame of the motion sequence (and re-randomised every frame i.e. every 71 or 155 ms), and the texture in the remaining blocks was dynamic (i.e. re-randomised every screen refresh, 12 ms). In texture contrast reversals, all static texture became dynamic, and vice-versa.

2.3.5. Orientation defined patterns

All blocks were filled with a random 50% black/white line pattern, best described as follows. A single row of 12 random microtexture elements was drawn across the top of each block. Subsequent rows were generated by duplicating this first row in the next row, but shifting the row either to the right or to the left by one element width to draw a pattern of random lines tilted either $-45°$ (anticlockwise from vertical), or $+45°$ (clockwise). Half of the blocks in the stimulus contained $-45°$ lines, and the rest contained $+45°$ lines (as depicted in Fig. 3). All random line textures were re-randomised between frames of the motion sequence. In texture contrast reversals, all random lines at $-45°$ were replaced with lines at $+45°$, and vice-versa.

2.3.6. Motion defined patterns

All blocks contained random black/white microtexture (12×12 pixel elements per block, 0 and 61 cd/m^2), which moved as follows. In each of the 12 vertical columns of 12 elements in each block, all elements were set to white (61 cd/m^2), except for one (randomly selected) element that was set to black (0 cd/m^2). In half of the blocks in the pattern (randomly selected), these dark texture elements drifted up through the block (with wrap-around), and in the remaining half the dark texture elements drifted down. Drift rate was 2.85 deg/s. All textures were re-randomised between frames. In texture contrast reversals, drift direction in each block reversed.

2.3.7. Depth defined patterns

Each frame was drawn on the monitor as a stereo-pair of patterns, each 6.8×6.8 arc deg, with their inner edges separated by 3.8 arc deg. The upper and lower edges of each pattern were given red-grey checked borders to aid stereo-fusion, and a central red fixation cross was displayed at zero disparity. Stereo-fusion was achieved using a prism stereoscope. All blocks in each frame contained random 50% black/white microtexture (12×12 pixel elements per block, 0 and 61 cd/m^2). Half of the blocks (randomly selected) were displayed at zero disparity, and the remaining blocks were displayed with 8.2 arc min of disparity (either all crossed or all uncrossed). All textures were re-randomised between frames. In texture contrast reversals, all crossed disparities became uncrossed, and vice-versa (zero-disparity blocks were unchanged).

2.4. Procedure

The seven different stimulus displays (Fig. 3) were tested in separate experimental sessions. Within a session, the six different conditions (three motion displays, Fig. 4, each at two frame durations) were presented in random order until 50 trials had accumulated for each. A single trial involved one five-frame presentation of a motion sequence, randomly selected to move either leftward or rightward, after which the observer pressed one of two response buttons to signify perceived direction. A small central red fixation cross was present continuously. During the 0.5 s inter-trial interval the display was uniform at the mean intensity of the pattern. Prior to the start of each session, observers were shown a few trials of the forward apparent motion stimulus (Fig. 4) for that session, to familiarise them with the display.

3. Results and discussion

Fig. 5 (top left) shows mean percentage of correct responses for the intensity defined pattern. The three pairs of columns correspond to data obtained using the three motion sequences depicted in Fig. 4, with the unshaded column of each representing data obtained using a frame duration of 71 ms, and the shaded column representing data obtained using a frame duration of 155 ms. Vertical bars represent standard errors. Responses to the Forward AM and reversed AM displays were scored as correct if they agreed with the direction of block displacement. Thus Forward AM responses should be above 50% (chance), and reversed AM responses should be below 50% (if reversed apparent motion was perceived). Responses to the four-stroke cycle were scored as correct if they agreed with the direction predicted by the forward AM transitions of the display.

It is clear that unidirectional apparent motion was perceived in the four-stroke cycle, since mean responses in this condition exceed 90% correct at both durations. It is also clear that both the Forward AM and reversed AM transitions contributed to the percept, since responses are well above chance in the former but below chance in the latter.

The remaining panels in Fig. 5 show the mean percentage of correct responses for contrast defined, orientation defined, and size defined patterns. All three displays show the same pattern of results as the intensity defined pattern, namely above-chance performance for Forward AM and four-stroke displays, but below-

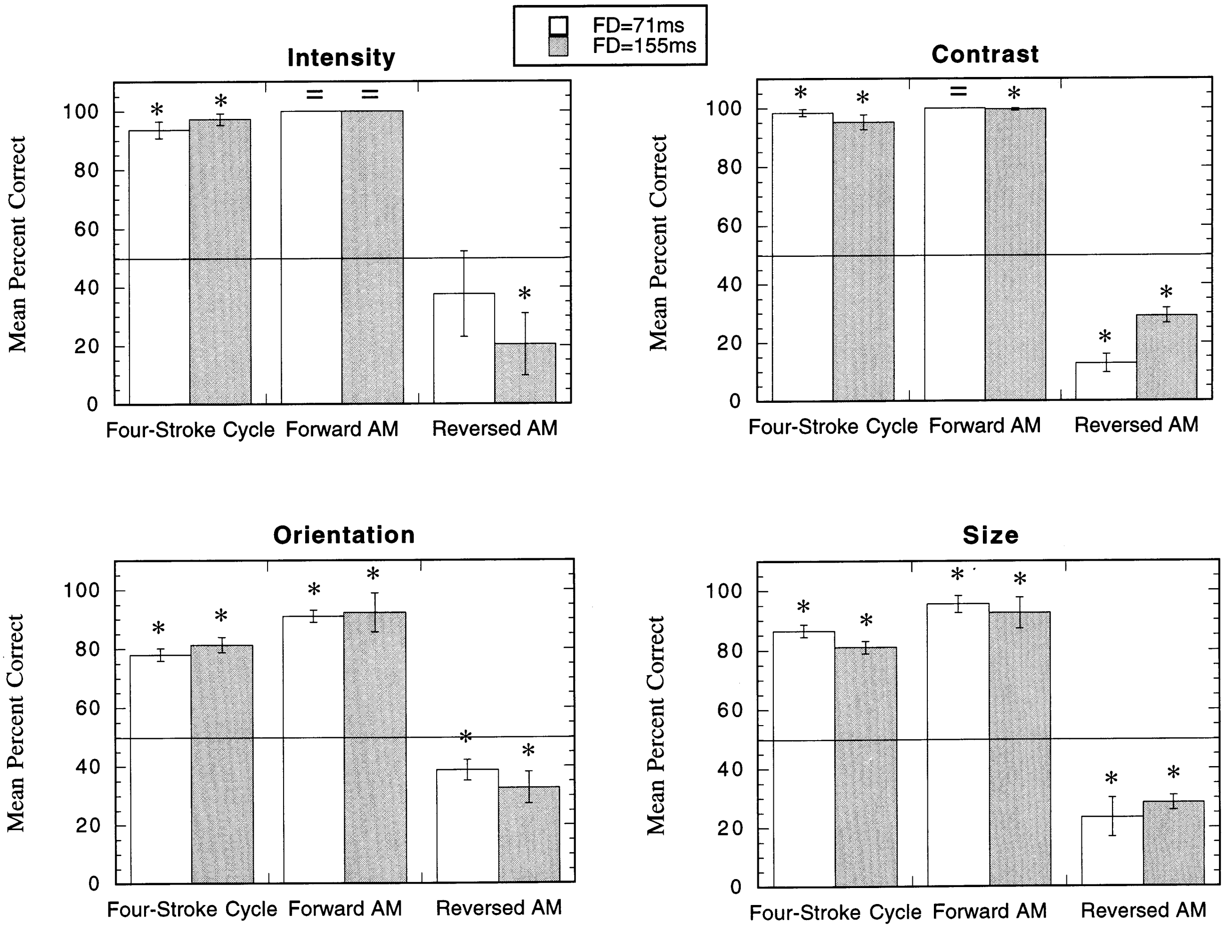

Fig. 5. Results for intensity, contrast, orientation, and size defined patterns. Each bar chart shows the mean percentage of correct responses to the three motion sequences illustrated in Fig. 4. Responses were scored as correct if they agreed with the direction of block displacement (forward transitions only in the case of four-stroke stimuli) i.e. 'right' for the upper two plots in Fig. 4, and 'left' for the bottom plot. Open bars show data at a frame duration of 71 ms, and shaded bars show data at a frame duration of 155 ms. * denotes responses that were significantly above or below chance (50%) according to t-tests (significance level 0.05, adjusted for the use of multiple tests). = denotes that no test was possible, since variance was zero.

chance performance for Reversed AM displays. Asterisks denote responses that are significantly above or below chance, according to t-tests (significance level adjusted for the use of multiple tests).

Fig. 6 shows the mean percentage of correct responses for dynamism defined, motion defined, and stereo-defined patterns. Responses to dynamism defined patterns are in the same direction as those to the first four displays, though performance in the reversed AM displays is closer to chance than in any of the other four conditions. For motion and stereo defined patterns there was no evidence that the four-stroke cycle was effective, since results for this pattern fell close to chance. Although forward motion was seen in Forward AM stimuli, no reversed motion was seen in Reversed AM stimuli. This discrepancy between the two components of the four-stroke cycle presumably accounts for the ineffectiveness of the four-stroke stimulus in these displays. The dynamism, motion, and stereo defined displays may be sensitive to exposure duration, since their texture definition is time-sensitive. However, we employed a long frame duration of 155 ms with this point in mind. Forward AM displays yielded at least 80% correct responses at this duration, so it cannot be argued that movement was simply not visible in dynamism, motion, and stereo defined displays.

4. Conclusions

Results show that both forward and reversed phi components of four-stroke motion gave a reliable impression of unidirectional motion in four of the seven displays tested. We can therefore conclude that second-order motion energy detectors exist in the visual system, and that a variety of texture-defined contours are visible to them. Current models of second-order motion energy detection (Wilson & Kim, 1994) involve the following sequence of operations:

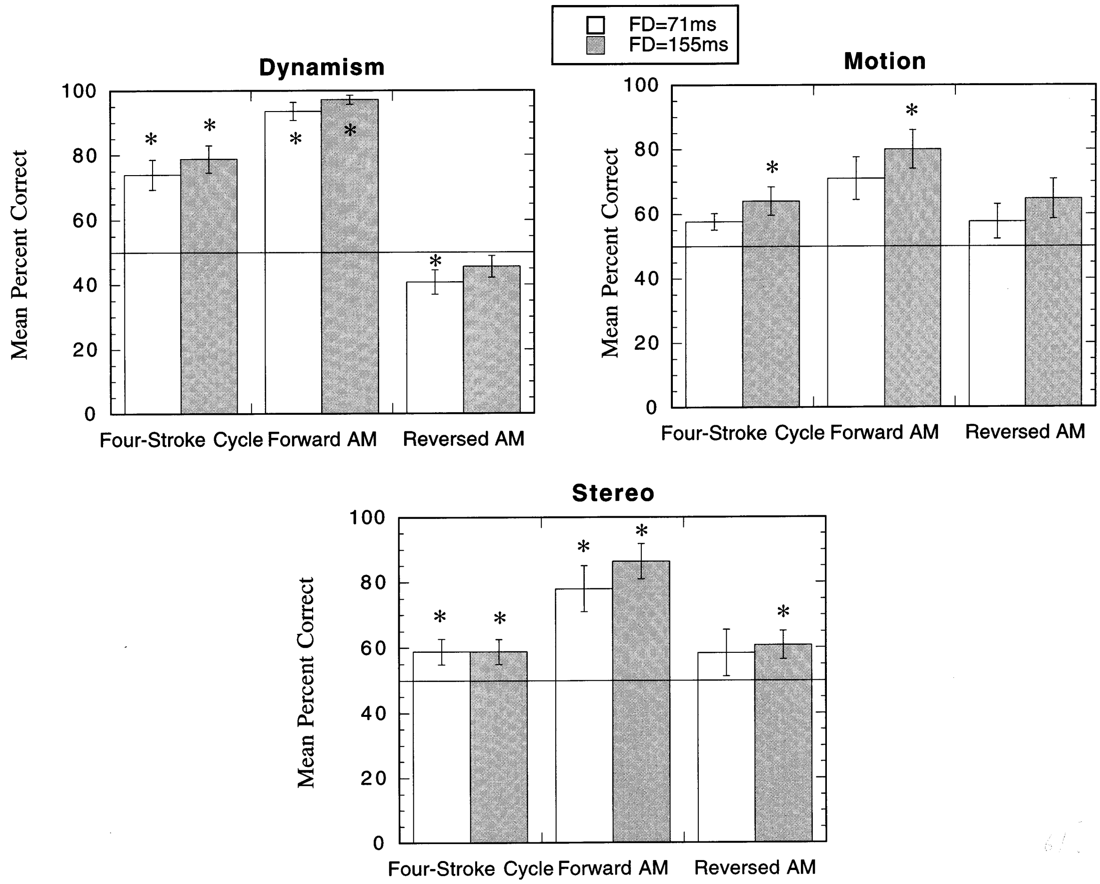

Fig. 6. Results for dynamism, motion, and stereo defined patterns. Conventions as in Fig. 5.

1. The image is passed through a bank of spatiotemporal filters. In physiological terms this operation may correspond to transmission through centre-surround ganglion cell receptive fields. If the image contains regions with different texture properties (e.g. high texture contrast versus low or zero contrast; coarse texture versus fine texture), these regions are likely to generate different levels of response modulation in the filters.
2. The resulting modulated 'neural' image is rectified (either full-wave or half-wave) to convert the texture-related modulation difference into a level (DC) difference in response.
3. The rectified neural image is passed through a second bank of low-frequency spatio–temporal filters, to smooth out ripples in response level.
4. The smoothed image is subjected to spatio–temporal energy analysis to extract motion (Adelson & Bergen, 1985).

It is not clear whether step (2) involves full-wave or half-wave rectification. On-centre and off-centre ganglion cells carry approximately half-wave rectified signals, so they could implement the first two steps in the sequence. Adaptation effects also indicate the presence of half-wave rectified signals in the motion system (Mather, Moulden & O'Halloran, 1991). On the other hand, there is also evidence for full-wave rectification during motion analysis (Solomon & Sperling, 1994; Mather & Tunley, 1995).

The most effective of our second-order displays require relatively simple texture-grabbing transforms, incorporating spatial filtering and rectification. All that is required is for the spatial filter to generate some difference in response to the different textures. For the least effective displays, simple spatial transformations are not sufficient to expose the texture modulation to energy analysis. The motion-defined display would require spatiotemporal filtering to extract texture velocity, while the stereo-defined display would require binocular processing to extract disparity. It is reasonable to conclude from the failure of these stimuli that such transforms do not feed into second-order motion analysis. According to previous studies, at least some forms of motion- and stereo-defined display are subject to motion analysis (Zanker, 1993; Patterson, Bowd, Phinney, Phondorf, Barton-Howard & Angilletta, 1994). However, there is also evidence (Anstis, 1980; Cavanagh, 1991; Smith, 1994; Lu & Sperling, 1995) that perception of second-order motion can be mediated by some form of attention-based, shape tracking process rather than by energy-based motion analysis. Feature-tracking can be excluded as an explanation for the four-stroke motion used here because, as discussed earlier, in four-stroke displays spatial features did not move unidirectionally, but oscillated in position over time. It may be that the effectiveness of motion- and stereo-defined displays in previous research as well as in the current experiment was actually due to a contribution from feature or object tracking. Although stereo-defined patterns do produce motion after effects (Patterson, Bowd, Phinney, Phondorf, Barton-Howard & Angilletta, 1994) they are relatively weak and require longer adaptation periods than other second-order stimuli (Nishida & Sato, 1995; Bex, Verstraten & Mareschal, 1996).

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References

Adelson, E. H., & Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. *Journal for the Optical Society of America*, *A2*, 284–299.

Anstis, S. (1970). Phi movement as a subtraction process. *Vision Research*, *10*, 1411–1430.

Anstis, S. (1980). The perception of apparent movement. *Philosophical Transactions of the Royal Society of London*, *B290*, 153–168.

Anstis, S. M., & Rogers, B. J. (1975). Illusory reversal of visual depth and movement during changes of contrast. *Vision Research*, *15*, 957–961.

Anstis, S. M., & Rogers, B. J. (1986). Illusory continuous motion from oscillating positive–negative patterns: implications for motion perception. *Perception*, *15*, 627–640.

Benton, C., Johnston, A., & McOwan, P. (1997). Perception of motion direction in luninance- and contrast-defined reversed-phi motion sequences. *Vision Research*, *37*, 2381–2399.

Bex, P., Verstraten, F., & Mareschal, I. (1996). Temporal and spatial frequency tuning of the flicker motion after effect. *Vision Research*, *36*, 2721–2727.

Burr, D. C., Ross, J., & Morrone, M. C. (1986). Seeing objects in motion. *Proceedings of the Royal Society of London*, *B227*, 249–265.

Carney, T., & Shadlen, M. N. (1993). Dichoptic activation of the early motion system. *Vision Research*, *33*, 1977–1995.

Cavanagh, P. (1991). Short-range versus long-range motion: not a valid distinction. *Spatial Vision*, *5*, 303–309.

Cavanagh, P., & Mather, G. (1989). Motion: the long and short of it. *Spatial Vision*, *4*, 103–129.

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*, 1986–2007.

Emerson, R. C., Bergen, J. R., & Adelson, E. H. (1992). Directionally selective complex cells and the computation of motion energy in cat visual cortex. *Vision Research*, *32*, 203–218.

Lu, Z., & Sperling, G. (1995). The functional architecture of human visual motion perception. *Vision Research*, *35*, 2697–2722.

Marr, D., & Ullman, S. (1981). Directional selectivity and its use in early visual processing. *Proceedings of the Royal Society of London*, *B211*, 151–180.

Mather, G., Moulden, B., & O'Halloran, A. (1991). Polarity specific adaptation to motion in the human visual system. *Vision Research*, *31*, 1013–1019.

Mather, G., & Murdoch, L. (1997). Order-specific and non-specific motion responses in the human visual system. *Vision Research*, *37*, 605–611.

Mather, G., & Tunley, H. (1995). Motion detection in interleaved random dots patterns. *Vision Research*, *35*, 2117–2125.

Morgan, M. J., & Ingle, G. (1994). What direction of motion do we see if luminance but not colour is reversed during displacement? Psychophysical evidence for a signed colour input to motion detection. *Vision Research*, *34*, 2527–2535.

Nishida, S. (1993). Spatiotemporal properties of motion perception for random-check contrast modulations. *Vision Research*, *33*, 633–645.

Nishida, S., & Sato, T. (1995). Motion after-effect with flickering test patterns reveals higher stages of motion processing. *Vision Research*, *35*, 477–490.

Patterson, R., Bowd, C., Phinney, R., Pohndorf, R., Barton-Howard, W., & Angilletta, M. (1994). Properties of stereoscopic (cyclopean) motion aftereffects. *Vision Research*, *34*, 1139–1147.

Reichardt, W. (1961). Autocorrelation, a principle for the evaluation of sensory information by the central nervous system. In W. Rosenblith, *Sensory communication*. Cambridge, MA: MIT Press, 303–317.

Sato, T. (1989). Reversed apparent motion with random patterns. *Vision Research*, *12*, 1749–1758.

Smith, A. T. (1994). The detection of second-order motion. In A. T. Smith, & R. Snowden, *Visual detection of motion*. London: Academic Press, 145–176.

Solomon, J., & Sperling, G. (1994). Full-wave and half-wave rectification in second-order motion perception. *Vision Research*, *34*, 2239–2257.

Wilson, H. R., & Kim, J. (1994). A model for two-dimensional motion perception: coherence and transparency. *Visual Neuroscience*, *11*, 1205–1220.

Zanker, J. (1993). Theta motion: a paradoxical stimulus to explore higher order motion extraction. *Vision Research*, *33*, 553–569.