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Order-specific and Non-specific Motion Responses in the Human Visual System

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A series of experiments measured direction discrimination in two-frame random block kinematograms. Blocks were presented against a uniform grey background, and were filled either with uniform grey (darker or brighter than the background; first-order blocks) or with random microtexture (isoluminant with the background; second-order blocks). Experiment 1 found that when blocks maintained their order from frame to frame, performance declined from near-perfect to chance levels as block displacement increased. When blocks switched order between frames, performance was generally worse (65–75% correct at best), but still above chance levels. Results from control experiments established that it is important to remove intensity cues in second-order patterns using a *psychophysical* technique, and that above-chance responses with order-switching patterns persisted, even when such intensity cues were removed or randomised. The last experiment measured the effects of block density manipulation. First-order and second-order patterns showed the same decline in D_{max} performance as pattern density increased, and results from patterns containing a mixture of first- and second-order blocks could be predicted from performance obtained with each set of blocks presented separately, except at very low densities. It is concluded that both order-specific and non-specific responses are available during motion analysis, but order-specific responses tend to predominate. © 1997 Elsevier Science Ltd. All rights reserved

First-order motion   Second-order motion   Random dot kinematograms   Motion perception

INTRODUCTION

Considered in purely physical terms, the distinction between first-order and second-order motion stimuli is very clear and straightforward. First-order stimuli contain stable and coherent spatio-temporal energy corresponding to the velocity of motion. Second-order stimuli do not contain coherent energy but, instead, motion information is conveyed by contours with dynamically changing and/or incoherent Fourier energy (texture borders, for instance). Considered in *psycho*physical terms, the distinction is less clear-cut. On the one hand, there is mounting evidence from motion discrimination studies for the existence of separate first- and second-order detectors (eg. Mather & West, 1993; Ledgeway & Smith, 1994; Solomon & Sperling, 1994; Holliday & Anderson, 1994) consistent with a scheme involving order-specific responses that are combined at a late stage of motion integration (eg. Wilson *et al.*, 1992; Nishida & Sato, 1995). On the other hand, order non-specific responses have also been reported in adaptation studies (eg. Turano, 1991; Ledgeway & Smith, 1994). The origin and importance of these responses is still not clear. They could arise from residual intensity cues in second-order stimuli, or from weak "cross-talk" between, for example, first-order stimuli and second-order detectors, or at the high-level integration stage where responses from all detectors are combined. The aim of experiments reported here was to shed some light on the strength and source of non-specific responses in motion detection tasks.

We began with the experiments on two-frame random block kinematograms (RBKs) conducted by Mather and West (1993). They found that patterns which switched order between frames could not support direction discrimination, indicating a complete absence of non-specific responses.The first experiment extended these initial observations using different stimulus conditions.

EXPERIMENT 1

In *order-matching*, RBKs blocks in the first frame are identical to those in the second frame (e.g., all first- or all second-order), except for a relative spatial shift between the frames that defines the motion cue (the top two stimuli in Fig. 1 illustrate first- and second-order matched RBKs).

In addition to these, Mather and West (1993) used *order-switching* RBKs in which the first frame contained only first-order intensity-defined blocks against a grey background, and the second frame contained second-order texture-defined blocks against a grey background

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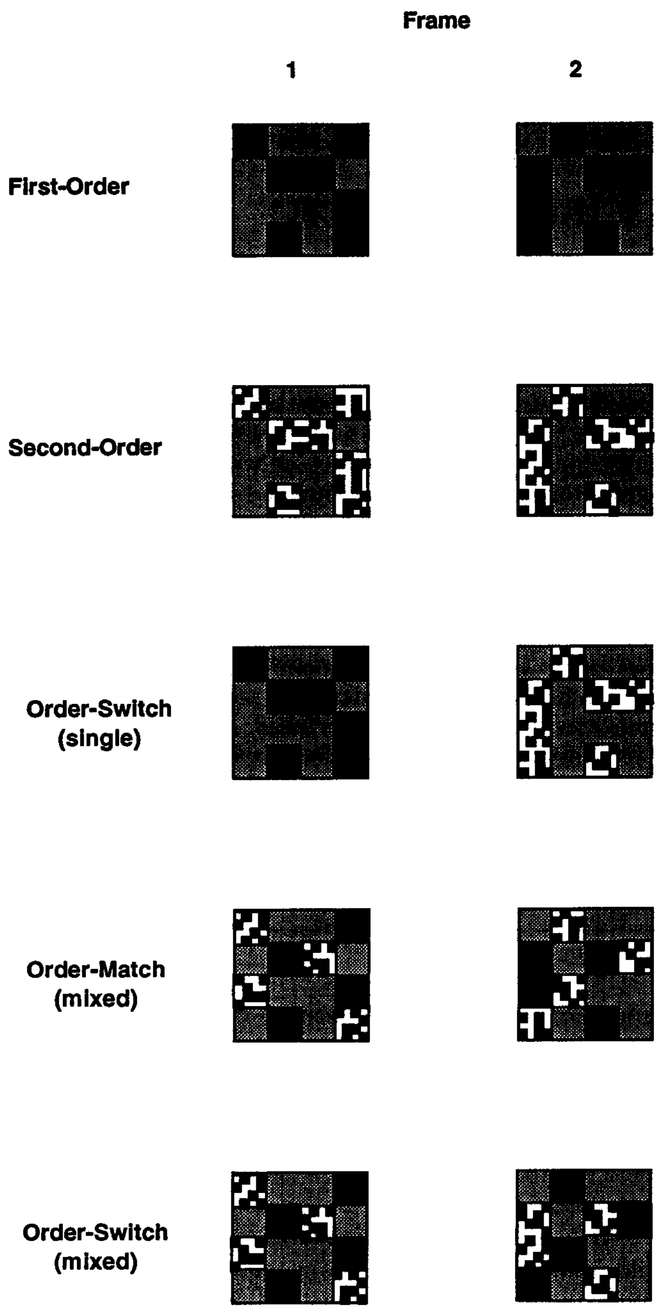

FIGURE 1. Schematic depiction of stimuli used in all experiments. The top row depicts a two-frame random block kinematogram containing first-order blocks. All blocks shift rightwards in the second frame, to offer a stimulus for motion detection. The second row depicts an equivalent kinematogram containing second-order blocks (note that texture is always re-randomised between frames). In the third row, all blocks are first-order in frame 1 and second-order in frame 2, but remain in the same spatial arrangement (apart from a spatial shift). In actual experimental stimuli the reverse order was also used. The bottom two rows depict kinematograms in which all frames contain a mixture of first- and second-order blocks. Blocks either maintain their definition from frame to frame (Order-Match), or switch order (Order-Switch). Actual stimuli involved 20×20 arrays of blocks (only 4×4 arrays are shown); first-order blocks could also be bright rather than dark as depicted; and second-order blocks contained 9×9 arrays of random microtexture (only 4×4 arrays are shown). In addition, displacement direction and magnitude varied randomly from trial to trial. Actual displacements used were 0.44, 1, 2 and 3 block widths (9.4, 21.2, 42.3 or 63.5 arcmin).

(or vice versa), again with a relative spatial offset between frames (third row in Fig. 1). Direction discrimination performance was good using order-matching patterns but at chance levels using order-switching patterns. On this basis Mather and West concluded that only order-specific responses were available. In their order-switching stimuli, all elements in one frame were one order, and all elements in the other frame were the alternate order (i.e., single-order frames). Hence the transition from frame 1 to frame 2 in these patterns involved a gross change in stimulus appearance, and a small change in mean luminance, which could possibly have masked any motion cue. At least, this arrangement admitted the possibility of observer bias since order-switching stimuli were easily distinguishable from order-matching stimuli. We therefore repeated the experiment, comparing results using single-order frames (as in Mather and West) with results when half of the blocks in each frame were first-order and half second-order (i.e., mixed order, bottom two rows in Fig. 1). Obviously, with mixed frames, order-matching and order-switching stimuli are visually similar, avoiding the possibility of deliberate observer bias. Is direction discrimination possible with the revised order-switching stimulus?

Method

Subjects. Five observers participated, both authors and three naïve but experienced observers.

Stimuli and apparatus. Apparatus comprised a PC-compatible computer equipped with a high performance raster graphics board, and an NEC Multisync Plus colour monitor (refresh rate 75 Hz). In between trials the monitor displayed a uniform grey background field (7.05×7.05 deg, 180×180 pixels), with a central red fixation cross. At the start of a trial, the fixation cross disappeared, and a two-frame random block kinematogram was presented against the grey background. The pattern contained a 20×20 array of blocks (each 9×9 pixels, or 21.15×21.15 arcmin square), and frame duration was 67 msec (5 refreshes), with no inter-frame-interval. Following stimulus presentation, all blocks disappeared and the fixation cross reappeared. The inter-trial interval was 750 msec. In all patterns, a random 160 of the available 400 block positions were filled. First-order blocks were all darker than the background field (at 13% contrast). Second-order blocks contained binary black–white single-pixel microtexture (53.5 and 0 cd/m^2). Three different kinematograms were constructed using these blocks, corresponding to the three lower stimuli depicted in Fig. 1. In the single-order pattern all blocks in one frame were first-order, and all blocks in the other frame were second-order (resulting in a small difference in mean luminance, as in Mather and West's stimuli). In mixed-order patterns, 80 blocks were solid, and 80 were filled with microtexture. In all second-order blocks, microtexture was re-randomised between frames.

Design and procedure. Frame-to-frame displacement

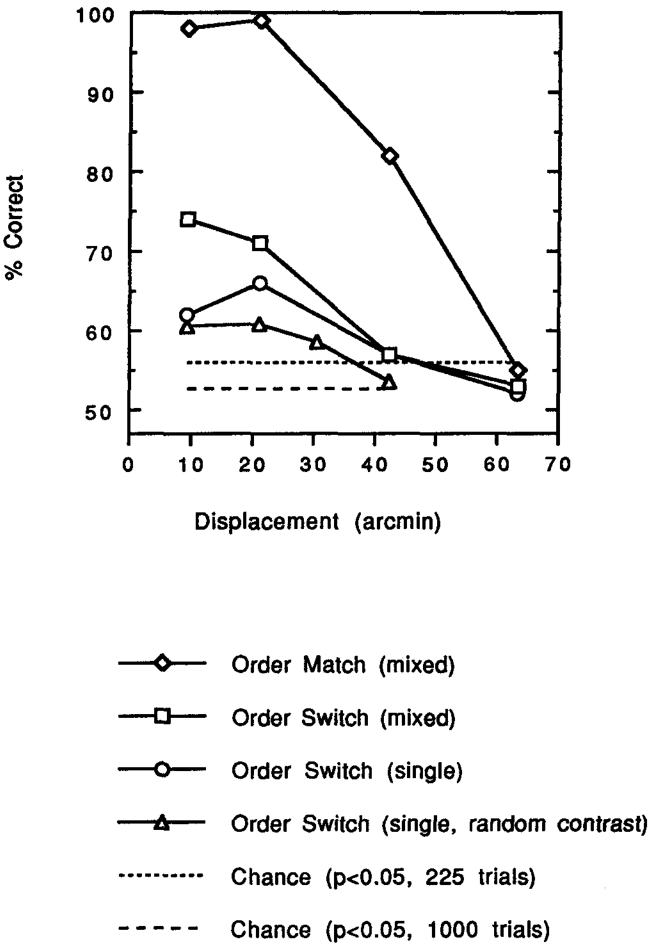

FIGURE 2. Results of Experiments 1 and 2, plotting mean per cent correct in a direction discrimination task as a function of displacement. Different curves represent results using different stimuli depicted in Fig. 1. Broken horizontal lines show the upper limit of chance responding according to cumulative binomial probability theory. For Experiment 1, chance = 56% (P 0.05, 225 trials); for Experiment 2, chance = 52.7% ($P < 0.05$, 1000 trials).

magnitude and direction varied from trial to trial. Following each presentation the observer was required to press one of two response keys to indicate perceived direction. Data were collected over a number of sessions. Minimally, 45 left/right direction responses were collected at each of four pattern displacements. Individual trials used novel block patterns, and randomly selected both the displacement direction and magnitude.

To avoid unwanted luminance cues in second-order stimuli, flicker photometry was used to derive a subjective luminance match between the microtexture and the grey background. A 7.05×7.05 deg field flickered repetitively at 25 Hz between uniform grey and bright/dark single-pixel microtexture. Observers adjusted the intensity of the uniform field to establish the point of minimum flicker (subjective isoluminance). Three settings were made by each observer at the start of each session, and the mean of these settings was taken to specify the intensity of the grey background for that observer in that session. (First-order blocks were set to 13% contrast relative to this background level. In pilot observations the same isoluminance settings were obtained at half the flicker rate, similar to the frame rate of the motion displays, but settings were more consistent at 25 Hz.)

Results and discussion

Figure 2 shows that data obtained from the order-match RBK (diamonds) conformed to a conventional psychometric function, with discrimination declining from near-perfect to chance levels as inter-frame displacement rose. Performance was much worse in order-switching patterns. The arrangement of blocks in each frame was important, in that discrimination was better at short displacements using frames that contained a mixture of first- and second-order blocks. However, even in the worst condition using single-order frames (circles), performance was well above chance levels for the two shortest displacements. A possible complication in mixed-order frames is that their mean luminance is lower than the luminance of the grey background (because half of the blocks present are dark), but only the grey background was used to establish isoluminance with second-order blocks.* This could mean that when order switches between frames there is a reversed motion signal generated by the transition from dark first-order blocks to second-order blocks that are slightly brighter than the mean intensity of the whole frame (or vice versa). The effect of this complication would be to suppress correct discrimination of direction in these patterns. However, although performance is generally lower than in other conditions, it is still in the region of 65–75% correct.

Results therefore indicate the presence of order non-specific responses during direction discrimination. The reason for the greater consistency in responses to order-switching patterns in this experiment compared to Mather and West's is not clear. Stimulus conditions were generally comparable, although density was slightly lower in the current experiment and only dark first-order blocks were used (Mather and West found no effect of block polarity). The second and third experiments tested a possible source of above-chance responses to order-switching patterns.

EXPERIMENT 2

In the first experiment, flicker photometry was used to arrive at a subjective match between second-order texture and uniform background. On average, isoluminance was achieved at a background intensity of 24.9 cd/m^2. However, this method of achieving subjective equality may not be accurate enough, or may be inappropriate because it does not allow for the intensity response of the *motion* system. We therefore ran two experiments to test whether cross-order matches in Experiment 1 could have been mediated by residual intensity cues.

In Experiment 2, we corrupted possible intensity cues in order-switching patterns by randomly varying (across

*We are grateful to an anonymous referee for pointing this out.

individual frames) the intensity of the uniform background on which blocks were presented. As a result, intensity-based signals varied randomly both in strength and in direction (reversals in contrast polarity lead to reversed energy signals; see Anstis, 1970; Anstis & Rogers, 1975).

Method

Subjects. Five observers took part, three of whom had participated in Experiment 1.

Apparatus and stimuli. The graphics card and display monitor were identical to that used in Experiment 1, but the host computer was replaced. There were two resulting changes to stimulus parameters: frame duration changed from 67 to 65 msec, and the bright pixels of the microtexture changed in intensity from 53.5 to 60.3 cd/m^2. Only the Order-Switch (single) stimulus was used (see Fig. 1). The first frame contained either all solid blocks, or all textured blocks. During the transition between frames all blocks switched order. The intensity of solid blocks was set to match the subjective mean intensity of textured blocks, established using flicker photometry as described above. The intensity of the grey background on which blocks were drawn was randomly selected for each stimulus frame from ten possible values, giving blocks a range of possible contrasts between -15 and $+15\%$.

Procedure. Data were collected over two sessions using the same procedure as given for Experiment 1. Two hundred responses were collected from each observer at each pattern displacement.

Results and discussion

Results are shown in Fig. 2 (triangles). Intensity randomisation did not entirely remove subjects' ability to match elements that change order from one frame to the next, but performance is relatively poor. As a further test for the presence of residual intensity cues, in Experiment 3 we compared the isoluminance settings determined by flicker photometry against settings determined by an apparent motion task.

EXPERIMENT 3

This experiment used only the Order-Switch (mixed) pattern from Experiment 1. Background intensity was parametrically varied in different presentations (the same background intensity was used in both frames of each presentation, unlike Experiment 2). First, consider trials in which *bright* first-order blocks become texture-defined second-order blocks during the frame transition. If the background is set lower than the mean intensity of both first- and second-order blocks, intensity-based cues would mediate a forward motion signal. If the background level is above the mean intensity of the second-order elements, but below the (bright) intensity of the first-order elements, then intensity cues would mediate a reversed motion signal (contrast reversal is known to result in reversed energy signals, as mentioned earlier). Now consider trials containing *dark* first-order blocks; backgrounds darker than the mean intensity of second-order dots but brighter than the (dark) first-order blocks should lead to reversed signals, while bright backgrounds should lead to forward motion signals. Thus, the psychometric function relating reported direction to background intensity using bright first-order blocks should be an inverted version of the function obtained using dark first-order blocks. The background intensity at which the two functions cross should specify the isoluminance value of the background.

Method

Subjects. Two observers participated, one of the authors and a naïve observer who had served in previous experiments.

Apparatus, stimuli, and procedure. Details correspond to those given in Experiment 2, except as follows. Only the Order-Switch (mixed) stimulus from Experiment 1 was employed. The background intensity in any one trial was selected randomly from a range of values between 14.8 and 35.6 cd/m^2. The intensity of all solid blocks in each trial was adjusted to maintain 13% contrast against the background (either brighter or darker in different presentations). No adjustments were made to the intensities of the microtexture in second-order blocks, which were fixed at 60.63 and 0 cd/m^2. Only one fixed displacement was used, equal to one block width (21.15 arcmin). Both observers completed five experimental sessions, each containing 360 trials in random order (9 background intensities $\times$ 2 first-order contrast polarities $\times$ 20 trials). A forced-choice right vs left response was required after each trial.

Results and discussion

Results are shown in Fig. 3. As expected, functions for dark and bright first-order blocks were mirror-images. The background intensity at the crossover point of the two functions, estimated by logistic regression (Berkson, 1953), agreed closely with isoluminance settings provided by flicker photometry, validating this technique as a method of removing intensity cues from second-order patterns. The isoluminance settings for both subjects in both tasks (about 23 cd/m^2) were well below the physical mean luminance of the microtexture (30.3 cd/m^2). The monitor was calibrated by placing a photometer against a large, uniformly bright area of the screen, and varying screen intensity while recording photometer output. The stated physical mean luminance of the microtexture is the average of the calibrated intensities used for bright and dark texture elements. However, the intensities of black and white pixels can depend on whether they are displayed as a fine texture or as uniform areas (Mulligan & Stone, 1989), so we checked that the discrepancy between perceptual isoluminance settings and calibrated mean intensities was not due to inaccurate calibration. The mean intensity of the texture was measured directly using a photometer which integrated over a small region of the pattern, and yielded a value of 30.2 cd/m^2. The mismatch between physical and psychophysical isoluminance settings presumably reflects nonlinear intensity

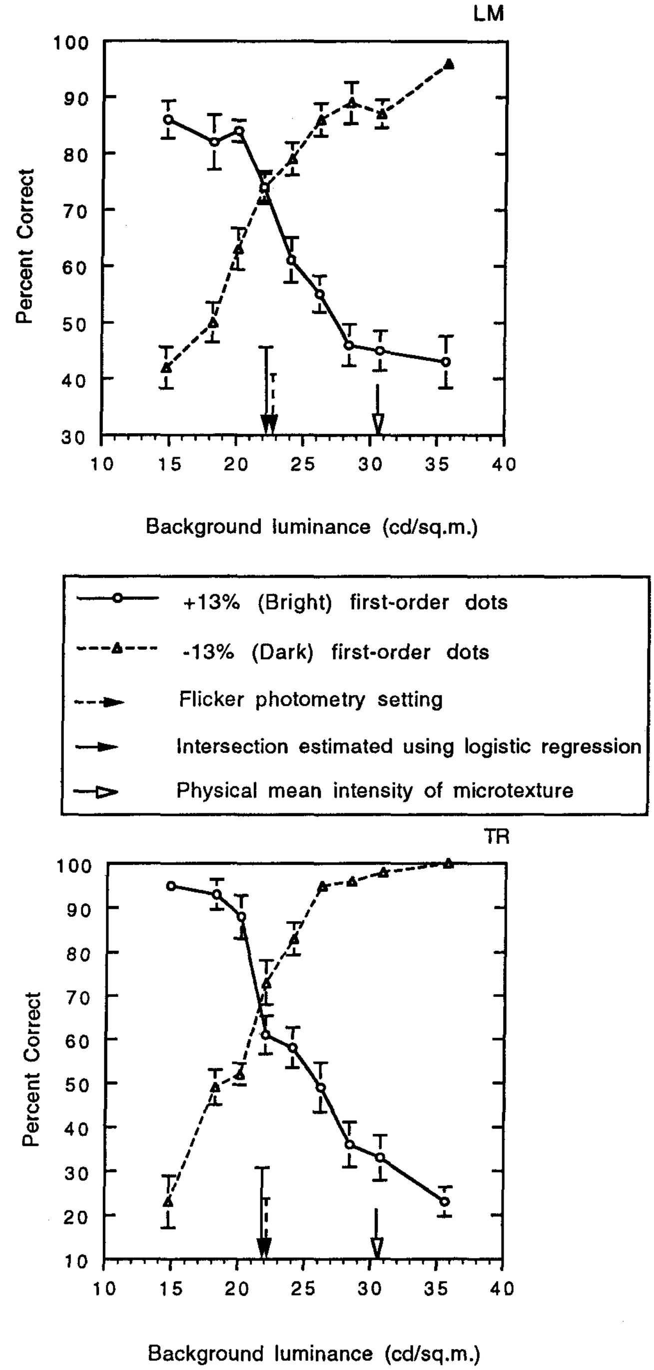

FIGURE 3. Results of Experiment 3, for two observers, showing per cent correct as a function of background intensity in order-switching random block kinematograms. Solid lines show results when the first-order frame in the kinematogram was always brighter than the background, and broken lines show results when the first-order frame was darker than the background. Error bars represent SE across sessions. Solid arrows on the abscissa locate the isoluminance point for the texture used in second-order frames established by flicker photometry (broken line) or by the cross-over point of the two best-fitting curves (solid line). Bars across the top of each arrow represent the SE of each estimate. The open arrow on the abscissa locates the physical mean intensity of the microtexture, measured directly using a photometer integrating over a small region of the pattern.

responses in the visual system, and reinforces the importance of using psychophysical matches to remove intensity cues in second-order patterns.

It is important to note that the two functions do not cross over at 50% correct, as we would expect if *only* intensity cues were used in order-switching stimuli, but at about 70% correct. This bias in favour of correct matches is consistent with earlier results, and must reflect the contribution of a visual process that can derive motion information from order-switching blocks regardless of contrast polarity (e.g., a process that is sensitive to the absolute value of the contrast of first-order blocks). A similar conclusion was reached by Papathomas *et al.* (1994) using a related technique.

EXPERIMENT 4

From the results of the first three experiments, we can conclude that motion response is maximal when stimulus order remains constant during motion sequences, and is impaired when the system is forced to integrate information across order switches. However, performance in such conditions is well above chance levels, and this effect cannot be attributed to residual intensity cues. As a final examination of the contribution of order-non-specific responses to discrimination performance, Experiment 4 manipulated element density in random block kinematograms.

It is already known that D_{max} falls as pattern density increases (Morgan & Fahle, 1992). Is the effect of pattern density similar in first- and second-order patterns, and how is the density effect modulated in patterns containing a mixture of first- and second-order blocks? First, we measured density effects in single order patterns.

Method

Subjects. Five observers took part, both authors and three naïve but experienced observers.

Stimuli, apparatus, and procedure. Equipment specifications and general stimulus parameters correspond to those given earlier, except that frame duration was now 71 msec. Initially, data were gathered using two different random block kinematograms. In first-order kinematograms, all blocks were uniformly brighter (or darker) than the background (13% contrast). In second-order kinematograms, all blocks contained random black–white single-pixel microtexture, as used in previous experiments. Texture was re-randomised between frames, and block arrangement was re-randomised between trials. The intensity of the grey background on which blocks were presented was established using flicker photometry, as before. Four different block densities were presented in different trials, 5, 10, 20 and 40%, and block displacement varied randomly between a predetermined set of possible values to permit estimation of D_{max} (the displacement yielding 80% accuracy, found by linear interpolation). Data were gathered over a number of experimental sessions.

Results and discussion

Means and SEs are shown in Fig. 4. Both first- and second-order patterns show the previously reported effect of pattern density on D_{max}, indicating that the same limits on performance apply. Morgan and Fahle (1992)

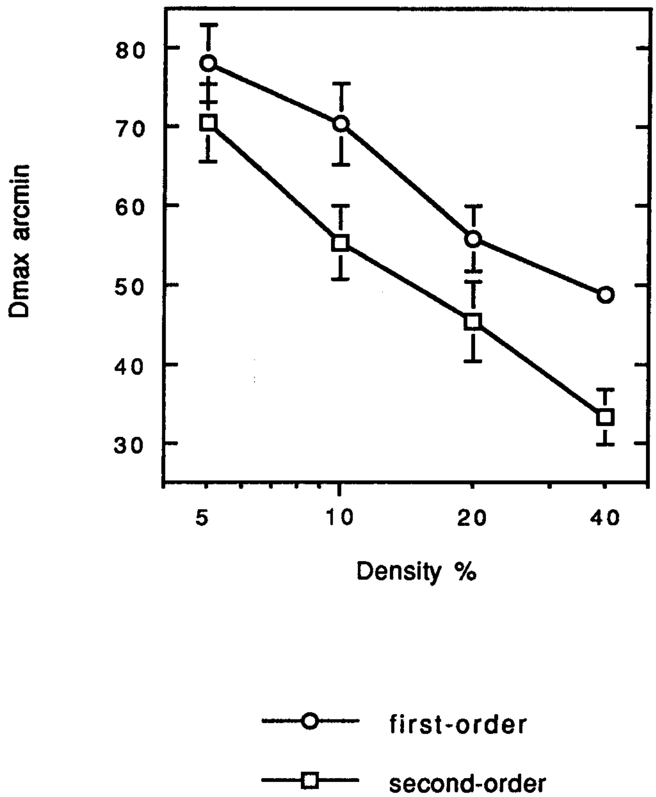

FIGURE 4. Results of Experiment 4, showing mean maximum displacement (D_{max}) as a function of block density for first-order patterns (circles) and second-order patterns (squares).

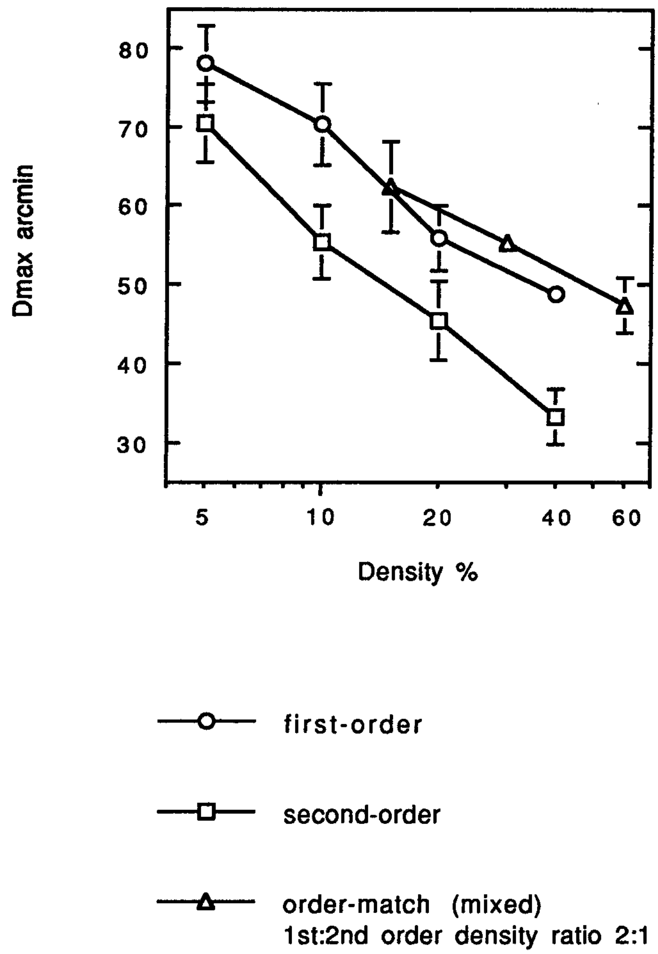

FIGURE 5. Comparison of results from single order and mixed order kinematograms. Triangles represent mean D_{max} values for patterns containing a 2:1 mixture of first- and second-order blocks, at the total density shown on the abscissa. Circles and squares plot D_{max} values for first- and second-order blocks, respectively, when presented separately at the densities shown (taken from Fig. 4).

demonstrate that the increasing probability of false matches at high densities plays a significant role in the decline in D_{max} scores.

To assess the contribution of non-specific responses at different densities, we measured D_{max} as a function of density in patterns containing a mixture of first- and second-order blocks (order was always matched across frames). The density of each order was chosen so that, when presented separately, the two sets of blocks supported similar levels of discrimination. For example, from inspection of Fig. 4 it is clear that D_{max} is roughly equivalent for first-order patterns at 10% density and second-order patterns at 5% density, so we measured discrimination in mixed patterns containing these two sets of blocks (i.e., combined density of 15%). If only order-specific responses contribute to discrimination, then D_{max} in such mixed patterns should correspond to the D_{max} measured with each set of blocks presented separately. If significant non-specific responses are present, then measured D_{max} should be lower than the value obtained with each set of blocks presented individually, due to "cross-talk" between the two sets of blocks in mixed patterns (i.e., an effectively higher density). Results for mixed patterns are shown in Fig. 5, along with data for single-order patterns replotted from Fig. 4.

The abscissa plots the total density of mixed patterns, and triangles represent data from these patterns. The open squares and circles plot D_{max} values obtained from the first- and second-order components in mixed patterns, respectively, at their individual densities. At the two higher densities, D_{max} in the mixed pattern corresponds to the D_{max} values obtained when first- and second-order components of the pattern are presented separately, indicating no cross-talk between the two components. Only at the lowest density is there evidence for a contribution from non-specific responses, since D_{max} for the mixed pattern is lower than the individual D_{max} values.

GENERAL DISCUSSION

Data from the four experiments presented here indicate that performance in motion discrimination tasks is optimal when stimuli maintain their order from frame to frame. Results from the last experiment show that when coherent information is available from within-order matches, incoherent cross-order matches have no disruptive effect except at very low pattern density. However, the earlier experiments indicate that when the *only* coherent cue available arises from cross-order matches, then the system can use them, though less effectively than within-order matches. Thus, in performance terms, the system shows a high degree of order-specificity, but can exploit non-specific cues when necessary.

It is tempting to conclude from this data, as Mather and West (1993) did, that the system possesses at least two populations of order-specific detector, one responsive to first-order motion stimuli, and a second responsive to second-order stimuli. Cross-order responses may reflect cross-talk at the level of one of these detector populations, or alternatively a contribution from a third, non-specific detector population. In a recent paper, Edwards and Badcock (1995) investigated interactions between first- and second-order dots using a coherence threshold paradigm. They found a mixture of order-specific and non-specific responses, and concluded that there are separate first- and second-order motion systems, but the latter has some response to first-order patterns. Edwards and Badcock used extremely low densities (less than 5%) so their results are consistent with those presented in Fig. 5 at the lowest density. Our data indicate that order-specific responses become dominant at higher densities.

A degree of caution is required when drawing inferences about multiple motion processes, because it may be possible to construct a single process that can respond to either order, provided that order remains consistent during motion (Ledgeway & Smith, 1994; Johnston & Clifford, 1995). However, given the evidence already accumulated in published studies (Wilson *et al.*, 1992; Gorea *et al.*, 1993; Ledgeway & Smith, 1994; Solomon & Sperling, 1994; Holliday & Anderson, 1994; Nishida & Sato, 1995), the multiple process scheme seems the most plausible working hypothesis for motion analysis.

CONCLUSIONS

The visual system shows a high degree of dependence on within-order matches during motion analysis, though in appropriate conditions responses to cross-order matches can be found. Results are consistent with current schemes involving multiple populations of order-specific motion detector.

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