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Evidence for global motion interactions between first-order and second-order stimuli

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Abstract. Recent research indicates that the early stages of visual-motion analysis involve two parallel neural pathways, one conveying information from luminance-defined (first-order) image features, the other conveying information from texture-defined (second-order) features. It is still not clear whether these two pathways converge during later stages of global motion integration. According to one account they remain segregated, and feed separate global analyses. In the alternative account, all responses feed a common stage of global analysis. Two perceptual phenomena are universally held to result from interactions between detector responses during global motion integration—direction repulsion and motion capture. We conducted two psychophysical experiments on these phenomena to test for segregation of first-order and second-order responses during integration. Stimuli contained two components, either two random-block patterns transparently drifting in different directions (repulsion measurements), or a drifting square-wave grating superimposed on an incoherent random-block pattern (capture measurements). Repulsion and capture effects were measured when both stimulus components were the same order, and when one component was first order and the other was second order. Both effects were obtained for all combinations of first-order and second-order patterns. Repulsion effects were stronger with first-order inducing patterns, and capture effects were stronger with second-order inducers. The presence of perceptual interactions regardless of stimulus order strongly suggests that responses in first-order and second-order pathways interact during global motion analysis.

1 Introduction

According to current physiological and psychophysical evidence, the early levels of visual-motion processing in human vision seem to contain two separate streams of information flow (eg Mather and West 1993; Ledgeway and Smith 1994; Zhou and Baker 1996). One stream (first-order, or Fourier) signals the movement of contours defined by simple luminance variation in the retinal image. The other stream (second-order, or non-Fourier) deals with the motion of contours defined by changes in textural properties in the image, even when there are no corresponding variations in average luminance (see figure 1 for example images). Since early detection processes are spatially localised, it is universally acknowledged that higher levels of analysis are required to resolve resulting ambiguities in their response (eg the aperture problem) and to segment the image into adjacent or transparent regions. However, it is still not clear how information in the two streams is integrated at higher levels. According to one current model of motion processing (Wilson and Kim 1994; Zhou and Baker 1996), the outputs of first-order and second-order motion analysers are pooled so that all participate in a single stage of global motion analysis (left-hand flow diagram in figure 1). Zhou and Baker (1996) found first-order and second-order motion analysers in cortical areas 17 and 18, and Wilson and Kim tentatively located global analysis in area MT. On the other hand, Edwards and Badcock (1995) and Nishida et al (1997) have argued that responses in the two streams "remain separate up to and including the level in the motion system at which global-motion signals are extracted" (Edwards and Badcock, page 2601). This scheme is depicted in the right-hand flow diagram of figure 1.

We sought to distinguish between the two schemes in psychophysical experiments, by examining two particular motion phenomena that are indicative of interactions during global motion integration: mutual repulsion and motion capture. The stimulus

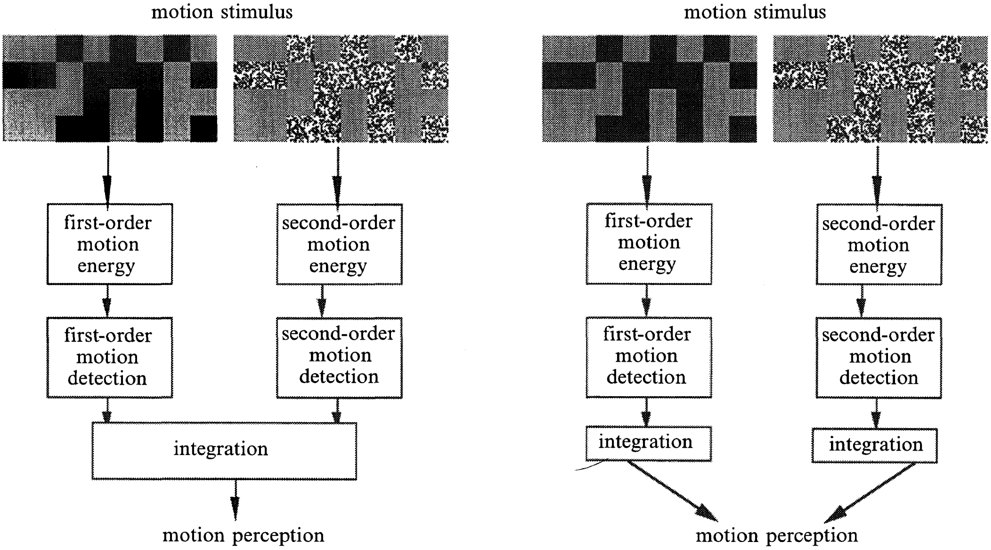

Figure 1. Hypothetical architectures for motion analysis in human vision. First-order motion stimuli contain features defined by intensity differences (black and grey random-block arrays in the top row); second-order stimuli contain features defined by texture variation (textured and grey random-block arrays in the top row). According to both schemes, the two stimulus classes are detected by separate populations of detectors. In the left-hand scheme, responses from the two populations are combined at a single stage of global motion analysis. In the right-hand scheme, separate global analyses are performed for each population.

contained two components, one first order (ie luminance defined) and the other second order (ie texture defined). We tested whether perceptual interactions were dependent on component order.

2 Experiment 1: Mutual repulsion

Marshak and Sekuler (1979), Mather and Moulden (1980), and Hiris and Blake (1996) reported that when two fields of coherently moving intensity dots are spatially superimposed, the apparent angle between their two directions is expanded. Kim and Wilson (1996) obtained a similar effect with second-order patterns. The phenomenon was explained by all authors in terms of mutual inhibition between directional signals during global analysis. If there are separate global analyses for first-order and second-order patterns, then we should find mutual repulsion when both directional components in the stimulus are first order and when both are second order, but no repulsion if one directional component is first order and the other is second order. On the other hand, a model based on common global analysis would predict mutual repulsion regardless of stimulus order. In the following experiment we tested these predictions.

2.1 *Methods*

2.1.1 *Observers.* Five experienced observers participated, both authors and three naive subjects.

2.1.2 *Apparatus and stimuli.* Patterns were generated by a PC equipped with an Imaging Technology graphics card, and displayed on a NEC Multisync monitor at a resolution of 512 × 512 pixels and a frame rate of 84 Hz. Stimuli were viewed through a cardboard mask of diameter 6.8 deg and consisted of two transparently moving random-block patterns presented by interleaving alternate frames of the TV display. A central red fixation cross was present at all times. Blocks (each subtending 20 min of arc × 20 min of arc) were drawn randomly at 25% density against a uniform grey background. Second-order blocks were filled with random black–white microtexture that was uncorrelated from frame to frame of the motion sequence. First-order blocks were either uniformly dark grey (22% contrast) or filled with random black–white microtexture that was correlated from frame to frame of the motion sequence. The latter stimulus was included to ensure a close match between first-order and second-order blocks, thus avoiding complications arising from differences in the visibility or spatial-frequency content of the two patterns. A flicker-photometry task was employed to arrive at a subjective brightness match between textured blocks and the grey background (see Mather and Murdoch 1997). In a given presentation, one block pattern (the 'inducer') moved vertically, while the other block pattern (the 'victim') moved in one of four directions clockwise from vertical (22°, 37°, 53°, or 79°). Six different combinations of first-order and second-order patterns were presented in different presentations (numbers in parentheses identify each pattern as either first order or second order):

Grey/Grey	Inducer, grey blocks (1); victim, grey blocks (1)
Unc/Unc	Inducer, uncorrelated texture blocks (2); victim, uncorrelated texture blocks (2)
Grey/Unc	Inducer, grey blocks (1); victim, uncorrelated texture blocks (2)
Unc/Grey	Inducer, uncorrelated texture blocks (2); victim, grey blocks (1)
Cor/Unc	Inducer, correlated texture blocks (1); victim, uncorrelated texture blocks (2)
Unc/Cor	Inducer, uncorrelated texture blocks (2); victim, correlated texture blocks (1).

Average velocity was 3.5 deg s^{-1} (there were slight velocity differences across different directions, due to the unavoidable quantisation effects of oblique displacements in video pixel arrays).

2.1.3 *Procedure.* After a single presentation (1.4 s), selected at random from all possible combinations of six stimulus conditions and four motion directions (each combination was presented twice), a white pointer appeared centred on the stimulus aperture. Using two response buttons, the observer adjusted the angle of the pointer to align it with the apparent direction of the pattern moving toward the right-hand hemifield. The observer signified that a setting was complete with a keyboard press, and a 0.5 s interval followed before the next trial began. Data were averaged across observers and trials.

2.2 *Results and discussion*

Results are shown in figure 2. Solid lines show data from all first-order (solid circles) and all second-order (open circles) stimuli. Dashed lines show data from stimuli in which one pattern was first order and the other was second order. The vertical axis plots the mean shift of apparent angular separation away from veridical, with positive values representing apparent expansion. In the absence of repulsion, all curves should cluster near zero on the ordinate. A directional repulsion effect was obtained in all conditions at small angular separations between the two patterns. The decline in repulsion as angular separation increased is very similar to that reported elsewhere (eg Hiris and Blake 1996, figure 2).

The data plots clearly fall into two groups, not on the basis of the similarity in order between the two patterns, but on the basis of the order of the inducing pattern. First-order inducing patterns generated more repulsion than second-order inducers. The greater potency of first-order patterns cannot be attributed to a simple contrast effect, because the same results were obtained with first-order patterns with zero mean contrast (vide the Cor/Unc and Unc/Cor conditions).

In an analysis of variance the main effects of stimulus condition and angular separation were significant (stimulus $F_{5,20} = 8.59$, $p = 0.0002$; angular separation $F_{3,12} = 7.85$, $p = 0.004$), as was their interaction ($F_{15,60} = 2.28$, $p = 0.012$).

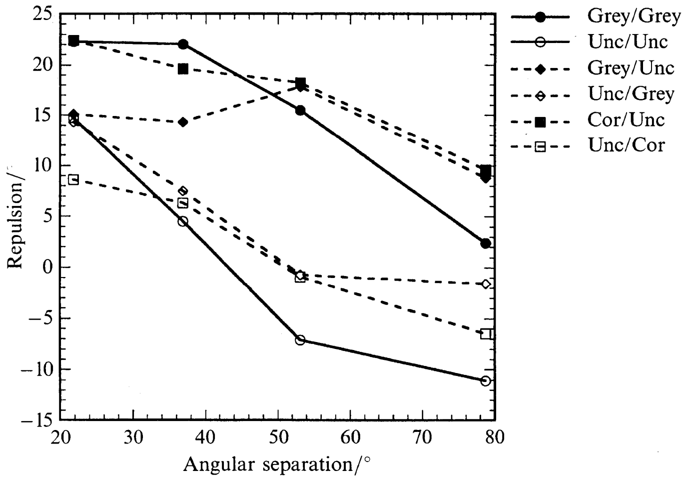

Figure 2. Results of an experiment to measure direction repulsion in transparently moving random-block arrays. Subjects viewed two transparently moving random-block patterns. Following each 1.4 s presentation, observers used two buttons to align the angle of an on-screen pointer with the apparent direction of one of the block patterns. Mean angular repulsion for five observers is plotted as a function of the angular difference between the moving components. Error bars are omitted for clarity, but standard errors were ±3.9° on average. Solid lines show results when both components were first order (solid circles) or both second order (open circles), and dashed lines show results when the two components were different in order. See text for details of the different stimulus conditions.

The presence of mutual repulsion effects between first-order and second-order patterns indicates that responses from the underlying mechanisms interact during motion analysis.

3 Experiment 2: Motion capture

Ramachandran and Cavanagh (1987) found that when a drifting low-frequency grating was superimposed on a dynamic visual-noise field, the incoherent motion of the latter was 'captured' by the former, so that the noise appeared to move along with the grating. This effect is commonly attributed to cooperative interactions during global motion integration (eg Kim and Wilson 1993). As a second test for interactions between first-order and second-order responses during motion analysis, we tested for motion capture of a second-order dynamic noise field by a drifting first-order grating and vice versa.

3.1 *Methods*

3.1.1 *Observers.* Five observers participated, four of whom also took part in the repulsion experiment.

3.1.2 *Apparatus and stimuli.* Unless stated otherwise, all details were identical to those for the previous experiment. Stimuli consisted of two transparently moving patterns, presented by interleaving alternate frames of the TV display. One pattern contained random blocks (20 min of arc × 20 min of arc), and the other pattern contained a vertical square-wave grating (spatial frequency 0.37 cycle deg^{-1}). In a given presentation either the blocks or the grating or both could be either first order or second order. First-order random blocks were uniformly dark against the grey background, and second-order blocks were filled with random black–white microtexture. First-order gratings consisted of alternating black and grey bars, and second-order gratings consisted of alternating microtextured and grey bars. The microtexture was always static during each frame of the motion sequence, but uncorrelated from frame to frame. As in previous experiments, a subjective match between the microtexture and the grey background was established by using a flicker-photometry task. In different presentations the random blocks either were displaced left (or right) from frame to frame (velocity 7.5 deg s^{-1}) or were uncorrelated from frame to frame. The grating, when present, always drifted left (or right) in steps of 0.19 cycle, at 11 deg s^{-1}. Two different first-order grating contrasts were employed in different sessions, 13% and 87%.

3.1.3 *Procedure.* In each trial of an experimental session, the observer was shown a single presentation (0.5 s) of one of eighteen possible stimuli (randomly ordered). Six of these stimuli were control displays that contained only random-block fields, either moving coherently leftward, moving coherently rightward, or incoherent, each either first order or second order. Twelve 'capture' stimuli were identical to these first six, except that the transparently drifting square-wave grating was superimposed on the random-block field. In six of the capture stimuli the grating was first order, and in the other six it was second order. The observer was instructed to fixate on the central marker, and to press a response key after each presentation to denote the perceived direction of the random-block field (ignoring the grating when present). Each of the eighteen stimuli was shown a total of thirty times in each session. Subjects performed in two sessions, one for each grating contrast, in counterbalanced order.

3.2 *Results and discussion*

All five observers were 100% accurate at reporting the direction of the block pattern when it was presented alone and moved coherently. Trials in which the block pattern moved incoherently in the absence of the grating produced chance reports of left vs right responses (the mean percentage of left responses was 46%, standard error 2.9%). However, when the drifting grating was also present, responses to the incoherent blocks were predominantly in the same direction as the drifting grating, as expected on the basis of capture. Analysis of variance on responses to the incoherent block patterns revealed that the effect of grating contrast was not significant, so data in figure 3 have been collapsed across this variable. The four columns represent the four

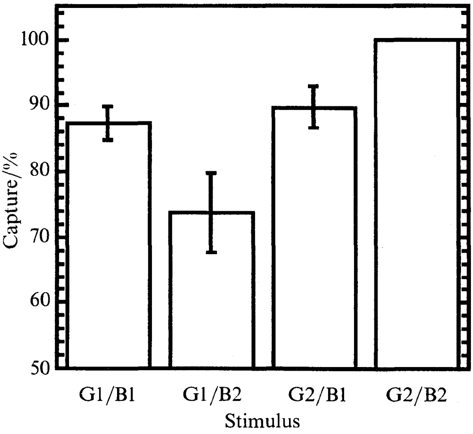

Figure 3. Results of an experiment to measure motion capture of a random-block pattern by a drifting square-wave grating. Stimuli consisted of two transparently moving patterns. One pattern contained random blocks (either first order or second order), and the other pattern contained a vertical square-wave grating (spatial frequency 0.37 cycle deg^{-1}, either first order or second order). In some presentations the random blocks were incoherent, and in others (not shown) they were displaced coherently. Subjects pressed one of two buttons to indicate the apparent direction of the block pattern. The vertical axis of the graph plots the mean percentage of trials in which the incoherent block pattern was seen to move in the same direction as the grating. Bars represent different combinations of first-order and second-order gratings (G1 and G2, respectively), and first-order and second-order blocks (B1 and B2, respectively). See text for details of other conditions and data.

possible combinations of two grating types and two dot pattern types, and are plots of the mean and standard error for each combination. Responses above 50% indicate that the incoherent motion of the blocks was captured by the motion of the grating. Second-order gratings captured the dot pattern significantly more than did first-order gratings ($F_{1,4} = 8.15$, $p = 0.046$), but there was no significant effect of block order.

4 Conclusions

Both repulsion and capture effects were obtained regardless of the order of the two components in each display. We conclude that responses from first-order and second-order motion analysers interact during global analysis. Wilson and Kim (1994) and Zhou and Baker (1996) argue in favour of a single stage of global motion analysis (left-hand scheme in figure 1), receiving pooled inputs from first-order and second-order mechanisms. Our results are consistent with this scheme, but we cannot rule out the possibility that separate first-order and second-order analyses do take place, but there is a third stage of analysis at which the outputs of these analyses interact to produce mutual repulsion and motion capture. Edwards and Badcock (1995) advocate separate first-order and second-order analyses. However, results from their two experiments (on motion coherence thresholds in very-low-density dot patterns) were rather inconclusive, since data from one experiment favoured common analysis and data from the other favoured separate analyses. We suggest that, on balance, the principle of Occam's razor favours one stage of global analysis rather than three.

A possible explanation for our results is that both first-order and second-order patterns were detected by conventional Fourier-based motion detectors, owing to residual intensity cues in second-order stimuli. However, we took care to use a flicker-photometry task to arrive at a subjective match between textured and grey blocks. Mather and Murdoch (1997) established that this procedure effectively removes intensity cues and produces matches that are consistent with a minimum-motion technique for eliminating these cues.

Given that first-order and second-order responses appear to be pooled at some stage during motion analysis, the question arises as to why the visual system generates second-order responses at all, rather than relying just on first-order responses. Different surfaces in natural images may vary along several perceptual dimensions simultaneously (eg intensity, colour, and texture), because of differences in reflectance and physical structure (eg surface markings, grain). Second-order responses allow surface segmentation and analysis even when intensity and colour differences are incoherent or absent. Models of second-order motion-energy detection form part of what might be called a 'second-order vision' system, since they share many features in common with theories of energy-based texture analysis in spatial vision (eg Malik and Perona 1990; Landy and Bergen 1991).

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