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Evidence for Separate Motion-detecting Mechanisms for First- and Second-order Motion in Human Vision

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Current theories of second-order motion perception postulate that such motion is detected by either a high-level mechanism which computes the temporal correspondences between "features" extracted from the image, or low-level motion mechanisms which operate on a nonlinear, neural transformation of the luminance profile of the image. Theories which favour the latter strategy either suggest that first- and second-order motion are detected by a common mechanism or else that distinct mechanisms exist for the two types of motion, both operating on similar principles. The aim of this study was to differentiate between these possibilities. Observers were required to judge the direction of multiframe motion sequences in which the frames alternated between sinusoidal variations in luminance (first order) and similar variations in contrast (second order). On each frame the modulation signal was displaced by some fraction of its spatial period. The motion sequences were designed such that integration of both types of frame (first and second order) would lead to unambiguous motion in a particular direction whilst separate analysis of first- or second-order frames alone would yield ambiguous motion. The results show clearly that observers were unable to integrate the first- and second-order frames of such motion sequences. However, when observers were presented with motion sequences in which the frames alternated between two, different types of second-order image (variations in the contrast or size of the elements constituting a random noise field) perceived direction was always consistent with integration of both image types. This is taken as support for models that suggest that first- and second-order motion are processed by distinct mechanisms in the visual system and that each mechanism is only sensitive to one type of motion. It is suggested that several varieties of second-order motion stimuli may be regarded as equivalent to contrast-modulated images when considered in terms of the effects of local spatiotemporal filtering operations carried out by the human visual system. In this respect, our results are consistent with the "texture grabber" concept of Werkhoven, Sperling and Chubb [(1993) *Vision Research*, *33*, 463–485].

Motion perception First-order motion Second-order motion Rectification

GENERAL INTRODUCTION

The study of motion processing by the visual system has recently begun to focus on the distinction between "first-order motion" and "second-order motion" (Cavangh & Mather, 1989). First-order motion stimuli are defined by spatiotemporal variations in luminance or colour in the retinal image and second-order motion stimuli are defined by spatiotemporal variations in other characteristics such as depth, contrast, or relative motion. Chubb and Sperling (1988, 1989a) have described several examples of second-order or "non-Fourier" motion stimuli which they term "drift-balanced". Fourier analysis, when applied to such stimuli, does not directly convey the perceived direction of motion because motion energy is equal in opposite directions. Chubb and Sperling offer formal proofs that their stimuli remain drift-balanced even after spatiotemporal filtering by the visual system and should therefore be invisible to conventional, low-level motion detectors which operate by detecting motion energy (e.g. Adelson & Bergen, 1985). Such a stimulus can be constructed by sinusoidally modulating the contrast of a two-dimensional (2-d), random noise field across space and time.

Although it is well established that observers can readily perceive second-order motion (e.g. Anstis, 1980; Cavanagh & Mather, 1989; Ramachandran, Rao & Vidyasagar, 1973), much uncertainty exists as to the mechanisms involved. However, two basic strategies for detecting second-order motion have been proposed and these are described below.

(i) Firstly, since second-order motion stimuli undoubtedly contain features (e.g. the high- and low-contrast regions or "bars" of a contrast-modulated noise field may be regarded as features) it is possible

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that motion perception is mediated by a high-level, feature-matching mechanism such as the long-range system proposed by Braddick (1980) or the post-attentive, feature-tracking mechanism proposed by Cavanagh (1991, 1992). A detailed model of motion detection based upon this principle has been developed by Ullman (1979). Ullman's "*minimal mapping theory*" provides algorithms for computing the most probable correspondences between primitive *elements* of figures (low-level "tokens") such as edges, lines, blobs and corners.

(ii) Secondly, several models have been developed that account for second-order motion perception in terms of low-level motion mechanisms and thus negate the need explicitly to encode features and the correspondences between them. These models fall into two main classes. Firstly, several computational models suggest that second-order motion perception is mediated by motion detectors which are separate from those used for detecting first-order motion but which operate on qualitatively similar principles. In particular, Chubb and Sperling (1988, 1989a) suggest that motion energy is introduced into the neural representation of the image by a process that can be modelled as rectifying the luminance profile of the image and that this energy is then detected conventionally. Werkhoven, Sperling and Chubb (1993) have recently developed a model of second-order motion perception based upon this principle. A somewhat similar idea has been proposed by Wilson, Ferrera and Yo (1992) and incorporated into a model of motion detection that can successfully predict the perceived direction of texture boundaries and type II plaids (Wilson & Mast, 1993).

A second possibility is that first- and second-order motion are detected by the same low-level mechanism. Two models have recently been presented in which a single, intensity-based mechanism detects both first- and second-order motion. One of these models, suggested by Grzywacz (1992) and published in abstract form, detects motion on the basis of the method of Chubb and Sperling (1988, 1989a) (i.e. band-pass filtering followed by rectification and motion energy detection) but dispenses with the separate, linear mechanism. The other model, by Johnston, McOwan and Buxton (1992), is based on the spatiotemporal gradient scheme of Marr and Ullman (1981).

In terms of human vision there is evidence that feature-based strategies may be used at least some of the time for the detection of second-order motion. For example, Smith (1994) has recently presented two experiments using complex, contrast-modulated motion stimuli which demonstrate that under conditions which are believed to favour the use of high-level, feature-based strategies [i.e. when an inter-stimulus interval (ISI) of 60 msec is introduced between updates of the position of the stimulus (Georgeson & Harris, 1990)], observers report motion in the direction of the "features". Furthermore, direction-identification performance under such conditions could be impoverished by the introduction of second-order noise masks constructed so as to specifically reduce the salience of the stimulus features.

However, there is also evidence that second-order motion is not detected exclusively by a high-level, feature-based mechanism. For example, in Smith's study (described above) he found that without an ISI observers report motion in a direction consistent with the use of low-level, motion-detecting strategies, rather than feature-tracking or matching, suggesting that the former normally dominate the perception of second-order motion. These results are supported by the finding that observers can reliably perceive motion in dense, briefly presented random-dot kinematograms (RDKs) in which the dots are defined by second-order characteristics such as variations in contrast. Such stimuli are assumed to preclude the involvement of feature-based motion processing (Cavanagh & Mather, 1989; Nishida, 1993).

Given that there is compelling evidence for the involvement of a low-level mechanism in the perception of second-order motion in human vision, an important issue concerns the nature of the mechanism involved. Despite the obvious parsimony of models that postulate the existence of a single, low-level mechanism sensitive to both first- and second-order motion, several lines of psychophysical evidence do not support this suggestion. For example, Chubb and Sperling (1989b) have produced motion displays that contain first- and second-order motion in opposite directions and have found that the perceived direction reverses according to viewing distance. These results were interpreted in terms of the existence of distinct mechanisms for the detection of first- and second-order motion. Harris and Smith (1992) found that second-order motion stimuli failed to elicit optokinetic nystagmus (OKN) whilst first-order motion stimuli of equal visibility did, again suggesting the existence of two distinct mechanisms, only one of which drives OKN. Recently, Mather and West (1993) constructed two-frame RDKs in which the random-dot pattern on each frame was defined by either first-order characteristics (the dots were defined by luminance) or second-order characteristics (the dots were composed of random texture that differed from the background in contrast). Observers were consistently able to detect the direction of RDK displacement for pairs of frames that were defined by the same characteristics (i.e. both frames were composed of either first- or second-order dots). However, when the frames of the RDK were defined by different characteristics direction-identification performance was at chance, implying that the observers were unable to integrate the two frames of the RDK. The study of Mather and West provides compelling evidence that first- and second-order motion are not encoded by a common motion mechanism.

The aim of the present study was to investigate further the integration of motion signals by the low-level mechanism or mechanisms responsible for encoding first- and second-order motion in human vision, in order to differentiate between current models of second-order motion perception. In contrast to the study of Mather and West (1993) multiframe motion sequences, rather than two-frame motion displays, were generally employed and periodic stimuli rather than random-dot patterns were used. Periodic stimuli are useful tools for studying the integration of first- and second-order motion signals because they allow precise predictions to be made concerning the perceived direction of motion as a function of the magnitude of the spatial displacement or phase shift on each image update (see below). Observers were required to judge the direction of motion sequences in which the display alternated between frames containing first-order information (luminance-modulated noise) and frames containing comparable second-order information (contrast- or size-modulated noise). The motion sequences were constructed so that integration of first- and second-order frames by the visual system should lead to an unambiguous percept of motion in a particular direction whilst separate analysis of the first- or second-order frames alone should yield ambiguous motion.

EXPERIMENT 1—CAN THE VISUAL SYSTEM INTEGRATE THE FIRST- AND SECOND-ORDER FRAMES OF A MULTIFRAME MOTION SEQUENCE?

Introduction

If first- and second-order motion are encoded by a single, low-level mechanism, that mechanism should be able to integrate the first- and second-order frames of a multiframe motion sequence. For example, in the case of a one-dimensional (1-d) sinusoidal modulation in luminance or contrast, when the spatial displacement on each image update is 0.25 cycles of the modulation frequency (f) (i.e. 90 deg phase shift) then observers should perceive motion in a consistent direction. However, if first- and second-order motion are detected by separate mechanisms then observers should perceive ambiguous motion when each image is displaced 0.25 cycles because the displacement between images of the same type (either first- or second-order) is 0.5 cycles of f (180 deg phase shift). Displacing a sinusoid 0.5 cycles of f leftward produces the same image as moving it 0.5 cycles rightward so, in principle, the true direction cannot be recovered.

Method

Observers

Two observers participated in the study and both had normal or corrected to normal acuity. Observer TL was one of the authors and observer CDJ was a paid volunteer who was unaware of the purpose of the experiment.

Apparatus and stimuli

All stimuli were eight-bit images generated by a *MATROX* image processing system and displayed on an APPLE, monochrome monitor with a frame (refresh) rate of 67 Hz and white P4 phosphor. The luminance of the monitor was carefully gamma-corrected using a look-up table so that luminance was a linear function of the digital representation of the image. Calibration was performed using second-order images similar to those employed in the experiments so that gamma-correction was accurate with respect to such stimuli. Any nonlinearity in the display could introduce moving distortion products (Henning, Hertz & Broadbent, 1975) into the second-order motion stimuli which would then be visible to a first-order motion-detecting mechanism. The stimuli were presented within a square window at the centre of the display and the window subtended an angle of 4 × 4 deg at the viewing distance of 1.2 m. The mean luminance of the square window and the remainder of the display area (which was homogeneous) was approx. 20 cd/m^2. A prominent fixation spot was located at the centre of the display, which was viewed binocularly.

Motion sequences were produced by alternating between frames containing second-order, contrast-modulated noise and frames containing first-order, luminance-modulated noise. All frames contained the same 2-d, static noise sample. On the first frame of a motion sequence 1-bit noise [see Fig. 1(b)] was multiplied by a 1 c/deg, vertical sine grating [Fig. 1(a)] to produce contrast-modulated noise. In the second frame the sine grating was displaced some fraction of its spatial period and added to the noise to produce luminance-modulated noise. On the third frame the sine grating was shifted again and multiplied, and so on. The speed of the motion sequences produced was maintained at 4.2 deg/sec (4.2 Hz) across different spatial displacements by manipulating the image update rate between 67 and 9.6 Hz. Each noise element subtended 2.8 × 2.8 arc min and was independently assigned with probability 0.5 to be either "white" or "black". There were 21 noise elements per spatial cycle of f. The mean contrast of the noise for the second-order frames was half the maximum possible (Michelson contrast of 0.45) and the amplitude of the contrast modulation (modulation depth) could be varied within the range 0.0–1.0 defined as:

$$\text{modulation depth} = (C_{\max} - C_{\min})/(C_{\max} + C_{\min})$$

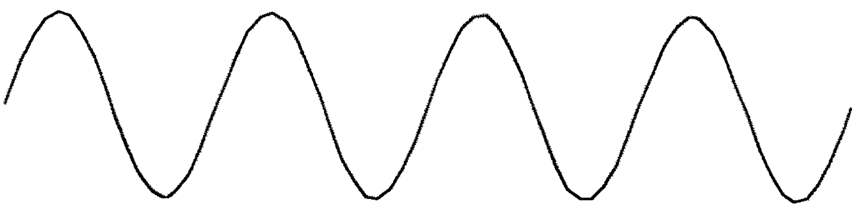
where $C_{\max}$ and $C_{\min}$ are the maximum and minimum local contrasts (Michelson) in the image. The luminance profile of a second-order frame is shown schematically in Fig. 1(c).

For the first-order frames the amplitude of the noise following addition with the sine grating was constant and was always equal to the mean amplitude of the noise in the second-order frames described previously. The amplitude of the luminance modulation (Michelson contrast or modulation depth) could be varied within the range 0.0–0.5 defined as:

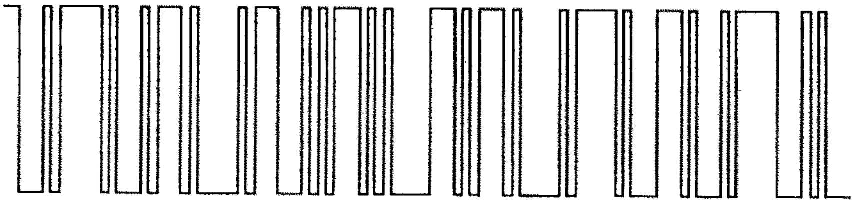
$$\text{modulation depth} = (L_{\max} - L_{\min})/(L_{\max} + L_{\min})$$

where $L_{\max}$ and $L_{\min}$ are the maximum and minimum mean luminances averaged over adjacent pairs of noise elements with opposite polarity in the image. The luminance profile of a first-order frame is shown schematically in Fig. 1(d).

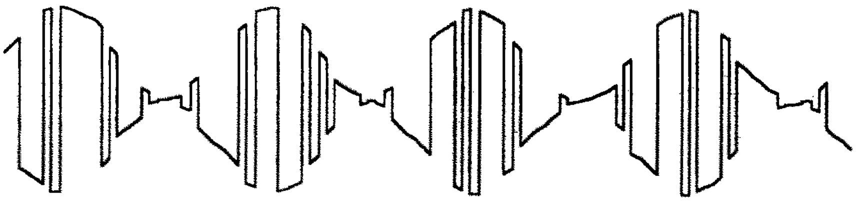
The first- and second-order images were presented at the same multiple of direction-identification threshold in order approximately to equate the images for suprathreshold visibility. However, additional studies revealed that this manipulation was not crucial (see



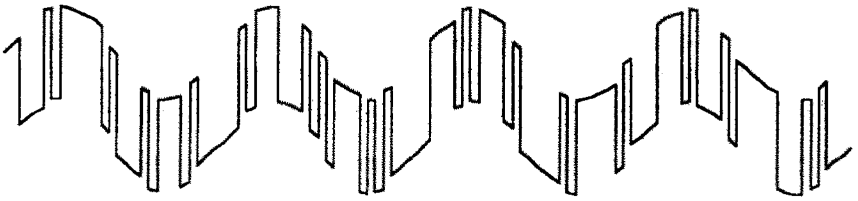
(a) Sine grating



(b) Binary noise field



(c) Contrast-modulated noise (second-order motion stimulus)



(d) Luminance-modulated noise (first-order motion stimulus)

FIGURE 1. Luminance profiles of the first- and second-order images used. Each trace represents a horizontal section through an image and shows how luminance changes as a function of spatial position. Second-order images were composed of contrast-modulated noise (c) produced by multiplying a static, binary noise field (b) by a sine grating (a). For the purposes of multiplication the noise was signed (range −1 to +1) and the modulation signal was unsigned (range 0–1). First-order images were composed of luminance-modulated noise produced by summing a static, binary noise field (b) and a sine grating (a) and scaling. The noise field (carrier) was spatially broadband and its Fourier power spectrum was essentially flat for frequencies up to several octaves above the modulation frequency of that shown in (c). This was also true of the noise fields employed in Expts 1 and 2.

Results). Thresholds were individually measured for each observer using the method of constant stimuli and motion sequences identical to those described above with the exception that all frames contained only first- or second-order images.

The suprathreshold modulation depth of the contrast-modulated noise was always 1.0 and the modulation depths of the first-order images were scaled accordingly so that all image types were presented at the same multiple of their respective thresholds. For example, this was approx. 6.4 times threshold for observer TL and the modulation depths of the contrast-modulated noise and luminance-modulated noise were 1.0 and 0.10, respectively. The corresponding values for observer CDJ were 1.0 and 0.11, respectively.

Procedure

Direction-identification performance was measured using the method of constant stimuli. In each run of trials the observer was presented with 70 motion sequences each lasting 1.5 sec and was required to identify the direction of motion (either rightward or leftward) using two response buttons. Motion sequences were separated by a 4 sec interval containing a homogeneous field of mean luminance 20 cd/m^2. In each run of trials seven spatial displacements were used ranging from 1/16 (0.063) to 7/16 (0.44) cycles of *f*. The magnitude of the spatial displacement on each image update was constant throughout each trial but randomized from trial to trial (with the constraint that no value was repeated until all seven had been presented consecutively). The direction of the displacement was either leftward or rightward and was randomized between trials. Each observer completed eight runs of trials.

Results and Discussion

Weibull functions (Weibull, 1951) were fitted to the resulting data and the results are plotted as the percentage of trials on which the observer reported motion in the "correct" direction (the direction of the displacement) as a function of the displacement on each image update, expressed as a fraction of the spatial period of *f*.

Although performance is plotted as the percentage of trials on which observers reported motion in the "correct" direction (direction of the displacement), the term "correct" is arbitrary in the sense that theoretically a single motion mechanism accessing both types of image could consistently signal motion in either the "correct" or "incorrect" direction depending on whether the high-luminance regions of the luminance-modulated noise correspond to the high-contrast regions of the contrast-modulated noise, following the nonlinear operation(s) that are hypothesised to occur prior to motion analysis, or to the low-contrast regions. In Fig. 2 the "correct" direction refers to the direction in which the low-contrast regions were displaced relative to the low-luminance regions on consecutive frames (or equivalently the direction in which the high-contrast regions were displaced relative to the high-luminance regions).

The crucial point to note is that for spatial displacements of 0.25 cycles of *f*, the magnitude of the displacement between consecutive images of the same type is 0.5 cycles of *f*. Thus, separate analysis of first- and second-order motion predicts ambiguous motion. However, a single motion mechanism accessing both types of image in the sequence predicts perception of unambiguous motion in the direction of the displacement (100% correct) or the opposite direction (0% correct—see above) because motion is adequately sampled (4 times per cycle). The observed level of performance is at chance at 0.25 cycles displacement for both observers suggesting that separate mechanisms exist for the perception of first- and second-order motion (e.g. Chubb & Sperling, 1988, 1989a; Wilson *et al.*, 1992).

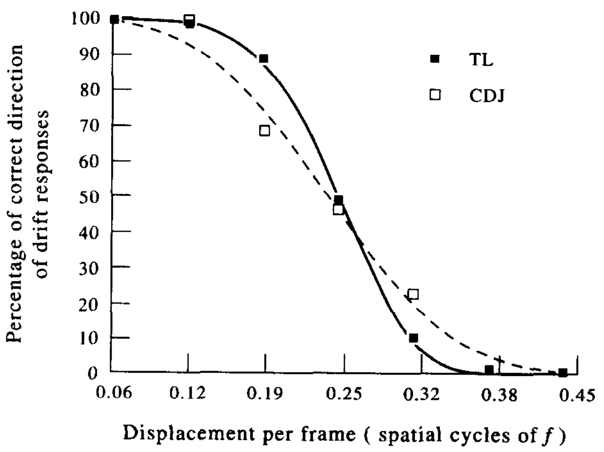


FIGURE 2. Psychometric functions for two observers for motion sequences containing alternating contrast- and luminance-modulated noise. The spatial frequency of the modulation signal (*f*) was 1.0 c/deg and the speed of the motion sequences was maintained at 4.2 deg/sec.

A single motion mechanism predicts perception of motion in a single, consistent direction up to displacements approaching 0.5 cycles of *f*. Separate analysis of first- and second-order motion predicts correct direction perception between 0 and 0.25 cycles of *f*. Aliasing (0% correct) is predicted between 0.25 and 0.5 cycles of *f* because the displacement between images of the same type is between 0.5 and 1.0 cycles of *f*. From Fig. 2 it is apparent that this is the observed result for both observers.

Despite the fact that the first- and second-order images were equated for visibility, the lack of integration of frames by a common motion mechanism could be the result of a mismatch in the effective modulation depths of the first- and second-order images. To eliminate this possiblity, control data were obtained using motion sequences in which all frames contained luminance-modulated noise but modulation depth (Michelson contrast) was different between consecutive frames. For all displacements, motion was reliably perceived in the correct (displacement) direction for modulation depth differences of at least a log unit (e.g. modulation depths of 0.5 and 0.05), demonstrating that the first-order frames are integrated despite the modulation depth mismatch.

The failure to find integration of first-order images and second-order images when the displacement on each image update was 0.25 cycles of *f* was not due to the particular frame duration used for this condition (i.e. 60 msec). When the frame duration was varied in the range 15–194 msec observers always perceived ambiguous motion for displacements of 0.25 cycles of *f* (data not shown). Furthermore, in the present experiment (see Fig. 2) when the magnitude of the spatial displacement on each image update was $\leqslant 0.25$ cycles of *f*, motion in an unambiguous direction was consistently reported for frame durations ranging from 15 to 45 msec and 75 to 104 msec, respectively. Similarly, introducing an ISI in the range 50–194 msec between the first- and second-order images in the motion sequence (conditions which supposedly impair low-level motion-detecting mechanisms and favour the use of high-level, feature-matching or -tracking processes) had no effect on the observers' performance. That is, ambiguous motion was always seen for spatial displacement of 0.25 cycles of *f*.

The pattern of results found cannot be explained by an artefact due to the presence, in the retinal image, of distortion products arising from a brightness nonlinearity in the display or an early nonlinearity in the visual system (e.g. Burton, 1973; Derrington, 1987; MacLeod, Williams & Makous, 1992). Such distortion products would be expected to introduce first-order (luminance) components into the contrast-modulated images at the modulation frequency so that all frames of the motion sequences would effectively contain first-order images. If this were the case, when the magnitude of the spatial displacement was 0.25 cycles of *f*, one would expect observers consistently to perceive motion in either the direction of the displacement or the opposite direction, depending on the nature of the nonlinearity in question. The fact that this did not occur suggests that the gamma-correction used was highly accurate with respect to the stimuli employed and that any early brightness nonlinearity in the visual system is too small to explain the visibility of contrast-modulated noise.

EXPERIMENT 2—EVIDENCE IN SUPPORT OF MULTIPLE FILTERING PRIOR TO RECTIFICATION AND MOTION ANALYSIS

Introduction

The results of Expt 1, in common with those of Mather and West (1993), support models that postulate the existence of separate, low-level mechanisms for the detection of first- and second-order motion. Indeed, the results suggest that the mechanism responsible for encoding second-order motion at a particular spatio-temporal scale is apparently not sensitive to first-order motion at the same scale. This is consistent with the model of Wilson *et al.* (1992) which predicts that the second-order motion-detecting mechanism will be "blind" to the first-order frames of the motion sequences used in Expt 1. In the second-order motion-detecting pathway of this model, the image is convolved with a set of band-pass spatial filters and the outputs of these are then squared (or rectified) and then filtered at a different (one-octave lower) spatial frequency prior to motion analysis. Within such a scheme a sinusoidal luminance modulation on the scale at which motion analysis occurs will not survive the first filtering operation.

The results, however, are not consistent with models based on the scheme suggested by Werkhoven *et al.* (1993). They propose a second-order motion-detecting mechanism in which a single, low-pass spatial filter precedes rectification and motion energy detection. Such a filter would pass first-order signals at the spatial frequency of motion detection, as well as the lower spatial frequency components of a modulated carrier (e.g. noise). One would therefore expect such a motion mechanism to detect both first- and second-order frames of the motion sequences employed in Expt 1 and so to signal motion in a consistent direction for all spatial displacements. This was not the observed result. However, if the nonlinear transformation following filtering is full-wave (as opposed to half-wave) rectification or squaring, this operation would effectively double the fundamental spatial frequency of first-order images (and introduce harmonics) but not second-order images as shown schematically in Figs 3 and 4. Some previous experiments support the notion that second-order motion-detection requires full-wave as opposed to half-wave rectification (Chubb & Sperling, 1989b). Within such a scheme a motion energy detector operating at any one spatial scale would not be expected to integrate the two image types because motion energy would lie at different spatial frequencies.

In order to differentiate between the models of Werkhoven *et al.* and Wilson *et al.*, observers were required, in Expt 2, to identify the direction of motion of a two-frame motion sequence in which the display alternated between one frame containing luminance-modulated noise and a second frame containing contrast-modulated noise. However, the spatial frequency of the luminance modulation in the first-order frame was half that of the contrast modulation in the second-order frame. The model of Wilson *et al.* (1992) predicts that observers should not perceive motion in such a display because first-order signals within the second-order pathway cannot survive both filtering operations. However, the model of Werkhoven *et al.* (1993), assuming full-wave rectification, predicts that observers should perceive motion in the direction of the displacement for such two-frame displays because following rectification, the first- and second-order inputs to the motion analysis stage will be at the same spatial frequency. The scheme of Werkhoven *et al.* (1993) with half-wave rectification predicts that observers should not perceive motion, since frequency doubling does not occur, but does not predict the results of Expt 1.

Method

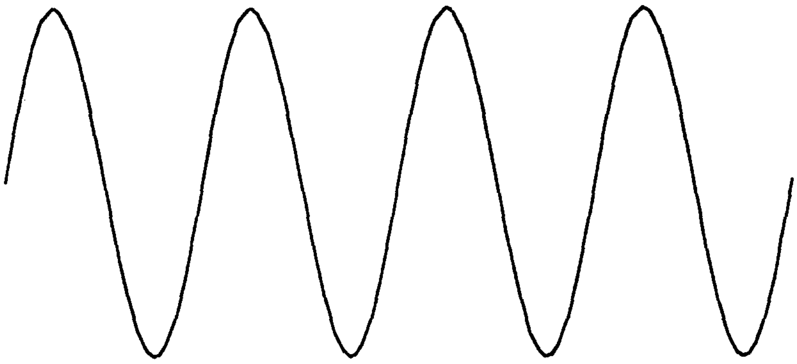
Observers

Two observers participated in the study and both had normal acuity. Observer TL was one of the authors and observer PJB was an experienced psychophysical observer who was, however, unaware of the purpose of the experiment.

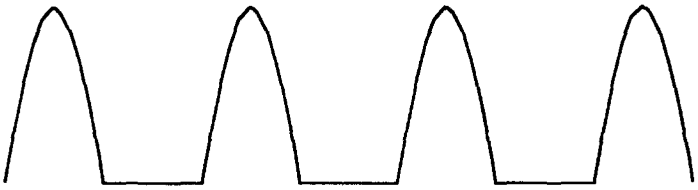
Apparatus and stimuli

All stimuli were generated and displayed in an identical manner to that described for Expt 1. However, two-frame motion sequences were employed in order to isolate the hypothetical second-order motion-detecting mechanism. Multiframe motion sequences would simultaneously activate both the first- and second-order motion-detecting mechanisms (e.g. the first-order motion-detecting mechanism would respond to the motion of the first-order frames) and confound the results because direction-identification performance would not reflect the activity of the second-order motion-detecting mechanism alone. Three types of two-frame motion sequence were investigated and these are described below.

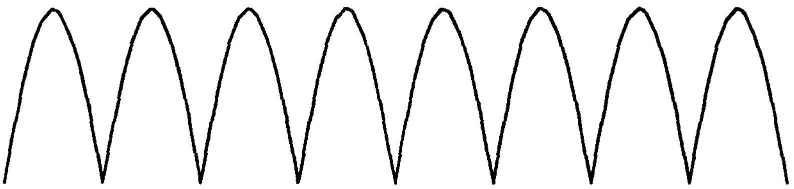
(i) Second-order motion sequences in which both frames contained contrast-modulated noise produced by multiplying 2-d, static noise by a vertical, 2 c/deg sine grating. The magnitude of the spatial displacement between frames was fixed at 0.125 deg (0.25 cycles of the modulation frequency).



(a) Sine grating



(b) Positive half-wave rectification



(c) Full-wave rectification

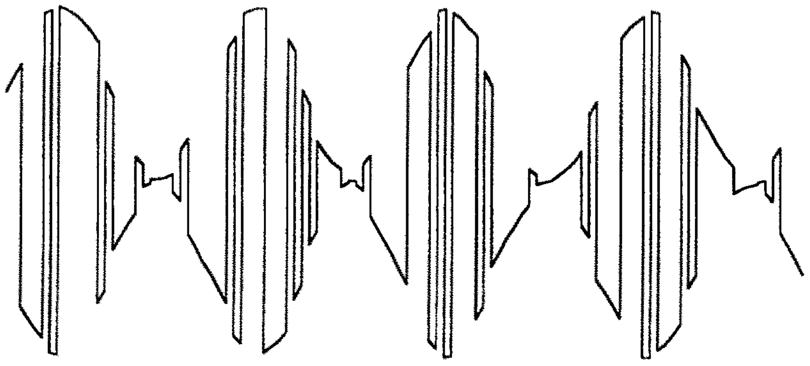
FIGURE 3. Luminance profiles of a sine grating (a), a half-wave rectified sine grating (b) and a full-wave rectified sine grating (c). Each trace shows how luminance changes as a function of spatial position in the horizontal dimension. Half-wave rectification following spatial filtering preserves the fundamental frequency of the sine grating whilst full-wave rectification results in frequency doubling. Both operations also introduce harmonics that are not present in the original stimulus shown in (a).

(ii) First-order motion sequences in which both frames contained luminance-modulated noise produced by adding 2-d, static noise to a vertical, 1 c/deg sine grating. The magnitude of the spatial displacement between frames was fixed at 0.125 deg (0.125 cycles of the modulation frequency).

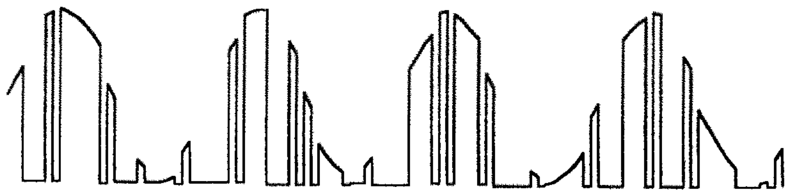
(iii) Mixed motion sequences in which one frame contained contrast-modulated noise and the other luminance-modulated noise. The order in which the first- and second-order frames were presented was varied randomly. The spatial frequency of the contrast-modulated noise was 2 c/deg and the spatial frequency of the luminance-modulated noise was 1 c/deg. The magnitude of the spatial displacement between frames was fixed at 0.125 deg.

For all three types of motion sequence the duration of each frame was 104 msec and both frames always contained the same noise sample which was identical in terms of its dimensions, density and contrast to the noise sample used in Expt 1.

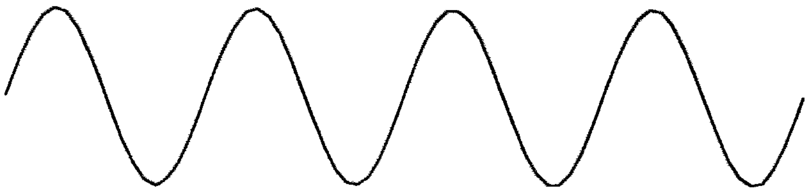
The first- and second-order images were presented at the same multiple of direction-identification threshold in order approximately to equate their suprathreshold visibility. However, pilot studies revealed that again this manipulation was not crucial. Thresholds were individually measured for each observer using the method



(a) Contrast-modulated noise



(b) Positive half-wave rectification



(c) Full-wave rectification

FIGURE 4. Luminance profiles of contrast-modulated noise (a), half-wave rectified contrast-modulated noise (b) and full-wave rectified contrast-modulated noise (c). Each trace shows how luminance changes as a function of spatial position in the horizontal dimension. Since contrast-modulated noise is spatially broadband, filtering at any arbitrary spatial frequency higher than the modulation frequency followed by either half- or full-wave rectification would be sufficient to introduce a luminance modulation at the same frequency as the modulation in contrast shown in (a). For clarity filtered stimuli are not shown because current models of second-order motion perception differ as to the nature and number of filters that are applied to the retinal image (see main text).

of constant stimuli and two-frame motion sequences identical to those described in (i) and (ii) above. The suprathreshold modulation depth of the contrast-modulated noise was always 1.0 and the modulation depth of the luminance-modulated noise was scaled accordingly so that both image types were presented at the same multiple of threshold. For example, this was approx. 4.6 times threshold for observer TL and the modulation depths of the contrast-modulated noise and luminance-modulated noise were 1.0 and 0.07, respectively. The corresponding values for observer PJB were also 1.0 and 0.07, respectively.

Procedure

Within each run of trials observers were presented with a total of 90 motion sequences (30 presentations of each type of motion sequence described above) and were required to identify the direction of motion of each using two response buttons. Trials of the three types were randomly interleaved. The direction of displacement was also randomised from trial to trial and was either leftward or rightward. The total duration of each motion sequence was 208 msec and motion sequences were separated by a 4 sec interval containing a homogeneous field of mean luminance 20 cd/m^2. Each observer completed a total of three runs of trials and from the resulting data the mean percentage of correct responses for each motion sequence was calculated for each observer.

Results and Discussion

Results are plotted in the form of histograms (see Fig. 5) showing the percentage of trials on which the observers reported motion in the correct direction (direction of the displacement) for each motion sequence type. It is apparent that when motion sequences were composed of two first-order frames (luminance-modulated noise) or two second-order frames (contrast-modulated noise) both observers consistently reported motion in the direction of the displacement. Indeed for both observers, performance was very close to 100% correct for these two types of motion sequence. However, from Fig. 5 it is also apparent that when motion sequences were composed of a first-order frame and a second-order frame, performance was at chance for both observers indicating that they were unable to integrate the two frames of the motion sequences.

Thus, the results of the present experiment, taken together with those of Expt 1, favour models of second-order motion that propose that the image is initially filtered at several different spatial scales (by band-pass filters) prior to full-wave rectification or squaring and motion analysis (e.g. Wilson *et al.*, 1992). The fact that the second-order motion-detecting mechanism appears to be insensitive to first-order motion is also consistent with the second, lower frequency filtering stage of Wilson *et al.*'s model. The results do not support models which suggest the existence of a single broadband filter prior to rectification and motion detection (e.g. Werkhoven *et al.*, 1993).

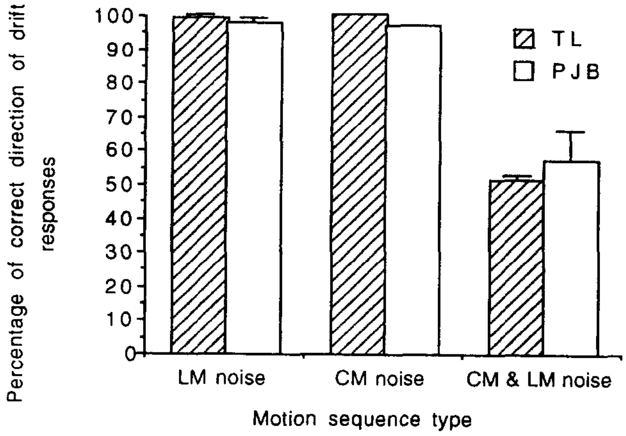


FIGURE 5. Histogram of the mean percentage of correct direction of drift responses for two-frame motion sequences containing either contrast-modulated (CM) noise, luminance-modulated (LM) noise or contrast- and luminance-modulated noise for both observers. The spatial frequency of the luminance modulation was 1 c/deg and the spatial frequency of the contrast modulation was 2 c/deg. The vertical line atop each bar (where visible) represents 1 SE.

Recently, a physiological study of the responses of motion-sensitive neurones in areas 17 and 18 of the feline cortex to luminance- and contrast-modulated stimuli has been reported (Zhou & Baker, 1993). Responses to drifting sine gratings and stationary high spatial frequency sine gratings with a drifting contrast modulation were compared. They found that the spatial frequency tuning of cells responsive to both types of motion stimuli was typically lower for contrast modulations than luminance modulations. This also supports the notion that second-order motion is detected on the basis of an early filtering stage, followed by a pointwise nonlinearity and a second, lower frequency spatial filtering stage. Within such a scheme a sinusoidal modulation in luminance at the spatial scale at which motion is detected will not survive the first filtering stage. Thus, one mechanism responds only to the first-order images in a motion sequence and the other only to the second-order images.

EXPERIMENT 3—INTEGRATION OF TWO DIFFERENT TYPES OF SECOND-ORDER IMAGE BY THE SECOND-ORDER MOTION MECHANISM

Introduction

The results of Expt 1 support models that suggest that first- and second-order motion are detected by separate, low-level mechanisms in the human visual system, at least for the classes of stimuli investigated. This raises and important question. Can the mechanism that encodes the motion of contrast-modulated noise also encode the motion of second-order stimuli defined by spatiotemporal variations in characteristics other than contrast? In order to investigate this possibility, multiframe motion sequences similar to those used in Expt 1 were constructed in which all frames contained second-order images. On consecutive frames, these images were defined by different second-order characteristics. If a single, nonlinear motion mechanism can integrate the frames of such a motion sequence, observers should always perceive motion consistently in a single direction for all spatial displacements on each image update less than 0.5 cycles of f. Alternatively, if specialised motion mechanisms exist for different types of second-order motion then such integration should not be possible. Motion sequences containing first- and second-order images were also investigated in order to extend the findings of Expts 1 and 2.

Method

Observers

Two observers participated in the study and both had normal acuity. Observer TL was one of the authors and observer MK was a paid volunteer who was unaware of the purpose of the experiment.

Apparatus and stimuli

All stimuli were generated and displayed in an identical manner to that described for Expt 1 with the following exceptions. Three types of motion sequence were investigated and these are described below.

(i) Motion sequences similar to those used in Expt 1 in which the display alternated between frames containing contrast-modulated noise and frames containing luminance-modulated noise. All frames contained 2-d, noise but this was replaced on each image update with a different random noise sample. This was to ensure that all motion sequences were perceptually as similar as possible [see (ii) below]. Each noise element subtended 3.75 × 3.75 arc min and was independently assigned with probability 0.5 to be either "white" or "black". There were 16 noise elements per spatial cycle of the contrast or luminance modulation. On the first frame of a motion sequence of this type, the noise was multiplied by a vertical, square-wave grating to produce contrast-modulated noise, in the second frame the square-wave grating was displaced some fraction of its spatial period and added to the noise to produce luminance-modulated noise. On the third frame the square-wave grating was shifted again and multiplied and so on. The fundamental spatial frequency (f) of the square-wave modulation was 1 c/deg.

(ii) Motion sequences in which the display alternated beween frames containing luminance-modulated noise and frames containing size-modulated noise. All frames contained 2-d noise but this was again replaced on each image update with a different random noise sample. The luminance-modulated noise was identical to that described in (i) above. The size-modulated noise was produced by modulating the size of the random elements constituting the noise with a 1-d, square-wave profile to give the appearance of a square-wave grating with a fundamental frequency of 1 c/deg defined by variations in noise element size. The mean size of the noise elements was always 3.75 × 3.75 arc min and again each element was independently assigned with probability 0.5 to be either "white" or "black". The modulation depth could be varied between 0.0 and 0.75 defined as:

$$\text{modulation depth} = (S_{\max} - S_{\min})/(S_{\max} + S_{\min})$$

where $S_{\max}$ and $S_{\min}$ are the sizes of the large and small noise elements, respectively. A space–time (x–t) plot of a rightward translating image of this type is shown in Fig. 6.

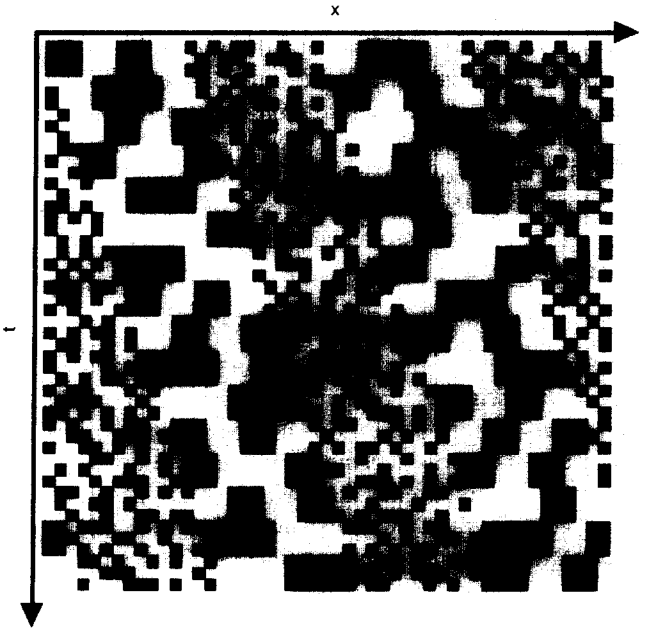


FIGURE 6. Space–time (x–t) plot of a square-wave, size-modulated noise pattern drifting rightwards. Such a second-order stimulus can be constructed by modulating the size of the random elements constituting a 2-d noise field with a drafting, 1-d, square-wave profile to give the appearance of a drifting square-wave grating defined by variations in the size of the noise elements. The noise on consecutive frames was uncorrelated (dynamic).

(iii) Motion sequences in which the display alternated between frames containing contrast-modulated noise and frames containing size-modulated noise. That is, all frames contained second-order images. All frames contained 2-d noise but this was again replaced on each image update with a different random noise sample. The contrast-modulated noise was identical to that described in (i) above and the size-modulated noise was identical to that described in (ii) above.

The speed of all motion sequences produced was maintained at 4.2 deg/sec (4.2 Hz) across different spatial displacements by manipulating the image update rate between 67 and 9.6 Hz.

The first- and second-order images were presented at the same multiple of direction-identification threshold in order approximately to equate their suprathreshold visibility. However, once again pilot studies revealed that this manipulation was not crucial for the present experiment. Thresholds were individually measured for each observer using the method of constant stimuli and motion sequences identical to those described above with the exception that all frames contained only first- or second-order images (of the same type). The suprathreshold modulation depth of the size-modulated noise (the stimulus to which sensitivity was lowest) was always 0.5 and the modulation depths of the contrast- and luminance-modulated images were scaled accordingly so that all image types were presented at the same multiple of their respective thresholds. For example, this was approx. 2.7 times threshold for observer TL and the modulation depths of the size-modulated noise, contrast-modulated noise and luminance-modulated noise were 0.5, 0.42 and 0.04, respectively. The corresponding values for observer MK were 0.5, 0.49 and 0.05, respectively.

Procedure

Direction-identification performance was measured using an identical procedure to that described for Expt 1.

Results and Discussion

Results are plotted as the percentage of trials on which the observers reported motion in the correct direction (direction of the displacement) as a function of the displacement on each image update, expressed as a fraction of the spatial period of f.

Figure 7 shows psychometric functions for two observers when the frames of the motion sequence

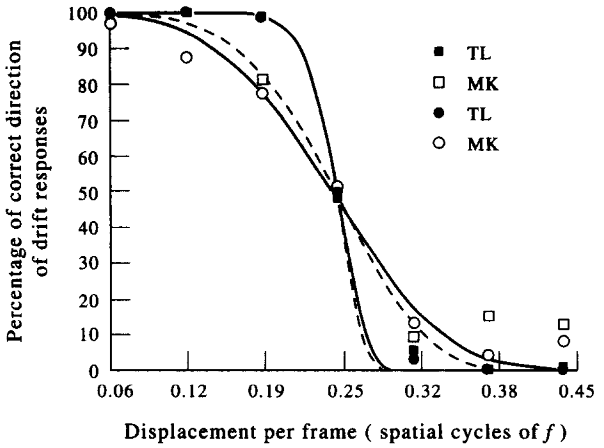


FIGURE 7. Psychometric functions for two observers for motion sequences containing alternating (square-wave) contrast- and luminance-modulated noise (solid lines) and motion sequences containing alternating (square-wave) luminance- and size-modulated noise (dashed lines). The fundamental spatial frequency of the modulation signal (*f*) was 1.0 c/deg and the speed of the motion sequences was maintained at 4.2 deg/sec.

alternated between either luminance-modulated noise and contrast-modulated noise, or luminance-modulated noise and size-modulated noise. For the latter, the "correct" direction refers to the direction in which the small-element regions were displaced relative to the low-luminance regions on consecutive frames (or equivalently the direction in which the large-element regions were displaced relative to the high-luminance regions). The results were almost identical to those found in Expt 1 in that the observers were unable to integrate the first- and second-order frames of the motion sequences when the magnitude of the spatial displacement on each image update was 0.25 cycles of *f*. This provides further support for the existence of separate motion detectors for first- and second-order motion.

Figure 8 shows direction-identification performance for both observers when the frames of the motion sequence alternated between contrast-modulated noise and size-modulated noise. Again, the term "correct" refers to the direction in which the small-element regions of the size-modulated noise were displaced relative to the low-contrast regions of the contrast-modulated noise (or equivalently the direction in which the large-element regions were displaced relative to the high-contrast regions). This is because pilot studies revealed that the perceived direction of motion was always determined by the positions of the small-element regions relative to the low-contrast regions. From Fig. 8 it is apparent that for all spatial displacements motion was always seen in the correct direction although there was a tendency for direction-identification performance to deteriorate when the magnitude of the spatial displacement was 0.44 cycles of *f* (i.e. approached 0.5 cycles of *f*) as expected. Thus, these results suggest that the motion of both types of second-order image is encoded by a common motion mechanism distinct from that used for detecting first-order, luminance-defined motion.

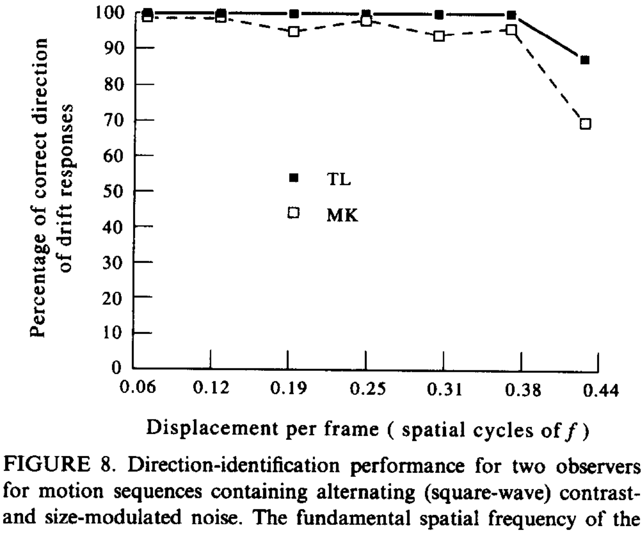


FIGURE 8. Direction-identification performance for two observers for motion sequences containing alternating (square-wave) contrast- and size-modulated noise. The fundamental spatial frequency of the modulation signal (*f*) was 1.0 c/deg and the speed of the motion sequences was maintained at 4.2 deg/sec.

GENERAL DISCUSSION

The results of all three experiments suggest that first- and second-order motion are detected by separate, low-level motion mechanisms in human vision and agree with those of Mather and West (1993). The present results contrast with those of Cavanagh, Arguin and Von Grunau (1989) who also investigated the integration of first- and second-order motion. They reported that observers perceived apparent motion between two alternating discs when they were defined with respect to their backgrounds by differences in luminance, colour, binocular disparity, texture or relative motion. Motion was also perceived between disks that were defined by different stimulus attributes but motion strength (as measured by the minimum spatial separation between the disks at which motion was just visible) was on average 25% less than that measured for pairs of disks defined by the same attribute. The apparent discrepancy with the present results can be resolved by proposing that the effects found by Cavanagh *et al.* (1989) were mediated by the operation of a high-level, feature-based mechanism while our results reflect the activity of low-level, motion-detecting mechanisms. There is evidence that low-level mechanisms are normally used for detecting second-order motion, but that feature-based strategies are also sometimes used (e.g. Cavanagh & Mather, 1989; Nishida, 1993; Smith, 1994). The stimuli of Cavanagh *et al.* (1989) are unfavourable for low-level, motion-detecting mechanisms because of the large spatial separation (3–4 deg) between successive positions of the target, and so it is likely that motion perception was mediated by a high-level, feature-based mechanism. In the case of our own stimuli, the spatial separations used do favour low-level processes. Furthermore, although it is not clear what the corresponding first- and second-order features are in motion sequences of the type employed in the present experiments, a high-level mechanism that was able to match first- and second-order features would be expected to signal motion consistently in one direction for all spatial displacements of the images examined and this was not the case. Integration of first-order images and second-order images was also not observed when an ISI was introduced between successive updates of the motion sequence (see Results and Discussion of Expt 1) in order to impair low-level motion detection and favour the use of high-level, motion-detecting strategies. Thus, performance in all three experiments was likely to be governed by the operation of low-level motion-detecting mechanisms.

In terms of low-level motion detection, our results clearly favour the existence of separate motion-detecting mechanisms for the analysis of first-order motion and second-order motion. Although we do not completely rule out the possibility that a model based upon a single motion-detecting mechanism (e.g. Grzywacz, 1992; Johnston *et al.*, 1992) may be able to accommodate our results, several other lines of psychophysical evidence are difficult to interpret within this framework. For example, the finding that second-order motion stimuli, unlike similar first-order motion stimuli, fail to elicit OKN (Harris & Smith, 1992) seems to point clearly to separate motion-detecting mechanisms. Neither are the results consistent with a second-order motion-detecting mechanism that rectifies (or squares) the output of a single band-pass or low-pass filter prior to motion energy analysis (Werkhoven *et al.*, 1993). If half-wave rectification followed filtering, the spatial frequency of first-order and second-order images would effectively be preserved and one would expect integration of first- and second-order frames (of the same modulation frequency f) by the motion mechanism. However, this was not the observed result for Expts 1 and 3. If a full-wave rectification operation were employed instead of half-wave rectification, spatial frequency doubling of the first-order, but not second-order, frames would occur prior to motion analysis and thus one would expect integration of motion sequences containing first- and second-order images of the type used in Expt 2. Clearly, this was not the case.

Our results support models that postulate the existence of separate, low-level motion mechanisms for first- and second-order motion, each mechanism being insensitive to stimuli of the other class. For example, that the second-order motion-detecting mechanism is insensitive to the first-order frames of the motion sequences is consistent with the model of Wilson *et al.* (1992) in which the image is filtered at one spatial scale, squared and then filtered at a different scale (i.e. lower frequency). In this scheme, no sinusoidal luminance modulation in the retinal image will survive both spatial filtering operations.

The finding that observers were able to integrate the frames of a motion sequence when spatial structure on consecutive frames was defined by different second-order characteristics (Expt 3) suggests that several varieties of second-order motion may be detected by a single, nonlinear motion mechanism. The observation that the perceived direction of motion was determined by the positions of the small-element regions of the size-modulated noise relative to the low-contrast regions of the contrast-modulated noise has important implications concerning the nature of the nonlinear operations performed on the second-order images prior to motion analysis. The fact that frequency filtering by the human visual system must be localised to some extent, because it is not possible to measure variations in luminance over infinite distances and time, offers a plausible explanation of why motion was seen between the small-element and low-contrast, and the large-element and high-contrast, regions of the second-order images. Although the Fourier power spectrum of the noise constituting the size-modulated images is flat on a global scale, the power at any spatial frequency varies locally within the image. For the small-element regions, locally there is less power at low- to mid-range spatial frequencies than for the large-element regions (see Fig. 9). Most importantly, this local variation in power occurs at the same spatial frequency as the modulation signal. Thus, when spatially filtered, for example at one octave above the modulation frequency (Wilson *et al.*, 1992), the image is effectively contrast-modulated. This analysis is supported by our observation that increasing the physical contrast of the small-element regions (thereby increasing the local power of the noise) and reducing that of the large-element regions (thereby reducing the local power of the noise) resulted in a nulling of perceived motion when the magnitude of the local contrast difference between the small- and large-element regions of the size-modulated noise reached a certain value. This is equivalent to adding square-wave, contrast modulation into the image 180 deg out of phase with the size modulation. This finding was confirmed by several naive observers. Thus, the explanation of the psychophysical results found when motion sequences contained two, different second-order images, although tentative, does not conflict with current theories or models (e.g. Chubb & Sperling, 1988, 1989a; Wilson *et al.*, 1992) and remains within the bounds of the known anatomy and physiology of the visual system. In this respect, our conclusions are in line with the "texture grabber" concept of Werkhoven *et al.* (1993). A texture grabber can be characterised as a mechanism which measures the amplitude or "activity" of a texture, with indifference to the spatial structure of the texture that gives rise to the activity. Werkhoven *et al.* (1993), following Chubb and Sperling (1988, 1989a), propose a mechanism which filters and rectifies the image and then locally quantifies the magnitude of the resulting signal, which is proportional to the local contrast in the original image. A texture grabber sensitive to local variations in contrast could not distinguish a contrast signal derived from the presence of contrast-modulated noise from one arising from size-modulated noise. Our results (Expt 2) do not, however, support the suggestion of Werkhoven *et al.* that there is only one such texture grabber mediating second-order motion detection.

It seems likely that other types of second-order motion stimuli might also reduce to contrast modulation when considered in this way. For example, consider an image

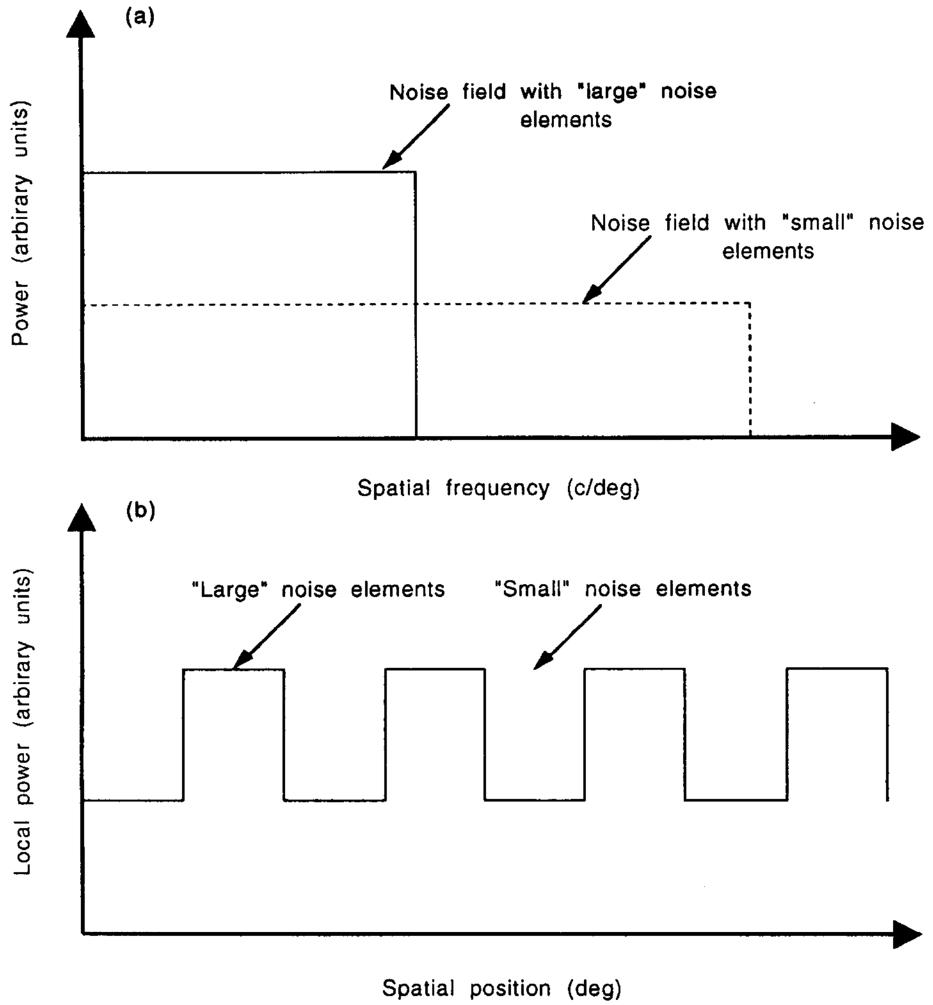


FIGURE 9. Schematic diagram of the Fourier power spectrum of unmodulated random noise composed of either "large" or "small" noise elements (a). The total power or energy remains constant (as indicated by the area under the spectrum) but the power at low- to mid-range spatial frequencies is less for noise composed of "small" elements than noise composed of "large" elements. For the small-element regions of square-wave, size-modulated noise locally there is less power at these frequencies than for the large-element regions (b). After spatial filtering the size-modulated noise is equivalent to contrast-modulated noise.

in which the flicker rate of a random noise field is modulated by a drifting sine-wave profile. In the temporal domain, the power at any temporal frequency will vary locally in the image at the same spatial frequency as the modulation in flicker rate. As a consequence, when temporally filtered by a texture grabber the image is equivalent to a drifting sinusoidal modulation in contrast. Howeer, other types of second-order motion stimuli (e.g. those defined by spatiotemporal variations in relative motion or binocular disparity) are not so easy to fit into this framework.

In the present paper we have sought only to distinguish between the existence of separate or common motion-detecting mechanisms for first-order motion and second-order motion and have not attempted to address the processes that occur presumably after the initial stages of local motion extraction in human vision. Although phenomena such as cross-adaptation between first- and second-order motion patterns (e.g. Ledgeway, 1994; Turano, 1991) and coherence in mixed plaid patterns containing both first-order and second-order components (Stoner & Albright, 1992; but see Victor & Conte, 1992) superficially seem to favour a single motion-detecting mechanism, they can also be accommodated by models suggesting the existence of separate mechanisms for each type of motion that pool their output at some later stage of processing (e.g. Wilson *et al.*, 1992). Thus, it is apparent that our results do not preclude the existence of interactions between the outputs of distinct first-order and second-order motion detectors.

In summary, the human visual system seems to possess separate specialised motion-detecting mechanisms for first- and second-order motion. It is not clear at present whether specialised motion-detecting mechanisms exist for different types of second-order motion or whether a single, nonlinear mechanism can detect second-order motion however it is defined. In light of the fact that spatiotemporal filtering followed by nonlinear operations such as rectification or squaring alone will not reveal any useful Fourier components in the neural representation of some second-order stimuli (e.g. those defined by spatiotemporal variations in binocular disparity) the possibility remains that specialised motion mechanisms exist for some varieties of second-order motion. We are currently conducting experiments in order to address these issues as well as the role that high-level, feature-based motion processes play in the detection of both first- and second-order motion.

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