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Motion: The long and short of it

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Abstract—Several authors have proposed that motion is analyzed by two separate processes: short-range and long-range. We claim that the differences between short-range and long-range motion phenomena are a direct consequence of the stimuli used in the two paradigms and are not evidence for the existence of two qualitatively different motion processes. We propose that a single style of motion analysis, similar to the well known Reichardt and Marr–Ullman motion detectors, underlies all motion phenomena. Although there are different detectors of this type specialized for different visual attributes (namely first-order and second-order stimuli), they all share the same mode of operation. We review the studies of second-order motion stimuli to show that they share the basic phenomena observed for first-order stimuli. The similarity across stimulus types suggests, not parallel streams of motion extraction, one short-range and passive and the other long-range and intelligent, but a concatenation of a common mode of initial motion extraction followed by a general inference process.

1. INTRODUCTION

Many studies suggest that motion perception is mediated by two sub-systems. The distinction was first proposed by Braddick (1974) who named them the 'short-range' and 'long-range' processes (Fig. 1) and this terminology has now been widely adopted in the motion literature. The short-range process is thought to occur at a relatively early level of visual processing and is tentatively identified with directionally selective neurons in the striate cortex. The long-range process is thought to occur at a higher level of processing, with properties more akin to cognitive or interpretive processes than to the responses of single neurons. In two reviews published following a Royal Society discussion meeting, Braddick (1980) and Anstis (1980) set out the evidence in favour of the distinction and each summarized the major points in a table. Table 1 here combines their two tables and adds a few points that have appeared since that time.

According to these authors, the defining characteristic of the two motion processes is their spatio-temporal range: the short-range process operates over short distances and brief durations while the long range process operates over long distances and long durations. In addition, there are differences in response to dichoptic stimulation, chromatic stimuli, and the ability to produce motion aftereffects. Most important, the two processes are distinguished by qualitatively different methods of extracting motion information. The short-range process is supposed to correspond to low-level motion detectors that act passively and in parallel over the entire visual field whereas the long-range process is supposed to correspond to a more interpretive, cognitive mechanism that might identify forms and then track their positions over time.

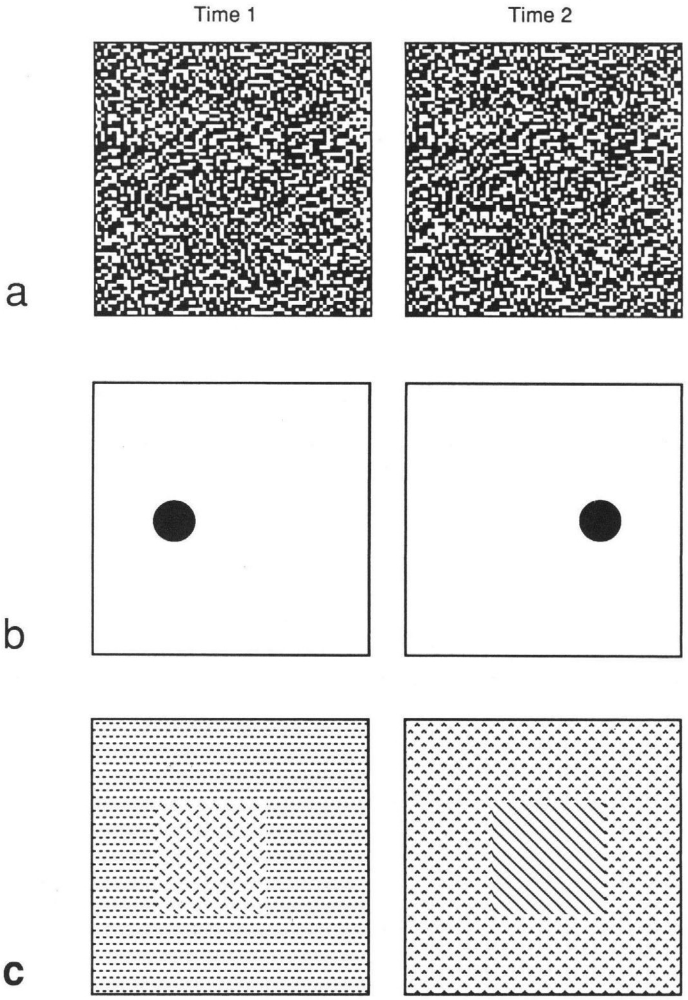

Figure 1. (a) Short-range motion. A kinematogram is created by alternating between two random dot fields. The position of a central region of identical dots is displaced in one frame compared to the other and this generates an impression of a square moving against the background. The maximum displacement for which the square remains visible was originally reported to be 15 arc min. (b) Long-range motion. An isolated stimulus, alternating in position can produce impressions of motion for displacements as large as 18 arc deg (Zeeman and Roelofs, 1953). (c) A second-order motion stimulus. The central patch, which differs from the surround in terms of texture in both panels, has the same mean luminance in both. The specific textures in the two panels (depicted, not shown here) are uncorrelated. There is therefore no information in the two panels that could activate spatiotemporal correlators based on luminance. Nevertheless, the alternation of these two panels produces a clear impression of motion (Ramachandran *et al.*, 1973).

Various mechanisms have been proposed as candidate models for the short-range process. Reichardt-type detectors compare the outputs of two input spatial filters that have spatially offset receptive fields (e.g., Reichardt, 1961; Barlow and Levick, 1965; van Santen and Sperling, 1985). Marr–Ullman detectors compare the change in filter response over time with the change over space to compute motion (Marr and Ullman, 1981). In many respects, these various detectors perform in very similar ways (van Santen and Sperling, 1985; Mather, 1988), and in the following discussion, low-level detectors will be referred to generically as comparators. No attempt will be made to favour one style of comparator rather than another (figures will depict a simple Reichardt-type comparator for purposes of illustration).

The only detailed model for long-range motion is radically different from short-range comparators. Ullman's (1979) model is based on similarity computations involving a set of matching primitives (correspondence tokens), and the final percept arises from a global cost–benefit analysis of available matches.

Although the short-range/long-range dichotomy is well entrenched in the literature, recent studies have failed to support the original distinctions upon which it was based. Short-range motion can be seen over long distances (Cavanagh *et al.*, 1985; Chang and Julesz, 1985) and long-range over short distances. Short-range motion can also be seen for colour stimuli (Cavanagh *et al.*, 1985; Sato, 1988) and, it is claimed, for dichoptic presentation (Shadlen and Carney, 1986). Long-range motion can produce motion aftereffects (von Grünau, 1986). Moreover, the distinction based on qualitative differences in motion processes does not appear to hold either: Lelkens and Koenderinck (1984) and Chubb and Sperling (1988) have modeled motion responses to what should be long-range stimuli using variations of low-level comparators.

This brief review shows that the main criteria which were said to discriminate between the two motion processes fail. We shall argue that the observed differences forming the basis of the claims for two motion processes may be more easily attributed to differences in the stimuli used in traditional short-range and long-range experiments than to differences between two motion processes.

Although the short-range/long-range dichotomy may be inappropriate, a different dichotomy specific to stimulus attributes may be useful: that is the distinction between first-order and second-order stimuli.

Table 1.
Properties of short-range and long-range motion processes (principally after Anstis (1980) and Braddick (1980), with some additions).

Short-range	Long-range
Short spatial range (< 15 arc min) Braddick (1974)	Operates over many degrees Kolers (1972)
Brief temporal range (80–100 ms ISI) Braddick (1974)	ISI up to 500 ms Mather (1989)
Motion aftereffect Banks and Kane (1972)	No motion aftereffect Papert (1964), Anstis (1980)
Not dichoptic Braddick (1974)	Dichoptic Shipley *et al.* (1945)
No response to colour Ramachandran and Gregory (1978)	Response to colour Ramachandran and Gregory (1978)
Low-level neural comparator	Responsive to higher-level correspondences that do not activate motion detectors
Passive motion response, velocity space computations (Adelson and Movshon, 1982)	Cooperative processes, inference

A first-order motion process responds to the displacement of first-order differences in luminance and perhaps colour. First-order statistics specify the frequency with which individual points in an image have specified intensity or colour values. Two areas in an image differ in their first-order statistics if they have different mean luminances or spectral compositions. First-order detectors therefore correspond to the extensively studied directionally selective units of the striate cortex. These units respond well to drifting luminance contours and each unit has a fairly narrow preferred range of directions (Hubel and Wiesel, 1968; De Valois *et al.*, 1982). The response of directionally selective units to colour-defined stimuli, if any, is not well understood (Hubel and Wiesel, 1968; Michael, 1978a, b, 1979; although see Albright, 1987, and Saito, *et al.*, 1989, for directional responses to colour stimuli for units in area MT).

We have identified colour and luminance as first-order properties because they characterize responses to visual stimuli at the earliest level, the retinal ganglia (De Valois and De Valois, 1975). Colour and luminance information is preserved with little modification through the lateral geniculate up to the striate cortex. Directionally selective neurons in the striate cortex react to displacements of regions defined by this first-order information.

Two areas may have the same mean luminance and colour, but differ in their spatial, temporal, or ocular distributions of luminance and colour. The two areas are then differentiated by second-order properties such as texture, motion or binocular disparity. Second-order statistics define the frequency with which specific combinations of intensity or colour values occur for *pairs* of points (e.g., both dark, or one dark and the other light). If the pairs of points belong to the same image but are separated spatially, then the second-order statistics define the textural properties of the image. If the pairs of points belong to different images representing two time frames in a motion sequence, the second-order statistics define the motion properties of the sequence. If the pairs of points belong to a stereo-pair of images then the statistics define the depth properties of the stereo image.

The second-order stimulus attributes of spatial structure, movement, and disparity emerge as new properties in the responses of neurons in the striate cortex. A second-order motion process, if such a process exists, would respond to displacement of second-order differences in luminance or colour, even in the absence of first-order differences (Fig. 2). A standard directionally selective unit would detect no net motion in the displacement of the border separating two such regions and yet these stimuli do produce clear impressions of motion (Julesz, 1971; Ramachandran *et al.*, 1973; Pantle, 1978; Petersik *et al.*, 1978; Anstis, 1980; Lelkens and Koenderinck, 1984; Chubb and Sperling, 1988; Turano and Pantle, 1989).

If these second-order motion stimuli cannot be detected by directionally selective units in the striate cortex then perhaps the processes that do respond to these stimuli correspond to the qualitatively different class of motion analysers that has been labeled the long-range process. This possibility was outlined by Anstis in his 1980 review paper and he suggested that this type of stimulus would be ideal for isolating the characteristics of the long-range process or system 2, as he referred to it. However, the results of our tests show that second-order motion is qualitatively similar to first-order motion and differs only in degree, not in kind. Thus, we are able to produce stimuli that must activate different sets of motion detectors—those for first-order and those for second-order motion—but our evidence suggests that these different types of motion detectors operate on the same basis. We claim that this common

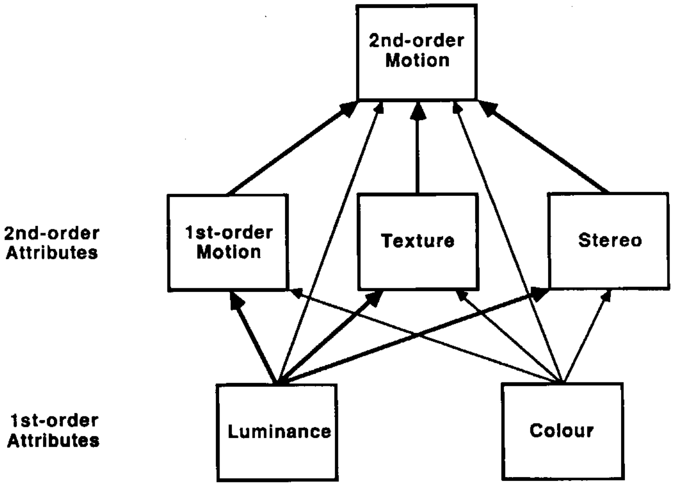

Figure 2. Hierarchy of stimulus attributes contributing to impressions of motion. First-order motion detectors are sensitive to the displacement of luminance contours and, weakly, to the diplacement of colour contours. Second-order motion detectors respond to displacement of second-order attributes even in the absence of displacement of first-order features. The detectors that are sensitive to second-order attributes may also produce motion responses to the displacement of first-order features.

mode of operation is a dense array of comparator-type motion detectors selective for various first- or second-order stimulus attributes. These detectors cover the visual field and operate in parallel.

We shall first review the original characteristics that distinguished between short-range and long-range motion processes and then describe the distinction between first- and second-order motion in more detail. We shall also consider the possibility that 'object file' motion processors (Treisman, 1986; Pylyshyn and Storm, 1988) might provide the model for a second class of motion analysis.

2. SHORT-RANGE AND LONG-RANGE MOTION PROCESSES

2.1. Spatial range

Apparent motion differs from real or continuous motion in that the stimuli are presented at discrete locations. The fact that this produces strong impressions of motion indicates that the motion system or systems may be integrating over fairly large distances. The discrete presentations used in apparent motion tasks accentuate the difficulty of matching stimuli across presentations and the maximum displacement for which motion can still be seen can be taken as a measure of the spatial integration area of the motion process.

The original justification for two motion processes came from the discovery of two very different spatial limits for motion perception. Prior to the 1970s, apparent motion had usually been studied using displacements of relatively simple stimuli (see Kolers, 1972). Good apparent motion was usually reported for displacements of up to several degrees of visual field. In 1960, Julesz introduced random dot stimuli into vision research and they were quickly adopted for the study of motion (Anstis, 1970; Julesz, 1971; Braddick, 1974). Braddick (1974) conducted an extensive study of the perception of motion in these random-dot 'kinematograms' consisting of a pair of random-dot patterns that alternated rapidly (see Fig. 1a). The dots in a rectangular area of one of the patterns were identical to those in a corresponding area of the other pattern but shifted slightly. Braddick reported that as long as the shift was smaller than about 15 min of visual angle, observers could perceive a rectangle oscillating back and forth against the background as the two patterns alternated. The 15 min limit, labeled D_{max}, was taken as the upper limit of the short-range system's ability to detect discrete displacements. Although the identification of a short-range process was based on the properties of random-dot kinematograms, the term was rapidly applied to any motion phenomenon that involved small displacements (Pantle and Picciano, 1976; Dick *et al.*, 1987). On the other hand, the apparent movement seen over much greater distances in classical stimuli was thought to be mediated by a second system, the long-range motion process. (The processes responsible for the perception of continuous or real motion are left somewhat ambiguous by this distinction.)

Since Braddick's original paper, however, numerous studies using kinematograms have reported D_{max} values that greatly exceed 15 min. Some of this variation can be attributed to the effect of retinal eccentricity on receptive field sizes: Baker and Braddick (1985a), for example, obtained D_{max} values approaching 2 deg of visual angle at an eccentricity of 10 deg. However, Nakayama and Silverman (1984) and Chang and Julesz (1983) found three- or four-fold variations in D_{max} independently of eccentricity when they manipulated the spatial frequency content of the random-dot kinematograms. Low-pass filtered stimuli gave the largest D_{max} values, about 1 deg at a filter centre frequency of 1 c/deg.

In fact, it appears that D_{max} scales linearly with the size of the elements in the random-dot field once the element size exceeds 15 min (Cavanagh *et al.*, 1985). Below that dot size, D_{max} appears to remain at a constant 15 min. It is not clear that there is any intrinsic limit on the largest spatial displacement over which apparent motion can be seen in random-dot stimuli; it is limited only by the size or spatial frequency content of the random-dot elements. We can directly relate the spatial frequency content of the stimulus to the size of the receptive field that responds to it. Larger stimuli activate units with larger receptive fields that can therefore respond to larger displacements (Fig. 3). Baker and Cynader (1986) showed that the optimum displacement for directionally selective units in the cat cortex (D_{opt} as opposed to D_{max}) also increases as a linear function of the unit's preferred spatial period up to a maximum of about 1.5 deg displacement.

While the traditional stimulus for studying short-range motion has become the random-dot kinematogram, long-range motion studies typically use individual shapes that are presented in succession at different spatial locations (Fig. 1b). Most of these studies pre-dated the arrival of the short- vs. longe-range distinction, but with the discovery of the 15 min displacement limit for kinematograms, it seemed that the large displacements involved in typical apparent motion studies must activate a different process (Braddick, 1974). This conclusion assumes that the displacement limit found for kinematograms made up of fine dots also applies to large isolated stimuli. However, as long as these isolated stimuli are defined by luminance (e.g., black disks on a white background), they should be quite effective in activating directionally selective units thought to be the basis of the short-range process: isolated shapes have complex Fourier spectra containing low spatial frequencies and, with large

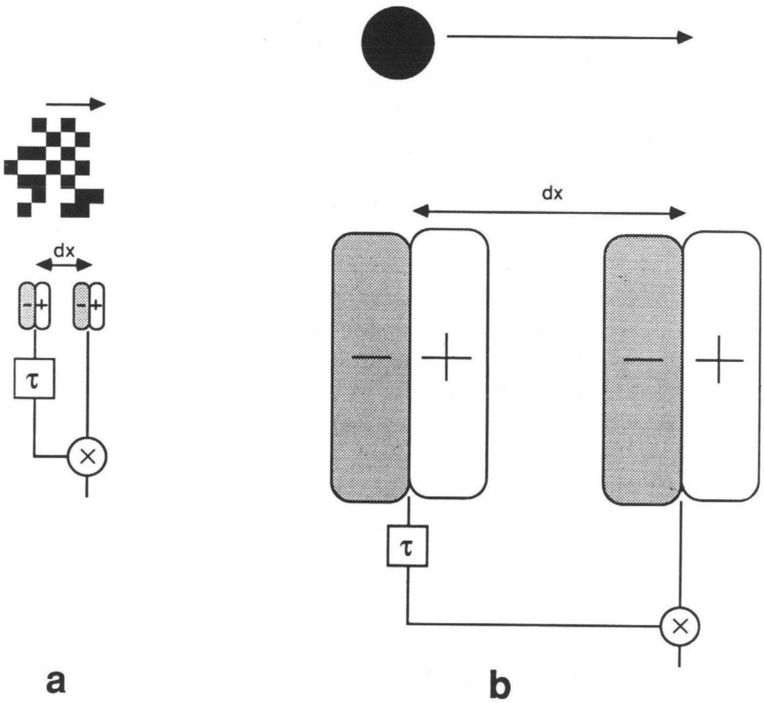

Figure 3. (a) The small elements of kinematograms activate motion detectors with small receptive fields that can respond only to relatively small displacements. The box denotes a time delay and the circle a correlation operator. The detector shown gives a maximum response to rightward motion of a particular speed determined by the detector's spatial offset, d*x*, and temporal delay, τ. (b) The large and/or isolated stimuli used in long-range apparent motion tasks can activate similar detectors with large fields that can respond to large displacements. In both cases the optimal separation, d*x*, for the two subfields in about one-quarter cycle (much less than the separation shown here), one half the width of the individual inhibitory and excitatory regions. The receptive fields shown here are oriented.

displacements, one or both of the alternating stimuli must fall on peripheral retinal locations. These stimuli should therefore be appropriate for comparator type detectors with large receptive fields that can respond to very large displacements (Fig. 3). A particular advantage of a single moving dot is that there are no false targets in the display—all directionally selective units will either respond with a signal appropriate to the true motion or not respond at all. We claim that the abrupt drop in the maximum displacement for dot displays that occurs when more than about ten or twenty dots are in the display (Sato, 1989) is a consequence of false targets falling within the displacement limit of detectors with the largest receptive fields and does not indicate a switch to a different motion process.

More recently, second-order stimuli such as texture-defined or stereo-defined shapes have been used for studying high-level motion processes (Julesz, 1971; Ramachandran *et al.*, 1973; Pantle, 1978; Anstis, 1980; Lelkens and Koenderinck, 1984; Green, 1986; Green and Odom, 1986; Chubb and Sperling, 1988; Turano and Pantle, 1989). Prazdny was particularly active in exploring motion (and stereo) using these stimuli (Prazdny, 1985a, b, 1986a, b, 1987). These stimuli cannot activate low-level detectors and we shall return to the results of studies using these stimuli later.

Finally, it should be remembered that, despite the emphasis on the maximum displacement over which stimuli produce impressions of motion, all stimuli, whether the classical short-range or long-range stimuli, also produce compelling impressions of motion for small displacements. In fact, the D_{min} measure, the smallest jumps producing an impression of motion, is in the same range as acuity measures: about 20 arcsec (Morgan and Ward, 1980; Baker and Braddick, 1985a).

To summarize, short-range motion stimuli can produce the perception of motion over very long distances and long-range motion stimuli can produce impressions of motion over very short distances. Whether or not there are two types of motion, the size of the stimulus displacement should not be used as the criterion to separate two different motion process and the results of studies that have used this criterion (e.g., Dick *et al.*, 1987) should be re-evaluated. In fact, a simpler hypothesis is that only one motion process is responsible for the impressions of motion reported in both paradigms. Before we can make such a claim, the characteristics of second-order motion must be examined. Motion of second-order stimuli cannot be detected by standard low-level motion detectors and may represent a separate type of motion analysis. We examine these stimuli in the second half of this paper.

2.2. *Temporal range*

Braddick (1974) reported that the perception of the oscillating square deteriorated progressively as the dark interstimulus interval (ISI) separating successive frames approached 100 ms. A more comprehensive study of the effects of ISI and stimulus exposure duration (Baker and Braddick, 1985a) concluded that 'short-range motion detection requires portions of each exposure to occur at about 40 ms separation in time.' Baker and Braddick found that motion was detected only when the ISI fell below about 100 ms.

In contrast, experiments which use typical 'long-range' stimuli find no such strict timing requirements for the perception of apparent motion. Kolers (1972) described a variety of experiments which found optimum apparent motion in simple geometric forms for ISIs ranging from 10 to 350 ms and Burt and Sperling (1981) reported even longer ISIs. Mather (1989) found that apparent motion could be seen in an alternating subjective figure for ISIs up to 500 ms.

The differences in temporal properties which are supposed to discriminate between the short- and long-range motion processes may be attributable to the different spatial frequency content of the stimuli used in the two paradigms: predominantly high spatial frequencies in short-range experiments with kinematograms (broad-band spectrum) and predominantly low spatial frequencies in long-range experiments using isolated stimuli (high-frequency roll-off in spectrum—energy decreases with inverse of spatial frequency in typical *sinc f* function). The temporal frequency tuning (and optimal timing) of a detector may correlate with its spatial frequency tuning. We may, however, expect some differences in the temporal properties of the motion processes for first-order and second-order stimuli (Mather, 1989).

2.3. *Adaptation*

Numerous studies have reported that a motion aftereffect occurs only when short-range stimuli are used. For long ISIs (Turano and Pantle, 1985), large spatial displacements (Banks and Kane, 1972), equiluminous colour stimuli (Cavanagh and Favreau, 1985; Mullen and Baker, 1985; Derrington and Badcock, 1985) or cyclopean stimuli (Papert, 1964; Anstis, 1980), motion aftereffects are often weak or completely absent. This loss may only be a question of degree. In these experiments, not only was the motion aftereffect often weak, but the initial impression of motion was also weak. If we compare the traditional short-range and long-range stimuli, it is evident that the short-range stimulus, and, in particular, random-dot kinematograms, cover a large spatial extent compared to the size of receptive field of the detectors responding to the motion. These stimuli should therefore activate large numbers of detectors. The spatial extent of long-range motion stimuli, such as a single oscillating dot, would typically be of the same order as the size of the receptive field that we claim would respond to it (Fig. 3). The number of adapted detectors must therefore be relatively low. In the case of a sampled stimulus such as that used by Banks and Kane (1972), only units that straddled at least two sampled positions could be adapted and the number of adapted units must therefore increase as the spacing between samples decreases. The reported differences in adaptation may therefore be attributable to the differences in the stimuli and not to differences in the nature of the motion processes. The same argument could be made concerning the difficulty of eliciting optokinetic nystagmus using long-range stimuli (Narayan *et al.*, 1982).

Recently, using a more sensitive measurement technique, von Grünau (1986) has reported motion aftereffects following adaptation to stimuli classified as long-range motion stimuli.

2.4. *Ocularity*

Braddick (1974) reported that when the two frames of a random-dot kinematogram were presented dichoptically (e.g., frame 1 to the left eye and frame 2 to the right eye) motion perception was abolished. In contrast, earlier studies of typical long-range stimuli (Shipley *et al.*, 1945; Ammons and Weitz, 1951) did obtain reports of apparent motion under dichoptic viewing conditions, though it was weaker than that seen under monocular or binocular viewing conditions.

A possible flaw in Braddick's technique is that after-images may have interfered with the motion detection under dichoptic presentation. For example, if the left eye received frame 1, then while the right eye received frame 2, the left eye received a dark uniform field. This dark interval alternating with the stimulus frame in each eye may have interfered with motion detection. To avoid this problem, we generated dichoptic random dot kinematograms with two interwoven sequences so that both eyes always received a patterned stimulus (Fig. 4). In frame 1, two uncorrelated dot patterns were presented to the two eyes simultaneously. In frame 2, the left eye's field was presented to the right eye (with a lateral displacement of the central square of dots), and the right eye's field was presented to the left eye (with a corresponding displacement). Even with these conditions, motion is never detected. However, when the uncorrelated fields do not cross eyes between frames, motion can be detected without difficulty.

Kinematograms are not the only stimulus for which dichoptic presentation disrupts the perception of motion. Georgeson and Shackleton (1988) recently found that the well-known missing-fundamental motion illusion (Adelson, 1982; Adelson and Bergen, 1985), easily explained using first-order detectors, only occurred under monoptic viewing conditions.

It may be that the motion detectors which respond to luminance correlations in random-dot kinematograms cannot operate interocularly (except when there are only

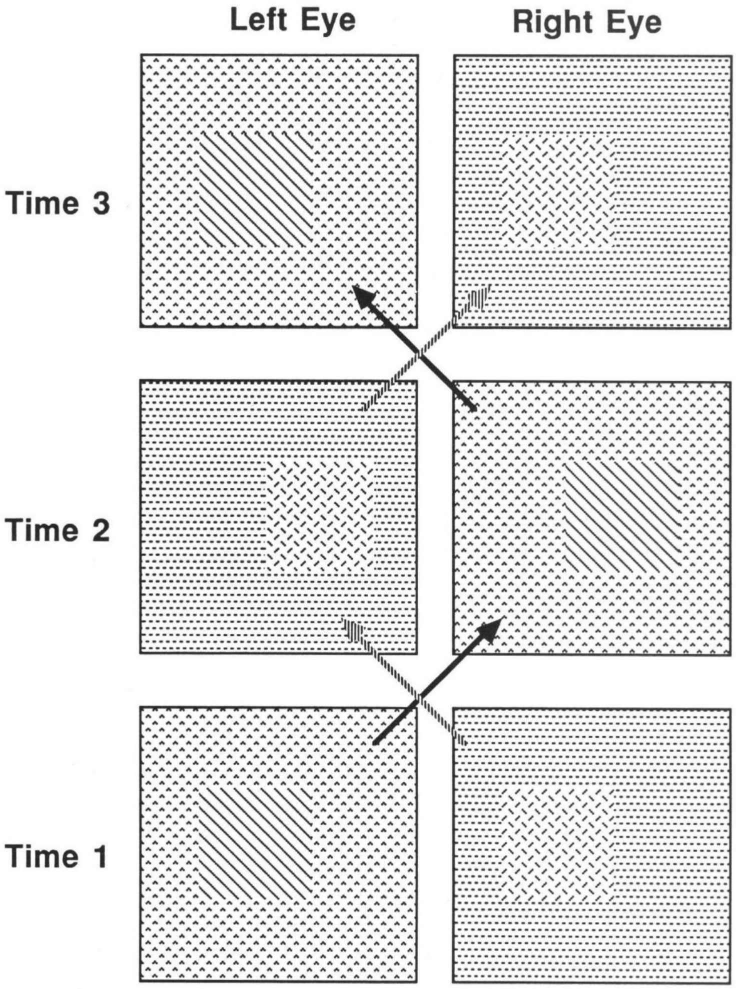

Figure 4. Two sequences of a dichoptic kinematogram stimulus are interwoven so that each eye receives continuous stimulation. Frame 1 in the left eye is correlated with frame 2 in the right eye and vice versa. At any given instant, the left and right eye stimuli are always uncorrelated. No motion is seen. Each correlated sequence produces a kinematogram with a moving central square that is clearly visible if continuously presented to a single eye rather than switching eyes on each frame.

a few dots in the display, Sato, 1989). On the other hand, Shadlen and Carney (1986) obtain motion perception from dichoptic stimulation with random-element displays, so this question remains to be resolved.

2.5. Colour

Both Braddick (1980) and Anstis (1980) include colour response as a criterion for differentiating two subsystems. They based their claim on the report by Ramachandran and Gregory (1978) that motion in a random-dot kinematogram disappeared at equiluminance. Ramachandran and Gregory (1978) presented a kinematogram where the white and black dots were replaced with red and green ones and all observers reported the absence of motion near the equiluminance point. Ramachandran and Gregory also reported that motion did not disappear at equiluminance if two simple line targets were alternated instead of random-dot figures. They therefore claimed that the short-range process could not respond to equiluminous stimuli but the long-range process could. However, a more recent study (Cavanagh *et al.*, 1985) demonstrated that motion can be perceived in equiluminous kinematograms provided that the successive frames are not separated by the dark ISI used by Ramachandran and Gregory (1978). The maximum displacements that produced impressions of motion (D_{max}) were always lowest near equiluminance and, moreover, the reduction in D_{max} was similar for the random-dot stimuli and for single bar stimuli. This study found no grounds for claiming two motion processes on the basis of response to colour. Although the impressions of motion were qualitatively similar for luminance-defined and colour-defined stimuli, there was a dramatic difference in the clarity of the subjective figure created by the moving square of dots. Both studies (Ramachandran and Gregory, 1978; Cavanagh *et al.*, 1985) reported that at equiluminance the moving region produced neither a sharp edge at its border nor an impression of a square floating above the background. These characteristics were very evident as soon as luminance contrast was reintroduced.

Drifting equiluminous stimuli also produced impressions of motion (Cavanagh *et al.*, 1984), although the gratings appeared to move more slowly than stimuli with luminance contrast. Despite this degradation of motion response for colour stimuli, it is possible to null the motion of a luminance grating with the opposing motion of an equiluminous colour grating (Cavanagh and Anstis, 1986). A luminance grating of about 10% contrast was required in order to null the motion of a saturated red/green equiluminous grating. Gorea and Papathomas (1989) have also reported that colour can provide a sufficient stimulus for motion perception even when competing against luminance tokens moving in the opposite direction. Finally, three studies reported that motion aftereffects could be obtained following adaptation to drifting equiluminous stimuli (Cavanagh and Favreau, 1985; Derrington and Badcock, 1985; Mullen and Baker, 1985), although these were often weaker than the aftereffects generated by stimuli with luminance contrast. Aftereffects induced by coloured stimuli transfered to luminance tests and *vice versa.*

These results suggest that colour and luminance contribute to a common motion process at some level although the contribution of colour to this process appears to be degraded in some respects. There is no evidence to suggest that two separate, qualitatively different motion processes are involved.

2.6. Cooperative processes

There are several demonstrations that high-level inferences play a role in the interpretation of some motion stimuli. Rock (1983) has shown that context and expectation can greatly influence perceived motion, and Ramachandran and Anstis (1986) have shown that rules which they call momentum, occlusion and common path seem to apply in certain motion displays (Fig. 5). This 'intelligent' behaviour is typically ascribed to the long-range motion process given that the short-range process is thought of as a low-level, passive transducer of motion energy that should be unaware of, and unaffected by, context. There is, however, no evidence that low-level motion signals cannot be modified by context and no evidence that the motion signals in the demonstration of Ramachandran and Anstis (1986) and Rock (1983) did not,

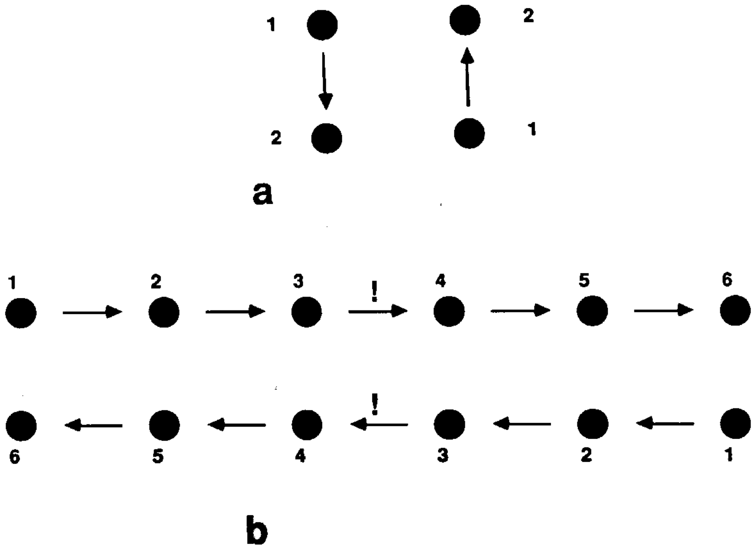

Figure 5. (a) Two spots of light at time 1 that alternate with two others at time 2 produce an impression of up and down motion when the dots are closer together vertically than horizontally as shown here. (b) This same dot array, when imbedded in a sequence of horizontal motions, is seen as part of continuous horizontal motion and the vertical motion is not perceived. This effect of context, described as a momentum effect by Ramachandran and Anstis (1986), is one of many examples of 'intelligent' perception described by Ramachandran and Anstis (1986) and by Rock (1983).

in fact, arise from low-level detectors. A recent computational model of low-level motion analysis (Yuille and Grzywacz, 1988) can predict many cooperative phenomena in motion perception. It is simpler to assume that cooperative processes can act on and influence motion signals independently of their source. Cooperative processes should be thought of as a common aspect of motion analysis that is applied to any signal and not an aspect of only one particular motion process.

2.7. *Motion without correlated luminance*

A large range of complex motion phenomena can be modeled well with comparator type motion detectors. In particular, reversed apparent motion (Anstis and Rogers, 1975), missing fundamental motion (Adelson, 1982; Adelson and Bergen, 1985), compound grating motion and the effects of temporal transients on static luminance edges (Mather, 1984; Moulden and Begg, 1986) have all been successfully modeled with these detectors (Adelson and Bergen, 1985; van Santen and Sperling, 1985; Watson and Ahumada, 1985; Mather, 1988). These models are all based on spatio-temporal cross-correlations of luminance energy and this is of course sufficient to predict simple motion phenomena in addition to the more complex ones mentioned above (Mather, 1987).

There are, however, several motion phenomena that cannot be explained with this class of motion detector. Ramachandran *et al.* (1973) reported the perception of apparent motion in a two-frame display consisting of two completely uncorrelated dot patterns (Fig. 1c). Each frame consisted of a square region of random visual noise that could be discriminated against a background of a different random noise, having the same mean luminance but different second-order statistics. The position of the square patch in the second frame was displaced laterally relative to the position of the patch in the first frame. There were no correlations between the dot patterns in the two frames and yet a clear impression of to and fro motion of the patch was produced when the frames were alternated. The perception of motion in the absence of correlated luminance information has also been reported for stimuli defined by relative motion (Petersik *et al.*, 1978; Anstis, 1980; Prazdny, 1986a, b, 1987), random-dot stereograms (Julesz, 1971; Prazdny, 1986a, b, Papathomas *et al.*, 1988), flicker (Lelkens and Koenderinck, 1984; Mather *et al.*, 1984; Prazdny, 1986a, b, 1987; Chubb and Sperling, 1988) and texture (Pantle, 1978; Turano and Pantle, 1989).

The perception of motion for this type of stimulus has been taken as key evidence for a second, qualitatively different motion process, the long-range process. Anstis (1980), for example, characterized the analysis of these higher-order motion stimuli as the identification of form followed by the extraction of motion and contrasted it to the response of low-level detectors to a kinematogram in which the extraction of motion precedes the perception of form. This comparison does not do full justice to the low-level process, however, since the low-level detectors must also extract form (the local distribution of dots picked up by the detectors' receptive fields) before generating a motion signal. Although, in the case of the kinematogram, the distribution of local motion signals also defines a global form (a second-order form), the nature of the initial motion process for both the low-level and high-level stimuli is similar. The motion response to both starts with an extraction of form, the difference is the level at which the form becomes explicit—a very low-level for kinematograms and a higher level for stimuli without correlated luminance. These higher-order stimuli do not require a new principle of motion, they need only an expanded definition of shape, one that includes regions defined by second-order attributes such as texture, motion, or binocular disparity (Fig. 6).

2.8. *Summary*

The psychophysical evidence shows that the principal differences that have been claimed to discriminate between short-range and long-range motion processes can be attributed to stimulus differences in the two paradigms. There is no evidence that qualitatively different processes are involved. There is a dichotomy, however, between low-level motion detectors that respond to the spatiotemporal luminance (and perhaps colour) energy in the stimulus and higher-level detectors that can respond to spatiotemporal correlations of properties such as texture, binocular disparity or motion in the absence of any first-order correlation. These detectors may well operate in the same fashion as the first-order motion detectors, that is, by virtue of spatiotemporal comparators that respond not to luminance profiles but to borders defined by texture, or by relative motion, or by binocular disparity (Fig. 6).

In order to determine whether second-order stimuli produce motion impressions with qualitatively different characteristics from those produced by first-order stimuli, we examined several motion phenomena using second-order stimuli.

3. CHARACTERISTICS OF MOTION FOR SECOND-ORDER STIMULI

Chubb and Sperling (1988) have used the term 'drift-balanced' to refer to a class of stimuli that are invisible to low-level, luminance-based, motion detectors. However,

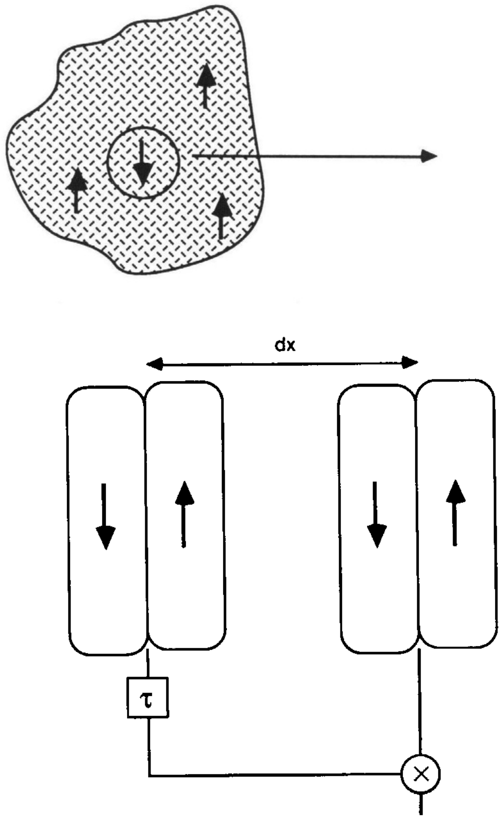

Figure 6. A Reichardt-type motion detector where the input receptive fields respond to different directions of motion in the two regions of the field (Frost and Nakayama, 1983; Nakayama and Loomis, 1974). This detector will respond to the displacements of borders between areas having different directions of motion. For example, a disk defined by relative motion (a kinematogram) is presented for a brief instant and then replaced with a second disk at a slightly different position, defined by the relative motion of a new set of dots, uncorrelated with the first set. This stimulus produces an impression of motion (Petersik *et al.*, 1978; Cavanagh *et al.*, 1989). The detector shown here has an oriented receptive field structure and the optimal separation, dx, between the two subfields would be one-quarter cycle. These detectors would be useful in computing figure-ground segregation when two patterns are moving with different directions or speeds (Reichardt and Poggio, 1976).

we prefer the more general term 'second-order' stimuli as defined at the beginning of the paper since some second-order stimuli are not drift-balanced. For example, consider a second-order, relative-motion grating. We can construct this grating from vertical strips of random texture moving upward, alternating with strips of random texture moving downward, and then let the contours dividing upward from downward motion drift leftward. Even though the textures themselves move only up or down, this stimulus produces a compelling impression of leftward motion. This stimulus has significant motion signals for low-level detectors—but these signals are in the up and down directions and, in fact, it is these signals that define the grating's second-order form and direction of motion. This grating is not drift-balanced in

Chubb and Sperling's (1988) classification, since the expected directional luminance energy is greater than zero in the vertical direction (except for the limited case of an integration area that is an even integer multiple of the bar width).

The purpose of the studies we shall describe was to compare the characteristics of first- and second-order motion when produced by otherwise identical stimulus conditions. We examined six situations: the strength of apparent motion seen between disks defined by various attributes (Cavanagh *et al.*, 1989), the effect of aperture size on the discrimination of the motion of first-order and second-order gratings, the perception of plaids made up of orthogonal second-order gratings, the transparency of superimposed first- and second-order gratings moving in opposite directions, the recovery of three-dimensional shape from second-order motion (Cavanagh and Ramachandran, 1988) and the perception of second-order kinematograms. Only the first of these tests involved apparent (stepwise) motion, the rest involved closer approximations to continuous motion (as sampled by our 30 Hz display). Since we wished to compare first- and second-order stimuli in identical situations, we took care to keep the stimulus parameters within the resolvable spatial and temporal resolution limits for second-order stimuli, generally less than 3 c/deg for spatial variations (Nakayama and Tyler, 1981; Tyler, 1974) and about 10 Hz for temporal variations (Nakayama and Tyler, 1981).

3.1. Intra- and interattribute apparent motion

The stimulus consisted of two disks which alternated at 2.0 Hz (Cavanagh *et al.*, 1989). Each disk could be defined by a difference in luminance, colour, binocular disparity, texture, or motion with respect to the random dot background. The observer's task was to decrease the separation between the two disks until motion was just visible. This separation was taken as an indication of motion strength. When the two disks that alternated were defined by the same attribute, the motion strength was comparable for all attributes, varying by at most a factor of 2. Motion could also be seen between disks defined by any two different stimulus attributes (Fig. 7a) and the motion strength showed no systematic variation as a function of the attributes involved. The motion strength measured for interattribute stimuli was, on average, about 75% of that measured for intra-attribute combinations.

These results support the previous reports of the perception of motion for various second-order stimuli (texture, binocular disparity, relative motion) and show that the strength of this motion is comparable to that seen with an otherwise identical first-order (luminance) stimulus. These findings are consistent with recent physiological recordings in area MT which demonstrate similar responses to moving contours whether defined by colour or luminance (Saito *et al.*, 1989; Charles and Logothetis, 1989) or by colour, luminance or relative motion (Albright, 1987).

Finally, returning to the psychophysical restults, motion was also perceived for alternations between disks defined by very different attributes such as texture and colour or luminance and relative motion (Cavanagh *et al.*, 1989). This perception of the motion of a form despite the change in the attributes that defined it suggests that there are detectors that combine signals across attributes (Fig. 7b). The strength of this interattribute motion was somewhat less ($D_{\max}$ reduced by 20%) than that for motion between two disks defined by the same attribute, indicating that there must be attribute-specific detectors as well (see also Green, 1986; Green and Odom, 1986).

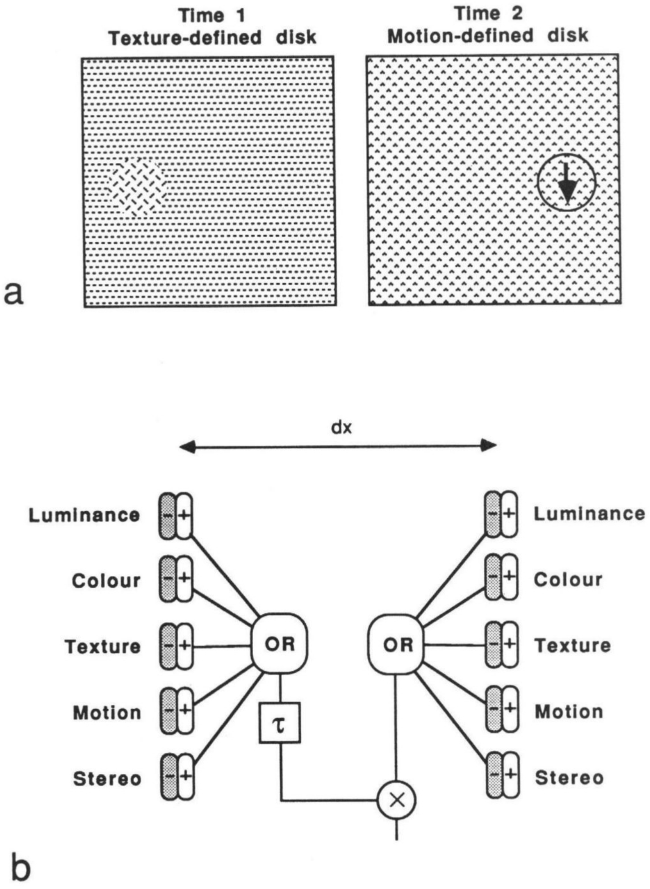

Figure 7. (a) Interattribute stimuli. Alternation between two disks that are defined by different attributes produces compelling impressions of motion (Cavanagh *et al.*, 1989). (b) A motion detector would have to combine the inputs from all stimulus attributes before crosscorrelation in order to respond to such a stimulus. Receptive fields are again depicted as oriented fields and the separations d*x*, of the two subfields should be optimally one-quarter cycle.

3.2. Aperture size

If second-order motion involves the identification of stimulus tokens that are matched over successive frames while first-order motion involves integrating spatiotemporal energy, we might expect a difference in the minimum aperture size through which unambiguous motion could be seen in the two cases. We therefore generated two grating displays, one a simple luminance sinewave (first-order) and the other a dynamic texture sinewave (second-order). The texture sinewave was produced by spatially modulating the contrast of a dynamic random dot field with a sinusoidal function (mean luminance remained constant). The dots were replaced with an entirely new field every 30th of a second and, at the same time as the dots were replaced, the contrast envelope could also shift left or right. This produced continuous motion of the contrast envelope with no coherent motion of the individual dots. This stimulus and others like it have been studied extensively by Chubb and Sperling (1988) and they have shown that these stimuli produce no net motion signal in low-level motion detectors that compute spatiotemporal crosscorrelations of luminance.

In each trial, either the texture or luminance grating was presented, oriented vertically and viewed through a vertical aperture. The observers decreased the aperture width until they could no longer identify the direction of the grating's motion. For both first- and second-order stimuli, the minimum window width for which the direction was just lost was approximately one-quarter of a cycle of the grating. This was true over a fairly broad range of spatial (0.25–2.0 c/deg) and temporal frequencies (2.0–7.5 Hz).

Both first- and second-order motion processes therefore appear to require access to approximately the same amount of a grating cycle to determine the direction of stimulus motion.

3.3. Plaids

When a vertical sinewave grating drifting to the right is superimposed on a horizontal sinewave drifting upwards, the resulting impression is a plaid pattern drifting in a diagonal direction. Adelson and Movshon (1982) described how the perceived direction of this compound stimulus can be determined from the direction and speed of the component gratings through a velocity space computation. In their view, the motion of this compound grating was derived from the signals of low-level, directionally selective units that respond to luminance and not from processes that might track individual features in the drifting plaid. Could such a derivation also work for plaids made of second-order stimuli? A velocity space derivation could not depend on low-level luminance detectors in this case since these do not respond to second-order stimuli.

For second-order stimuli, we used the same dynamic texture gratings that we used in the aperture test but now we superimposed (linear addition) a vertical and a horizontal texture grating. The resulting motion impression was clearly diagonal. We also tested grids defined by binocular disparity and relative motion and they too appeared to move in the same direction as a similar luminance-defined grid.

Whatever process determines the perceived direction of plaids, it appears to operate in a similar manner for both first- and second-order stimuli. If, in fact, the plaid motion is derived from the component velocities, this implies that there are directionally-selective detectors for first- and second-order stimuli that must have some common characteristics.

Alternatively, the motion of the plaids could be determined by tracking individual features in either first- or second-order plaids. The individual features that stand out in a plaid are the 'blobs' formed at the intersections of the bars of the two gratings. Gorea and Lorenceau (1989) have claimed that the motion of the blobs determines the motion perception for plaids; Welch (1989), on the other hand, has argued that the motions of the component gratings determine the motion of the plaids. An interesting test of the blob hypothesis can be performed with multiattribute plaids—plaids that combine one grating defined by, say, luminance with another defined by, say, relative motion. The intersection of the bars of these two gratings then produces a 'blob' that is defined by different attributes around its contour, e.g., luminance on the top and bottom but relative motion on the left and right, and it should be difficult to construct a detector for such blobs. Studies with multiattribute plaids (Albright and Stoner, 1989; Kooi *et al.*, 1989; Krauskopf *et al.*, 1989) do not resolve the debate, however; multiattribute plaids do show less coherence (the two gratings may appear to slide over each other) than single attribute plaids but, nevertheless, they do show some coherence.

3.4. *Transparency*

When two luminance-defined gratings are superimposed and drifted in opposite directions, they can either compete and produce a net impression of motion in one direction or the other, or they can appear transparent so that both directions are visible at the same time. Transparency occurs when the two gratings have spatial frequencies that differ by a factor of four or more, competition occurs when they have the same spatial frequency.

We tested whether the impressions of transparency and competition would occur for second-order stimuli. Dynamic texture gratings were superimposed and drifted in opposite directions. When the two gratings had the same spatial frequency, the perceived motion was always in the direction of the component with the higher amplitude contrast envelope. When the two components had similar amplitudes neither direction was seen, only a stationary flickering field. When the two grating had spatial frequencies differing by a factor of 4 (0.25 and 1.0 c/deg), they appeared transparent, drifting through each other.

When a luminance (first-order) and a dynamic texture (second-order) grating were superimposed, the same phenomena were observed: competition when they had the same spatial frequency and transparency when their spatial frequencies differed by a factor of four. When they both had the same spatial frequency, the two motions nulled each other when the luminance grating had about 10% contrast.

Again, the characteristics of first- and second-order stimuli appear to be qualitatively quite similar.

3.5. *Kinetic depth effects*

From observations using a random dot display in which the dots were arranged on a rotating invisible sphere, Petersik (1980) concluded that kinetic depth was a long-range phenomenon. More recently, Mather (1989) found that depth was seen in such a display only in conditions which allow motion detection in conventional random dot kinematograms depicting frontoparallel motion (Braddick, 1974). Can second-order stimuli produce impressions of three-dimensional structure? Landy *et al.* (1987) have claimed that stimuli defined by texture do not allow the recovery of structure from motion whereas Prazdny (1986) reported that he could obtain structure from motion using stimuli defined by dynamic texture. We have examined (Cavanagh and Ramachandran, 1988) these contradictory claims and found that they were both correct and that the differences were due to the stimuli used in the two experiments. Prazdny (1986) used explicit, wire-frame figures whose two-dimensional silhouette was defined by texture as the object rotated. We used similar figures defined by texture, relative motion, or binocular disparity and found compelling three-dimensional recovery. Landy *et al.* (1987) used scattered disks on a three-dimensional surface and defined those disks, relative to the background, by dynamic texture. When we repeated structure from motion tests using similar stimuli, disks on the surface of a rotating sphere, we also found very little impression of depth when the disks were defined by dynamic texture, relative motion, or binocular disparity even though the motions of the individual disks could be resolved.

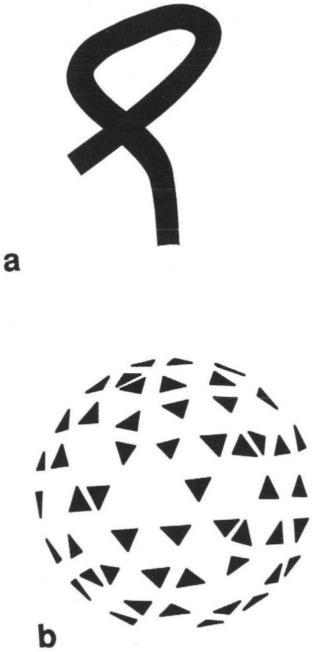

Figure 8. Kinetic depth effects with second-order stimuli. (a) Three-dimensional structure is recovered for second-order stimuli whose total visible surface is explicitly represented such as this silhouette of a paper clip. (b) Little depth is seen for second-order stimuli where a subjective surface must be recovered. These stimuli are shown here as first-order stimuli, defined by luminance. When presented as second-order stimuli the dark areas are filled with dynamic texture and the light areas filled with a uniform gray of the same mean luminance as the texture.

We argued that second-order stimuli can support the recovery of structure from motion as long as the stimulus was explicitly represented. When the stimulus was incomplete, no subjective figure (i.e., sphere) was perceived and no structure was recovered from the motion. It is already well known that subjective figures are only strongly perceived in static stimuli when they are defined by luminance (Brussell *et al.*, 1977; Gregory, 1977; Cavanagh, 1987; Ejima and Takahashi, 1988). Our data suggest that the loss of structure from motion for stimuli involving subjective completion is therefore a failure in the completion step and not the motion extraction. The difference between first- and second-order stimuli here does not appear to have its source in two qualitatively different motion processes.

3.6. Kinematograms

Normal kinematograms are produced from random dot fields where the black and white dots are defined by luminance. We examined kinematograms where the dots are distinguished from each other by second-order properties. We constructed a pattern of random checks where each check was either a patch of uniform grey or a patch of dynamic texture. We then set a square area of these checks into motion in one direction and the background checks into motion in the opposite direction. The relative motion of the two areas could be seen but, like equiluminous coloured kinematograms and unlike luminance-defined kinematograms, there was no segregation of the square from the background, no evident edge between the oppositely moving regions and no impression of one area floating above the other. Thus, similar to the results for kinetic depth effect described above, the second-order stimulus produced impressions of motion but no impression of a subjective figure (this would be a third-order shape).

3.7. *Eccentricity*

The motion response to second-order stimuli appears to drop rapidly in the periphery (Turano and Pantle, 1989). This loss of response is seen first as a slowing of the apparent velocity and then as a loss in stimulus visibility. The rate of loss appears to be much more rapid than that seen with luminance-defined stimuli (Campbell and Maffei, 1978) and suggests that test displays should not extend very far into the periphery.

3.8. *Summary*

Our brief review shows that second-order stimuli may produce less robust impressions of motion in some instances but it did not reveal any evidence of a qualitatively different mechanism responding to second-order motion. The one striking difference we did find, the loss of subjective figures, is more likely a consequence of the processes responsible for completing subjective contours than of those that extract motion. It has already been shown for static figures that luminance contrast is necessary for robust perception of subjective contours and we feel that is the cause of the loss of the subjective square in the second-order kinematogram and the loss of the three-dimensional recovery in the incomplete, second-order, rotating stimuli.

An important finding was the similarity for first- and second-order stimuli in the aperture width necessary for discriminating motion direction. This result certainly suggests that a similar comparator mechanism underlies motion perception for the two types of stimuli. The receptive fields that contribute to the comparator must respond to different stimulus attributes in the two cases, but beyond the characteristics of the initial receptive fields, the mechanisms can be otherwise identical.

There are many more questions to raise about the nature of the receptive fields that contribute to a second-order motion detector. How do they respond to the second-order differences? Chubb and Sperling (1988) have presented an explicit model for detecting dynamic textures that assumes a rectification of image intensities before the crosscorrelation stage. No one has yet offered explicit models for detecting the motion of regions defined by binocular disparity or relative motion but these might involve opponent-motion (Frost and Nakayama, 1983; Nakayama and Loomis, 1974; Frost *et al.*, 1981; Frost *et al.*, 1988) or opponent-depth receptive fields. It would be interesting to determine the spatial structure of these receptive fields: whether or not they are oriented, and whether or not they operate at several spatial scales. The similarity of the results for first- and second-order motion in our aperture and transparency experiments suggests that second-order receptive fields exist at different spatial scales in much the same manner as do the first-order receptive fields that respond to luminance.

It is interesting to note that the characteristics of motion seen with stimuli defined by colour resemble in many respects those seen with second-order stimuli. The apparent velocity of both is slowed relative to a luminance-defined stimulus moving at the same rate. Motion aftereffects are relatively weak in both cases. The subjective figure seen in a kinematogram is lost for both colour and second-order stimuli. Certainly, the response to colour is more like that to second-order stimuli than that to luminance, the other stimulus attribute that we have labeled first-order. This uncertainty concerning the classification of colour stimuli detracts from the usefulness of the first-order vs. second-order classification—on the basis of phenomenology, our categories might be better described as luminance-based vs. 'everything else'. However, the physiological basis for the motion response to colour stimuli is not yet clear and we feel that it is more appropriate to pay attention to the cortical level at which the stimulus attribute emerges than the characteristics of the perceived motion in order to classify the type of detector. A receptive field that has an opponent-colour organization requires one less step to construct than one with an opponent-texture or opponent-motion organization. It requires the same number of steps as an opponent-luminance organization.

3.9. *Object files*

There is one aspect of some long-range motion concepts that does differ from our suggestion of second-order detectors. The 'object files' concept of motion (Treisman, 1986) and Pylyshyn and Storm's (1988) FINST (finger of instantiation) operator assume that when an object appears, a file on the object is opened and that any change in its position contributes to an impression of motion (Fig. 9). Low-level detectors may guide this object tracking function but the role of low-level operators is not made explicit in these models. The key aspect is that each object file 'process' may be arbitrarily connected to any point in the visual field as a dedicated processor. The object file process must still solve the correspondence problem to know which object at time $t+1$ corresponds to which at time t and so must engage in some similarity computations (computing crosscorrelations in some stimulus domain) but these need be neither specific to spatial location nor direction as each process should be capable of tracking a given object over an arbitrary path of positions and directions. On the other hand, the comparator mechanisms that we have discussed are location specific: they cover the visual field with an array of detectors operating in parallel, each analyzing one and only one area of the visual field. We should therefore be able to identify 'object file' processes by examining the spatial organization of motion-sensitive units in visual cortex: dedicated processors that could be allocated to arbitrary spatial locations should be characterized by receptive fields that respond to any region of the visual field. However, in regions up to and including area MT, directionally selective units have localized receptive fields (Hubel and Wiesel, 1968; Zeki, 1980; Baker *et al.*, 1981; De Valois *et al.*, 1982; Felleman and Kaas, 1984) that provide a range of scales and preferred directions at each location—properties expected for comparator-type mechanisms. There are units with receptive fields covering very large areas in the inferotemporal cortex (Gross, 1973) but, unlike those in area MT, they do not appear to be directly involved with motion analyses. Overall, these results might appear to rule out the possibility of 'object file' motion processors, but a specialized processor need show neither spatial nor directional selectivity, so it is not clear that physiologists have asked the right questions to reveal their presence.

There is also an assumption that there is only a limited number of these object file processors available to track objects (Pylyshyn and Storm, 1988). Although there are capacity limits that restrict our ability to follow several independent motions at

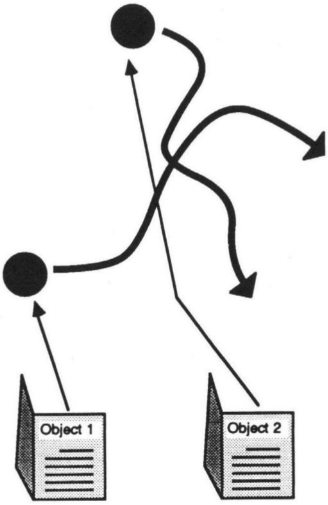

Figure 9. Object files (Treisman, 1986; Pylyshyn and Storm, 1988). A limited number of dedicated processors could be associated with individual objects at arbitrary locations in the visual field and track their movements.

one time (a place-keeping, or shell game task), there do not appear to be capacity limits on perceiving the motion of fields of multiple first-order or second-order elements (e.g., kinematograms). The limit does not appear to act at the level of motion extraction, therefore, but at some higher level. In general, although the object file concept of motion perception allows us to examine a few of its operating principles, it needs to be elaborated in more detail before it can place testable constraints on the underlying physiological mechanisms.

4. CONCLUSIONS

Our paper had two purposes. The first was to argue that the reported differences between short- and long-range motion were the result of the different stimuli used in the two paradigms and not an indication of two qualitatively different motion processes. We found little evidence from previous studies for qualitative differences based on the short-range vs. long-range distinction. The best candidates for two separate motion processes appeared to be those of first-order vs second-order motion detectors.

The second purpose of our paper was therefore to examine whether first- and second-order stimuli generate impressions of motion by way of different mechanisms. Since we found no evidence that second-order motion involved a different style of motion detector, we attribute to second-order motion processes the same organization that is assumed for first-order motion processes: arrays of local, spatiotemporal comparators that cover the visual field and operate in parallel (Fig. 10, we include in these operators ones that respond to moving contours independently of the attributes defining the contours, Cavanagh *et al.*, 1989). Many seemingly different implementations have been proposed for these operators (Reichardt, 1961; Barlow and Levick, 1965; Marr and Ullman, 1981; Adelson and Bergen, 1985; van Santen and Sperling, 1985; Watson and Ahumada, 1985) but none

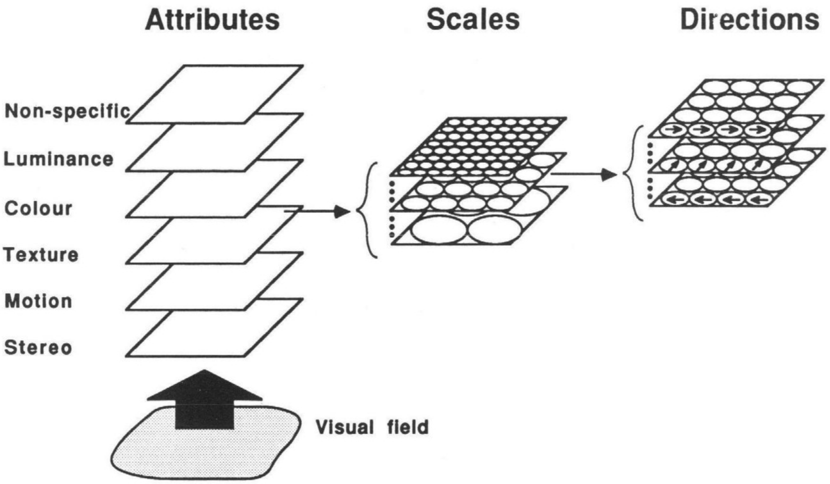

Figure 10. The visual field is covered by arrays of detectors for each stimulus attribute as well as an array that responds to motion independently of the attributes defining the stimulus contours. Several scales and several directions of motion are represented for each array.

of the evidence we have considered discriminates critically among them. We also assume that the signals from all of these detectors can trigger cooperative, context-dependent processing independently of the level of the detectors (Fig. 10).

In one sense, our suggestion that all motion is analyzed by variations on simple detectors is trivial. How else could motion be detected but through spatiotemporal comparison? Are not all mechanisms reduceable to some variant of a motion-detecting, receptive field? Our answer is yes, even token matching (Ullman, 1979), problem solving (Rock, 1983) and 'object file' (Treisman, 1986; Pylyshyn and Storm, 1988) processes must engage in spatiotemporal comparisons at some level. However, we are claiming that the similarity of the initial motion extraction for all types of stimuli extends beyond the basic detector style to include similarities in the arrangements of detector arrays (Fig. 10). More important, this initial similarity across stimulus types suggests, not parallel streams of motion extraction, one short-range and passive and the other long-range and intelligent, but a concatenation of a common mode of initial motion extraction followed by a general inference process. Freeing this inference process from the misleading short-range/long-range dichotomy allows it to be studied within the general framework of cooperative processes (Rosenfeld *et al.*, 1976; Poggio *et al.*, 1986).

In summary, we suggest that there is only one style of motion processing in the visual system: one that starts with several arrays of spatiotemporal comparators—spatially localized processors that operate in parallel. The visual field is therefore covered several times over with sufficient detectors to respond to various first- and second-order stimulus attributes at several spatial scales and directions for each attribute. The signals from these detectors can be augmented or modified by cooperative, context-dependent processes. The 'intelligent' analyses provided by these cooperative interactions should be associated with all the motion detectors and not with only one particular subclass of detector. We do not find evidence for the special purpose motion processors such as those suggested by Treisman (1986) or Pylyshyn and Storm (1988) which would be dedicated to individual objects as opposed to spatial locations. However, it is not clear that any current psychophysical or physiological tests would be sensitive to these detectors.

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REFERENCES

Adelson, E. H. (1982). Some new motion illusions, and some old ones, analyzed in terms of their Fourier components. *Invest. Ophthalmol. Visual Sci.* (*Suppl.*) **27**, 291.

Adelson, E. H. and Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. *J. Opt. Soc. Am. A* **2**, 284–299.

Adelson, E. H. and Movshon, J. A. (1982). Phenomenal coherence of moving gratings. *Nature* **300**, 523–525.

Albright, T. D. (1987). Isoluminant motion processing in macaque visual area MT. *Soc. Neurosci Abs.* **13**, 1626.

Albright, T. D. and Stoner, G. R. (1989). Motion perception survives figural cue heterogeneity. *Invest. Ophthalmol. Visual Sci.* (*Suppl.*) **30**, 74.

Ammons, C. H. and Weitz, J. (1951). Central and peripheral factors in the phi phenomenon. *J. Exp. Psychol.* **42**, 327–332.

Anstis, S. M. and Rogers, B. J. (1975). Illusory reversal of visual depth and movement during change of contrast. *Vision Res.* **15**, 957–962.

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

Anstis, S. M. (1980). The perception of apparent movement. *Phil. Trans. R. Soc. Lond.* **B290**, 153–168.

Baker, C. L. and Braddick, O. J. (1985a). Eccentricity-dependent scaling of the limits for short-range apparent motion perception. *Vision Res.* **25**, 803–812.

Baker, C. L. and Braddick, O. J. (1985b). Temporal properties of the short-range process in apparent motion. *Perception* **14**, 181–192.

Baker, C. L. and Cynader, M. S. (1988). Space–time separability of direction selectivity in cat striate cortex neurons. *Vision Res.* **28**, 239–246.

Baker, J. F., Petersen, S. E., Newsome, W. T. and Allman, J. (1981). Visual response properties of neurons in four extrastriate visual areas of owl monkey (*Aotus trivergatus*): a quantitative comparison of the medial (M), dorsomedial (DM), dorsolateral (DL) and middle temporal (MT) areas. *J. Neurophysiol.* **45**, 387–406.

Banks, W. F. and Kane, D. A. (1972). Discontinuity of seen motion reduces the visual motion aftereffect. *Percept. Psychophys.* **12**, 69–72.

Barlow, H. B. and Levick, W. R. (1965). The mechanism of directionally selective units in the rabbit retina. *J. Physiol.* (*Lond.*) **178**, 477–504.

Braddick, O. (1974). A short-range process in apparent motion. *Vision Res.* **25**, 839–847.

Braddick, O. (1980). Low-level and high-level processes in apparent motion. *Phil. Trans. R. Soc. Lond.* **B290**, 137–151.

Brussell, E. M., Stober, S. R. and Bodinger, D. M. (1977). Sensory information and subjective contour. *Am. J. Psychol.* **90**, 145–156.

Burt, P. and Sperling, G. (1981). Time distance and feature trade-offs in visual apparent motion. *Psychol. Rev.* **88**, 171–195.

Campbell, F. W. and Maffei, L. (1981). The influence of spatial frequency and contrast on the perception of moving patterns. *Vision Res.* **21**, 713–721.

Cavanagh, P. (1987). Reconstructing the third dimension: Interactions between color, texture, motion, binocular disparity and shape. *Comp. Vision, Graphics Image Process.* **37**, 171–195.

Cavanagh, P. (1988). Pathways in early vision. In: *Computational Processes in Human Vision: An Interdisciplinary Perspective.* Z. Pylyshyn (Ed.). Ablex, Norwood, NJ, pp. 254–289.

Cavanagh, P. and Anstis, S. M. (1986). Do opponent-color channels contribute to motion? *Invest. Ophthalmol. Visual Sci. (Suppl.)* **27**, 291.

Cavanagh, P., Arguin, M. and von Grünau, M. (1989). Interattribute apparent motion. *Vision Res.* **29**, 1197–1204.

Cavanagh, P., Boeglin, J. and Favreau, O. E. (1985). Perception of motion in equiluminous kinematograms. *Perception* **14**, 151–162.

Cavanagh, P. and Favreau, O. E. (1985). Color and luminance share a common motion pathway. *Vision Res.* **25**, 1595–1601.

Cavanagh, P. and Ramachandran, V. S. (1988). Structure from motion with equiluminous stimuli. Paper presented to the *Annual meeting of the CPA*, Montreal, June.

Cavanagh, P., Tyler, C. W. and Favreau, O. E. (1984). Perceived velocity of moving chromatic gratings. *J. Opt. Soc. Am. A* **1**, 893–899.

Chang, J. J. and Julesz, B. (1983). Displacement limits for spatial frequency filtered random-dot cinematograms in apparent motion. *Vision Res.* **23**, 1379–1385.

Charles, E. R. and Logothetis, N. K. (1989). The reponses of middle temporal (MT) neurons to isoluminant stimuli. *Invest. Ophthalmol. Visual Sci. (Suppl.)* **30**, 427.

Chubb, C. and Sperling G. (1988). Drift-balanced random stimuli: a general basis for studying non-Fourier motion perception. *J. Opt. Soc. Am. A* **5**, 1986–2007.

De Valois, R. L. and De Valois, K. K. (1975). Neural coding of color. In: *Handbook of Perception*, Vol. 5, *Seeing*. E. C. Carterette and M. P. Friedman (Eds.). Academic Press, New York, pp. 117–166.

De Valois, R. L., Yund, E. W. and Helper, N. (1982). The orientation and direction selectivity of cells in macaque visual cortex. *Vision Res.* **22**, 531–544.

Derrington, A. M. and Badcock, D. R. (1985). The low level motion system has both chromatic and luminance inputs. *Vision Res.* **25**, 1874–1884.

Dick, M., Ullman, S. and Sagi, D. (1987). Parallel and serial processes in motion detection. *Science* **237**, 400–402.

Ejima, Y. and Takahashi, S. (1988). Illusory contours induced by isoluminant chromatic patterns. *Vision Res.* **28**, 1367–1377.

Felleman, D. J., Kaas, J. H. (1984). Receptive field properties of neurons in middle temporal visual area (MT) of owl monkeys. *J. Neurophysiol.* **52**, 488–513.

Frost, B. J. and Nakayama, K. (1983). Single visual neurons code opposing motion independent of direction. *Science* **220**, 744–745.

Frost, B. J., Cavanagh, P. and Morgan, B. (1988). Deep tectal cells in pigeons respond to kinematograms. *J. Comp. Physiol.* **162**, 639–647.

Frost, B. J., Scilley, P. L. and Wong, S. C. P. (1981). Moving background patterns reveal double opponency of directionally specific pigeon tectal neurons. *Exp. Brain Res.* **43**, 173–185.

Georgeson, M. A. and Shackleton, T. M. (1988). Monocular motion sensing, binocular motion perception, *Perception* **17**, 349.

Gorea, A. and Lorenceau, J. (1989). Motion perception in compound stimuli is 'blob'-dependent. *Invest. Ophthalmol. Visual Sci. (Suppl.)* **30**, 388.

Gorea, A. and Papathomas, T. V. (1989). Motion processing by chromatic and achromatic pathways. *J. Opt. Soc. Am. A* **6**, 590–602.

Gregory, R. L. (1977). Vision with isoluminant colour contrast: 1. A projection technique and observations. *Perception* **6**, 113–119.

Green, M. (1986). What determines correspondence strength in apparent motion? *Vision Res.* **26**, 599–607.

Green, M. and Odom, J. V. (1986). Correspondence matching in apparent motion: Evidence for three-dimensional spatial representation. *Science* **233**, 1427–1429.

Gross, C. H. G. (1973). Visual functions of the inferotemporal cortex. In: *Handbook of Sensory Physiology*. Vol. VII/3B: *Visual Centers in the Brain*. R. Jung (Ed.). Springer-Verlag, Berlin, pp. 451–483.

Hubel, D. H. and Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *J. Physiol. (Lond.)* **195**, 215–243.

Julesz, B. (1960). Binocular depth perception of computer generated patterns. *Bell. Syst. Tech. J.* **39**, 1125–1162.

Julesz, B. (1971). *Foundations of Cyclopean Perception*. University of Chicago Press, Chicago, IL.

Kolers, P. A. (1972). *Aspects of Motion Perception*. Pergamon Press, New York.

Kooi, F. L., De Valois, K. K., Grosof, D. H. and Switkes, E. (1989). Coherence properties of colored moving plaids. *Invest. Ophthalmol. Visual Sci. (Suppl.)* **30**, 74.

Krauskopf, J., Farell, B. and Movshon, J. A. (1989). Phenomenal coherence of moving chromatic gratings. *Invest. Ophthalmol. Visual Sci. (Suppl.)* **30**, 74.

Landy, M. S., Sperling, G., Dosher, B. A. and Perkins, M. E. (1987). Structure from what kinds of motion? *Invest. Ophthalmol. Visual Sci. (Suppl.)* **28**, 233.

Lelkins, A. M. M. and Koenderink, J. J. (1984). Illusory motion in visual displays. *Vision Res.* **24**, 1083–1090.

Marr, D. and Ullman, S. (1981). Directional selectivity and its use in early visual processing. *Proc. R. Soc. London* **B211**, 151–180.

Mather, G. (1984). Luminance change generates apparent movement: implications for models of directional specificity in the human visual system. *Vision Res.* **24**, 1399–1405.

Mather, G. (1987). The dependence of edge displacement thresholds on edge blur, contrast, and displacement distance. *Vision Res.* **27**, 1631–1637.

Mather, G. (1988). Models of the motion detector: which ones predict known illusions of movement? *Perception* **17**, 350.

Mather, G. (1989). Early motion processes and the Kinetic Depth Effect. *Q. J. Exp. Psychol.* **41A**, 183–198.

Mather, G. (1989). Temporal properties of apparent motion in subjective figures. *Perception*, in press.

Mather, G., Cavanagh, P. and Anstis, S. M. (1985). A moving display which opposes short-range and long-range signals. *Perception* **14**, 163–166.

Michael, C. R. (1978a). Color vision mechanisms in monkey striate cortex: simple cells with dual opponent-color receptive fields. *J. Neurophysiol.* **41**, 1233–1249.

Michael, C. R. (1978b). Color-sensitive complex cells in monkey striate cortex. *J. Neurophysiol.* **41**, 1250–1266.

Michael, C. R. (1979). Color-sensitive hypercomplex cells in monkey striate cortex. *J. Neurophysiol.* **42**, 726–744.

Morgan, M. J. and Ward, R. (1980). Conditions for motion flow in dynamic visual noise. *Vision Res.* **20**, 431–435.

Moulden, B. and Begg, H. (1986). Some tests of the Marr-Ullman model of movement detection. *Perception* **15**, 139–155.

Mullen, K. T. and Baker, C. L. (1985). A motion after effect from an isoluminant stimulus. *Vision Res.* **25**,685–688.

Nakayama, K. (1984). Biological image processing: a review. *Vision Res.* **25**, 625–660.

Nakayama, K. and Loomis, J. M. (1974). Optical velocity patterns, velocity-sensitive neurons, and space perception: a hypothesis. *Perception* **3**, 63–80.

Nakayama, K. and Silverman, G. H. (1984). Temporal and spatial characteristics of the upper displacement limit for motion in random dots. *Vision Res.* **24**, 293–299.

Nakayama, K., and Tyler, C. W. (1981). Psychophysical isolation of movement sensitivity by removal of familiar position cues. *Vision Res.* **21**, 427–433.

Narayan, V., Lakshminarayan, V. and Schor, C. (1982). Short but not long range apparent motion stimulates OKN, OKAN, and vection. *Invest. Ophthalmol. Visual Sci. (Suppl.)* **22**, 124.

Pantle, A. J. (1978). On the capacity of directionally selective mechanisms to encode different dimensions of moving stimuli. *Perception* **7**, 261–267.

Pantle, A. J. and Picciano, L. (1976). A multistable movement display: evidence for two separate motion systems in human vision. *Science* **193**, 500–502.

Papathomas, T. V., Gorea, A., Julesz, B. and Chang, J.-J. (1988). The relative strength of depth and orientation in motion perception. *Invest. Ophthalmol. Visual Sci. (Suppl.)* **29**, 449.

Papert, S. (1964). Stereoscopic synthesis as a technique for localizing visual mechanisms. *MIT Quart. Prog. Rep.* **73**, 239–244.

Petersik, J. T. (1980). The effects of spatial and temporal factors on the perception of stroboscopic rotation simulations. *Perception* **9**, 271–283.

Petersik, J. T., Hicks, K. I. and Pantle, A. J. (1978). Apparent movement of successively generated subjective figures. *Perception* **7**, 371–383.

Poggio, T., Torre, V. and Koch, C. (1985). Computational vision and regularization theory. *Nature* **317**, 314–319.

Prazdny, K. (1985a). Some new phenomena of motion perception. *Biol. Cybernet.* **52**, 187–194.

Prazdny, K. (1985b). Stereopsis from kinetic and flicker edges. *Percept. Psychophys.* **36**, 490–492.

Prazdny, K. (1986a). What variables control (long range) apparent motion? *Perception* **15**, 37–40.

Prazdny, K. (1986b). Three-dimensional structure from long-range apparent motion. *Perception* **15**, 619–625.

Prazdny, K. (1987). An asymmetry in apparent motion of kinetic objects. *Bull. Psychonomic Soc.* **25**, 251–252.

Pylyshyn, Z. W. and Storm, R. W. (1988). Tracking multiple independent targets: evidence for a parallel tracking mechanism. *Spatial Vision* **3**, 151–224.

Ramachandran, V. S. and Anstis, S. M. (1986). The perception of apparent motion. *Sci. Am.* **254(6)**, 80–87.

Ramachandran, V. S., Rao, V. M. and Vidyasagar, T. R. (1973). Apparent movement with subjective contours. *Vision Res.* **13**, 1399–1401.

Ramachandran, V. S. and Gregory, R. (1978). Does colour provide an input to human motion perception? *Nature* **275**, 55–56.

Reichardt, W. (1961). Autocorrelation, a principle for the evaluation of sensory information by the central nervous system. In: *Principles of Sensory Communication.* W. A. Rosenblith (Ed.). Wiley, New York, pp. 303–317.

Reichardt, W. and Poggio, T. (1976). Visual control of orientation behaviour in the fly. *Q. Rev. Biophys.* **9**, 311–375.

Rock, I. (1983). *The Logic of Perception.* MIT Press, Cambridge, MA.

Rosenfeld, A., Hummel, R. and Zucker, S. W. (1976). Scene labelling by relaxation operations. *IEEE Trans. Syst. Man Cybernet.* **6**, 420–433.

Saito, H., Tanaka, K., Isono, H. Yasuda, M. and Mikami, A. (1989). Directionally selective response of cells in the middle temporal area (MT) of the macaque monkey to the movement of equiluminous opponent color stimuli. *Exp. Brain Res.*, in press.

Sato, T. (1988). Direction discrimination and pattern segregation with isoluminant chromatic random-dot cinematograms. *Invest. Ophthalmol. Visual Sci.* (*Suppl.*) **29**, 449.

Sato, T. (1989). Motion and depth perception with dichoptic-sequential presentation of random-dot patterns. *Invest. Ophthalmol. Visual Sci.* (*Suppl.*) **30**, 74.

Shadlen, M. and Carney, T. (1986). Mechanisms of human motion perception revealed by a new cyclopean illusion. *Science* **232**, 95–97.

Shipley, W. C., Kenney, F. A. and King, M. E. (1945). Beta movement under binocular, monocular, and interocular stimulation. *Am. J. Psychol.* **58**, 545–549.

Treisman, A. (1986). Features and objects in visual processing. *Sci. Am.* **255(5)**, 114B–125.

Turano, K. and Pantle, A. (1985). Discontinuity limits for the generation of visual motion aftereffects with sine- and square-wave gratings. *J. Opt. Soc. Am. A* **2**, 260–266.

Turano, K. and Pantle, A. J. (1989). On the mechanism that encodes the movement of contrast variations: velocity discrimination. *Vision Res.* **29**, 207–221.

Tyler, C. W. (1974). Depth perception in disparity gratings. *Nature* **251**, 140–142.

Ullman, S. (1979). *The Interpretation of Visual Motion.* MIT Press, Cambridge, MA.

van Santen, J. P. H. and Sperling, G. (1985). Elaborated Reichardt detectors. *J. Opt. Soc. Am. A* **2**, 300–321.

von Grünau, M. W. (1986). A motion aftereffect for long-range stroboscopic apparent motion. *Percept. Psychophys.* **40**, 31–38.

Watson, A. B. and Ahumada Jr., A. J. (1985). Model of human visual-motion sensing. *J. Opt. Soc. Am. A* **2**, 322–342.

Welch, L. (1989). The perception of moving plaids reveals two motion-processing stages. *Nature* **337**, 734–736.

Yuille, A. L. and Grzywacz, N. M. (1988). A computational theory for the perception of coherent visual motion. *Nature* **333**, 71–74.

Zeeman, W. P. C. and Roelofs, C. O. (1953). Some aspects of apparent motion. *Acta Psychol.* **9**, 159–181.

Zeki, S. M. (1980). The representation of colours in the cerebral cortex. *Nature* **284**, 412–418.