Counter-Changing Luminance: A Non-Fourier, Nonattentional Basis for the Perception of Single-Element Apparent Motion

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Motion perception was studied for generalized apparent motion stimuli composed of 2 simultaneously visible elements whose luminance alternated between 2 values (only 1 element is visible at a time for standard apparent motion). It was demonstrated that 1st-order motion energy is neither necessary nor sufficient for the perception of apparent motion. Instead, it was found that counter-changing luminance—simultaneous luminance changes at 2 element locations—is the informational basis for perceiving luminance-defined apparent motion: Motion starts where luminance changes toward the background luminance value and ends where luminance changes away from the background luminance. The results were not attributable to either 2nd-order motion mechanisms (for which rectification precedes the computation of motion energy) or attention-based, 3rd-order motion mechanisms.

Single-element apparent motion has been a central perceptual phenomenon since the earliest days of experimental psychology (Exner, 1875; Wertheimer, 1912). In the standard version, a visual element, say a spot of light, is alternately presented against a dark background in one of two nearby spatial locations; it appears for a finite period of time in one location and almost instantly disappears and reappears for a finite period of time in its other location. Over a wide range of spatial and temporal conditions, a single element is perceived moving smoothly through the space between the two locations.

Despite its historical importance, the status of the apparent motion phenomenon has been uncertain. Because displacements are discontinuous, it has been commonplace, even very recently, to assume that the apparent motion percept is an illusion (e.g., Bor- ing, 1942; Coren, Ward, & Enns, 1999; Goldstein, 1999; Kolers, 1972; Rock, 1975). The Gestaltists attributed it to “short-circuited” electrical fields in the brain (e.g., Köhler, 1920/1938; Wertheimer, 1912), and Anstis (1978) to a “quirk” in our visual system. Shepard (1981, 1984) has argued that apparent motion is a construction, somewhere between perceiving (continuous) motion and imagining it. That is, motion is included in perceptual representations that are constructed for discontinuously displaced objects because real objects are constrained to move continuously through space.

The assertion that motion perceived for discontinuously displaced objects must be an illusion or a rule-constrained construction is likely to have stemmed from the assumption that the absence of physically continuous movement meant that there was no motion-specifying information in the apparent motion stimulus. However, Fourier-based analyses of motion energy (Adelson & Bergen, 1985) have shown that apparent motion stimuli are spatially and temporally sampled versions of continuous motion, both containing common motion-specifying information (in their low spatial and temporal frequencies). Such motion-specifying information can be detected for apparent motion stimuli, just as it is detected for continuous motion stimuli (Gibson, 1966).

In this article, we provide evidence for an alternative to Fourier-based motion energy as the informational basis for the luminance-defined perception of apparent motion. We begin by contrasting two descriptions of the standard apparent motion stimulus. The first emphasizes events occurring sequentially; an object with greater-than-background luminance appears first at one location and then at another. This change in the spatial location with the highest luminance magnitude was defined as first-order motion information by Cavanagh and Mather (1989).1 Fourier-based analysis of first-order motion energy (Adelson & Bergen, 1985; van Santen & Sperling, 1985; Watson & Ahumada, 1985), described subsequently, provides a potential informational basis for the perception of motion for both discontinuously and continuously displaced objects.

A second description, one that emphasizes events occurring simultaneously rather than sequentially, is in keeping with Gibson’s (1968) proposal that perception of apparent motion is based on changes in stimulus pattern rather than changes in stimulus location. That is, when an object with greater-than-background luminance is removed from one location and shifted discontinuously to a second location, the luminance at the first spatial location (the starting point of the motion) changes toward the

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1 An example of a second-order apparent motion stimulus is a Gabor patch shifted back and forth between two spatial locations. The Gabor patch is a localized spatial frequency grating whose contrast is modulated by a two-dimensional Gaussian distribution such that the average luminance of the patch at each of its locations is the same as the background luminance. Hence, there is no first-order information specifying motion for the patch.
luminance of the background while at the same time the luminance at the other spatial location (the ending point of the motion) changes away from the luminance of the background. We refer to this potential motion-specifying stimulus information as **counter-changing luminance**. It differs from first-order motion information in that it depends on the direction of simultaneous luminance changes (relative to the background luminance) rather than a sequence of luminance magnitudes. Counter-changing luminance also can be the basis for the perception of motion for continuously displaced objects. That is, when an object with greater-than-background luminance moves continuously from one location to the next, the luminance at the location the object just occupied changes toward the background luminance, and at the same time the luminance at the location the object currently occupies changes away from the background luminance.

Although both first-order (Fourier) motion energy and counter-changing luminance are present for standard apparent motion stimuli, we have created a number of apparent motion stimuli for which they are separable. Motion perception (or its absence) for these stimuli indicates that the presence of counter-changing luminance, not first-order motion energy, is the basis for luminance-defined perception of single-element apparent motion.

### Analysis of First-Order Motion Energy

We begin with a description of how the presence of first-order motion information is specified by the two-dimensional, space–time Fourier transformation of the time-varying luminance at each element location of a standard apparent motion stimulus (e.g., Adelson & Bergen, 1985; van Santen & Sperling, 1985). Although particular spatial and temporal parameters have been selected to make the computational results concrete, the conclusions are not parameter dependent. In our initial examples, first-order (Fourier) motion energy is analyzed for two stimuli with discontinuously changing luminance values.

The first example is a standard single-element apparent motion stimulus that always results in the perception of rightward motion (two frames are represented in Figure 1a): A small 12° × 12° min of arc squared (luminance: 130.1 cd/m²) is presented for 267 ms against a darker background (6.9 cd/m²) that is 2.5° wide and 1.5° high and then replaced by an identical square element located 42 min of arc to its right, again for 267 ms. (The spatial and luminance values for the example have been selected for correspondence with values in the examples and experiments that follow.)

The second example has the same elements in the locations just described. Both elements are simultaneously illuminated for 267 ms and then simultaneously darkened (element luminance = back-

![Figure 1](graphical_representation.png)

**Figure 1.** Graphical representation of two frames of a standard apparent motion stimulus (a) and a flicker stimulus (b). Superimposed on the two-dimensional Fourier space–time transforms for these stimuli (c and d) are the areas over which motion energy is integrated for rightward (R) and leftward (L) motion directions, as well as the calculated first-order directional energy (R – L).
ground luminance) for 267 ms, resulting in the perception of flicker (Figure 1b).

Presented in Figure 1c and Figure 1d are the two-dimensional, space-time Fourier transformations (in the horizontal direction) for these stimuli. The transformations, which include the background box, are limited to two frames to avoid mixing motion energy for successive motions in opposite directions. Each point on these motion energy diagrams represents the energy for a particular combination of spatial and temporal frequencies; bright locations represent higher energy than dark locations. It can be seen that discontinuously changed luminance values are highly complex in the Fourier domain, with many replications of sub-regions with similar energy distributions. These replications result from the sampling artifacts that distinguish discontinuously from continuously displaced stimuli (Adelson & Bergen, 1985).

The presence of motion-specifying first-order information is indicated qualitatively when high energy locations are oriented with respect to the origin of the motion energy diagram (Fleet & Langley, 1994). The direction and speed specified by the first-order motion information depend on the slope of the oriented motion energy. Positive slopes specify leftward motion, negative slopes specify rightward motion, steep slopes specify fast motion, and shallow slopes specify slow motion. A slope of zero specifies a speed of 0°/s (stationarity rather than motion).

In addition to the qualitative determination of whether motion energy is oriented, a quantitative measure of first-order directional energy (DE) is introduced. DE is a variable representing the direction and magnitude of the motion specified by first-order luminance information. For the stimuli studied in this article, positive DE values specify rightward motion, negative values specify leftward motion, and magnitudes near zero specify stationarity rather than motion. Measurement of DE is useful in revealing the presence of oriented energy when it is not easily visualized in the motion energy diagram and in matching the magnitude of first-order motion energy in otherwise contrasting experimental conditions. DE is calculated by integrating motion energy over equal areas within the upper-left and upper-right quadrants of the space-time Fourier transform. The integration areas for these examples (and the remainder of this study) are denoted in Figure 1c and Figure 1d. The range of integration is restricted to low temporal frequencies between 0 and 0.8 Hz and low spatial frequencies between 0 and 0.4 (or between 0 and −0.4) cycles per degree to eliminate the influence of the replications that distinguish discontinuously from continuously displaced stimuli (Adelson & Bergen, 1985). (Roughly similar results are obtained when the integration area is increased by a factor of 10 along each dimension.) The energy at each combination of spatial and temporal frequency within these ranges is summed, the summed energy in the upper-left quadrant reflecting the presence of rightward energy (R), the summed energy in the upper-right quadrant reflecting the presence of leftward energy (L), and the difference of these summed energies (R − L) constituting first-order DE: First order DE = R − L.

The presence of first-order energy specifying rightward motion for the standard apparent motion stimulus is indicated qualitatively by the negative slope (orientation) of the motion energy diagram and quantitatively by positive values of DE (Figure 1c). The absence of motion-specifying first-order energy for the flicker stimulus is indicated qualitatively by the absence of orientation in the motion energy diagram and quantitatively by a zero DE value (Figure 1d). Stationarity is specified rather than motion.

The qualitative and quantitative comparison of the standard apparent motion and flicker stimuli reflects the feasibility of first-order motion energy providing the informational basis for the perception of apparent motion. However, as indicated earlier, rightward motion also is specified by counter-changing luminance for the standard apparent motion stimulus; perceived motion would start at the element for which luminance changes toward the background luminance value and end at the element for which luminance changes away from the background luminance value (see Figure 1a).

Generalized Single-Element Apparent Motion

A generalized version of single-element apparent motion was first described by Johansson (1950) and more recently studied systematically by Hock, Kogan, and Espinoza (1997). For the generalized version, elements are simultaneously visible at both locations of the apparent motion stimulus, with the luminance of one element different from that of the other (instead of only one element being visible at a time, as with standard apparent motion). Johansson (1950) found that motion could be perceived through the space between the two elements when the luminance of one was continuously decreased while at the same time the luminance of the other was continuously increased. Hock et al. (1997) modified Johansson’s paradigm by simultaneously presenting two elements (small squares) with different luminance values and exchanging these values during successive, discrete frames; when the luminance of one square was continuously decreased, the luminance of the other was discontinuously increased (Figure 2). They found, over a wide range of element and background luminance values, that the likelihood of perceiving motion varies with a unit-free measure of stimulus contrast, the background-relative luminance contrast (BRLC). The BRLC is the difference in the luminance values for each element (L1 − L2) divided by the difference between the average luminance of the element (Lm) and the luminance of the background (Lb): (L1 − L2)/(Lm − Lb). Standard single-element apparent motion is a special case of the generalized version. It is established by making the lower luminance value (L1) of each element equal to the luminance of the background (Lb), so only one of the two elements is visible at a time, first at one location and then at the other. The BRLC for standard apparent motion is 2.0, regardless of the particular luminance values that are presented.

Analysis of first-order motion energy for the generalized version of single-element apparent motion is based on a stimulus with the same elements, interelement distance, frame duration, and background luminance as the previously analyzed standard apparent motion stimulus. Now, however, the BRLC for each element is 0.8 rather than 2.0. The stimulus is graphically illustrated in Figure 3a, and the two-dimensional Fourier transformation of the time-varying luminance is presented in Figure 3b. The orientation of the motion energy diagram specifies motion in the rightward direction.

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2 The BRLC at an element location is twice the Michelson contrast, but only if the background luminance is zero (and the luminance of both elements is greater than or less than the background luminance).
(the calculated first-order DE is 0.43), but it can be seen from Figure 3a that counter-changing luminance at the two element locations also specifies rightward motion; that is, the luminance of the left element changes toward the background luminance value, and simultaneously the luminance of the right element changes away from the background value. Motion is almost always perceived for this example (Hock et al., 1997), but as is the case for standard apparent motion, it is not possible to distinguish between counter-changing luminance and first-order motion energy as the basis for the motion percept, because both are present. Moreover, increasing the time-varying stimulus contrast (as measured by the BRLC) increases the magnitude of the change in luminance toward and away from the background luminance at each element location and also increases the first-order DE. As illustrated in Figure 3c for stimuli with the same BRLC value at each element location, the relationship between BRLC and DE is linear. This was the case for all of the luminance configurations tested in the experiments described subsequently (although the magnitudes of DE and the slope of the function relating DE to BRLC varied).
Experimental Plan

The results of seven experiments are reported. Experiment 1 determined whether first-order motion energy is sufficient for the perception of apparent motion when counter-changing luminance is absent, and Experiment 2 investigated whether first-order motion energy contributes to motion perception when counter-changing luminance is present. Experiment 2 determined whether the effect of counter-changing luminance can instead be explained by an attention-based, feature-tracking mechanism (Cavanagh, 1992; Lu & Sperling, 1995a, 1995b). Experiments 3 and 4 were concerned with whether the influence of counter-changing luminance on motion perception is based not on simultaneous luminance decrements and increments but, more specifically, on the directions of the luminance changes relative to the background luminance (i.e., toward the background luminance at one element location and away from it at the other element location). It was confirmed in Experiment 5 that counter-changing luminance specifies not just motion, but motion in a particular direction (starting at the element for which luminance changes toward the background luminance and ending at the element for which luminance changes away from the background luminance). Experiment 6 determined whether a second-order motion mechanism in which nonlinear rectification precedes the determination of first-order motion energy (Chubb & Sperling, 1988; Lu & Sperling, 1995b) could be the basis for the perception of single-element apparent motion between elements of opposite luminance polarity. Finally, Experiment 7 examined the potential contribution of an attention-based, third-order motion mechanism (Cavanagh, 1992; Lu & Sperling, 1995a, 1995b) to the perception of apparent motion in the presence and absence of counter-changing luminance.

Experiment 1

The purpose of this experiment was to examine the necessity and sufficiency of first-order motion information versus counter-changing luminance as the luminance-defined informational basis for the perception of single-element apparent motion. In the co-changing condition, luminance values were selected such that first-order motion energy was present but counter-changing luminance was not. In the counter-changing condition, both potential sources of motion information were present.

The first two (of eight) frames of a stimulus from the co-changing condition are illustrated in Figure 4a. The BRLC values for the left and right elements are 0.6 and 1.8, respectively. The orientation of the two-dimensional Fourier transform for this stimulus (Figure 4d) indicates that first-order motion energy specifies motion in the rightward direction. However, as indicated in Figure 4a, luminance increased simultaneously at both element locations from Frame 1 to Frame 2 (in the experiment, it then decreased simultaneously during Frame 3, and so on), so there is no counter-changing luminance at the two element locations.

The first two frames of a stimulus from the counter-changing condition with corresponding BRLC values are illustrated in Figure 4b. Its two-dimensional Fourier transform (Figure 4e) again specifies rightward motion. However, in contrast with the co-changing example, luminance decreases for the left element while simultaneously increasing for the right element, so there is counter-changing luminance at the two element locations specifying rightward motion (see Figure 4b).

Although rightward motion is specified by first-order motion energy for the two frames of the co-changing and counter-changing stimuli illustrated in Figure 4a and Figure 4b, there is much more rightward DE (calculated values of DE are more positive) for the counter-changing stimulus (DE = 0.59) than for the co-changing stimulus (DE = 0.29). However, a match in DE can be obtained by reducing the BRLC for the right element of the counter-changing stimulus. The first two frames of a counter-changing stimulus with BRLC values of 0.6 at both the left and right element locations are illustrated in Figure 4c. Its two-dimensional Fourier transform (Figure 4f) also specifies rightward motion, but now the DE (0.29) matches that of the co-changing condition in Figure 4b.

If the presence of first-order motion energy is sufficient for the perception of motion, it would be perceived equally often in both the co-changing and counter-changing conditions when DEs are matched (additional matches were created at other values of DE, as described subsequently). However, if motion perception requires decreases in luminance at one element location accompanied by increases in luminance at the other element location, motion would be perceived only in the counter-changing condition.

Method

Stimuli. Stimuli were presented with a Power Macintosh 7300/180 computer. Two small squares with variable luminance were centered within a darker rectangular box (2.5° × 1.5° high; luminance, $L_0 = 6.9 \text{cd/m}^2$), which in turn was centered in the screen of a Viewsonic 15GA monitor (screen luminance: $<0.001 \text{cd/m}^2$). The squares, which always were simultaneously visible, subtended a visual angle of $12 \times 12$ min of arc and were $42$ min of arc apart (center to center) when viewed from a distance of 35.8 cm (viewing distance was maintained by a head restraint).

For both conditions, the luminance of the element on the left always alternated between 46.9 and $81.0 \text{cd/m}^2$ ($L_1$ and $L_2$), resulting in a BRLC value of 0.6, and the luminance of the element on the right alternated between different pairs of luminance values, either 55.5/72.5, 52.5/75.5, 49.7/78.3, 46.9/81.0, 35.5/92.5, 21.1/106.9, 18.2/109.8, 15.3/112.7, or $12.5/115.5 \text{cd/m}^2$, resulting in BRLC values of 0.3, 0.4, 0.5, 0.6, 1.0, 1.5, 1.6, 1.7, or 1.8, respectively. The average luminance value for each element, $L_m$, always was 64.0 $\text{cd/m}^2$.

Stimuli in the two conditions differed with respect to the frame-to-frame directions of luminance change for the two elements. (There were eight frames per trial, each with a duration of 267 ms.) For co-changing stimuli, luminance values simultaneously increased and simultaneously decreased at both element locations. Both elements were at their lower luminance value during odd-numbered frames (the luminance of the left element was greater), and both were at their higher luminance value during even-numbered frames (the luminance of the right element was greater). For counter-changing stimuli, decreases in luminance at one element location occurred simultaneously with increases in luminance at the other element location. During odd-numbered frames, the left element was at its higher luminance value and the right element at its lower luminance value. During even-numbered frames, the left element decreased in luminance to its lower value, and the right element increased in luminance to its higher value. Calculated DEs were matched for the co-changing and counter-changing

3 For both the co-changing and counter-changing versions of this luminance configuration, the direction of motion specified by first-order motion energy is determined by whether the luminance of the right element increases (rightward motion) or decreases (leftward motion) in relation to the relatively unchanged luminance of the element on the left.
conditions on the basis of the BRLC of the element on the right (BRLC was fixed at 0.6 for the left element). The four matches are listed in Table 1.

**Design.** The orthogonal combination of two conditions (co-changing and counter-changing luminance) and nine BRLC values resulted in 18 distinctive trials, each of which was repeated six times within each block of 108 trials (trial order was randomized in sub-blocks of 18 trials). There were two blocks of trials during each of two testing sessions.

**Procedure.** Participants were instructed to fixate midway between the two squares. After each trial, they indicated whether or not they had perceived motion through the space between the two squares anytime during the trial by pressing one of two designated keys on the computer keyboard (they did not judge motion direction, which alternated between leftward and rightward over the course of each eight-frame trial). They were instructed to press the space bar if they were unsure of their response.

**Participants.** The 3 participants were one of the authors, a graduate student at Florida Atlantic University, and an undergraduate student who was naive with respect to the purpose of the experiment.

**Results**

Motion was never perceived in the co-changing condition, regardless of the BRLC values, but was perceived in the counter-changing condition. This difference was obtained even for BRLC values of the right element that resulted in equal DE in the two conditions (these DE matches are linked by broken lines in Figure 5). If there was sufficient first-order motion energy for motion to be perceived for counter-changing stimuli, why was motion not perceived for co-changing stimuli with matching DE? It can be concluded from the results for the co-changing condition that the presence of first-order motion energy is not sufficient for motion to be perceived. The contrasting results for the counter-changing condition indicate that decreases in luminance at one element location and increases in luminance at the other element location are necessary for the luminance-defined perception of apparent motion.

Simultaneous Decrements and Increments?

**Additional Results**

A simple additional experiment confirmed that luminance decrements and increments must occur at both element locations if motion is to be perceived. During successive frames of this addi-
tional experiment, the luminance of the left element remained constant at 68.5 cd/m² (BRLC = 0), while that of the right element alternated between 28.4 and 108.6 cd/m² (BRLC = 1.3), with one value above and the other below the luminance of the left element. This provided successive luminance decrements and increments for the right element (but not the left), and analyses of first-order motion energy specified the frame-to-frame alternation of rightward and leftward motion over a succession of frames, with a first-order DE value of 0.35. This stimulus was randomly mixed in a block of 108 trials with a counter-changing stimulus having similar DE (0.32; BRLC = 0.6 for both elements; note that the particular luminance values for this stimulus, 50.0 and 87.0 cd/m², were different from those in the main portion of the experiment).

Averaging the results for 2 observers (1 naive), motion was perceived on 93% of the trials for the counter-changing stimulus but never for the stimulus with BRLC values of 0 for one element and 1.3 for the other (despite the similarity in DE for the two stimuli). This indicated that (a) the presence of first-order motion energy is not sufficient for the perception of motion (replicating the results of the main experiment) and (b) changes in luminance for both elements are necessary for motion to be perceived on the basis of counter-changing luminance.

Experiment 2

The results of Experiment 1 indicated that the presence of first-order motion energy in the co-changing condition was not sufficient for the perception of apparent motion. Motion was not perceived in the absence of counter-changing luminance at the two element locations. In this experiment, we investigated whether first-order motion energy can contribute to motion perception in the presence of counter-changing luminance. To do so, we introduced a spatial gradient in luminance magnitudes across the two element locations: The average luminance for the right element was three times larger than the average luminance (\(L_m\)) for the left element. This was the spatial asymmetry condition. In the contrasting spatial symmetry condition, the average luminance was the same for both elements. The spatial gradient for the spatial asymmetry condition was significant because it affected the magnitude of first-order DE, as shown subsequently.

Counter-changing luminance specifies rightward motion for both the spatial asymmetry and symmetry conditions (the first two of eight frames are illustrated in Figure 6a and Figure 3a, respectively; BRLC = 0.8 for both elements in both examples). The orientation of the two-dimensional Fourier transforms (Figure 6b and Figure 3b) also specifies rightward motion for both examples. However, there is approximately 40% more first-order DE for the spatial symmetry stimulus (DE = 0.43) than for the spatial asymmetry condition.

Table 1: Values of Background-Relative Luminance Contrast for the Co-Changing and Counter-Changing Conditions That Produce Matching Values of First-Order Directional Energy

<table>
<thead>
<tr>
<th>Co-changing condition</th>
<th>Counter-changing condition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left element</td>
<td>Right element</td>
</tr>
<tr>
<td>0.6</td>
<td>1.8</td>
</tr>
<tr>
<td>0.6</td>
<td>1.7</td>
</tr>
<tr>
<td>0.6</td>
<td>1.6</td>
</tr>
<tr>
<td>0.6</td>
<td>1.5</td>
</tr>
</tbody>
</table>

Figure 5. Experiment 1: Proportions of trials during which motion was perceived in the co-changing and counter-changing conditions as a function of the background-relative luminance contrast (BRLC) of the right element, for participants L.G. (top), M.R. (middle), and C.P. (bottom). The BRLC value of the left element was always 0.6. Included in each graph are broken lines linking values in the two conditions with matching values of first-order directional energy (DE). The results were obtained for the stimuli illustrated in Figure 4.
that is, the calculated difference between rightward and leftward motion energy is larger (and more positive) for the spatial symmetry stimulus. If first-order motion energy contributes to the perception of apparent motion in the presence of counter-changing luminance (Experiment 1 showed that it makes no contribution in the absence of counter-changing luminance), larger BRLC values would be required to perceive motion in the spatial asymmetry condition than in the spatial symmetry condition. This would be necessary to account for the difference in first-order DE between the two conditions. (Figure 3c shows that the magnitude of first-order DE increases with increases in BRLC.)

Method

With the exception of the luminance values of the elements, this experiment was identical to that of Experiment 1. In the spatial asymmetry condition, the luminance of the left element alternated between pairs of values, either 32.9/35.6, 31.5/37.0, 30.1/38.4, 28.8/39.7, 27.4/41.1, 26.0/42.5, 24.7/43.8, 23.3/45.2, or 21.9/46.6 cd/m², resulting in BRLC values of 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, or 0.9, respectively (the average luminance value was 34.2 cd/m²). The luminance of the right element in that condition alternated between different pairs of values, either 98.0/107.5, 93.2/112.3, 88.4/117.1, 83.6/121.9, 78.8/126.7, 74.0/131.5, 69.2/136.3, 64.4/141.1, or 59.6/145.9 cd/m², also resulting in BRLC values ranging from 0.1 to 0.9 (the average luminance value was 102.7 cd/m²). In both conditions, the BRLC values for a particular trial were always the same at each element location. Counter-changing luminance was present for both conditions; when luminance decreased for one element, it increased for the other.

The 3 participants were volunteer undergraduate students at Florida Atlantic University who were naive with respect to the purpose of the experiment. During each of four testing sessions, they participated in three blocks of 144 randomly ordered spatial symmetry and spatial asymmetry condition trials.

Results

For each of the participants, motion was perceived for somewhat smaller BRLC values in the spatial asymmetry condition than in the spatial symmetry condition (Figure 7). If perception of motion were influenced by first-order motion energy, the opposite result would have been obtained. That is, motion would have been perceived more easily (for smaller BRLC values) in the spatial symmetry condition because there was more DE than in the spatial asymmetry condition. It can be concluded that first-order motion energy does not contribute to the perception of single-element apparent motion, regardless of whether counter-changing luminance is present (Experiment 2) or absent (Experiment 1).

Feature Tracking? Additional Results

It might be argued that the effects on motion perception attributed to the detection of counter-changing luminance are in reality the result of an attention-based, feature-tracking mechanism (Cavanagh, 1992; Lu & Sperling’s, 1995a, 1995b, third-order motion). Indeed, there were two potentially trackable stimuli features in the spatial symmetry condition, the brighter element and the occurrence of a luminance increment (or decrement). Both shifted back and forth between the two element locations during successive frames.

A simple experiment based on a two-frame version of the spatial asymmetry condition provided evidence against feature tracking as an alternative to the detection of counter-changing luminance. The duration of the first frame was 6,268 ms, and that of the second frame was 267 ms. The purpose of the long-duration first frame was to eliminate the possibility of motion being perceived through the attentional tracking of luminance increments; they were too far apart in time. The purpose of the spatial asymmetry condition was to eliminate the possibility of motion being perceived through the attentional tracking of the brighter element; the brighter element always remained in the same location in that condition. To minimize anticipation of a particular motion direction, both leftward and rightward motion were possible at the onset of Frame 2. For some trials, the luminance decreased for the left element and increased for the right element (rightward motion); for other, randomly mixed trials, the luminance increased for the left element.
and decreased for the right element (leftward motion). BRLC values ranged from 0.1 to 0.9.

As in the main experiment, whether or not motion was perceived (tested with 2 observers, 1 naive) was affected by increases in BRLC; motion was perceived for an average of 90% of the trials when the BRLC was 0.9. This indicated that the perception of single-element apparent motion, which we have been attributing to the detection of counter-changing luminance, cannot be attributed instead to attention-based feature tracking, which was eliminated as a factor in this experiment. (The possible influence of attention-based motion mechanisms in other circumstances is not ruled out.)

### Experiment 3

The purpose of this experiment was to show that simultaneous luminance decrements and increments at the two element locations are not sufficient for the perception of motion. That is, the luminance change at one element location must be toward the luminance value of the background, and the luminance change at the other element location must be away from the luminance value of the background. In contrast with the preceding experiments, one element was presented against a white background and the other against a black background (Figure 8a).

The first two frames of a stimulus from the *would-otherwise-be-motion* condition are graphically illustrated in Figure 8b. During Frame 2, the luminance of one element decreases while, at the same time, the luminance of the other element increases (BRLC = 0.6 for both). If these luminance values were presented against a uniformly dark background, flicker rather than motion would be perceived. However, as can be seen in Figure 8c, when these luminance values are presented against a mixed white–black background, the luminance of one element changes toward the luminance value of the background, while the luminance of the other element changes away from the background value (and so on for the remaining frames). If motion perception requires counter-changing luminance toward and away from background luminance values, motion would be perceived in this condition.

#### Method

The background for the elements (a rectangular box that was 2.5° wide and 1.5° high) was divided such that the left half was white (luminance: 171.2 cd/m²) and the right half was black (luminance: <0.001 cd/m²). The luminance for the remainder of the screen was 6.9 cd/m². Luminance at both element locations alternated between pairs of values, either 81.2/90.1, 77.1/94.2, 72.6/98.6, 68.5/102.7, 64.0/107.2, 59.9/111.3, 55.8/115.4, 51.4/119.9, or 47.3/124.0 cd/m², resulting in BRLC values from 0.1 to 0.9 for both the white and black backgrounds (the average luminance for each element was 85.6 cd/m²). In the would-otherwise-be-motion condition, the left element was at its lower luminance value and the right element at its higher luminance value during odd-numbered trials, and the reverse was the case during even-numbered frames. In the would-otherwise-be-flicker condition, both elements were at their higher luminance value during odd-numbered frames and their lower luminance value during even-numbered frames. The stimuli, procedure, and design were otherwise as in the preceding experiments.

The 3 participants were one of the authors, a graduate student at Florida Atlantic University, and an undergraduate student who was naive with respect to the purpose of the experiment. They participated in four blocks of 108 randomly ordered trials during a single testing session. After each trial, they indicated whether or not they perceived motion through the space between the two squares (motion direction, which alternated between leftward and rightward over the course of each eight-frame trial, was not judged).

#### Results

With the exception of a few trials for one participant, motion was not perceived in the would-otherwise-be-motion condition despite luminance decrements at one element location occurring simultaneously with luminance increments at the other element location.
The failure to perceive motion can be attributed to the background-relative direction of the luminance decrements and increments. When the left element’s luminance increased toward the luminance of its white background, the right element’s luminance decreased, but toward the luminance of its black background (and then both away from their background luminance values, and so on).

Motion was perceived in the would-otherwise-be-flicker condition for sufficiently large BRLC values (Figure 9). This was the result of the background-relative direction of the luminance decrements and increments. When the luminance of the two elements is the same during a frame and is simultaneously increased for both elements during the next frame, the luminance of the element on the left changes toward that of the white background while at the same time the luminance of the element on the right changes away from that of the black background.4

4 Simultaneous lightness contrast would tend to make the elements appear darker against the white background and lighter against the dark background, and could have affected the discriminability of the high and low luminance values at each location. Because this was true for both the would-otherwise-be-motion and the would-otherwise-be-flicker conditions, simultaneous contrast effects could not have been responsible for the difference in motion perception between the two conditions.
**Differences in First-Order Directional Energy?**

**Additional Results**

Although oriented energy was not easily visualized for the Fourier transforms shown in Figure 8d and Figure 8e, there was more first-order DE in the would-otherwise-be-flicker condition than in the would-otherwise-be-motion condition (with BRLC values matched). To address the possibility that motion was not perceived for the latter because the DE level was too low, we created a would-otherwise-be-motion stimulus for which the BRLC value was 1.4 for each element location; the DE for the first two frames was 0.52. This stimulus was randomly mixed in a block of 108 trials with a would-otherwise-be-flicker stimulus in which the BRLC value was 0.6 for each element location; its DE for the first two frames was 0.55. The different motion directions specified by the first-order motion energy (negative DE values indicate more leftward than rightward energy, and vice versa for positive values) were of no importance in this experiment because motion was never reported for the would-otherwise-be-motion condition. That is, when tested with 2 observers (1 naive), perception of motion was reported for an average of 99% of the trials for the would-otherwise-be-flicker stimulus and 0% of the trials for the would-otherwise-be-motion stimulus. It was confirmed, therefore, that motion perception depends on the presence of background-relative counter-changing luminance.

**Experiment 4**

In this experiment, the objective was to demonstrate again that counter-changing luminance must be in relation to background luminance if motion is to be perceived, but under conditions for which there was no potentially interfering luminance boundary between the elements (as in Experiment 3; see Figure 8a). The background in this experiment was a uniform gray, the left element was always lighter than the background, and the right element was always darker than the background.

During the second frame of the background-relative/co-changing condition (Figure 10a), the right element’s luminance decreases while the left element’s luminance increases; however, the luminance changes for both elements are simultaneously away from the background value (and then simultaneously toward the background, and so on for the remaining frames). Motion perception was not expected. During the second frame of the background-relative/counter-changing condition (Figure 10b), the luminances of both elements simultaneously increase, but the changes in luminance are toward the background luminance for the right element and away from the background luminance for the left element (and so on for the remaining frames). Motion perception was expected for sufficiently large BRLC values.

**Method**

In this experiment (as well as Experiments 5 and 6), the entire screen was at the background luminance ($L_b$) of 85.6 cd/m². There was no rectangular box, as in the preceding experiments. The lighter-than-background element on the left alternated between one of nine pairs of luminance values, 134.4/140.0, 131.9/142.1, 129.3/144.7, 126.7/147.3, 124.1/149.8, 121.6/152.4, 119.0/155.0, 116.4/157.5, or 113.9/160.1 cd/m², resulting in BRLC values ranging from 0.1 to 0.9 ($L_m/H = 137.0$ cd/m²). The darker-than-background element on the right also alternated between one of nine pairs of luminance values, 31.7/36.8, 29.1/39.4, 26.5/42.0, 24.0/44.5, 21.4/47.1, 18.8/50.0, 16.3/52.2, 13.7/54.8, or 11.1/57.4 cd/m², again resulting in BRLC values ranging from 0.1 to 0.9 ($L_m/H = 34.3$ cd/m²).

In the background-relative/co-changing condition, the left element was at its low luminance value and the right element at its high luminance value during odd-numbered frames. This was reversed during even-numbered frames. In the background-relative/counter-changing condition, the left and right elements were at their lower luminance values during odd-numbered frames and their higher luminance values during even-numbered frames. The stimuli, procedure, and design were otherwise as in the preceding experiments.

The 3 participants were one of the authors and 2 undergraduate students at Florida Atlantic University. The latter 2 individuals were naive with respect to the purpose of the experiment. All 3 participated in four blocks of 108 randomly ordered trials during a single testing session.

**Results**

Motion was not perceived in the background-relative/co-changing condition despite the simultaneous occurrence of luminance decrements for one element and luminance increments for the other (Figure 11). As in Experiment 3, the failure to perceive...
motion can be attributed to the background-relative direction of the luminance decrements and increments. When the luminance of the darker-than-background right element decreased away from the luminance of the gray background, the luminance of the darker-than-background right element increased, but also away from the luminance of the gray background (and then both toward the background luminance value during the next frame, and so on).

Motion was perceived in the background-relative/counter-changing condition for sufficiently large BRLC values, despite the occurrence of simultaneous luminance increments and decrements.

Figure 10. Experiments 4 and 5: Graphical representation of two frames of stimuli in the background-relative/co-changing (a) and background-relative/counter-changing (b) conditions, as well as the two-dimensional Fourier space–time transforms and calculated first-order directional energies for these stimuli (c and d).

Figure 11. Experiment 4: Proportions of trials during which motion was perceived in the background-relative/co-changing and background-relative/counter-changing conditions as a function of background-relative luminance contrast (BRLC), for participants L.G. (left), D.N. (middle), and M.A.R. (right). The results were obtained for the stimuli illustrated in Figure 10.
at the two element locations (Figure 11). When the luminance of the darker-than-background right element increased toward the luminance of the gray background, the luminance of the lighter-than-background left element increased away from the luminance of the gray background, creating the counter-changing basis for the perception of apparent motion.

Differences in first-order DE were not a factor in this experiment. As indicated in Figure 10b and Figure 10d, there was less energy in the background-relative/counter-changing condition (when motion was perceived) than in the background-relative/co-changing condition (when motion was not perceived).

**Experiment 5**

In describing counter-changing luminance as the basis for the perception of apparent motion, we have emphasized that direction as well as motion is specified; that is, motion starts at the element for which luminance changes toward the background luminance and ends at the element for which luminance changes away from the background luminance. The purpose of this experiment was to confirm that counter-changing luminance specifies not just motion, but the direction of the motion. That is, the experiment determined whether observers can discriminate between leftward and rightward motion when it is specified by counter-changing luminance.

**Method**

Trials in this experiment were composed of two frames, the first with a duration of 1,017 ms (which allowed more than sufficient time for fixation between the two elements at the start of each trial) and the second with a duration of 267 ms. Luminance values for the lighter-than-background element (which was always on the left) and the darker-than-background element (which was always on the right) were as in the background-relative/counter-changing condition of the preceding experiment. In the luminance-decrease condition, luminance values were at their high value during Frame 1 and their low value during Frame 2. Rightward motion was specified in this condition; the luminance of the left element changed toward that of the background, and the luminance of the right element changed away from that of the background. In the luminance-increase condition, luminance values were at their low value during Frame 1 and their high value during Frame 2; leftward motion was specified by counter-changing luminance. Participants were required to make two responses at the end of each trial, the first to indicate whether or not they perceived motion and the second to indicate the direction of the perceived motion (if motion was perceived).

The 2 participants were one of the authors and an undergraduate student at Florida Atlantic University who was naive with respect to the purpose of the experiment. They participated in four blocks of 108 randomly ordered trials during a single session.

**Results**

When BRLC values were high enough for motion to be perceived, motion was almost always perceived in the direction (either left or right) predicted on the basis of counter-changing luminance (Figure 12). This confirmed that counter-changing luminance provides the specifical stimulus information, not just for the perception of motion, but also for the perception of motion direction.

**Experiment 6**

The experiments reported thus far have presented evidence against first-order motion energy as a basis for the perception of single-element apparent motion. However, Chubb and Sperling (1988) and Lu and Sperling (1995b) have argued for the existence of a second-order motion mechanism in which nonlinear rectification precedes the determination of Fourier motion energy. Such a mechanism could not have had any impact on the results of Experiments 1 and 2 (rectification would have no effect because the elements' luminance values were all of the same polarity; i.e., all luminances were greater than the background luminance), but it is conceivable that perception of single-element apparent motion was influenced by such a second-order mechanism in Experiments 3 through 5 (luminance values were higher than the background luminance value for one element and lower than the background luminance value for the other). The purpose of this experiment was to determine whether the perceived motion in the counter-changing luminance condition was influenced by such a second-order motion mechanism.
to distinguish the potential influence of a second-order mechanism from that of a motion mechanism that responds to counter-changing luminance as the basis for the perception of apparent motion between elements of opposite luminance polarity.

Two-frame co-changing and counter-changing stimuli that were tested in this experiment are graphically illustrated in Figure 13a and Figure 13b (BRLC = 0.6 for the left element and 1.3 for the right element). Calculation of first-order DE indicated that leftward motion was specified for both stimuli, with more leftward energy for the co-changing (DE = 0.29) than the counter-changing (DE = −0.17) stimulus. (The motion energy diagrams are not depicted.)

Rectified versions of the stimuli are graphically represented in Figure 13b and Figure 13c (note the similarity of the configuration of these rectified luminances to the configuration in Experiment 1; see Figure 4a and Figure 4b). Rectification makes all luminance values positive in relation to the background luminance, possibly by combining the responses of ON-center receptive fields for the element with greater-than-background luminance and OFF-center receptive fields for the element with less-than-background luminance. Oriented energy is not easily visualized for the two-dimensional Fourier transformation of the rectified stimulus versions in Figure 13e and Figure 13f; however, second-order DE could be calculated as before (i.e., by integrating over the same

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**Figure 13.** Experiment 6: Graphical representation of two frames of stimuli in the co-changing (a) and counter-changing (b) conditions, as well as the rectified versions of these stimuli (c and d). Also presented are the two-dimensional Fourier space–time transforms and calculated second-order directional energies for the rectified stimuli (e and f).
ranges of temporal and spatial frequencies and subtracting the energy in the leftward direction from the energy in the rightward direction). Calculations for these examples indicate that rightward motion was specified, but with more second-order DE for the counter-changing stimulus (DE = 0.28) than the co-changing stimulus (DE = 0.10).

If the perception of motion for these polarity-reversed stimuli depends on either a first- or second-order motion energy mechanism, motion will be perceived in both conditions (or in neither condition if DE levels are too small). If, instead, the perception of motion depends on a mechanism that responds to counter-changing luminance, motion (rightward) will be perceived, but only in the counter-changing condition.

Method

The background was a uniform gray (luminance: 68.5 cd/m²), the left element had an average luminance of 102.8 cd/m² (the element was always lighter than background), and the right element had an average luminance of 34.3 cd/m² (the element was always darker than background). The luminance of the right element always alternated between 12.0 and 56.5 cd/m², resulting in a BRLC value of 1.3. The luminance of the left element alternated between pairs of luminance values, either 101.0/104.5, 99.3/106.2, 97.6/107.9, 95.9/109.6, 94.2/111.3, 92.5/113.0, 90.8/114.7, 89.0/116.4, or 87.3/118.2 cd/m², resulting in BRLC values ranging from 0.1 to 0.9.

As in the preceding experiment, there were two frames per trial, the first with a duration of 1,017 ms and the second with a duration of 267 ms. During Frame 2 of the co-changing condition, luminance increased for the left element and decreased for the right element (away from the background luminance for both elements). During Frame 2 of the counter-changing condition, both elements decreased in luminance (the left element toward the background luminance and the right element away from the background luminance).

The 2 participants were one of the authors and an undergraduate student at Florida Atlantic University who was naive with respect to the purpose of the experiment. They participated in four blocks of 108 randomly ordered trials during a single session. After each trial, the participants indicated whether or not they had perceived motion and, if they had, the direction of the perceived motion.

Results

Motion was perceived in the counter-changing condition when BRLC values were sufficiently high, and then only in the rightward direction specified by the counter-changing luminance (Figure 14). It was never perceived in the co-changing condition. If motion perception for these reversed polarity stimuli depended on the response of a rectification-dependent, second-order motion mechanism, motion would have been perceived in both conditions (unless there was insufficient second-order motion energy for it to be perceived in the co-changing condition).

Differences in Second-Order Directional Energy?

Additional Results

To rule out the possibility that motion would have been perceived in the co-changing condition if there was sufficient second-order DE, a co-changing stimulus with BRLC values of 0.2 and 2.0 for the left and right elements (second-order DE = 0.27) was randomly mixed in a block of 108 trials with a counter-changing stimulus in which BRLC values were 0.6 and 1.3 for the left and right elements (second-order DE = 0.28). The results of the main experiment were confirmed. For 2 observers (1 naive), perception of motion was reported for 100% of the trials with the counter-changing stimulus and 0% of the trials with the co-changing stimulus.

If there was sufficient second-order motion energy for motion to be perceived for counter-changing stimuli, why was it not perceived for co-changing stimuli with matching second-order DE? It can be concluded that the presence of second-order motion energy is not sufficient for motion to be perceived. The perception of apparent motion in only the counter-changing condition therefore can be attributed to a mechanism responsive to counter-changing luminance.

Figure 14. Experiment 6: Proportions of trials during which motion was perceived in the counter-changing and co-changing conditions as a function of background-relative luminance contrast (BRLC), for participants L.G. (left) and M.R. (right). When motion was perceived, it was always rightward. The results were obtained for two-frame presentations (illustrated in Figure 13).
luminance rather than a second-order mechanism, even when motion takes place between elements with opposite luminance polarity.

Experiment 7

The initial purpose of this experiment was to determine, in the absence of counter-changing luminance, whether the perception of apparent motion could result from the attentional tracking of an identifiable visual element (Cavanagh, 1992; Lu & Sperling, 1995a). The second purpose was to determine whether the perception of motion is affected by attentional tracking when motion is specified by counter-changing luminance.

The experiment was based on the stimuli of Experiment 3; the left and right elements were presented against white and black backgrounds, respectively (Figure 8). It was anticipated that attentional tracking would be possible when motion direction is not specified by counter-changing luminance (this is the direction-neutral condition, which corresponds to the would-otherwise-be-motion condition of Experiment 3). The reason is that the same luminance values appear successively at each element location. If motion can be perceived as a result of attentional tracking, it was hypothesized that the frequency with which it is perceived would depend on whether observers fix their attention midway between the elements, or whether they attend to one element and allow their attention to shift back and forth between the two element locations (see Lu & Sperling, 1995a, for similarly contrasting instructions). Whether or not attention affects motion perception when counter-changing luminance is present was tested in the direction-specified condition, which corresponds to the would-otherwise-be-flicker condition of Experiment 3.

Method

Lu and Sperling’s (1995b) results indicate that third-order motion is best perceived for stimuli with low spatial and temporal frequencies. On this basis, the size of the visual elements was increased by a factor of four (to \(48 \times 48\) min of arc), the center-to-center distance between the squares was doubled (to \(1.4^\circ\)), and the size of the white and black boxes surrounding the elements was doubled (to \(2.5^\circ\) wide and \(3.0^\circ\) high). The effect of these increased spatial dimensions was to concentrate more of the spatial variation in luminance in lower spatial frequencies. Also modified was the duration of each frame (again eight frames per trial). It was increased to \(534\) ms, concentrating more of the temporal variation in luminance in lower temporal frequencies. BRLC values for the direction-neutral and direction-specified conditions were as in Experiment 3 (stimuli from these conditions were randomly mixed in blocks of 108 trials).

In the attention-fixed condition, observers were instructed to maintain their attention midway between the two elements, at the white–black boundary. In the attention-shifted condition, participants were instructed to attend to one or the other of the elements and to shift their attention back and forth between the two element locations; they were not required to maintain fixation midway between the elements (eye movements were not monitored in either condition). They indicated, by pressing one of two designated keys on the computer keyboard, whether or not they perceived motion through the space between the two elements anytime during the trial.

There were four blocks of trials during each of two testing sessions. In the attention-fixed and attention-shifted conditions, testing occurred during alternating blocks, their order counter-balanced across testing sessions and participants. The 2 participants were one of the authors and an undergraduate student at Florida Atlantic University who was naive with respect to the purpose of the experiment. After each trial, they indicated whether or not they perceived motion through the space between the two squares (they did not judge motion direction, which alternated between leftward and right over the course of each eight-frame trial when it was perceived).

Results

Perception of motion in the direction-neutral condition was strongly attention dependent for both participants (Figure 15a). Relatively little motion was perceived when attention was fixed midway between the elements, but motion was perceived with high frequency (depending on the BRLC) when attention was shifted between the two element locations. This evidence that single-element apparent motion can be perceived as a result of attentional tracking means that the second part of the experiment (the direction-specified condition) provided a meaningful test of whether attentional tracking affects motion perception when counter-changing luminance is present.

The results for the direction-specified condition (Figure 15b) indicated that attentional tracking is not required for perceiving motion when it is specified by counter-changing luminance; it was perceived with high frequency when attention was fixed midway between the elements. There was relatively little influence of motion. When attention was shifted between the two element locations, there was a small enhancement of motion perception in the direction-specified condition for one participant (M.R.) and no effect for the other (L.G.).

General Discussion

Informational Basis for the Perception of Apparent Motion

It can be concluded from the results reported in this article that counter-changing luminance is the informational basis for the luminance-defined perception of single-element apparent motion. Motion is perceived when the luminance at one element location changes toward its background luminance value (the start of the perceived motion path) and the luminance at the other element location changes away from its background luminance value (the end of the perceived motion path). Even though superficially there is no physical movement for discontinuously displaced objects, at a deeper level of stimulus analysis there is motion-specifying stimulus information (counter-changing luminance) whose detection results in the perception of motion.\(^5\) Perception of apparent motion cannot be considered an illusion or a rule-constrained perceptual construction (Shepard, 1981, 1984) when it is specified by detectable information in the stimulus.

The nature of the motion-specifying stimulus information (the co-occurrence of opposing luminance changes at different spatial locations) is consistent with Gibson’s (1968) assertion, more than 30 years ago, that perception of apparent motion is based on

\(^5\) Analogously, Ginsburg (1975) has shown that there is a potential informational basis for the subjective contours perceived for the Kanizsa triangle. When image processing of the stimulus removes high spatial frequency information, the contours that were physically present but hidden in the image are revealed.
changes in stimulus pattern rather than changes in stimulus location. Characterizing the relevant information as a pattern is justified by evidence that apparent motion depends on simultaneous luminance relationships rather than sequences of luminance magnitudes. The requisite directions of luminance change at each spatial location are determined in relation to the background luminance, toward it at one location and away from it at the other.

As indicated in the introduction, the motion of continuously as well as discontinuously displaced objects can be based on counter-changing luminance. When an object that differs in luminance from its background moves continuously from one location to the next, the luminance at the location the object just occupied changes toward the background luminance, and at the same time the luminance at the location the object currently occupies changes away from the background luminance. Identification of counter-changing luminance as the informational basis for the luminance-defined perception of single-element apparent motion therefore is compatible with previous psychophysical studies indicating that continuous motion and discontinuous motion are based on the same detecting mechanisms (e.g., Burr & Ross, 1982), as well as previous neurophysiological evidence indicating that directionally selective neurons in Areas V1 and MT respond to both continu-

Figure 15. Experiment 7: Proportions of trials during which motion was perceived in the attention-fixed and attention-shifted conditions for direction-neutral (a) and direction-specified (b) stimuli, as a function of background-relative luminance contrast (BRLC), for participants L.G. (top left and bottom left) and M.R. (top right and bottom right). The results were obtained for stimuli similar to those illustrated in Figure 8 (see text).
Mechanisms for the Perception of Apparent Motion

In addition to development of evidence for counter-changing luminance as the informational basis for the perception of apparent motion (and, implicitly, the existence of motion-detecting mechanisms that respond to this information), other alternatives have been ruled out. Most important, it has been shown that mechanisms that respond to first-order motion energy (Adelson & Bergen, 1985; van Santen & Sperling, 1985; Watson & Ahumada, 1985) do not influence the perception of single-element apparent motion, regardless of whether counter-changing luminance is present (Experiment 2) or absent (Experiment 1). Also ruled out is the possibility that the effects on motion perception attributed to counter-changing luminance are in reality the result of attention-based, feature-tracking mechanisms (Cavanagh, 1992; Lu & Sperling’s, 1995a, 1995b, third-order motion). It has been shown that apparent motion is perceived on the basis of counter-changing luminance when there are no trackable features in the apparent motion stimulus (see Additional Results section, Experiment 2). Experiment 6 addressed the potential influence of second-order motion mechanisms (Chubb & Sperling, 1988; Lu & Sperling, 1995b), which entail a stage of nonlinear rectification preceding the determination of Fourier motion energy. Such a mechanism could potentially influence perception of apparent motion when luminance values are higher than the background luminance value for one element and lower than the background luminance value for the other element. However, the results of Experiment 6 show that the perception of apparent motion between elements with opposite luminance polarity does not depend on a mechanism responsive to second-order motion energy. Finally, Experiment 7 showed that an attention-based, third-order mechanism could result in the perception of apparent motion when counter-changing luminance was absent but had relatively little effect when counter-changing luminance was present.

Grossberg and Rudd’s (1992) theory. Grossberg and Rudd have proposed a theory of apparent motion perception in which presentation of elements at successive locations produces spatially overlapping, Gaussian distributions of activation, one decreasing in strength (when the element at the start of the motion path is removed) and the other increasing in strength (when the element at the end of the motion path is presented). The elements are assumed to be sufficiently close relative to the bandwidth of the Gaussian distributions of activation for the sum of these distributions to be a single-peaked Gaussian distribution of activation. It is argued on this basis that the apparent motion percept results from the peak of the summed distributions shifting over time, from the start toward the end of the motion path.

Grossberg and Rudd’s (1992) theory is consistent with the results obtained for the generalized apparent motion stimulus when the average luminance value ($L_{ave}$) is the same at the two element locations (e.g., the spatial symmetry condition of Experiment 2). The BRLC value would determine the difference in strength between the Gaussian distributions at each element location and, thereby, the amount of shift for the peak of the summed Gaussian distribution. However, the account seems problematic when average luminance values ($L_{ave}$) are substantially different at the two element locations, as in the spatial asymmetry condition of Experiment 2. For the latter, the summed Gaussian distributions would always be dominated by the brighter element, so there would be relatively little shift in the peak of the summed Gaussian distributions when the luminance of the elements changes. Nonetheless, motion is perceived more easily (at lower BRLC values) in the spatial asymmetry condition than in the spatial symmetry condition (even though there would be a larger shift in the peak of the summed Gaussian distributions for the latter). Also problematic for the theory is the co-changing condition of Experiment 1. In that condition, the right element undergoes substantially larger changes in luminance than the left element, with the result that the luminance on the right is alternately greater than and less than the luminance on the left. Grossberg and Rudd’s theory would predict substantial shifts in the peak of the summed Gaussian distribution at the two locations, yet motion never is perceived.

The Reichardt detector. The Fourier-based models of Adelson and Bergen (1985), van Santen and Sperling (1985), and Watson and Ahumada (1985) are founded on Reichardt’s (1961) correlational model of motion detection. Reichardt’s motion detector is composed of pairs of retinally separated subunits that respond to visual elements appearing in different spatial locations at different points in time. Rightward motion is detected for a laterally separated pair of subunits by delaying the activation of the subunit on the left and multiplying the delayed response by the activation produced by the element when it reaches the subunit on the right. (The opposite is the case for the detection of leftward motion.) Because both the rightward and leftward motion detectors would artifactualy respond to the sustained stimulation of both subunits by a static stimulus, the Reichardt model requires the subtractive comparison of the activation for each direction.

The results reported in this article are not readily accounted for by Reichardt detectors. Illustrative is the two-frame apparent motion stimulus that is the basis for the additional results reported at the end of Experiment 2. Motion was perceived for this stimulus even though the durations of the first and second frames were 6,268 and 267 ms, respectively. If motion is perceived on the basis of simultaneous changes in luminances at the start of the second frame (as we have argued), the required delay would be 0 ms, which is inconsistent with a Reichardt detector designed to detect sequentially occurring visual events. Alternatively, if motion is perceived on the basis of the onset asynchrony of the two frames, a Reichardt detector with a delay of 6,268 ms would be required. Not only is such a long delay unlikely for a motion detector, but the first frame in that experiment could have been much longer than 6,268 ms. Motion would be perceived provided that observers maintained attention midway between the two element locations.

Proposed Mechanism for the Detection of Counter-Changing Luminance

The temporal delay inherent in the Reichardt model (and, equivalently, the low-pass temporal filtering introduced in Fourier-based versions) thus serves two functions: (a) It allows for a multiplicatively combined response to spatially separated events occurring at different times, and (b) it establishes, along with the retinal location of the individual subunits, the directional selectivity of the motion detector (i.e., motion starts at the subunit with the delay and ends at the location of the nondelayed subunit). In contrast, a
mechanism responsive to counter-changing luminance would be based on the principle that the essential information for motion perception is carried by changes occurring at different spatial locations but at the same time. Because of this simultaneity, there would be no need to introduce temporal delays to establish the combined response of pairs of detecting units to retinally separated events. The directional selectivity of the motion detector can therefore be determined not by which of the pair of subunits carries the delay, but by which of the pair of subunits responds to changes in luminance toward the background luminance value (the starting point of the motion) and which responds to changes in luminance away from the background luminance (the endpoint of the motion). Because the responses of each subunit would be based on changes in luminance, they would not be activated by a static stimulus; thus, there is no need to subactively compare the responses of detectors that respond selectively to opposite directions of motion to eliminate artifactual motion responses to static stimuli (as is the case for the Reichardt detector).

The mechanism we propose for the detection of apparent motion is therefore a simplified version of the Reichardt detector in which both subunits are based on ON-center receptive fields, both are based on OFF-center receptive fields, or one is based on ON-center receptive fields and the other is based on OFF-center receptive fields (the latter to account for motion perception between elements of opposite luminance polarity, as in Experiments 3–7). Regardless of their composition, both subunits in a pair would respond transiently to changes in luminance, one responding to changes in luminance toward the background luminance value and the other responding to changes in luminance away from the background luminance value. The multiplicative combination of these responses would reflect the requirement that both changes occur in order for motion to be perceived (see Additional Results section, Experiment 1). A potential neurophysiological basis for units that respond to increases and decreases in luminance is suggested by the transient responses observed in motion-sensitive ganglion cells in the cat retina (Y-type cells; Enroth-Cugell & Robson, 1966; Hochstein & Shapley, 1976), although it is conceivable that inhibitory interactions with X-type cells (Singer & Bedworth, 1973) also contribute to whether or not motion is perceived (e.g., Banta & Breitmeyer, 1985; von Grünau, 1978). The time scale of these transient responses (and, thus, the degree to which departures from simultaneity are tolerated) remains to be determined by psychophysical experiments introducing temporal delays between the occurrence of luminance changes toward and luminance changes away from the luminance of the background.

The development of a model such as the one just described would be constrained by the results of a recent study conducted by Anstis, Smith, and Mather (2000). They found that when light and dark elements (presented against a gray background) are exchanged during discrete frames, the competition between motion in opposite directions (mediated by overlapping ON-center and OFF-center cells) is resolved in favor of the element that contrasts most with the background. More specifically, the relative strength of the competing motions of the light and dark elements was found to depend on each element’s Weber fraction, the element–background luminance difference divided by the background luminance (not BRLC, which, for Anstis et al.’s stimuli, would be 2.0 for motions detected independently by ON-center and OFF-center receptive fields, regardless of the background luminance value). Further investigation is necessary to determine whether or not this inconsistency with Hock et al.’s (1997) BRLC measure of time-varying luminance contrast is restricted to BRLC values near the 2.0 level that is characteristic of standard apparent motion.

References


