

Detection of Counter-Changing Contrast: Second-Order Apparent Motion Without Postrectification Motion-Energy Analysis or Saliency Mapping/Feature Tracking

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The perception of 2nd-order, texture-contrast-defined motion was studied for apparent-motion stimuli composed of a pair of spatially displaced, simultaneously visible checkerboards. It was found that background-relative, counter-changing contrast provided the informational basis for the perception of 2nd-order apparent motion; motion began where contrast changed toward the contrast value of the background checkerboard and ended where contrast changed away from the background value. The perceived apparent motion was not attributable to either postrectification motion-energy analysis or saliency-mapping/feature-tracking mechanisms. Parallel results for 1st-order, luminance-defined motion (H. S. Hock, L. A. Gilroy, & G. Harnett, 2002) suggest that counter-changing activation provides a common basis for the perception of both luminance- and texture-contrast-defined apparent motion.

The dominant contemporary approach for understanding low-level motion perception entails the Fourier-based analysis of motion energy, a computational methodology based on the assumption that motion is detected through the spatiotemporal filtering of the motion stimulus (Adelson & Bergen, 1985; van Santen & Sperling, 1985; Watson & Ahumada, 1985). The research reported in this article examined the perception of apparent motion when it is not based on the detection of motion energy. (The role of motion-energy detection under other circumstances is not addressed.)

The possibility that motion energy would not be the basis for apparent-motion perception arises because the motion-energy signal for the apparent-motion stimulus can be obscured by energy artifacts that are by-products of the discontinuous spatial and temporal sampling that distinguishes apparent-motion from continuous-motion stimuli (Mather, 1994). Consistent with this possibility, Hock, Gilroy, and Harnett (2002) provided experimental evidence that apparent-motion perception for their first-order, luminance-defined elements was indeed not based on the detection of motion energy. They showed instead that the perception of apparent motion resulted from the detection of *counter-changing luminance*. That is, for motion to be perceived, it was necessary for there to be a change in luminance toward the background luminance value at one element location, accompanied by a change in luminance away from the background luminance value at another location. (See also Lappin, Tadin, & Whittier, 2002, who used the term *dipole contrast change* rather than counter-changing luminance.)

If luminance-defined apparent motion can be perceived without the analysis of motion energy, it can be asked whether apparent

motion defined by other stimulus attributes can likewise be perceived without the analysis of motion energy. Lu and Sperling (1995b, 2001) have proposed a three-mechanism model to account for motion defined by different stimulus attributes, all three mechanisms of which require a final stage of “standard motion analysis,” the Fourier-based analysis of motion energy. The first- and second-order motion mechanisms are distinguished by second-order motion perception, requiring detection by rectifying “texture grabbers” prior to motion-energy analysis (Chubb & Sperling, 1988; Werkhoven, Sperling, & Chubb, 1993). The third-order motion mechanism likewise entails motion-energy analysis, but now following the formation of a time-varying, feature-saliency map (Blaser, Sperling, & Lu, 1999; Lu & Sperling, 1995a, 1995b).

The focus of the current study was on the perception of second-order, texture-contrast-defined apparent motion. The objectives were to show that (a) parallel to the results for luminance-defined motion, the motion-specifying stimulus information is *counter-changing contrast*, a change in the texture contrast at one element location toward the contrast value of the background, accompanied by a change in texture contrast at another location away from the contrast value of the background, and (b) the perception of second-order apparent motion does not depend on the postrectification analysis of motion energy (Chubb & Sperling, 1988), the formation of a saliency map (Lu & Sperling, 1995a), or feature tracking (Cavanagh, 1992).

Hock et al.’s (2002) study of luminance-defined apparent motion was based on a generalized single-element apparent-motion stimulus (Johansson, 1950; Hock, Kogan, & Espinoza, 1997). For this stimulus, two square elements with different, greater-than-background luminance values were simultaneously visible (Figures 1a and 1b), and the luminance values were exchanged over a succession of frames. As with standard apparent motion, a special case of generalized apparent motion for which only one element is visible at a time, motion can be perceived between the two element locations, given appropriate spatial and temporal conditions. Hock et al. (1997) found that motion was perceived more frequently

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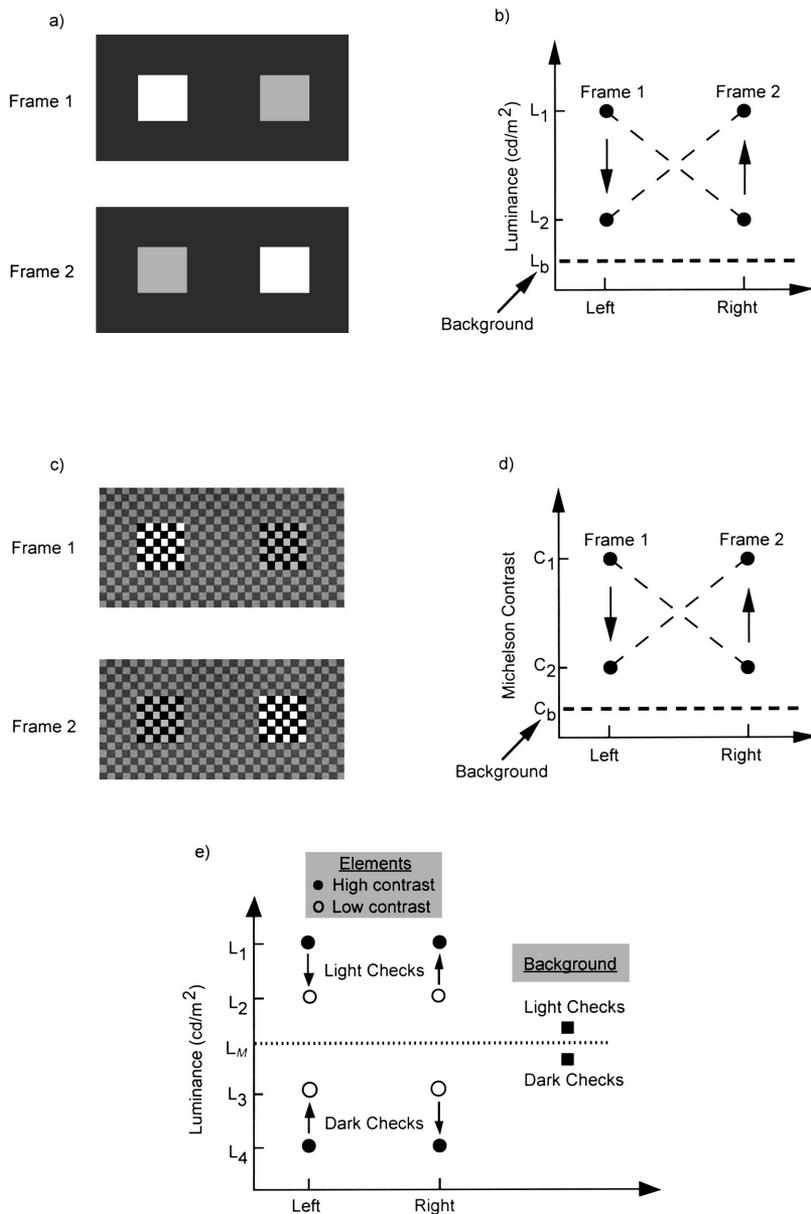


Figure 1. An illustration of the first two frames of a generalized, luminance-defined apparent-motion stimulus (a) and a graphical representation of its changing luminance (L) values (b). An illustration of the two frames of a generalized, texture-contrast-defined apparent-motion stimulus (c) and a graphical representation of its changing contrast (C) values (d). The luminance values for the light and dark checks composing the checkerboard elements were equally above and below the same mean (M) luminance value.

when there were larger changes in luminance at each element location and when element luminance values were more similar to the luminance of the background.

The arrangement of luminance values for the generalized apparent-motion stimulus was varied by Hock et al. (2002) to create stimuli that distinguished between counter-changing luminance and motion energy as the informational basis for the perception of first-order apparent motion. The key stimulus was one for which there was a small change in luminance at one location and a much larger change in luminance at a nearby location (the

average luminance was the same at the two locations). When the luminance values were simultaneously changed at both locations, the higher luminance value was first at one of the locations, then at the other, back and forth during successive frames. Hock et al. (2002) found that motion was perceived only when luminance values simultaneously changed in opposite directions at the two element locations (counter-change). Motion was never perceived when luminance values simultaneously changed in the same direction (co-change), despite motion energy being equated in the two conditions. (This was the model for Experiment 3 of the

current study, which determined whether the postrectification analysis of motion energy is required for the perception of second-order, texture-contrast-defined apparent motion.)

The results of six experiments are reported in this article. They were conducted with second-order, texture-contrast-defined apparent-motion stimuli (Figures 1c and 1d) that were homologues of the generalized, first-order luminance-defined apparent-motion stimulus illustrated in Figures 1a and 1b (also called *crossed-phi* and *crossover stimuli*; Watson, 1986; Mather & Anstis, 1995; Werkhoven et al., 1993). The stimuli, checkerboard squares composed of small, spatially alternating light and dark checks, were presented against a checkerboard background that differed only in contrast from the checkerboard elements (luminance values are detailed in Figure 1e). Experiments 1 and 2 provided evidence that the perception of second-order, texture-contrast-defined apparent motion depended on the detection of background-relative, counter-changing contrast for the two checkerboards. The remaining experiments confirmed this while ruling out alternative motion-detecting mechanisms.

Experiment 1

As described above, the likelihood of motion being perceived for first-order, luminance-defined stimuli increases with the magnitude of the luminance changes at each location (Hock et al., 1997), provided that the luminance changes are in opposite background-relative directions (Hock et al., 2002). Luminance changes specify motion only when the luminance at one location changes toward the luminance value of the background, and the luminance at another location changes away from the luminance value of the background. The purpose of this experiment was to determine whether the likelihood of perceiving second-order, texture-contrast-defined motion likewise depends on the magnitude of the counter-changing contrast and, further, whether the direction of perceived motion likewise depends on the background relativity of the counter-changing contrast (i.e., motion begins where contrast changes toward the background contrast and ends where it changes away from the background contrast).

To test this hypothesis, we changed the contrast of each checkerboard element simultaneously in opposite directions (the size of the change varied randomly between trials), but the contrast of the background checkerboard was lower than the contrast values of the checkerboard elements in one condition and higher than the contrast values of the checkerboard elements in the other condition. The background relativity of counter-changing texture contrast would be indicated if the same contrast changes of the checkerboard elements resulted in different perceived motion directions in the two conditions.

The first two frames of a stimulus from the low-contrast background condition are illustrated in Figure 2a. The left and right checkerboards are at different contrast values during Frame 1. During Frame 2, one decreases to its lower contrast value (toward the background contrast), while the other increases to its higher contrast value (away from the background contrast). If the magnitude of the contrast change is sufficiently large for motion to be perceived, the expectation for this example is that the perceived motion direction would be rightward.

The first two frames of a stimulus from the high-contrast background condition are illustrated in Figure 2b. The contrast changes

for the left and right checkerboards are identical to those for the low-contrast background condition, but now the decrease in contrast of the left checkerboard is away from the background contrast, and the increase in contrast for the right checkerboard is toward the background contrast. If the magnitude of the contrast change is sufficiently large for motion to be perceived, the expectation for this example is that the perceived motion direction would be leftward.

Method

Stimuli. The stimuli were presented, with a Power Macintosh 7300/180 computer, in the center of the darkened screen of a Viewsonic 15GA monitor (screen luminance: $<.001$ cd/m²). The viewing distance, 35.8 cm, was maintained by a head restraint. Two checkerboard elements were presented 2.4° apart, center-to-center, against a 7.2° × 4.8° checkerboard background. Each checkerboard element was a 1.2° × 1.2° square composed of 64 smaller (9 × 9 min), spatially alternating light and dark squares (checks). The luminance values for the checks were equally above and below the mean luminance value of 58.5 cd/m², the same mean luminance as the checkerboard background, which also was composed of 9 × 9 min light and dark checks.¹

Michelson contrast values for the checkerboard elements and the luminance values used to create them are listed in Table 1. Contrast changes for the elements ranged from .100 to .300, and the average contrast always was .500. The background checkerboard, which was presented both during and between trials, had a Michelson contrast of .200 in the low-contrast background condition (luminance values were 70.20 and 46.80 cd/m² for the light and dark checks, respectively) and .800 in the high-contrast background condition (luminance values were 105.30 and 11.70 cd/m² for the light and dark checks, respectively).

Four blocks of trials were completed during a single testing session, two for each of the two background-contrast conditions. Each block contained 108 trials: six repetitions of the 18 trials, determined by the orthogonal combination of nine element contrast changes and two possible directions of contrast change. Decreases in contrast for the left checkerboard were accompanied by increases in contrast for the right checkerboard for 9 of the trials, and vice versa for the other 9 trials, so both leftward and rightward motion directions were possible during each block of trials. Trial order was randomized within subblocks of 18 trials.

Procedure. There were two frames per trial. The first frame was presented for 1,017 ms, which allowed sufficient time for participants to fixate between the two checkerboard elements at the start of each trial. Participants were instructed to maintain fixation during the entire trial. The duration of the second frame was 267 ms. After each trial, participants pressed designated keys on the computer keyboard to indicate whether or not they perceived motion and, if they did, whether the motion direction was rightward or leftward (they pressed the spacebar instead if they were unsure of their response).

Participants. The three participants were one of the authors and two undergraduate students at Florida Atlantic University. The latter were naive with respect to the purpose of the experiment.

¹ The luminances used to establish the contrast values of the checkerboards were selected from a look-up table with premeasured values. Although there were fluctuations in the average luminance measured for each checkerboard contrast value, these were small and nonsystematic and therefore unlikely to have influenced the results obtained in this or the other experiments reported in this article.

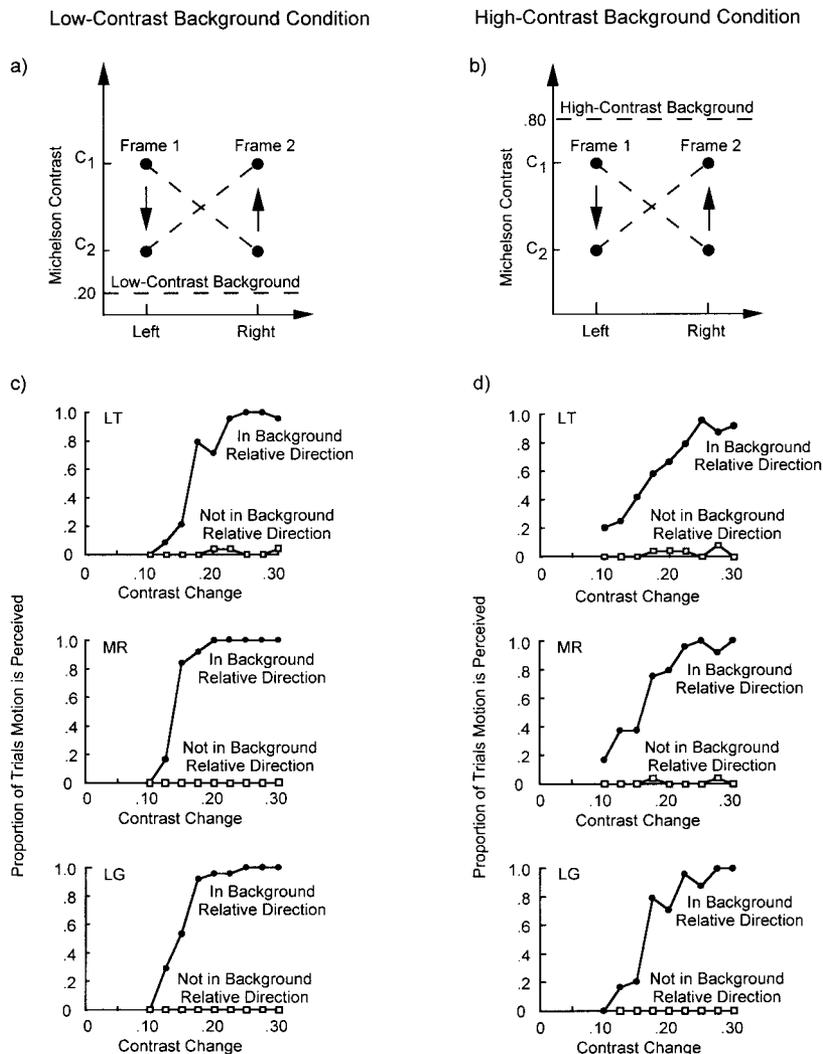


Figure 2. Experiment 1: Graphical representation of changing contrast (C) values for the two frames of the low-contrast (a) and high-contrast (b) background conditions. The proportions of trials in which motion was perceived in the counter-change-specified direction by 3 participants (LT, MR, and LG) for the low-contrast (c) and high-contrast (d) background conditions as a function of the magnitude of the contrast change.

Results

The results, presented in Figures 2c and 2d, are based on trials for which participants clearly perceived motion or nonmotion. (*Unsure* responses, which were not included, occurred for an average of approximately 1% of the trials. This proportion was typical of the other experiments in this study.) Because the results for the leftward and rightward motion directions were similar, they have been combined and graphed on the basis of whether or not motion was perceived in the direction predicted by background-relative, counter-changing contrast.

It was found that the likelihood of motion being perceived increased with increases in the magnitude of contrast change and, further, that identical contrast changes of the checkerboard elements resulted in motion being perceived in opposite directions, depending on whether the contrast of the checkerboard back-

ground was less than or greater than the contrast of the elements. It was the checkerboard most different from the background that was perceived to be moving (the high-contrast checkerboard element in the low-contrast background condition and the low-contrast checkerboard element in the high-contrast background condition). Motion always started at the location where contrast changed toward the background contrast and ended at the location where contrast changed away from the background contrast.

Discussion

The results of the experiment indicate that the perceived motion direction for second-order apparent motion depends on changes in the texture contrast of the elements relative to the texture contrast of the background. Mather and Anstis (1995) reached a similar conclusion regarding this dependence on the background in exper-

Table 1
Michelson Contrast Values and Corresponding Luminance Values for Light and Dark Checks Composing Each Checkerboard Element in Experiments 1 and 4

| Michelson contrast | Check (cd/m ²) | | Alternating Michelson contrast | Check (cd/m ²) | | Contrast change |
|--------------------|----------------------------|-------|--------------------------------|----------------------------|-------|-----------------|
| | Light | Dark | | Light | Dark | |
| .550 | 90.68 | 26.33 | .450 | 84.83 | 32.18 | .100 |
| .563 | 91.41 | 25.59 | .438 | 84.09 | 32.91 | .125 |
| .575 | 92.14 | 24.86 | .425 | 83.36 | 33.64 | .150 |
| .588 | 92.87 | 24.13 | .413 | 82.63 | 34.37 | .175 |
| .600 | 93.60 | 23.40 | .400 | 81.90 | 35.10 | .200 |
| .613 | 94.33 | 22.67 | .388 | 81.17 | 35.83 | .225 |
| .625 | 95.06 | 21.94 | .375 | 80.44 | 36.56 | .250 |
| .638 | 95.79 | 21.21 | .363 | 79.71 | 37.29 | .275 |
| .650 | 96.53 | 20.48 | .350 | 78.98 | 38.03 | .300 |

Note. Michelson contrast values that were alternated for each checkerboard element are paired in each row of the table, and the magnitude of contrast change for each pair is indicated. Average Michelson contrast was .500 for each pair.

iments that varied both the texture of the elements (e.g., their density) and the texture of the backgrounds. They found that the element texture that was most different from the background texture was the one that was perceived as moving.

The perception of motion for both the high-contrast and the low-contrast background conditions in the current experiment indicated that changes in texture contrast above and below the contrast value of the background texture were encoded. There is as yet no neurophysiological evidence that there are ON and OFF channels for detecting spatial differences in texture contrast that correspond to the well-established ON and OFF channels for detecting spatial differences in luminance. However, the results of this experiment are consistent with the existence of such channels, perhaps in the form of “texture grabbers” (Chubb & Sperling, 1991) that are sensitive to the texture of both the checkerboard elements and their background.

Experiment 2

As a further test of the background relativity of second-order motion perception, we conducted an experiment with the same two-frame design as in Experiment 1 but with the contrast of the background (.500) midway between the contrast values of the two checkerboard elements. The contrast of the left checkerboard alternated between .150 and .450, whereas the contrast of the right checkerboard alternated between .850 and .550. Motion was not perceived when the contrast of the two checkerboard elements simultaneously changed in opposite directions (Figure 3a), because contrast was changing in the same background-relative direction. However, motion was perceived when the contrast of the two checkerboard elements simultaneously changed in the same direction, because contrast was changing in opposite background-relative directions. For the stimulus illustrated in Figure 3b, motion started at the location of the highest contrast checkerboard (its contrast changed toward the background’s contrast) and ended at the location of the lowest contrast checkerboard (its contrast changed away from the background’s contrast). The reverse was the case for the stimulus illustrated in Figure 3c. The establishment of a featural correspondence between checkerboard elements with

similar texture contrast clearly had no bearing on the motion perceived for these stimuli. (Parallel results for first-order stimuli were reported by Hock et al., 2002.) Further evidence against motion perception depending on a feature-tracking mechanism is presented in the experiments that follow.

Experiment 3

Werkhoven et al. (1993) have provided evidence for rectifying detectors (texture grabbers) that linearly transform texture-contrast values into “activity,” which becomes the basis for the analysis of motion energy. Assuming such a transformation, the purpose of this experiment was to determine whether the perception of second-order, texture-contrast-defined motion requires the postrectification analysis of motion energy or depends instead on the detection of counter-changing contrast (or counter-changing activation).

Counter-changing and co-changing conditions were defined by whether contrast simultaneously changed in opposite directions or in the same direction at each element location. Texture-contrast values were selected such that postrectification motion energy was present in both conditions, but contrast changed in opposite background-relative directions only in the counter-changing condition.

Figure 4a illustrates the first two (of eight) frames of a stimulus from the co-changing condition. Assuming a linear relationship between contrast and activity (Werkhoven et al., 1993), the activity values of the hypothetical texture-detecting units responding to these contrasts (.57 and .43 for the left checkerboard; .73 and .27 for the right checkerboard) were arbitrarily set at 100 times the contrast. The orientation of the 2-D Fourier transform for the time-varying contrast/activity at each location indicates that the postrectification motion energy specifies leftward motion for this stimulus (Figure 4d). However, contrast decreases simultaneously at both checkerboard locations from Frame 1 to Frame 2 (then increases simultaneously from Frame 2 to Frame 3, and so on), so motion is not specified by counter-changing contrast.

Figure 4b illustrates the first two frames of a stimulus from the counter-changing condition with the same contrast values as those

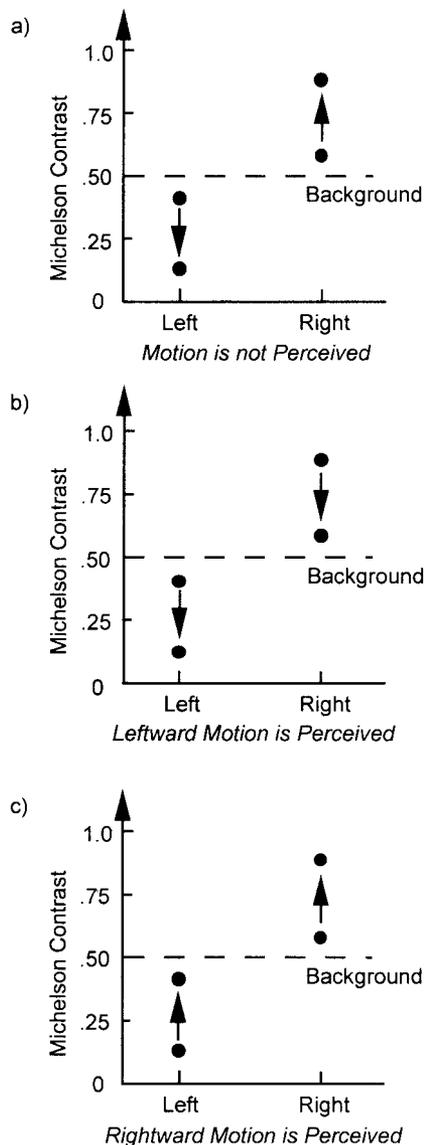


Figure 3. Experiment 2: Graphical representation of changing contrast values for the two frames of checkerboards whose contrast values changed in the opposite absolute directions but the same background-relative direction (a). Graphical representation of changing contrast values for the two frames of checkerboards whose contrast values changed in the same absolute direction but opposite background-relative directions (b and c).

in the co-changing condition. The orientation of the 2-D Fourier transform (Figure 4e) again specifies leftward motion, but unlike with the co-changing stimulus, contrast increases for the left element while it simultaneously decreases for the right element, so counter-changing contrast at the two element locations also specifies leftward motion.

Stimuli from the counter-changing and co-changing conditions were matched with respect to their postrectification motion energy on the basis of a measure of *directional energy* (DE), which quantitatively represents the direction and magnitude of the oriented energy in the motion-energy diagram. (This measure is very

similar to Doshier, Landy, & Sperling's, 1989, *directional power*.) Although DE was determined for only two frames of the apparent-motion sequence, in order to avoid mixing energy from motion in opposite directions, the calculated values applied equally to all the frame changes during the trial. As in Hock et al. (2002), the calculation entailed the integration of motion energy over equal areas, starting at the origin of the upper-left and upper-right quadrants of the space-time Fourier transform (the areas are indicated in Figures 4d–4f). The integrated energy reflects the presence of rightward (R) and leftward (L) energy, respectively, and the difference between them (R–L) constitutes the DE. Positive values specify rightward motion, whereas negative values specify leftward motion.

For the current experiment, the integration range was between spatial frequencies of 0 and 0.1 cycles/° (or 0 and –0.1 cycles/°) and between temporal frequencies of 0 and 0.8 Hz. These ranges were selected in order to eliminate the contribution of the replications in the motion-energy diagram that distinguish discontinuously from continuously displaced stimuli. However, similar matches in motion energy between the counter-changing and co-changing stimuli were obtained when the integration range was increased. Moreover, the matches were the same when they were determined by calculating the response of Adelson and Bergen's (1985) motion-energy detector to the stimuli.² (It is evident from the experimental results reported below that the particular method used to calculate motion energy is not critical.)

As can be seen in Figures 4d and 4e, when the alternating contrast values in the counter-changing and co-changing conditions were the same, there was more postrectification DE in the counter-changing condition. However, a match in DE was found by changing the alternating contrast values for the right checkerboard of the counter-changing stimulus from .73/.27 to .59/.41 (Figure 4c). The DE for this stimulus (–0.18; Figure 4f) was the same as in the co-changing example in Figure 4a. If the perception of second-order motion depends on the detection of postrectification motion energy, motion would be perceived equally often in the co-changing and counter-changing conditions for stimuli with matching DE (there were additional DE matches at other contrast values). However, if motion perception requires decreased contrast for one checkerboard accompanied by increased contrast for the other, motion would be perceived only in the counter-changing condition.

Method

Stimuli. Checkerboards were constructed and presented as in the preceding experiments. The checkerboard on the left always alternated between contrast values of .430 and .570, resulting in a contrast change of .140. The checkerboard on the right alternated between nine different pairs of contrast values (Table 2), resulting in contrast changes ranging from .060 to .460 (the average contrast was .500). The contrast of the background checkerboard was .200 (luminance values were 70.2 and 46.8

² This was done by fitting space-time oriented filters to two frames of the postrectification activity values for the counter-changing and co-changing stimuli, in accordance with Adelson and Bergen's (1985) motion-energy detector. The spatial filters were maximally sensitive at 0.5 cycles/°, and the temporal filters were maximally sensitive at 10.5 Hz. We thank David Nichols for implementing the model and carrying out the computations.

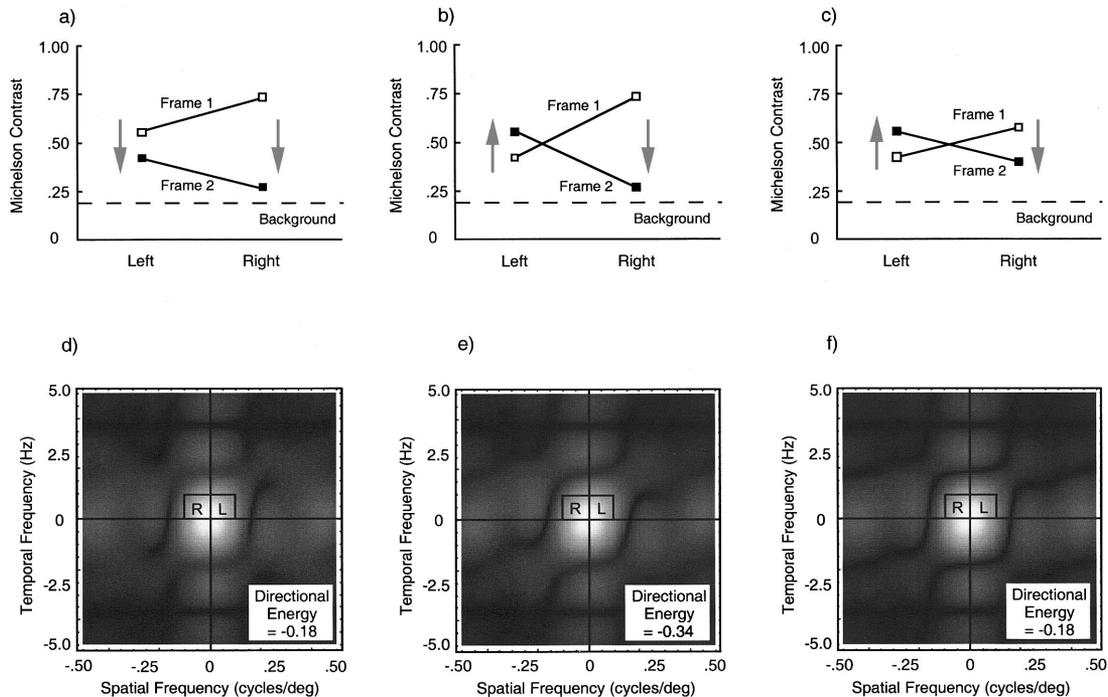


Figure 4. Experiment 3: Graphical representation of two frames of a co-changing apparent-motion stimulus with alternating contrast values of .43 and .57 for the left-hand checkerboard and alternating contrast values of .27 and .73 for the right-hand checkerboard elements (a); a counter-changing apparent-motion stimulus with the same alternating contrast values (b); and a counter-changing apparent-motion stimulus with the same alternating contrast values of .41 and .59 for the right-hand checkerboard elements (c). The 2-D Fourier space-time transforms and calculated values of postrectification directional energy (DE) for these stimuli (d–f; see text for details of how these values were calculated).

cd/m^2 for the light and dark checks, respectively), and the average luminance for the checkerboard elements and the checkerboard background was 58.5 cd/m^2 .

There were eight frames per trial, each with a duration of 267 ms. In the co-changing condition, the contrast for each checkerboard element was at its higher value during odd-numbered frames and at its lower value during even-numbered frames. In the counter-changing condition, the left checkerboard was at its lower contrast value and the right checkerboard at its higher contrast value during odd-numbered frames, and the left checkerboard increased in contrast to its higher value and the right checkerboard decreased in contrast to its lower value during even-numbered frames. Calculated values of postrectification DE were matched for four stimuli (see Figure 5).

Design. The orthogonal combination of two conditions (co-changing and counter-changing) and nine values of contrast change resulted in 18 distinctive trials, each of which was repeated six times within each block of 108 trials (trial order was randomized in subblocks of 18 trials). There were four blocks of trials during a single testing session. Participants (both of the authors and an undergraduate student at Florida Atlantic University who was naive with respect to the purpose of the experiment) indicated after each trial whether or not they perceived motion between the checkerboards at any time during the trial. (They did not judge motion direction, which alternated between left and right over the course of each trial for which motion was perceived.)

Results

Motion was perceived in the counter-changing condition by all three participants. As in the preceding experiments, the likelihood

of motion perception increased with the magnitude of contrast change (in this experiment, the magnitude changed only for the checkerboard on the right). Motion was not perceived in the co-changing condition, even for contrast changes that resulted in values of calculated postrectification DE that were the same as those in the counter-changing condition (floor effects obscured differences between the conditions for matches with low values of DE). If the postrectification analysis of motion energy was the basis for the perception of second-order, texture-contrast defined apparent motion, motion would have been perceived equally often for counter-changing stimuli and co-changing stimuli with matching DE.

The evidence that contrast-defined apparent motion did not depend on the analysis of postrectification energy was not scale dependent. We reduced both the size of the checkerboard elements (two columns of checks: width = 12 min from a viewing distance of 54 cm) and the distance between them (center-to-center distance = 24 min, again from a viewing distance of 54 cm). Once again, motion was perceived in the counter-changing but not the co-changing condition.

Discussion

It can be concluded from the fact that motion was perceived only for the counter-changing stimuli that the detection of contrast changes in opposite directions at the two element locations was the

Table 2
Michelson Contrast Values and Corresponding Luminance Values for Light and Dark Checks Composing Each Checkerboard Element in Experiment 3

| Michelson contrast | Check (cd/m ²) | | Alternating Michelson contrast | Check (cd/m ²) | | Contrast change |
|--------------------|----------------------------|-------|--------------------------------|----------------------------|-------|-----------------|
| | Light | Dark | | Light | Dark | |
| Left checkerboard | | | | | | |
| .430 | 83.66 | 33.35 | .570 | 91.85 | 25.16 | .140 |
| Right checkerboard | | | | | | |
| .470 | 86.00 | 31.01 | .530 | 89.51 | 27.50 | .060 |
| .450 | 84.83 | 32.18 | .550 | 90.68 | 26.33 | .100 |
| .430 | 83.66 | 33.35 | .570 | 91.85 | 25.16 | .140 |
| .410 | 82.49 | 34.52 | .590 | 93.02 | 23.99 | .180 |
| .370 | 80.15 | 36.86 | .630 | 95.36 | 21.65 | .260 |
| .330 | 77.81 | 39.20 | .670 | 97.70 | 19.31 | .340 |
| .310 | 76.64 | 40.37 | .690 | 98.87 | 18.14 | .380 |
| .290 | 75.47 | 41.54 | .710 | 100.04 | 16.97 | .420 |
| .270 | 74.30 | 42.71 | .730 | 101.21 | 15.80 | .460 |

Note. Michelson contrast values that were alternated for each checkerboard element are paired in each row of the table, and the magnitude of contrast change for each pair is indicated. Average Michelson contrast was .500 for each pair.

basis for the perception of second-order, texture-contrast defined apparent motion. The complete absence of motion perception in the co-changing condition indicated that the same pattern of results would be obtained regardless of the particular method used to calculate postrectification DE.

It might be argued that the motion perceived in this experiment was the result of either a feature-tracking mechanism (Cavanagh, 1992; Verstraten, Cavanagh, & Labianca, 2000) or a mechanism responding to changes in the salience of the checkerboards at each element location (Lu & Sperling's, 1995a, third-order mechanism; Mather & Anstis, 1995). If either were the case, motion perception would have been possible in the co-changing condition of this experiment, because the higher contrast checkerboard was alternately in the left- and right-hand element locations. This alternation provided a feature that could have been tracked between the two element locations, and it could also have been the basis for the formation of a time-varying feature-salience map. Nonetheless, motion was never perceived in the co-changing condition. There was no counter-changing contrast.

Experiment 4

As discussed earlier, Mather and Anstis (1995) have found that motion is perceived when two different textures, simultaneously visible at two element locations, are exchanged over a series of discrete frames and, further, that the element that appears to be moving is the one that is most different from the background. They attributed this background dependence to the relative salience of the elements, arguing that motions in opposite directions were possible for each of the simultaneously presented textures, but the motion signal is stronger for the texture that is more salient relative to the background. However, Mather and Anstis's "salience account" is inconsistent with results for luminance-defined motion indicating that motion is perceived more often when the alternating

luminance of the elements is closer to the background luminance value (i.e., the motion signal is stronger when the elements are less salient with respect to the background; Hock et al., 1997). The purpose of this experiment was to further address the salience explanation for our texture-defined stimuli by determining whether the likelihood of perceiving second-order apparent motion would be influenced in the same way by the similarity in contrast of the checkerboard elements and background.

Method

As illustrated in Figure 6a, the contrast of the checkerboard background was either .100 (luminance values of the light and dark checks were 64.35 and 52.65 cd/m²), .200 (luminance values of the light and dark checks were 70.20 and 46.80 cd/m²), or .300 (luminance values of the light and dark checks were 76.05 and 40.95 cd/m², respectively). Each trial was composed of eight 267-ms frames, and there were nine distinctive trials corresponding to the nine contrast changes of the checkerboard elements (listed in Table 1), each of which was repeated six times within each block of 54 trials. Three blocks of trials, one for each value of background contrast, were presented once during each of six testing sessions (their order was counterbalanced). After each trial, participants indicated whether or not they perceived motion between the elements at any time during the trial.

Results

Three psychometric functions are presented for each participant, one for each value of background contrast, in Figure 6b. As in the preceding experiments, motion perception increased with increases in the contrast change of the checkerboard elements. However, there was an additional effect of the background contrast. Motion was perceived more often for higher values of background contrast, values that were closer to the contrast values of the checkerboard elements.

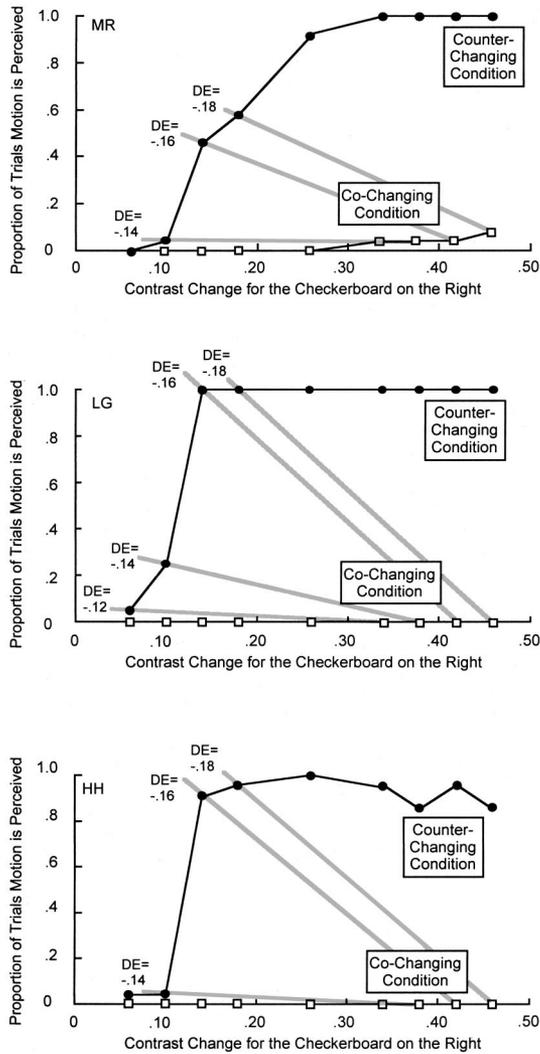


Figure 5. Experiment 3: The proportion of trials in which motion was perceived in the counter-changing and co-changing conditions by 3 participants (MR, LG, and HH) as a function of the magnitude of the contrast change for the checkerboard on the right. (The contrast change for the checkerboard on the left was always .14.) Gray lines link stimuli in the two conditions with matching values of postrectification directional energy (DE). These results were obtained for the stimuli illustrated for two frames in Figure 4.

Discussion

The results of this experiment converge with those of Hock et al. (1997) in indicating that the likelihood of motion being perceived increases with both the magnitude of the counter-changing luminance/contrast of the elements and the similarity of their luminance/contrast to the luminance/contrast of the background. The evidence that apparent motion strength was greater when the elements were more similar in luminance or contrast to the background (when they were less salient) is the opposite of what would be expected on the basis of Mather and Anstis's (1995) salience account.

Experiment 5

The preceding experiments showed that the presence of contrast changes that could provide the basis for salience mapping was not sufficient for the perception of texture-contrast defined apparent motion. That is, motion was not perceived in the co-changing condition of Experiment 3, even though the location with the higher contrast was changed from one frame to the next, and the same contrast change that was sufficient for motion to be perceived in Experiment 4 resulted in less rather than more motion perception when the background contrast was made more salient relative to the background. The purpose of this experiment was to

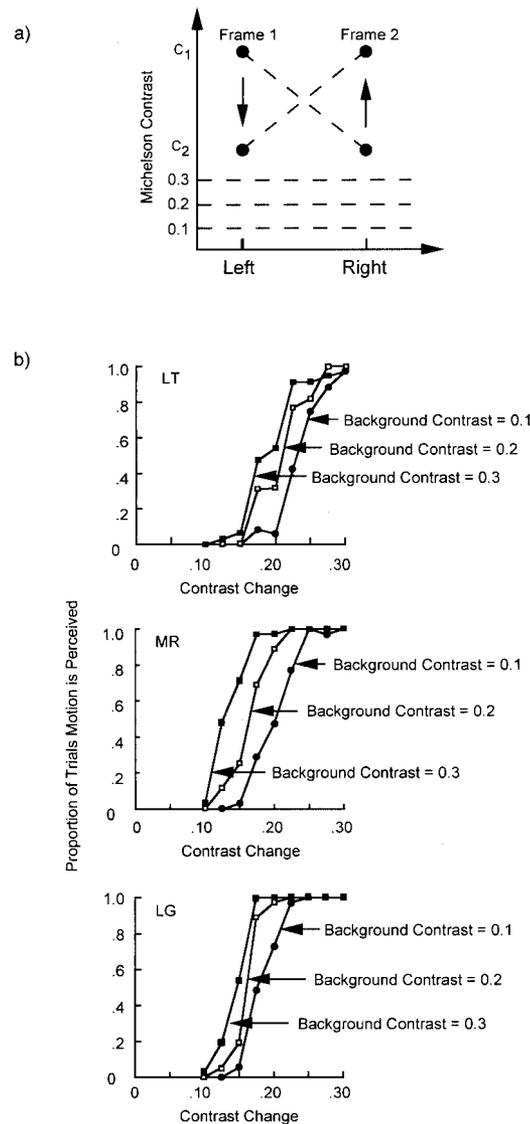


Figure 6. Experiment 4: Graphical representation of the changing contrast (C) values for the first two frames and the three values of background contrast (indicated by broken lines; a). The proportions of trials in which motion was perceived by 3 participants (LT, MR, and LG) for each value of background contrast as a function of the magnitude of the contrast change (b).

determine whether changes in the location of the more salient element are necessary for apparent-motion perception.

Stimuli were created for which texture-contrast values at one element location always were greater than texture-contrast values at the other element location (the top of Figure 7a). With this design, there was no change in the location with the most salient feature because the highest contrast was always at the same location. Nonetheless, one checkerboard decreased in contrast toward the contrast value of the background while the other checkerboard increased in contrast away from the contrast value of the background, so counter-changing contrast was always present. If motion is perceived for this stimulus, it would provide additional

evidence for counter-changing contrast as the basis for the perception of texture-contrast-defined apparent motion while ruling out the possibility that changes in the location with the higher salience are necessary for the perception of apparent motion.

Method

For all conditions, the mean luminance of the checkerboard elements and the checkerboard background was constant at 58.5 cd/m^2 . The contrast of the checkerboard on the left ($M = .300$) was always lower than the contrast of the checkerboard on the right ($M = .700$). Michelson contrast values and the luminance values used to create them are listed in Table 3. The magnitude of the contrast changes was the same for the left and right checkerboard elements during each trial and varied randomly between .100 to .300 from one trial to the next. The background Michelson contrast was .200 (luminance values were 70.2 and 46.8 cd/m^2 for the light and dark checks, respectively).

Trials were composed of two frames (participants reported the direction of the perceived motion), the first with a duration of $1,017 \text{ ms}$ and the second with a duration of 267 ms . For half of the trials, contrast values decreased for the left checkerboard and increased for the right checkerboard during Frame 2; rightward motion was specified by counter-changing contrast. For the other half of the trials (randomly interleaved), contrast values increased for the left checkerboard and decreased for the right checkerboard during Frame 2; leftward motion was specified by counter-changing contrast. There were 18 distinctive trials produced by the orthogonal combination of nine contrast changes and two possible motion directions, each of which was repeated six times within each block of 108 trials. Two naive participants completed four blocks of trials during a single testing session. After each trial, they indicated whether or not they perceived motion and, if they did, whether the motion was rightward or leftward.

Results

Motion perception increased with increases in the magnitude of contrast change, and it was always perceived in the direction specified by counter-changing contrast (Figure 7b). This was the case despite the checkerboard with the more salient (higher) contrast always remaining in the same location, indicating that changes in the location of the most salient feature were not necessary for the perception of apparent motion. Furthermore, because the higher contrast value never changed location, it could not have been the basis for attentive feature tracking (Cavanagh, 1992; Verstraten et al., 2000).

Another possible featural basis for salience mapping/feature tracking was the sequence of contrast increments, at one element location with the onset of Frame 1 and then at the other element location with the onset of Frame 2. We eliminated this sequence as a factor by increasing the duration of Frame 1 to 6 s . Motion again was perceived, but it could not have been based on the sequence of contrast increments because the resulting motion would have been too slow to be perceived.

Further evidence that motion perception was not due to either feature tracking or salience mapping was obtained by determining the maximum temporal frequency at which motion could be seen. With the same spatial dimensions as in the preceding experiments, the contrast for each checkerboard element varied between .200 and 1.0, and the contrast of the checkerboard background was set

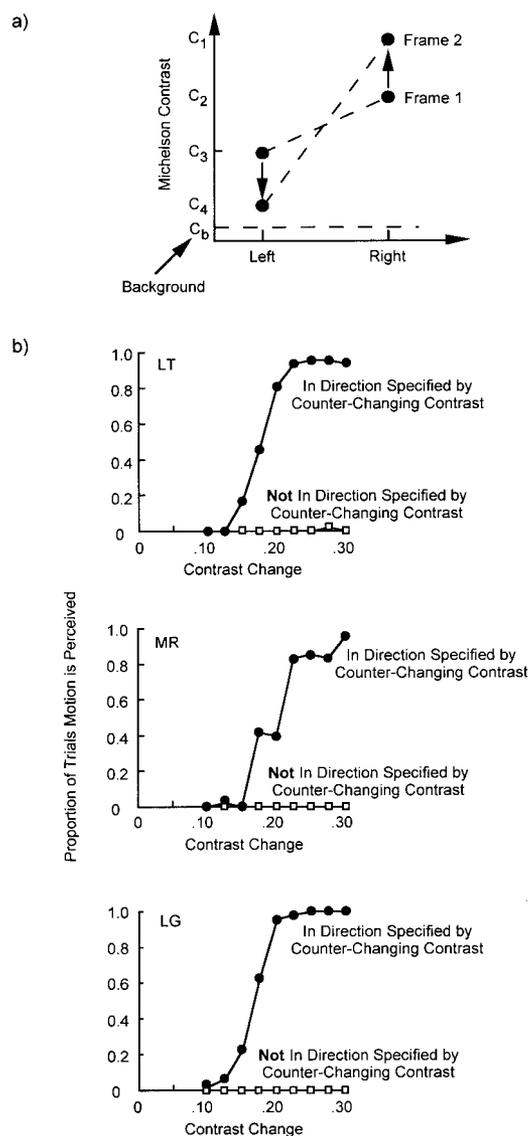


Figure 7. Experiment 5: Graphical representation of the changing contrast (C) values for the first two frames of a stimulus for which texture contrast was always greater for the right- than for the left-hand checkerboard (a) and the proportions of trials in which motion was perceived in the counter-change-specified direction by 3 participants (LT, MR, and LG) as a function of the magnitude of the contrast change (b).

Table 3
Michelson Contrast Values and Corresponding Luminance Values for Light and Dark Checks Composing Each Checkerboard Element in Experiment 5

| Michelson contrast | Check (cd/m ²) | | Alternating Michelson contrast | Check (cd/m ²) | | Contrast change |
|--------------------|----------------------------|-------|--------------------------------|----------------------------|-------|-----------------|
| | Light | Dark | | Light | Dark | |
| Left checkerboard | | | | | | |
| .350 | 78.98 | 38.03 | .250 | 73.13 | 43.88 | .100 |
| .363 | 79.71 | 37.29 | .238 | 72.39 | 44.61 | .125 |
| .375 | 80.44 | 36.56 | .225 | 71.66 | 45.34 | .150 |
| .388 | 81.17 | 35.83 | .213 | 70.93 | 46.07 | .175 |
| .400 | 81.90 | 35.10 | .200 | 70.20 | 46.80 | .200 |
| .413 | 82.63 | 34.37 | .188 | 69.47 | 47.53 | .225 |
| .425 | 83.36 | 33.64 | .175 | 68.74 | 48.26 | .250 |
| .438 | 84.09 | 32.91 | .163 | 68.01 | 48.99 | .275 |
| .450 | 84.63 | 32.18 | .150 | 67.28 | 49.73 | .300 |
| Right checkerboard | | | | | | |
| .750 | 102.38 | 14.63 | .650 | 96.53 | 20.48 | .100 |
| .763 | 103.11 | 13.89 | .638 | 95.79 | 21.21 | .125 |
| .775 | 103.84 | 13.16 | .625 | 95.06 | 21.94 | .150 |
| .788 | 104.57 | 12.43 | .613 | 94.33 | 22.67 | .175 |
| .800 | 105.30 | 11.70 | .600 | 93.60 | 23.40 | .200 |
| .813 | 106.03 | 10.97 | .588 | 92.87 | 24.13 | .225 |
| .825 | 106.76 | 10.24 | .575 | 92.14 | 24.86 | .250 |
| .838 | 107.49 | 9.51 | .563 | 91.41 | 25.59 | .275 |
| .850 | 108.23 | 8.77 | .550 | 90.68 | 26.63 | .300 |

Note. Michelson contrast values that were alternated for each checkerboard element are paired in each row of the table, and the magnitude of contrast change for each pair is indicated. Average Michelson contrasts were .300 for each pair in the left checkerboard and .700 for each pair in the right checkerboard.

at .200. Apparent motion was perceived for temporal frequencies as high as 9–10 Hz, greater than reported temporal frequency limits for salience mapping (3–5 Hz; Lu & Sperling, 1995b) and attentive tracking (4–8 Hz; Verstraten et al., 2000).

Experiment 6

Finally, it might be argued that the checkerboards in this study were not truly second-order stimuli, so the reported results might not pertain to second-order motion perception. This could be the case if the integration of luminance values for the light and dark checks by receptive fields large enough to encompass each checkerboard element were not perfectly linear (Smith & Ledgeway, 1997). The imperfectly averaged luminance of the checkerboard elements would then differ for each of their alternating contrast values and the background checkerboard, so motion perception could be based artifactually on a first-order, luminance-based mechanism.

To test this possibility, we made the average luminance of the checkerboard background less than the average luminance of the checkerboard elements in the low-luminance background condition and greater than the average luminance of the elements in the high-luminance background condition. As illustrated in Figures 8a–8c, changes in imperfectly averaged luminance would be confounded with changes in contrast in the low-luminance background condition. Rightward motion would be perceived because of either background-relative changes in imperfectly averaged

luminance or background-relative changes in contrast. In the high-luminance background condition, however, motion based on artifactual first-order information would be in the leftward direction, opposite of the direction expected on the basis of counter-changing contrast (Figures 8d–8f). The perceived motion direction therefore would be different in the high- and low-luminance background conditions if motion were based on artifactual changes in first-order luminance but not if it were based on changes in second-order contrast (the latter because the contrast of the background would remain lower than the contrast values of the checkerboard elements in both conditions).

Method

The contrast of each checkerboard element alternated between .700 (on the basis of luminance values of 68.0 and 12.0 cd/m² for the light and dark checks, respectively) and .300 (on the basis of luminance values of 52.0 and 28.0 cd/m² for the light and dark checks, respectively). The contrast changes always were in opposite directions at the two checkerboard locations, so motion almost always was perceived. During separate blocks of trials, the contrast of the background checkerboard was fixed at .100, but its average luminance was either 77.5 cd/m² (greater than the luminance of any of the checks composing the checkerboard elements) or 10.0 cd/m² (less than the luminance of any of the checks composing the checkerboard elements). There were two frames per trial, the first presented for 1,017 ms and the second for 267 ms. After each trial, participants indicated the direction of the perceived motion.

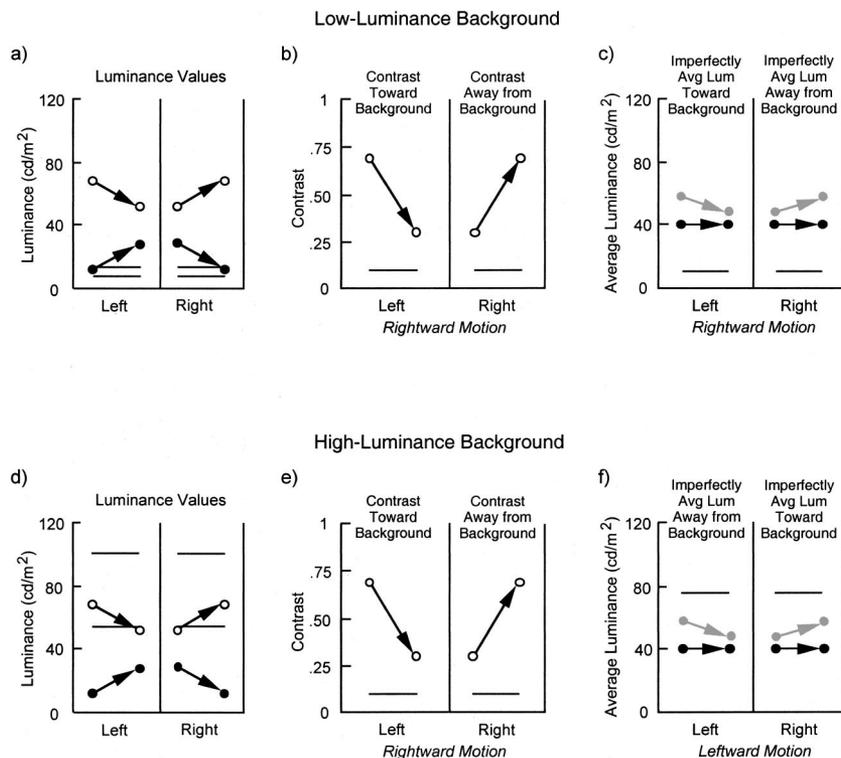


Figure 8. Experiment 6: The luminance values for the checks composing each checkerboard element (open and filled circles) and the checkerboard background (horizontal bars) in the low- and high-luminance background conditions (a and d). Michelson contrast values for the two checkerboard elements (open circles) and their background (horizontal bars; b and e). The average luminance (Avg Lum) for each checkerboard element (filled circles) and their background (horizontal bars; c and f). Although the actual average luminance of the checks was constant for the checkerboards, it was assumed for the purposes of this experiment that luminance was imperfectly averaged as a result of nonlinear integration (indicated in light gray).

Results

Motion was always perceived in the direction consistent with the contrast rather than the average luminance of the checkerboard background (the latter was either greater than or less than the average luminance of the checkerboard elements). In the high-luminance background condition, one motion direction was predicted on the basis of the low contrast of the checkerboard background, and the opposite motion direction was predicted on the basis of the high average luminance of the checkerboard background. Motion was always perceived in the direction determined by the contrast, indicating that it was based on the second-order characteristics of the checkerboard elements and not on artifactual first-order information that might have been created by imperfect luminance averaging.

General Discussion

Motion Energy Analysis?

As discussed in the introduction, Hock et al. (2002) found that the perception of first-order, luminance-defined apparent motion does not require the analysis of motion energy and instead depends on the detection of counter-changing luminance (i.e., simultaneous changes in luminance toward and away from the background

luminance value at different element locations). In parallel with those of Hock et al. (2002), the results of the current Experiment 3 indicate that the perception of second-order, texture-contrast-defined apparent motion does not require the postrectification analysis of motion energy; it depends instead on the detection of counter-changing contrast.

Background Relativity

Also parallel to Hock et al.'s (2002) results for luminance-defined motion is the current evidence that motion is perceived only when contrast values at each element location change in opposite directions relative to the contrast value of the background: The perceived motion path starts at the element location where contrast changes toward the background contrast, and it ends at the element location where contrast changes away from the background contrast (Experiment 1). This is the case even when the motion starts at the highest contrast value and ends at the lowest contrast value, or vice versa (Experiment 2). Background relativity also affects the likelihood of motion perception; motion is perceived more often when element contrast values are more similar to the contrast value of the background texture (Experiment 4).

Saliency Mapping/Feature Tracking?

There is substantial evidence that feature tracking/saliency mapping could not have been responsible for motion perception in our paradigm. (a) In Experiment 2 (with the background contrast midway between the contrast values of the elements), perceived apparent motion started at the checkerboard with the highest contrast and ended at the checkerboard with the lowest contrast, and vice versa. Establishing a featural correspondence between checkerboard elements with similar texture contrast is not necessary for motion perception. (b) Apparent-motion perception based on feature tracking or saliency mapping was possible in the co-changing condition of Experiment 3 because the higher contrast checkerboard alternated between the two element locations. Nonetheless, motion was never perceived (there was no counter-changing contrast). (c) Apparent-motion strength is greater when the elements are more similar in luminance or contrast to the background (i.e., when they are less salient with respect to the background; Experiment 4). (d) Changes in the location of the more salient element are not necessary for apparent motion perception; motion can be perceived even when the higher (presumably more salient) contrast value never changes location (Experiment 5). We argue, for the same reason, that contrast could not serve as a feature for attentive feature tracking, and it has been shown as well that the only other imaginable featural basis for attentive tracking—a sequence of contrast increments—could not have been the basis for motion perception. (e) Motion can be perceived at temporal frequencies exceeding reported limits for saliency mapping and attentive feature tracking (*Results* section of Experiment 5, third paragraph).

Counter-Changing Activation and a Proposed Motion-Detection Mechanism

The parallel results obtained for spatiotemporal changes in luminance (Hock et al., 2002) and spatiotemporal changes in texture contrast (the current study) suggest that apparent motion is perceived as a result of a mechanism that responds to counter-changing activation, regardless of the stimulus changes that are responsible for the opposite changes in activation at each element location. Consistent with this hypothesis, Hock and Gilroy (2002) have found that motion can be perceived between a zero-contrast, uniform-luminance square presented on a zero-contrast, uniform-luminance background and a nearby texture-contrast-defined checkerboard square presented on a checkerboard background. (Similar results were obtained by Cavanagh, Arguin & von Grünau, 1989.) That changes in activation at each element location were the basis for the apparent motion perceived between luminance- and texture-contrast-defined stimuli is indicated by evidence for transitivity and local integration. That is, changes in luminance and contrast with equivalent effects on motion perception were interchangeable, and motion perception depended on the net activation change resulting from simultaneous background-relative luminance and contrast changes at the same element location.

A possible mechanism for detecting counter-changing activation (resulting from changes in luminance, texture contrast, or both) would, in the style of the Reichardt motion detector (Reichardt, 1961), be composed of a pair of subunits whose transient responses

to changes in activation are multiplicatively combined. The directional selectivity of the proposed mechanism would be established by the direction of activation change; that is, motion would start at the subunit that is excited when its input activation decreases and end at the subunit that is excited when its input activation increases. Unlike the Reichardt detector (or the inhibition-based motion-detecting mechanism proposed by Barlow & Levick, 1965), this mechanism would not require delaying the response of one subunit prior to combining it with the response of the other subunit to establish directional selectivity. Also unlike the standard Reichardt detector, this mechanism would not require the subtractive comparison of the outputs of detectors with opposing directional selectivity to prevent motion from being signaled when the input activation to the two subunits simultaneously increased or simultaneously decreased. Motion would be signaled by the proposed mechanism only when input activation was changing in the opposite direction at the two subunits.

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