Available online at www.sciencedirect.com
SCIENCE DIRECT®
Vision Research 45 (2005) 661–675
Vision Research
www.elsevier.com/locate/visres

A common mechanism for the perception of first-order and second-order apparent motion

Howard S. Hock *, Lee A. Gilroy

Department of Psychology, Florida Atlantic University, 777 Glades Road, P.O. Box 3091, Boca Raton, FL 33431-0991, USA

Received 24 April 2003; received in revised form 30 December 2003

Abstract

A common mechanism for perceiving first-order, luminance-defined, and second-order, texture-contrast defined apparent motion between two element locations is indicated by: (1) transitivity—whether or not motion is perceived is inter-changeably affected by activationally equivalent luminance and contrast changes at each location, (2) local integration—whether or not motion is perceived depends on the net activation change resulting from simultaneous background-relative luminance and background-relative contrast changes at the same element location, and (3) inseparability—apparent motion is not perceived through independent first- or second-order mechanisms when luminance and contrast co-vary at the same location. These results, which are predicted by the response characteristics of directionally selective cells in areas V1, MT, and MST, are not instead attributable to changes in the location of the most salient element (third-order motion), attentive feature tracking, or artifactual first-order motion. Their inconsistency with Lu and Sperling's [Lu, Z., Sperling, G. (1995a). Attention-generated apparent motion. *Nature 377*, 237, Lu, Z., Sperling, G. (2001). Three-systems theory of human visual motion perception: review and update. *Journal of the Optical Society of America A 18*, 2331] model, which specifies independent first- and second-order mechanisms, may be due to computational requirements particular to the motion of discrete objects with distinct boundaries defined by spatial differences in luminance, texture contrast, or both.

Keywords: Motion; Apparent motion; First-order; Second-order

1. Introduction

There are by now a vast number of research articles concerned with whether one or two mechanisms are required for the detection of motion for first-order, luminance-defined stimuli, and second-order, texture-contrast-defined stimuli. Clifford and Vaina (1999) have compiled a long list of articles addressing this issue, with some psychophysical results consistent with a common mechanism (e.g., Johnson & Benton, 1997; Johnson & Clifford, 1995a; Taub, Victor, & Conte, 1997; Turano, 1991; Turano & Pantle, 1989; Victor & Conte, 1992), and others consistent with separate mechanisms for first- and second-order motion stimuli (e.g., Harris & Smith, 1992; Ledgeway & Smith, 1994; Lu & Sperling, 1995a; Mather & West, 1993; Nishida, 1993; Scott-Samuel & Smith, 2000).

To date, however, the issue of a common mechanism has not been comprehensively addressed for apparent motion stimuli composed of discrete, object-like elements. Such elements have distinct, closed boundaries that can be defined by spatial differences in any nonmotion attribute, including differences in luminance and texture contrast. It makes good computational sense that the motion of an object would be determined by a common mechanism responding to the combined effects

* Corresponding author. Fax: +1 561 297 2160.
E-mail address: hockhs@fau.edu (H.S. Hock).

0042-6989/$ - see front matter © 2004 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2004.09.039

of changes in luminance and texture contrast (and potentially, changes in other attributes as well). The alternative would require a decision among the different, possibly conflicting motion signals generated by each of the object's attributes. Objects can move in only one direction at a time, so establishing the net activation change at each object location prior to detection by a common motion mechanism provides a distinct computational advantage for the perception of object motion. Psychophysical evidence for a single first/second-order mechanism for the apparent motion of discrete objects would be consistent with neurophysiological results indicating that directionally selective neurons in areas V1, MT, and MSTd respond to both first-order, luminance-defined and second-order, texture-contrast defined motion (Albright, 1992; Chaudhuri & Albright, 1997; Geesaman & Andersen, 1996; O'Keefe & Movshon, 1998; Olavarria, DeYoe, Knierem, Fox, & Van Essen, 1992; Stoner & Albright, 1992; Zhou & Baker, 1993). It would be consistent as well with the results of computational simulations (Baloch, Grossberg, Mingolla, & Nogueria, 1999; Johnston & Clifford, 1995b).

Hock, Gilroy, and Harnett (2002) have demonstrated that the apparent motion of object-like first-order visual elements is specified by background-relative, counter-changing luminance. (Also called dipole contrast change; Lappin, Tadin, & Whittier, 2002.) For motion to be perceived, the luminance at one element location must change toward the luminance of the background while the luminance at a second element location changes away from the luminance of the background (Fig. 1a and d). Hock et al. (2002) ruled out Fourier-analyzed motion energy as the motion-specifying information for luminance-defined apparent motion by creating stimuli for which there was adequate motion energy for motion perception, but no counter-changing luminance; motion was not perceived. Additional research has indicated, analogously, that the apparent motion of object-like second-order visual elements is specified by background-relative, counter-changing texture contrast (Gilroy & Hock, 2004). For motion to be perceived, the contrast at one element location must change toward the contrast of the background while the contrast at a second element location changes away from the contrast of the background (Fig. 1b and e). Post-rectification motion energy was ruled out as motion-specifying information for texture-contrast defined apparent motion by creating stimuli for which there would be adequate post-rectification motion energy for motion perception, but no counter-changing contrast; motion was not perceived. Although these results do not constitute evidence against motion energy detection in general, they indicate that it is not the basis for first- and second-order apparent motion perception of discrete, object-like elements. They are thus consistent with the assertion that the potential motion energy signal for apparent motion stimuli is obscured by energy artifacts that are by-products of discontinuous spatial and temporal sampling (Fleet & Langley, 1994; Mather, 1994).

The parallel results for luminance and contrast change in the studies described above led us to consider the possibility of a common first/second-order mechanism that would result in the perception of apparent motion between a second-order, contrast-defined element and a first-order, luminance-defined element. Consistent with previous research (Cavanagh, Arguin, & von Grünau, 1989), we observed that motion can be perceived when the contrast of a square checkerboard decreases toward the contrast of its background, while at the same time, the luminance of a nearby square with uniform luminance increases away from the luminance of its background (Fig. 1c and f), and vice versa. Motion is not perceived when the luminance and contrast of the elements simultaneously increase or simultaneously decrease relative to their backgrounds. When it is perceived, motion always begins at the location where activation decreases (e.g., the contrast of the left-hand element decreases toward the background contrast) and ends at the location where activation increases (the luminance of the right-hand, uniform-luminance element increases away from the background luminance). This example of contrast-to-luminance motion is consistent with a common first/second-order mechanism because there is incomplete motion-specifying information for independent first- and second-order mechanisms. [1]

In the experiments that follow, we examine the properties expected of a common first/second-order mechanism if the perception of apparent motion for object-like elements is indeed based on such a mechanism. As in Hock et al. (2002) and Gilroy and Hock (2004), the experiments are based on a generalized apparent motion paradigm in which elements are simultaneously visible at two locations, and the elements' luminance and/or contrast are simultaneously changed. [2] Combinations of changes in luminance and contrast toward and away from the luminance and contrast of their background serve as the basis for predicting whether or not motion would be perceived.

[1] Although the stimulus elements in this experiment were relatively large in order for the checkerboards to be easily perceived, contrast-to-luminance motion could be perceived when the size of the elements was reduced to three min and the center-to-center distance between them was reduced to 6 min.

[2] This paradigm, which was first described for luminance-defined elements by Johansson (1950), was refined by Hock, Kogan, and Espinoza (1997). Other versions of generalized apparent motion stimuli have involved the swapping of black and white elements that are simultaneously presented against a gray background (Anstis & Mather, 1985), as well as the swapping of simultaneously presented elements that differ in texture (Mather & Anstis, 1995) and spatial frequency (Watson, 1986; Werkhoven, Sperling, & Chubb, 1993).

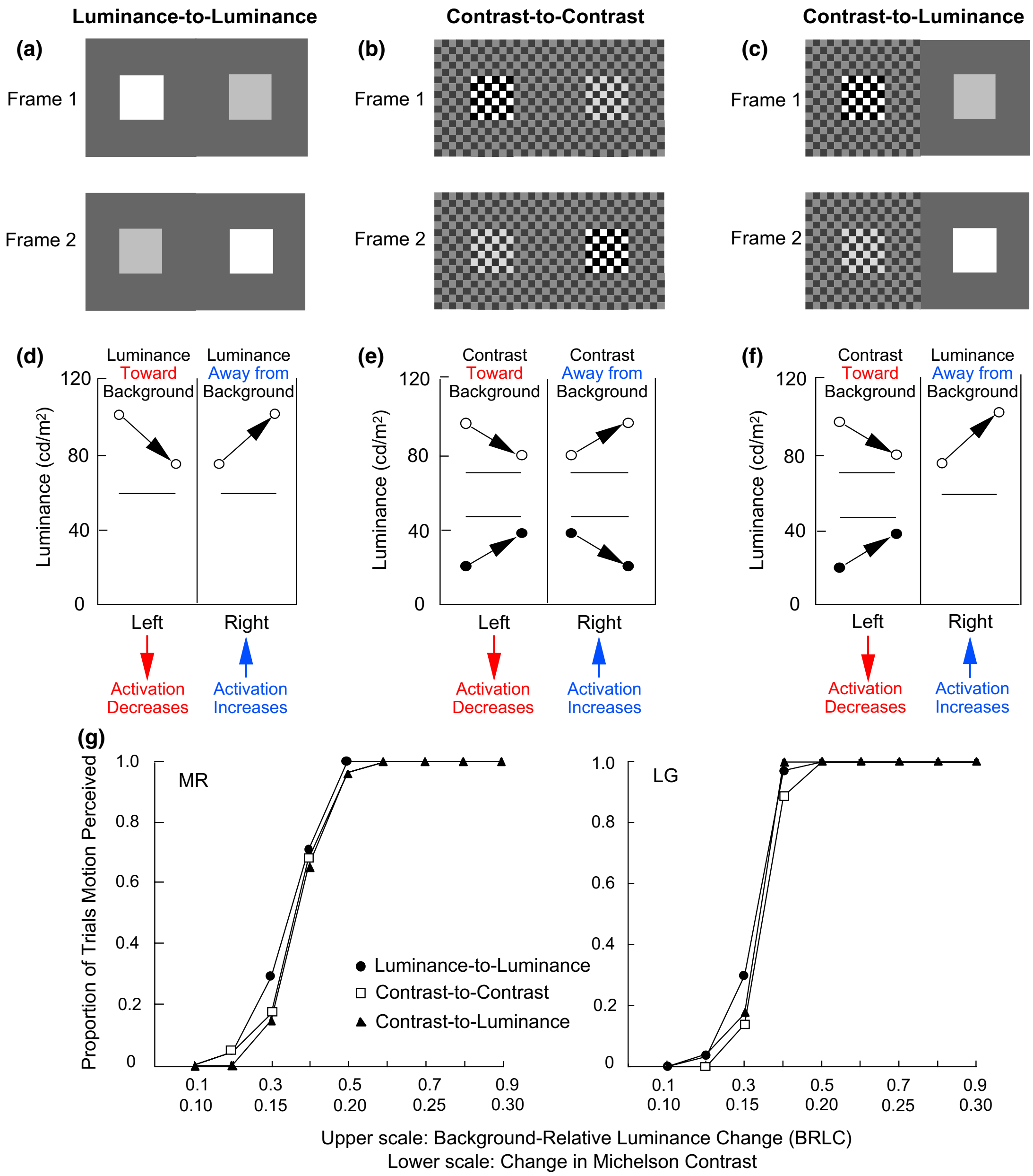

Fig. 1. Stimulus description and results for Experiment 1. (a–c) Illustration of two frames of the stimuli in the Luminance-to-Luminance, Contrast-to-Contrast, and Contrast-to-Luminance conditions. (d–f) Graphical representation of the luminance and contrast values for the stimuli above them (luminance values alternate between 74.7 and 101.3 cd/m^2; BRLC = 0.9; Michelson contrast values alternate between 0.65 and 0.35). The background luminance of the uniform-luminance elements is indicated by a horizontal line. For the checkerboard background of the checkerboard elements, luminance values of the light and dark checks are indicated by a pair of horizontal lines. For the checkerboard elements, luminance values of light and dark checks are indicated respectively by open and filled circles. Arrows indicate how luminance values change for both the uniform-luminance and checkerboard elements from the first to the second frame. (g) The proportion of trials during which motion was perceived as a function of the BRLC values of the uniform-luminance elements and/or the contrast change of the checkerboards.

2. General method

Pairs of 1.2 × 1.2 deg elements were simultaneously presented with a Power Macintosh 7300/180 computer. The elements were 2.4 deg apart (center-to-center), and centered within a 7.2 × 4.8 deg rectangular background (which was in turn centered in the screen of a Viewsonic 15GA monitor; screen luminance <.001 cd/m^2). Viewing distance was maintained at 35.8 cm with a head restraint. Luminance-defined elements were squares with uniform luminance presented against a uniform-luminance background. Texture-contrast defined elements were square checkerboards composed of 64 spatially alternating light and dark squares (each check was 9 × 9 min) presented against a lower contrast checkerboard background, which also was composed of

9 × 9 min checks. Unless indicated otherwise, the average luminance of the checkerboard elements and their checkerboard background was the same, and the same as the uniform-luminance background of the uniform-luminance elements. Changes in luminance and/or contrast at one element location were simultaneous with changes in luminance and/or contrast at the other element location. Each trial was composed of eight frames with alternating luminance and/or contrast. The frame-to-frame temporal frequency of alternation was 1.9 Hz in Experiments 1 and 5, and varied between 1.0 and 10.0 Hz in Experiments 2, 3 and 4.

Instructions to maintain fixation midway between the two element locations was stressed in order to minimize the potential influence of attentive feature tracking (Cavanagh, 1992; Verstraten, Cavanagh, & Labianca, 2000). After each trial, subjects indicated whether or not they perceived motion across the space between the elements anytime during the trial by pressing 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). The spacebar was pressed on the infrequent occasions when they were unsure of their response.

3. Experiment 1: Transitivity

The purpose of this experiment was to determine whether changes in luminance and changes in texture contrast that are matched with respect to the frequency of perception of luminance-to-luminance motion and contrast-to-contrast motion are inter-changeable with respect to their effect on whether or not contrast-to-luminance motion is perceived. This evidence for transitivity would be consistent with the existence of a common motion mechanism (Werkhoven et al., 1993). It would indicate that the activation changes produced by changes in luminance and texture contrast are crucial for the perception of apparent motion, irrespective of whether the source of the activation changes lies in the first-or second-order characteristics of the apparent motion stimulus.

3.1. Method

The selection of luminance values for the uniform-luminance elements in the Luminance-to-Luminance condition (Fig. 1a and d) was based on the perception of apparent motion for luminance-defined elements depending on their background-relative luminance change (BRLC), which is calculated by dividing the change in an element's luminance by the difference between its mean luminance and the luminance of its background (Hock et al., 1997). With the background luminance fixed at 58.5 cd/m^2, the pairs of luminance values were 86.5/89.5, 85.0/91.0, 83.6/92.4, 82.1/93.9, 80.6/95.4, 79.2/96.8, 77.7/98.3, 76.3/99.8, or 74.7/101.3 cd/m^2, resulting in BRLC values ranging from 0.1 to 0.9. The selection of texture contrast values for the Contrast-to-Contrast condition (Fig. 1b and e) was based on evidence that motion perception for sinusoidally varying textures depends on the change in their Michelson contrast (e.g., Kulikowski & Tolhurst, 1973; Pantle & Sekuler, 1969). For the checkerboards, the Michelson contrast is the difference in luminance between the light and dark checks divided by the sum of their luminance values. Pairs of contrast values were. 55/.45, .56/.44, .58/.42, .59/.41, .60/.40, .61/.39, .63/.37, .64/.36, or .65/.35, resulting in contrast changes ranging from 0.10 to 0.30. The Michelson contrast of the checkerboard background was 0.2 (light checks = 70.2 cd/m^2; dark checks = 46.8 cd/m^2).

The texture contrast and luminance values for the Contrast-to-Luminance condition (Fig. 1c and f) were combinations of values from the Contrast-to-Contrast and Luminance-to-Luminance conditions (e.g., .55/.45 with 86.5/89.5 cd/m^2; .56/.44 with 85.0/91.0 cd/m^2; and so on). The frame duration for each eight-frame trial was 267 ms (temporal frequency = 1.9 Hz). There were four blocks of trials in each of the three conditions (54 trials per block; 9 pairs luminance and/or contrast changes, with 6 repetitions).

3.2. Results

In the Contrast-to-Luminance condition, a checkerboard element presented against a checkerboard background was paired with a uniform-luminance element presented against a uniform-luminance background. In creating these pairs, it was assumed that equal frequency of motion perception in the Luminance-to-Luminance and Contrast-to-Contrast conditions meant that there were equal changes in activation for both attributes. As can be seen in Fig. 1g, the psychometric functions for the Contrast-to-Luminance condition overlapped the functions for the Luminance-to-Luminance and Contrast-to-Contrast conditions. This provided evidence for transitivity: Changes in luminance and texture contrast that have equivalent effects on whether or not motion is perceived are inter-changeable, consistent with a common first/second-order motion mechanism that responds to counter-changing activation at the two element locations.

4. Experiment 2: Local integration

The luminance changes that contribute to the perception of contrast-to-luminance motion need not be based on an element with uniform luminance presented against a uniform-luminance background, as in Experiment 1. Motion also can be perceived for pairs of checkerboard elements presented against a common checkerboard background when one checkerboard element changes in contrast while its average luminance remains constant, and the other changes in average luminance while its contrast remains constant (a stimulus from the Contrast-to-Average-Luminance condition is graphically illustrated in Fig. 2a–c). The proviso is that the change in contrast at one location, and the change in average luminance at the other location, are in opposite

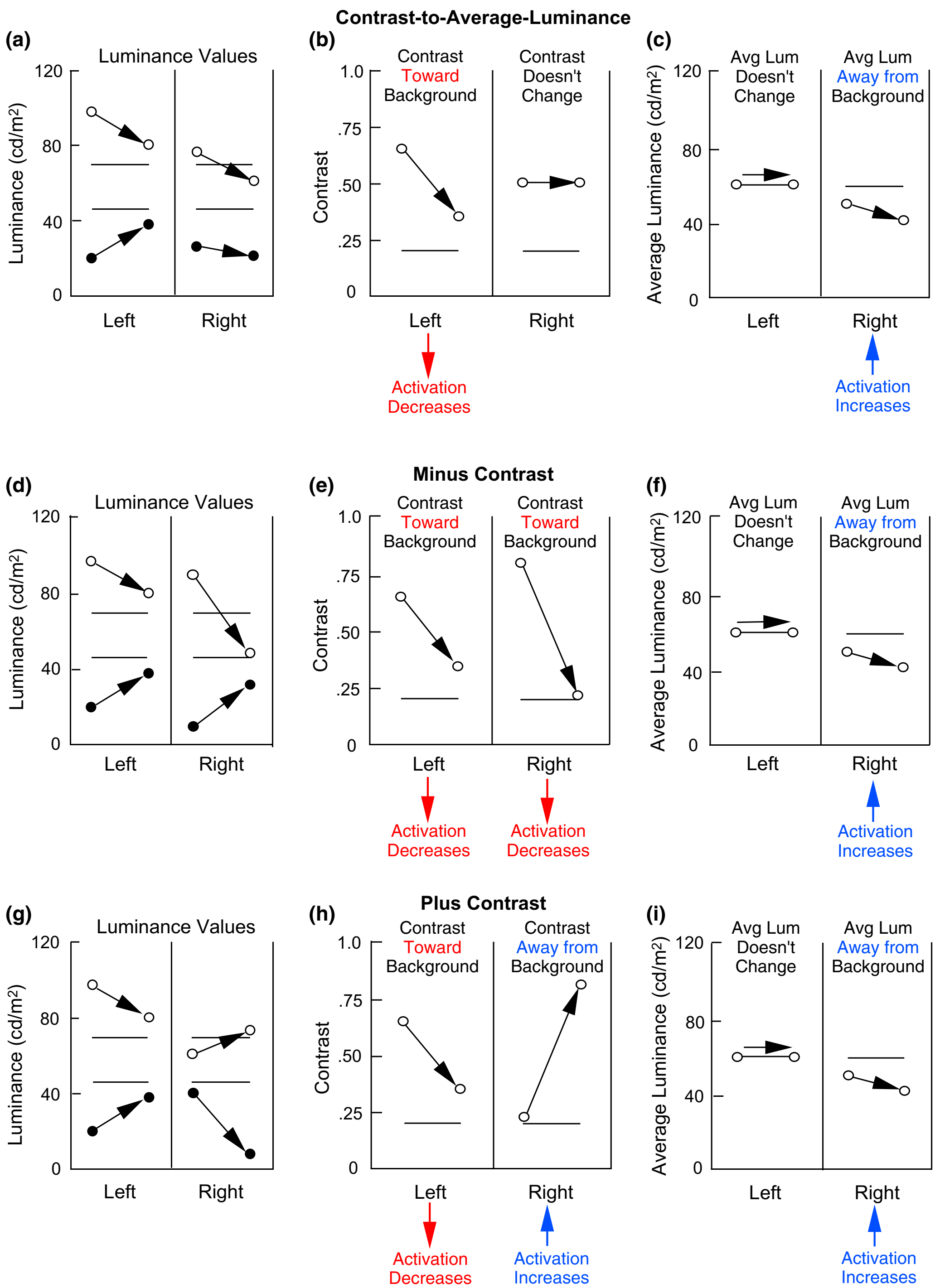

Fig. 2. Stimulus description for Experiment 2. Indicated are check-luminance (a, d, g), Michelson contrast (b, e, h), and average luminance (c, f, i) values for the checkerboard elements and their checkerboard background. In the Contrast-to-Average-Luminance condition, changes in the left-hand checkerboard's contrast toward the contrast of the background (b) are accompanied by the change in the right-hand checkerboard's average luminance away from the average luminance of the background (c). In the Minus Contrast condition, changes in contrast (e) and average luminance (f) are in opposite background-relative directions for the right-hand checkerboard. In the Plus Contrast condition, changes in contrast (h) and average luminance (i) are in the same background-relative direction for the right-hand checkerboard.

background-relative directions, producing counter-changing activation at the two locations.

If the perception of motion were based on a common first/second-order mechanism responsive to counter-changing activation, it would be expected to depend on the net change in activation produced by simultaneous changes in contrast and average luminance at the same location. This was investigated by simultaneously changing both attributes for the right-hand checkerboard element; only the contrast was changed for the left-hand checkerboard element.

In the Minus Contrast condition, the change in average luminance of the right-hand element was opposed by a contrast change in the opposite background-relative direction (Fig. 2d–f). That is, a decrease in the right-hand checkerboard's average luminance (away from the average luminance of the background) was accompanied by a simultaneous decrease in its contrast (toward the contrast of the background), and vice versa. In the Plus Contrast condition, the change in average luminance of the right-hand element was reinforced by a contrast change in the opposite background-relative direction (Fig. 2g–i). That is, the decrease in average luminance of the right-hand checkerboard away from the background's average luminance was accompanied by a simultaneous increase in its contrast away from the background's contrast, and vice versa.

The hypothesized differences in activation-change for the Contrast-to-Average-Luminance, Minus Contrast, and Plus Contrast conditions were assessed by determining the range of temporal frequencies over which apparent motion could be perceived. It was expected that the perception of motion would be susceptible to differences in activation change at high temporal frequencies because motion is more difficult to perceive for the brief frame durations of high frequency stimuli. This hypothesis followed from motion perception being based on the transient response of biphasic detectors to changes in luminance and/or contrast (e.g., Adelson & Bergen, 1985; Cai, DeAngelis, & Freeman, 1997; Strout, Pantle, & Mills, 1994; Watson & Ahumada, 1985). Apparent motion is harder to perceive at high temporal frequencies (brief frame durations) because the transient response of a biphasic detector to a luminance or contrast change at the start of each frame would not have reached its full activation before the opposite luminance or contrast change occurred at the end of the frame. [3]

4.1. Method

Two checkerboards were presented against a checkerboard background with a Michelson contrast of 0.2 and an average luminance of 58.5 cd/m^2. In all three conditions, the left-hand checkerboard element had a mean luminance of 58.5 cd/m^2 and alternated in contrast between 0.65 (light checks: 96.5 cd/m^2; dark checks: 20.5 cd/m^2) and 0.35 (light checks: 79.0 cd/m^2; dark checks: 38.0 cd/m^2). In the Contrast-to-Average-Luminance condition, the contrast of the right-hand checkerboard remained constant at 0.5 while its average luminance simultaneously alternated between 50.0 and 40.0 cd/m^2 (Fig. 2a–c). In the Minus Contrast condition, the contrast of the right-hand checkerboard decreased from 0.8 (light checks = 90.0, dark checks = 10.0 cd/m^2) to 0.2 (light checks = 48.0, dark checks = 32.0 cd/m^2) while its average luminance simultaneously decreased from 50.0 to 40.0 cd/m^2, and vice versa over successive frames (in opposite background-relative directions; Fig. 2d–f). In the Plus Contrast condition, the right-hand checkerboard's contrast increased from 0.2 (light checks = 60.0, dark checks = 40.0 cd/m^2) to 0.8 (light checks = 72.0, dark checks = 8.0 cd/m^2) while its average luminance simultaneously decreased from 50.0 to 40.0 cd/m^2, and vice versa over successive frames (in the same background-relative direction; Fig. 2g–i). Subjects were tested during three blocks of trials in each of the three conditions. There were 168 trials per block determined by 24 repetitions of 7 different temporal frequencies (1.0, 2.0, 4.0, 5.0, 7.0, 8.0, or 10.0 Hz).

4.2. Results

In the Minus Contrast condition, luminance and contrast changes were in opposite background-relative directions for the right-hand checkerboard. Consistent with the hypothesized reduction in activation change at that location, motion perception was limited to relatively low temporal frequencies compared with the Contrast-to-Average-Luminance condition (Fig. 3). In the Plus Contrast condition, both attribute changes were in the same background-relative direction for the right-hand checkerboard. Consistent with the hypothesized increase in activation change, motion was perceived for even higher temporal frequencies of contrast/luminance alternation than in the Contrast-to-Average-Luminance condition (Fig. 3). This evidence for local integration can be accounted for only by a common first/second-order motion mechanism. [4]

[3] Gilroy (2003) has shown that the perception of a single motion for a two-frame, luminance-defined apparent motion stimulus decreases as the duration of the second frame is decreased.

[4] The increased motion perception in the Plus Contrast condition could not have been due to the effect of luminance on contrast gain. The changes in luminance were in the direction opposite to the changes in texture contrast, so if the neural response to texture contrast decreased with decreases in average luminance, it would have decreased rather than increased motion perception in the Plus Contrast condition.

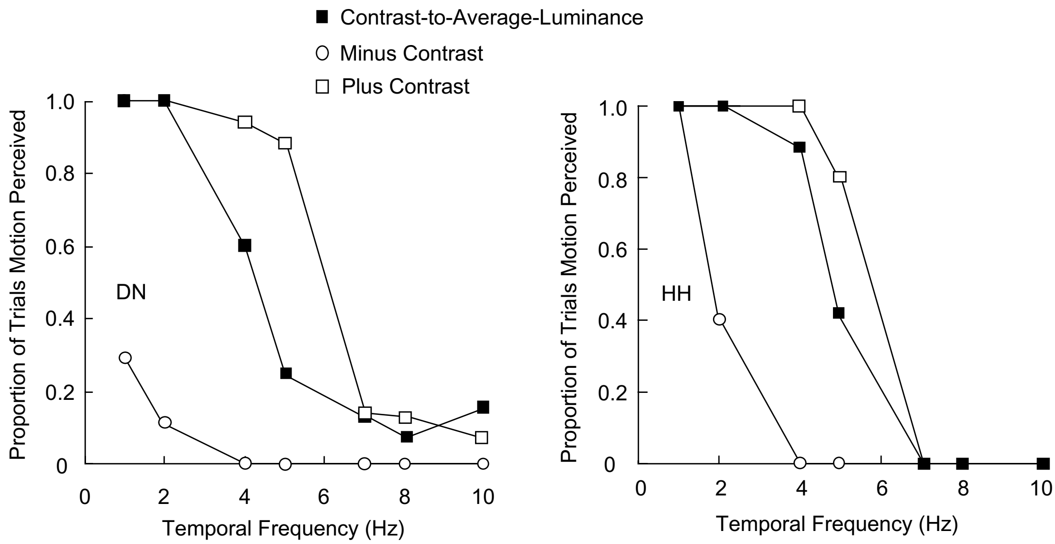

Fig. 3. Results for Experiment 2. The proportion of trials that motion was perceived as a function of the temporal frequency of contrast/luminance alternation.

5. Experiment 3: Inseparability

The above evidence for a common mechanism does not preclude its co-existence with independent first- and second-order mechanisms. It seems unlikely, however, that transitivity would have been observed in Experiment 1 if luminance-to-luminance motion was based on a first-order mechanism, contrast-to-contrast motion on a second-order mechanism, and contrast-to-luminance motion on still another, common first/second-order mechanism. We nonetheless tested this possibility by determining whether: (1) average-luminance-to-average-luminance motion would be affected by an opposing change in contrast for one of the checkerboard elements (the change in contrast would be "invisible" to an independent first-order mechanism), and (2) contrast-to-contrast motion would be affected by an opposing change in average luminance for one of the checkerboard elements (the change in average luminance would be "invisible" to an independent second-order mechanism).

5.1. Method

5.1.1. Part 1

Two checkerboards were presented against a checkerboard background with a Michelson contrast of 0.2 and an average luminance of 58.5 cd/m^2. In the Average-Luminance-to-Average-Luminance condition (Fig. 4a–c), the contrast of both checkerboards remained constant at 0.5 and their average luminance varied between 58.5 and 73.0 cd/m^2 (in opposite directions for the two checkerboards). In the Minus Contrast condition (Fig. 4d–f), the contrast of the right-hand checkerboard decreased from 1.0 to 0.2 while its average luminance increased from 58.5 to 73.0 cd/m^2, and vice versa over successive frames. If apparent motion could be based on an independent first-order mechanism, there would be no loss of motion perception in the Minus Contrast compared with the Average-Luminance-to-Average-Luminance condition.

5.1.2. Part 2

In the Contrast-to-Contrast condition (Fig. 5a–c), the contrast of both checkerboards varied between 0.2 and 0.8 (in opposite directions for the two checkerboards). The average luminance of both checkerboards was constant at 58.5 cd/m^2. In the Minus Average Luminance condition (Fig. 5d–f), the average luminance of the right-hand checkerboard decreased from 97.5 to 58.5 cd/m^2 while its contrast increased from 0.2 to 1.0, and vice versa over successive frames. If apparent motion could be based on an independent second-order mechanism, there would be no loss of motion perception in the Minus Average Luminance compared with the Contrast-to-Contrast condition.

In each part of the experiment, there were four blocks of trials for each of the two conditions (168 trials per block; 7 temporal frequencies with 24 repetitions).

5.2. Results

It was found in Part 1 that luminance-defined apparent motion was perceived only at relatively low temporal frequencies in the Minus Contrast compared with the Average-Luminance-to-Average-Luminance condition (Fig. 4g). This evidence for the inseparability of luminance changes from contrast changes co-occurring at

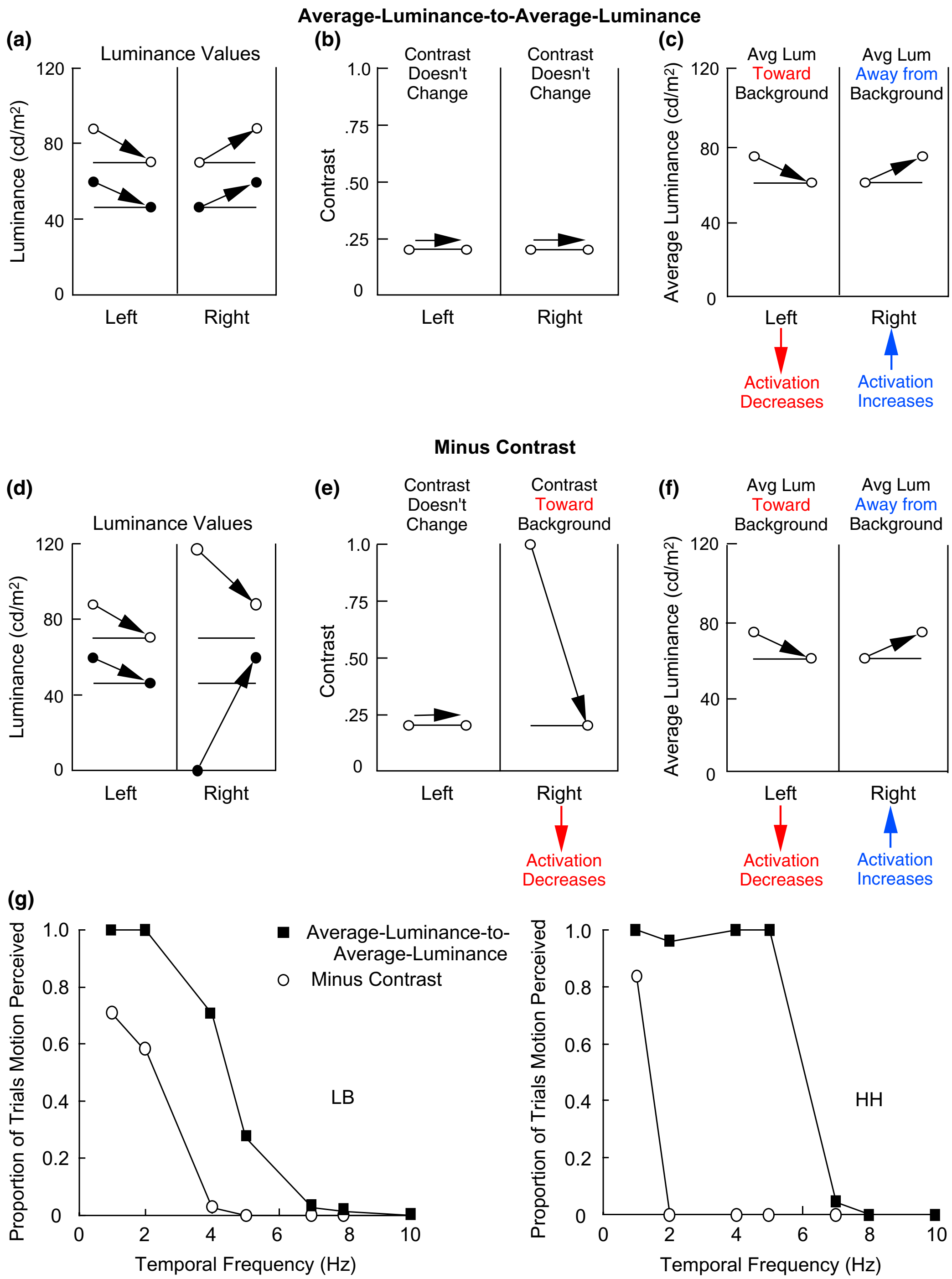

Fig. 4. Stimulus description and results for Experiment 3, Part 1. Indicated are check-luminance (a, d), Michelson contrast (b, e), and average luminance (c, f) values for the checkerboard elements and their checkerboard background. In the Average-Luminance-to-Average-Luminance condition, the change in the left-hand checkerboard's average luminance toward the average luminance of the background is accompanied by the change in the right-hand checkerboard's average luminance away from the average luminance of the background (c). In the Minus Contrast condition, changes in contrast (e) and average luminance (f) are in opposite background-relative directions for the right-hand checkerboard. (g) The proportion of trials that motion was perceived as a function of the temporal frequency of contrast/luminance alternation.

the same element location argued against the perception of apparent motion being based on an independent first-order mechanism.

It was found in Part 2 that contrast-defined apparent motion was perceived only at relatively low temporal frequencies in the Minus Average Luminance compared

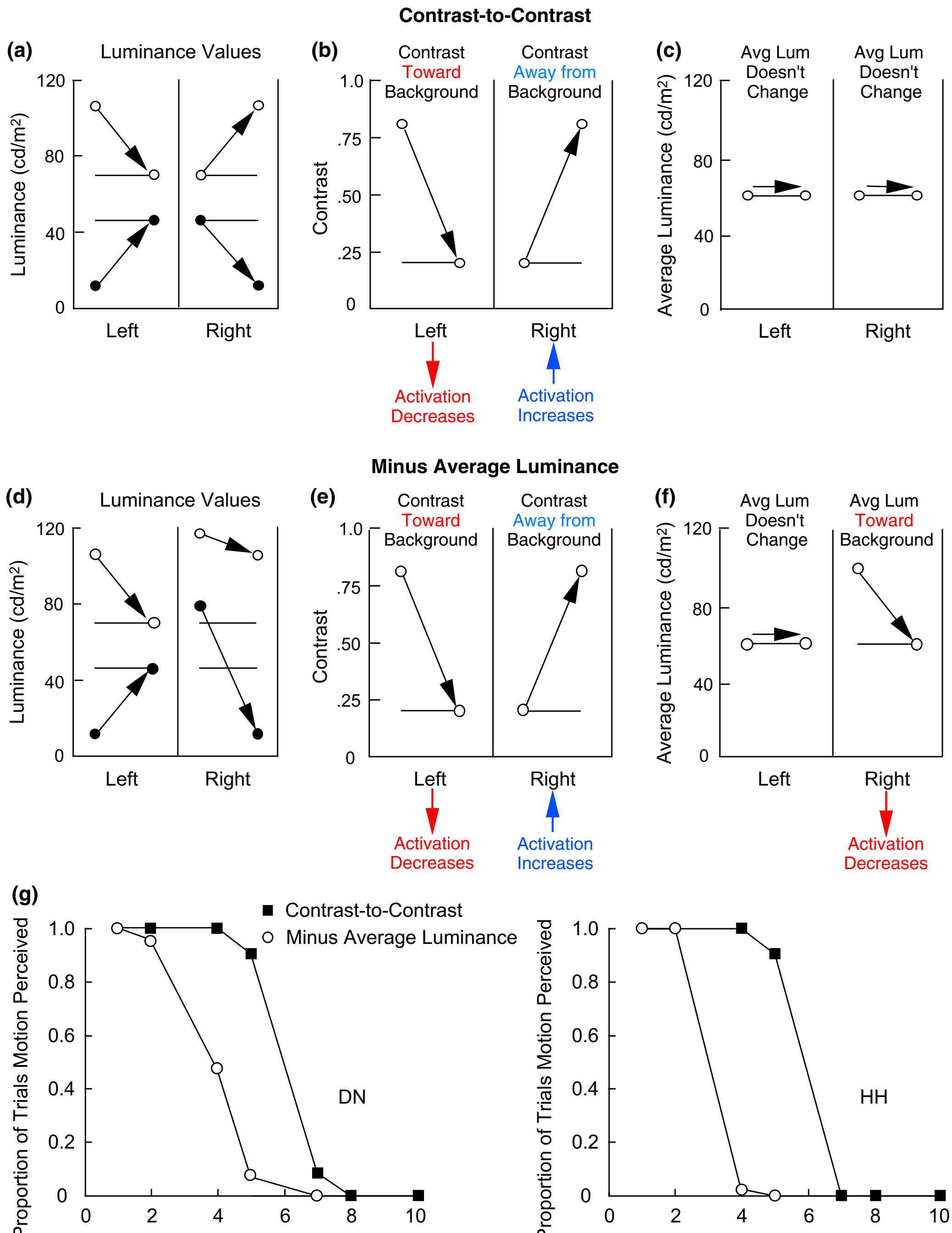

Fig. 5. Stimulus description and results for Experiment 3, Part 2. Indicated are check-luminance (a, d), Michelson contrast (b, e), and average luminance (c, f) values for the checkerboard elements and their checkerboard background. In the Contrast-to-Contrast condition, motion is perceived on the basis of the change in the left-hand checkerboard's contrast toward the contrast of the background accompanied by the change in the right-hand checkerboard's contrast away from the contrast of the background (b). In the Minus Average Luminance condition, changes in contrast (e) and average luminance (f) are in opposite background-relative directions for the right-hand checkerboard. (g) The proportion of trials that motion was perceived as a function of the temporal frequency of contrast/luminance alternation.

with the Contrast-to-Contrast condition (Fig. 5g). This evidence for the inseparability of contrast changes from average luminance changes co-occurring at the same element location argued against the perception of apparent motion being based on an independent second-order mechanism.

6. Experiment 4: Salience-mapping/feature tracking?

Rather than a common first/second-order mechanism, it might be claimed that the perception of contrast-to-luminance apparent motion is based on a third-order mechanism responsive to changes in the

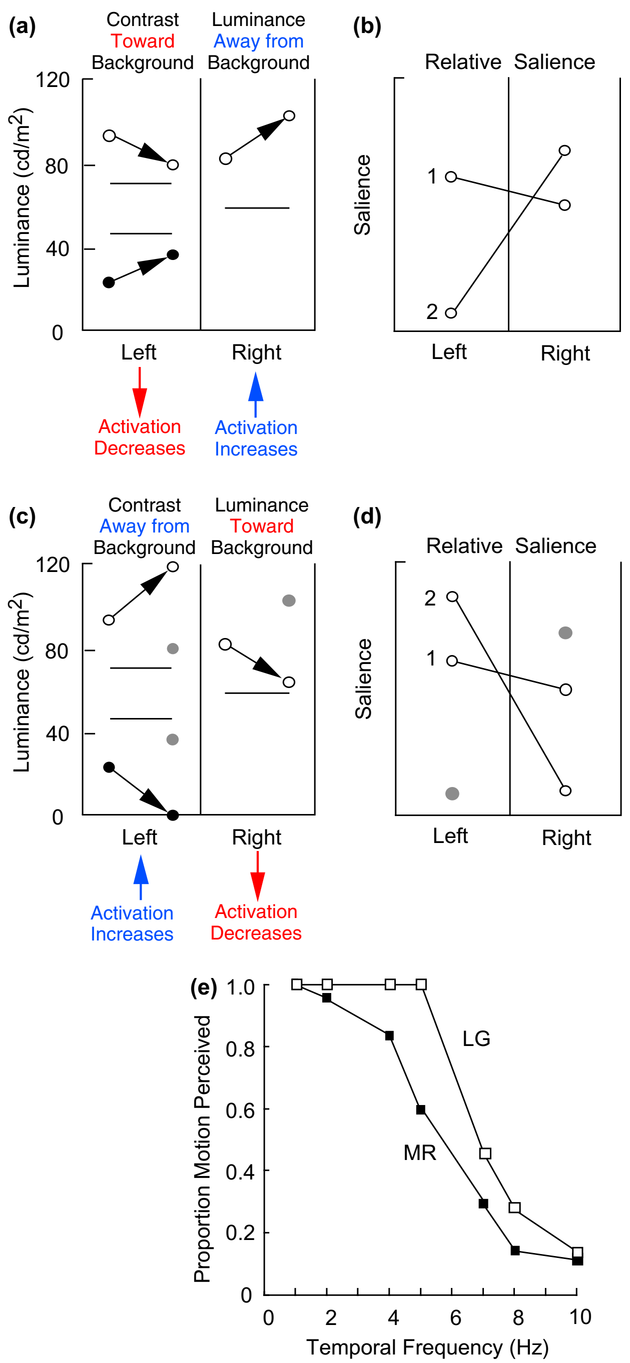

Fig. 6. Stimulus description and results for Experiment 4. (a) Graphical representation of luminance values for a split checkerboard/uniform-luminance stimulus from Experiment 1. The possibility of salience-based motion is illustrated in (b) by the left element being more salient during Frame 1 and the right element more salient during Frame 2. (c and d) Graphical representation of the split checkerboard/uniform-luminance stimulus tested in Experiment 4. Contrast and luminance values during Frame 2 were modified so that the checkerboard on the left always was more salient than the uniform-luminance element on the right (gray dots representing luminance and relative salience values before the stimulus from Experiment 1 was changed). (e) The proportion of trials that motion was perceived as a function of the temporal frequency of alternation of contrast and luminance values (motion was perceived even though there were no frame-to-frame changes in the location of the most salient element).

location with the most salient element (Blaser, Sperling, & Lu, 1999; Lu & Sperling, 1995a, 1995b, 2001; Mather & Anstis, 1995). This possibility, which is illustrated in Fig. 6a and b for a split checkerboard/uniform-luminance stimulus from Experiment 1, would mean that the checkerboard element on the left (when its contrast was high) was more salient than the uniform-luminance element on the right (when its luminance value was low). Then on the next frame, the uniform-luminance element on the right (when its luminance value was high) was more salient than the checkerboard on the left (when its contrast was low), and so on.

This third-order alternative was addressed by replacing the low contrast value of the checkerboard with a contrast value that was higher than its previously high contrast value, and the high luminance value of the uniform-luminance element with a luminance value that was lower than its previously low luminance value (the replaced values are indicated in gray in Fig. 6c and d). Following the salience assumption, the checkerboard element on the left would then be more salient than the uniform-luminance element on the right during every frame, so motion would not be perceived, if it depended on changes in the location that was most salient (because the most salient element never changed location).

6.1. Method

The stimuli were derived from the split checkerboard/uniform-luminance stimuli of Experiment 1. In the current experiment, the contrast of the checkerboard element alternated between 0.6 and 1.0 (rather than 0.6 and 0.4 in Experiment 1), and the luminance values of the uniform-luminance element alternated between 82.1 and 63.5 cd/m^2 (rather than 80.6 and 95.4 cd/m^2 in Experiment 1). The significance of these changes for the relative salience of the checkerboard and uniform-luminance elements is described above and illustrated in Fig. 6b and d. Subjects were tested during three blocks of 168 order-randomized trials (7 temporal frequencies with 24 repetitions).

6.2. Results

Contrast-to-luminance motion was perceived out to relatively high temporal frequencies (Fig. 6e), consistent with the texture contrast of the checkerboard element and the luminance of the uniform-luminance element changing in opposite background-relative directions. Motion would not have been perceived if it were based on a third-order, salience mechanism because the most salient element never changed location.

6.3. Additional results

In order to determine the temporal frequency limits of contrast-to-luminance apparent motion, we maximized the changes in contrast and luminance for the split checkerboard/uniform luminance stimulus. The Michelson contrast of the checkerboard element alternated between 1.0 (light checks: 117.0 cd/m^2; dark checks: 0 cd/m^2) and 0.2 (light checks: 70.2 cd/m^2; dark checks: 46.8 cd/m^2), and the uniform-luminance element alternated between 117.0 and 58.5 cd/m^2 (BRLC = 2.0). It was found then that motion could be perceived for temporal frequencies of up to 8.1 Hz for subject DN and 6.6 Hz for subject HH, clearly greater than the limit of 3–5 Hz for salience mapping (Lu & Sperling, 1995a, 2001).

6.4. Feature tracking

The perception of contrast-to-luminance motion in this experiment was unlikely to have been based on attentive feature tracking. There was neither a trackable feature nor a trackable change in salience for this stimulus. Measurements of the temporal frequency limits for attentive feature tracking have not been made for the kind of one-step, back-and-forth apparent motion studied in this article. However, Verstraten et al.'s (2000) evidence for three-step apparent motion suggests that the temporal frequency limits for the perception of contrast-to-luminance motion in the current experiment (6.6/8.1 Hz) were greater than would be expected on the basis of attentive feature tracking.

7. Experiment 5: First-order artifact?

Finally, we investigated the possibility that motion was perceived for the contrast-to-luminance stimuli through a strictly first-order motion mechanism. It was assumed in the preceding experiments that first-order information was eliminated for the checkerboard elements by matching their average luminance to the average luminance of their background. It remained possible, however, that the effective average luminance values for the checkerboard element and its background were mismatched because of nonlinearity in the integration of luminance values for the light and dark checks (Smith & Ledgeway, 1997). On this basis, the effective average luminance of the checkerboard elements (indicated in gray in Fig. 7c) could be different for its two, alternating contrast values, and both could be different from the effective average luminance of the checkerboard background. As a result, changes in the checkerboard's contrast toward the background contrast might be confounded with changes in its effective average luminance toward the effective average luminance of the background (as would changes away from the background during the next frame). Contrast-to-luminance motion therefore might have been based on a first-order mechanism responding to artifactual luminance changes for the left-hand, checkerboard co-occurring with actual luminance changes for the right-hand, uniform-luminance element (rather that a common first/second-order mechanism).

Although Papathomas, Gorea, and Chubb (1996) have devised a clever technique for establishing the effective luminance of texture-defined elements relative to luminance-defined elements, we have taken a different approach to ruling out the potential for artifactual first-order motion perception. This entailed reversing the potential confounding of the possible change in effective average luminance with the actual contrast change by making the luminance values of the light and dark checks of the checkerboard background greater than the luminance values of the light and dark checks of the checkerboard element. With this stimulus configuration, if there were changes in the checkerboard's effective average luminance, they would be away from the effective average luminance of the background. Changes in the checkerboard element's contrast would continue to be toward the contrast of the background (Fig. 7d–i).

When the change in luminance of the right-hand, uniform-luminance element is away from the background luminance (Fig. 7f), the counter-changing activation required for motion perception would not be established if motion depends on the change in the left-hand checkerboard's effective average luminance (activation then would increase at both locations). However, counterchange would be established, and motion perceived, if the activation change for the left-hand checkerboard results from its change in contrast (activation then would decrease at one location and increase at the other).

Conversely, when the change in luminance of the right-hand, uniform-luminance element is toward the background luminance (Fig. 7i), the counter-changing activation required for motion perception would be established, and motion perceived, if motion depends on the change in the checkerboard's effective average luminance (activation would then decrease at one location and increase at the other). However, counterchanging activation would not be established if the activation change for the left-hand checkerboard depends on the change in the checkerboard's contrast toward the background (activation then would decrease at both element locations).

7.1. Method

The split checkerboard/uniform-luminance stimulus tested in this experiment is detailed in Fig. 7d–f. The checkerboard half of the background had an average luminance of 77.5 cd/m^2 and a contrast of 0.1 (light checks: 85.3 cd/m^2; dark checks: 69.8 cd/m^2), and the uniform-luminance half of the background had a

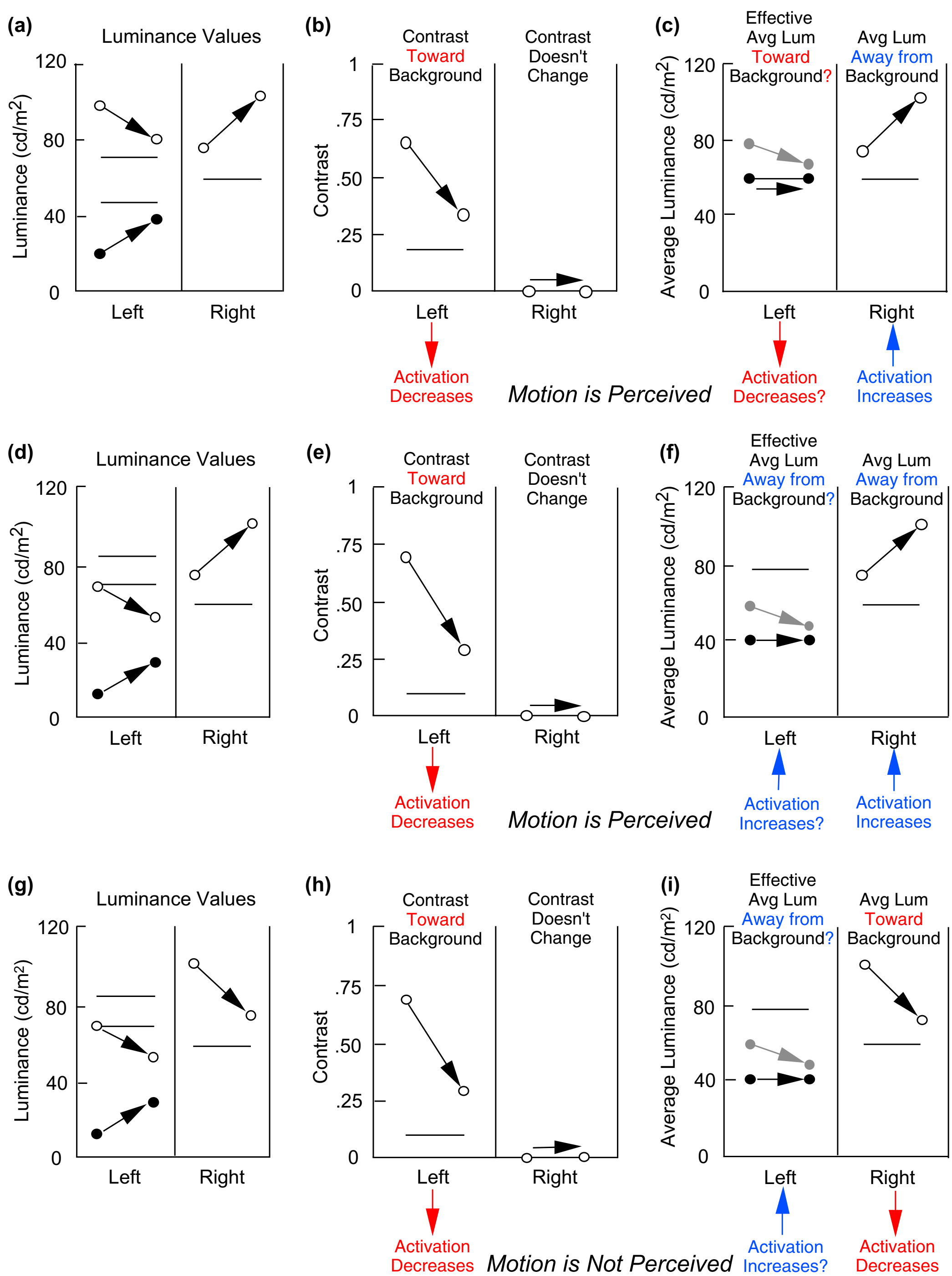

Fig. 7. Stimulus description and results for Experiment 5. Indicated are check-luminance (a, d, g), Michelson contrast (b, e, h), and average luminance (c, f, i) values for the checkerboard element and its checkerboard background, and the luminance values for the uniform-luminance element and its uniform-luminance background. Although the actual average luminance of the checks (indicated by black dots) is constant for the checkerboard, it was assumed for the purposes of this experiment that luminance is imperfectly averaged as a result of nonlinear summation (illustrated by light gray dots). It was found that motion is perceived for the stimulus depicted in (d–f) even though it could not have been based on a first-order mechanism. In addition, motion is not perceived for the stimulus depicted in (g–i), even though it would have been perceived if motion were based on a first-order mechanism (the latter assuming that there was a significant change in the effective luminance of the checkerboard elements when there contrast changed from one frame to the next).

luminance of 58.5 cd/m^2. The average luminance of the left-hand checkerboard element was 40.0 cd/m^2; its contrast alternated between 0.7 (light checks: 68.0 cd/m^2; dark checks: 12.0 cd/m^2) and 0.3 (light checks: 52.0 cd/m^2; dark checks: 28.0 cd/m^2). The uniform luminance of the right-hand element alternated between 74.7 and

101.3 cd/m^2 (BRLC = 0.9), either in the opposite background-relative direction to the contrast change of the left-hand checkerboard (Fig. 7d–f) or the same background-relative direction to the contrast change of the left-hand checkerboard (Fig. 7g–i). The temporal frequency of alternation was 1.9 Hz.

7.2. Results

Motion was perceived when the contrast and luminance changed in opposite background-relative directions (Fig. 7d–f). This could only have been based on a common first/second-order mechanism because the counter-changing activation required for motion perception would not have been present if it depended on changes in effective average luminance rather than changes in the contrast of the checkerboard element. This conclusion was reinforced by the absence of motion perception when the direction of luminance change was reversed for the right-hand, uniform-luminance element (Fig. 2g–i). In that case, when the luminance of the uniform-luminance element decreased toward the luminance of its background (decreasing activation), motion would have been perceived as a result of the change in effective average luminance of the left-hand checkerboard element away from its effective background luminance (increasing activation), if the effective average luminance were the basis for the perception of motion. Although it remained possible that the checkerboard element and its background were not perfectly matched in effective luminance, if there were mismatches they were too small to be the basis for first-order motion perception.

8. General discussion

The results of the experiments reported in this article are consistent with a common first/second-order motion mechanism that responds to activation changes at the two locations of an apparent motion stimulus, regardless of whether the activation changes are the result of changes in luminance, changes in texture contrast, or some combination of the two. Evidence was obtained for transitivity (the perception of apparent motion was inter-changeably affected by activationally equivalent luminance and contrast changes), local integration (the perception of apparent motion depended on the net activation change resulting from simultaneous background-relative luminance and background-relative contrast changes at the same element location), and inseparability (apparent motion was not perceivable through independent first- or second-order mechanisms when luminance and contrast co-varied at the same location). These results are inconsistent with Lu and Sperling's (1995, 2001) model, which argues for independent first- and second-order mechanisms. However, as indicated in the introduction, an important way in which the current experiments differ from those supporting independent mechanisms is that our apparent motion stimuli were composed of object-like elements with distinct boundaries defined by spatial differences in luminance and/or texture contrast. The existence of independent first- and second-order motion mechanisms is not ruled out for stimuli, like random cinematograms, for which object boundaries are not formed unless motion is perceived. In contrast with our results, evidence for transitivity is not obtained for random cinematograms when subjects detect shifts in blocks of randomly arranged luminance- and texture-defined elements (Mather & West, 1993), and evidence for local integration is not obtained when subjects detect motion direction for thin strips of interleaved luminance-modulated and contrast-modulated random dots (Scott-Samuel & Smith, 2000).

Cavanagh et al. (1989) have previously proposed an attribute-invariant common mechanism to account for the perception of mixed-attribute motion, including attributes other than luminance and texture contrast. Although they found that motion could be perceived between luminance-defined and texture-contrast-defined elements, they did not find evidence for the inter-changeability of luminance and contrast changes (i.e., transitivity); motion was perceived over larger inter-element distances for within- than between-attribute stimuli. This difference might have occurred because their dependent measure, the largest displacement for which motion could be seen, encouraged attentive feature tracking for within-attribute motion (when there were matching features to attentively track).

Our evidence for a common first/second-order mechanism is consistent with neurophysiological results indicating that motion sensitive neurons in V1, MT, and MST can respond to changes in luminance and as well as changes in texture contrast. A computational model for such neurons has been developed by Baloch et al. (1999). The evidence is also consistent with Gilroy and Hock's (2004) proposal that motion detection entails the detection of counter-changing activation, regardless of whether the activation changes are due to background-relative changes in luminance, texture contrast, or both. In the style of the Reichardt motion detector (Reichardt, 1961), their proposed motion detector is composed of a pair of subunits whose transient responses to changes in activation are multiplicatively combined. However, in contrast with the Reichardt detector (as well as Barlow & Levick's, 1965 inhibition-based motion detector), it is not necessary in the proposed model for directional selectivity to be established by delaying the response of one subunit prior to combining it with the response of the other subunit. Instead, directional selectivity is established by motion starting at the subunit that is excited by a decrease in its input activation and ending at the subunit that is simultaneously excited by an increase in its input activation. In further contrast with the standard Reichardt detector, the subtractive comparison of the outputs of detectors with opposing directional selectivity is not necessary to prevent motion from being signaled when the input activation to the two subunits simultaneously increases or simultaneously decreases. This is because motion is signaled in the proposed model only when input activation is changing in the opposite direction at the two subunits. A candidate neural mechanism for the proposed model is a receptive field with enmeshed OFF and ON subunits, like those observed for directionally selective complex cells in the visual cortex (Movshon, Thompson, & Tolhurst, 1978).

As a final note, the results reported in this article apply to discontinuously displaced objects, but counter-changing activation potentially can be the basis as well for perceiving the motion of continuously displaced objects. That is, when an object with greater than background luminance and/or texture contrast moves continuously from one location to the next, the luminance/contrast at the location the object had just occupied changes toward the background luminance/contrast, and at the same time, the luminance at the location the object now occupies changes away from the background luminance/contrast. Whether counter-changing activation is the basis for the perception of continuous object motion is the subject of future research.

References

Adelson, E. H., & Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America A, 2*, 284–299.

Albright, T. D. (1992). Form-cue invariant motion processing in primate visual cortex. *Science, 255*, 1141–1143.

Anstis, S. M., & Mather, G. (1985). Effects of luminance and contrast on direction of ambiguous apparent motion. *Perception, 14*, 167–179.

Baloch, A. A., Grossberg, S., Mingolla, E., & Nogueria, C. A. M. (1999). Neural model of first-order and second-order motion perception and magnocellular dynamics. *Journal of the Optical Society of America A, 16*, 953–978.

Barlow, H. B., & Levick, W. R. (1965). The mechanism of directionally selective units in rabbit's retina. *Journal of Physiology (London), 178*, 477–504.

Blaser, E., Sperling, G., & Lu, Z.-L. (1999). Measuring the amplification of attention. *Proceedings of the National Academy of Science, 96*, 11681–11686.

Cai, D., DeAngelis, G. C., & Freeman, R. D. (1997). Spatiotemporal receptive field organization in the lateral geniculate nucleus of cats and kittens. *Journal of Neurophysiology, 78*, 1045–1061.

Cavanagh, P. (1992). Attention-based motion perception. *Science, 257*, 1563–1565.

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

Chaudhuri, A., & Albright, T. D. (1997). Neuronal responses to edges defined by luminance vs temporal texture. *Visual Neuroscience, 14*, 949–962.

Clifford, C. W. G., & Vaina, L. (1999). A computational model of selective deficits in first and second-order motion processing. *Vision Research, 39*, 113–130.

Fleet, D. J., & Langley, K. (1994). Computational analysis of non-Fourier motion. *Vision Research, 34*, 3057–3079.

Geesaman, B. J., & Andersen, R. A. (1996). The analysis of complex motion patterns by form/cue invariant MSTd neurons. *Journal of Neuroscience, 16*, 4716–4732.

Gilroy, L. A. (2003). A transient mechanism for the perception of apparent motion. Dissertation, Florida Atlantic University.

Gilroy, L. A., & Hock, H. S. (2004). Detection of counter-changing contrast: second-order apparent motion without post-rectification motion energy analysis or salience-mapping/feature-tracking. *Journal of Experimental Psychology: Human Perception and Performance.*

Harris, L. R., & Smith, A. T. (1992). Motion defined by second-order characteristics does not evoke optokinetic nystagmus. *Visual Neuroscience, 9*, 565–570.

Hock, H. S., Gilroy, L., & Harnett, G. (2002). Counter-changing luminance: a non-Fourier, non-attentional basis for the perception of single-element apparent motion. *Journal of Experimental Psychology: Human Perception and Performance, 28*, 92–112.

Hock, H. S., Kogan, K., & Espinoza, J. K. (1997). Dynamic, state-dependent thresholds for the perception of single-element apparent motion: Bistability from local cooperativity. *Perception and Psychophysics, 59*, 1077–1088.

Johansson, G. (1950). *Configurations in event perception*. Uppsala: Almqvist & Wiksells Boktryckeri AB.

Johnson, A., & Benton, C. P. (1997). Speed discrimination thresholds for first and second-order bars and edges. *Vision Research, 37*, 2217–2226.

Johnson, A., & Clifford, C. W. G. (1995a). Perceived motion of contrast modulated gratings: predictions of the multi-channel gradient model and the role of full-wave rectification. *Vision Research, 35*, 1771–1783.

Johnston, A., & Clifford, C. W. G. (1995b). A unified account of three apparent motion illusions. *Vision Research, 35*, 1109–1123.

Kulikowski, J. J., & Tolhurst, D. J. (1973). Psychophysical evidence for sustained and transient neurons in the human visual system. *Journal of Physiology (London), 414*, 223–243.

Lappin, J. S., Tadin, D., & Whittier, E. J. (2002). Visual coherence of moving and stationary image changes. *Vision Research, 42*, 1523–1534.

Ledgeway, T., & Smith, A. T. (1994). Evidence for separate motion-detecting mechanisms for first- and second-order motion in human vision. *Vision Research, 34*, 2727–2740.

Lu, Z.-L., & Sperling, G. (1995a). Attention-generated apparent motion. *Nature, 377*, 237–239.

Lu, Z.-L., & Sperling, G. (1995b). The functional architecture of human visual motion perception. *Vision Research, 35*, 2697–2722.

Lu, Z.-L., & Sperling, G. (2001). Three-systems theory of human visual motion perception: review and update. *Journal of the Optical Society of America A, 18*, 2331–2370.

Mather, G. (1994). Motion detector models: Psychophysical evidence. In A. T. Smith & R. J. Snowden (Eds.), *Visual detection of motion* (pp. 117–143). London: Academic Press.

Mather, G., & Anstis, S. (1995). Second-order texture contrast resolves ambiguous apparent motion. *Perception, 24*, 1373–1382.

Mather, G., & West, S. (1993). Evidence for second-order motion detectors. *Vision Research, 33*, 1109–1112.

Movshon, J. A., Thompson, I. D., & Tolhurst, D. J. (1978). Receptive field organization of complex cells in the cat's striate cortex. *Journal of Physiology (London), 283*, 79–99.

Nishida, S. (1993). Spatiotemporal properties of motion perception for random-check contrast modulations. *Vision Research, 33*, 633–645.

O'Keefe, L. P., & Movshon, J. A. (1998). Processing of first- and second-order motion signals by neurons in area MT of the macaque monkey. *Visual Neuroscience, 15*, 305–317.

Olavarria, J. F., DeYoe, E. A., Knierem, J. J., Fox, J. M., & Van Essen, D. C. (1992). Neural responses to visual texture patterns in middle temporal area of the macaque monkey. *Journal of Neurophysiology, 68*, 164–181.

Pantle, A., & Sekuler, R. (1969). Contrast response of human visual mechanisms sensitive to orientation and direction of motion. *Vision Research, 9*, 397–406.

Papathomas, T. V., Gorea, A., & Chubb, C. (1996). Precise assessment of the mean effective luminance of texture patches—an approach based on reverse-phi motion. *Vision Research, 36*, 3775–3784.

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

Scott-Samuel, N. E., & Smith, A. T. (2000). No local cancellation between directionally opposed first-order and second-order motion signals. *Vision Research, 40*, 3495–3500.

Smith, A. T., & Ledgeway, T. (1997). Separate detection of moving luminance and contrast modulations: fact or artifact? *Vision Research, 37*, 45–62.

Stoner, G. R., & Albright, T. D. (1992). Motion coherence rules are form-cue invariant. *Vision Research, 32*, 465–475.

Strout, J. J., Pantle, A., & Mills, S. L. (1994). An energy model of interframe interval effects in single-step apparent motion. *Vision Research, 34*, 3223–3240.

Taub, E., Victor, J. D., & Conte, M. M. (1997). Nonlinear preprocessing in short-range motion. *Vision Research, 37*, 1459–1477.

Turano, K. (1991). Evidence for a common motion mechanism of luminance-modulated and contrast-modulated patterns: selective adaptation. *Perception, 20*, 455–466.

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

Verstraten, F. A. J., Cavanagh, P., & Labianca, A. T. (2000). Limits of attentive tracking reveal temporal properties of attention. *Vision Research, 40*, 3651–3664.

Victor, J. D., & Conte, M. M. (1992). Coherence and transparency of moving plaids composed of Fourier and non-Fourier gratings. *Perception and Psychophysics, 52*, 403–414.

Watson, A. B. (1986). Apparent motion occurs only between similar spatial frequencies. *Vision Research, 26*, 1727–1730.

Watson, A. B., & Ahumada, A. J. (1985). Model of human visual-motion sensing. *Journal of the Optical Society of America A, 2*, 322–341.

Werkhoven, P., Sperling, G., & Chubb, C. (1993). The dimensionality of texture-defined motion: a single channel theory. *Vision Research, 33*, 463–485.

Zhou, Y.-X., & Baker, C. L. (1993). A processing stream in mammalian visual cortex neurons for non-Fourier responses. *Science, 262*, 98–101.