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Multiplicative nonlinearity in the perception of apparent motion

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Abstract

Evidence is reported indicating that the perception of apparent motion is better predicted by the multiplicative combination of luminance changes at two element locations than by the sum or squared-sum of the luminance changes, or by the motion energy in the stimulus. Because the results were obtained with a stimulus for which motion was specified by simultaneous luminance changes, they support a Reichardt-style motion detector model, but without the asymmetrical delay specified by current versions. Motion direction in the modified model relies on asymmetrical stimulus information rather than asymmetrical delay. That is, one subunit of the detector responds to changes in luminance toward the background luminance (the start of the motion path), and the other to changes in luminance away from the background luminance (the end of the motion path).

1. Introduction

Despite the historical prominence of linear (Fourier) methods, experimental research has continued to uncover fundamental nonlinearities in the processing of visual information. One domain in which this has been of central importance is the perception of motion. Reichardt-style motion detector models specify that multiplicative nonlinearity is introduced when responses to luminance changes at different element locations are combined (Reichardt, 1961; van Santen & Sperling, 1985). Alternatively, Adelson and Bergen's (1985) motion energy detector introduces a squaring nonlinearity following the additive combination of responses to luminance changes at different locations. The experiments reported in this article distinguish between multiplicative and post-addition squaring nonlinearities in the perception of apparent motion.

The experiments are based on a generalized single-element apparent motion stimulus first described by Johansson (1950), who found that motion could be perceived between two simultaneously visible elements when their luminance values were varied sinusoidally, but 180° out-of-phase (i.e., the luminance increased for one element while it decreased for the other). In the current version, motion is perceived when the luminance values are discontinuously changed (Fig. 1a). The probability of motion perception increases when there are larger changes in luminance at each element location, and when element luminance values are more similar to the luminance of the background (Hock, Kogan, & Espinoza, 1997). [1] Standard apparent motion—when an element alternately appears at two different locations—is a special case in which the lower luminance value at each location is equal to the luminance of the background.

Hock, Gilroy, and Harnett (2002) have shown that the motion-specifying information in apparent motion stimuli is counter-changing luminance, simultaneous changes in luminance in opposite background-relative directions at two element locations. Motion begins at the element location where luminance changes toward the luminance of the background, and ends at the element location where luminance changes away from the

[1] This kind of luminance exchange also results in motion perception for repetitive stimuli in which motion direction is ambiguous. Hock, Park, and Schöner (2002) presented a long row of evenly spaced square elements with spatially alternating luminance values (both greater than the background luminance), and found that coherent unidirectional or oscillatory motion patterns were perceived when the luminance values of adjacent elements were exchanged during successive frames.

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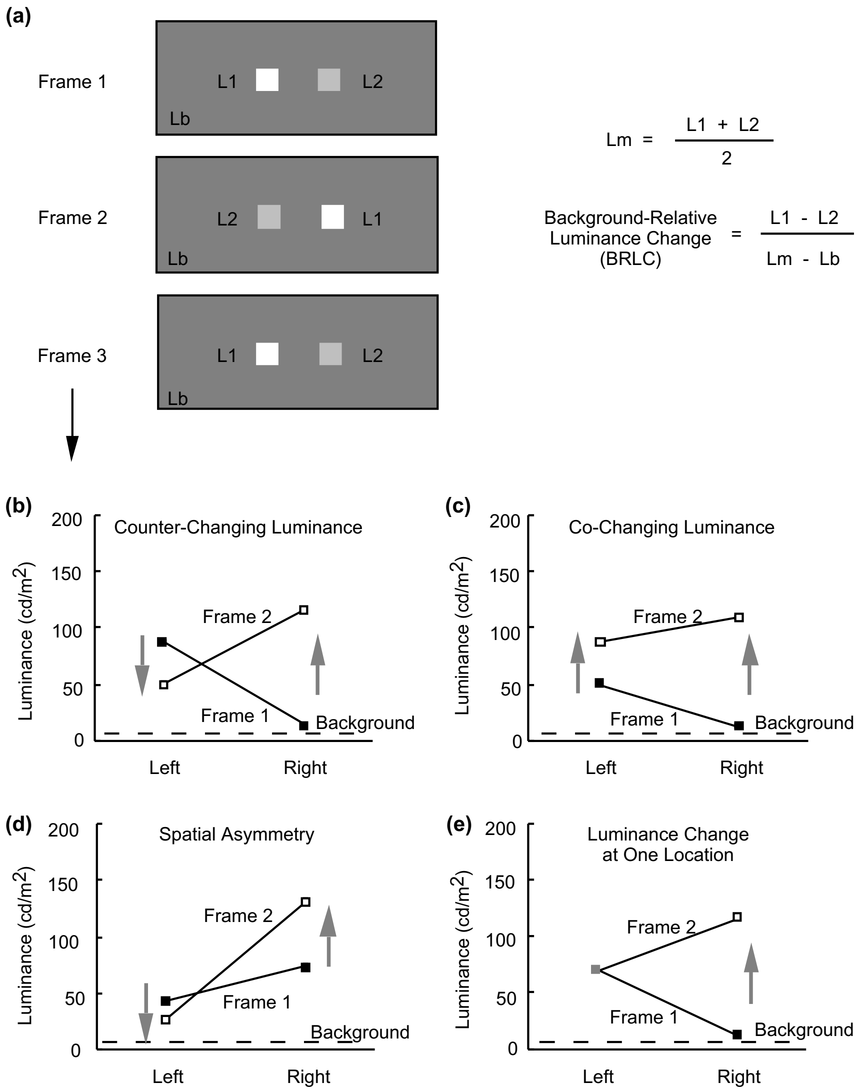

Fig. 1. (a) Illustration of generalized apparent motion stimulus and the formula for calculating background-relative luminance change (BRLC). (b) Stimulus for which there is counter-changing luminance at the two element locations; motion is perceived. (c) Stimulus for which there is co-changing luminance at the two element locations; motion is not perceived despite the presence of motion energy matched to that in the counter-changing condition. (d) Counter-changing stimulus with spatially asymmetric luminance values, ruling out attentive feature tracking and salience mapping as the basis for the perceived motion. (e) Motion is not perceived when luminance changes at one element location, despite the presence of motion energy.

luminance of the background. They created generalized apparent motion stimuli for which there was a small change in luminance at one location, and a much larger change in luminance at a nearby location (the time-averaged luminance was the same at both locations), so that the higher luminance value was first at one location, then at the other, back and forth during successive frames. Hock et al. found that motion was perceived when luminance changed in opposite directions at the two element locations (i.e., counter-changed), but never when luminance changed in the same direction (Fig. 1b and c). This was the case despite measurements of motion energy being equated in the two conditions. (The measurement procedure is described in Section 4.)

In addition to showing that the presence of motion energy is insufficient for apparent motion perception, Hock et al. showed that neither attentive feature tracking (Cavanagh, 1992) nor spatio-temporal changes in salience (Lu & Sperling, 1995) are required. The latter were eliminated as alternatives with a counter-changing stimulus for which there was no change in the location of the element with the higher luminance, and thus no trackable feature or change in the location of the most salient element (Fig. 1d). Motion nonetheless was perceived.

Motion, however, is not perceived when there is a luminance change at only one element location, even when motion energy is generated by frame-to-frame

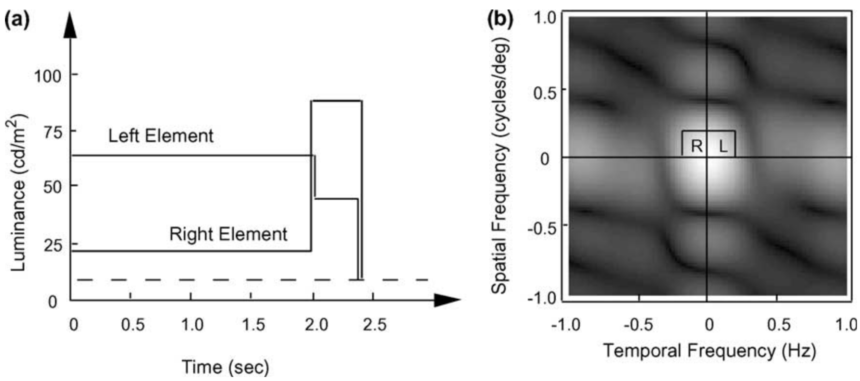

Fig. 2. (a) Graphical representation of a 2-frame apparent motion stimulus for which the BRLC is 0.4 for the left element and 1.4 for the right element. (b) Two-dimensional Fourier space/time transform for this stimulus. Superimposed on the Fourier transform are the areas over which motion energy is integrated for rightward (R) and leftward (L) motion directions. The calculated directional energy is R–L.

changes in the element location with the higher luminance (Fig. 1e). The requirement of a luminance change at *both* element locations suggests that the effects of the luminance changes are combined by multiplication (even if there is a high activation at one location, if there is no activation at the other, their product is zero—no motion signal). This would be consistent with the nonlinearity inherent in Reichardt-style motion detection models. In contrast, the effects of luminance change at different locations are combined by addition in Adelson and Bergen's (1985) motion energy detector; i.e., the luminance changes are detected by a single, space-time oriented filter that encompasses both locations. Given Hock et al.'s (2002) evidence that the perception of luminance-defined apparent motion is not based on the detection of motion energy, it was anticipated that the frequency with which motion is perceived would be better predicted by the multiplicative than the additive combination of luminance changes at the two element locations of the apparent motion stimulus (or by the square of the additive combination, as in Adelson and Bergen's model).

Experimental results consistent with multiplicative nonlinearity have been reported by van Santen and Sperling (1984, Experiment 3) for a multi-frame stimulus composed of five contiguous elements with sinusoidally modulated luminance, as well as 2-frame, random dot cinematograms (Morgan & Cleary, 1992) and phase-shifted sine gratings (Allik & Pulver, 1995; Georgeson & Georgeson, 1987; Morgan & Chubb, 1999). However, departures from multiplicativity were observed in the 2-frame experiments when low contrast cinematograms and gratings presented during one frame were masked by spatially overlapping, high contrast cinematograms and gratings presented during the other frame.

Multiplicative nonlinearity was tested in the current study with a stimulus composed of non-contiguous elements; small and large luminance changes occurred at different spatial locations, eliminating the possibility of masking (Fig. 1a). Although evidence for multiplicative nonlinearity would be consistent with Reichardt (1961) and elaborated Reichardt (van Santen & Sperling, 1985) detectors, these models also assume that the motion-specifying luminance changes at each location occur at different moments in time. They therefore introduce a delay in the activation of the initially stimulated subunit and multiply this delayed response by the activation of a subsequently stimulated subunit. An important feature of the current study was that the only possible motion-specifying stimulus information entailed *simultaneous*, counter-changing luminance at the two element locations. Both elements of the test stimulus were visible for 2 s, then their luminance values were simultaneously changed at the start of a 400 ms second frame (Figs. 1b and 2a). The delay required in order to combine the activational effects of the simultaneous luminance changes was zero, inconsistent with Reichardt-style detectors that are designed to detect sequential luminance changes. The purpose of the 2 s first frame was to introduce a long delay between the luminance increments occurring at the start of the first frame (when the pair of elements first appeared during a trial), and the luminance increment occurring at the start of the second frame. The time difference of 2 s was too long for motion to be perceived on the basis of a Reichardt detector with asymmetrical delay, so we could be confident that the perceived motion in this study was based on the simultaneous decreases and increases in luminance occurring at the start of the second frame. Evidence for the multiplicative combination of luminance changes at the two element locations therefore would be consistent with the nonlinearity of Reichardt-style motion detection, but without asymmetrical temporal delay.

2. Experiment 1

The magnitude of luminance change for each element was determined by its background-relative luminance change (BRLC); i.e., the difference between its high and low luminance values divided by the difference between its mean luminance and the luminance of the background (equation in Fig. 1a). Hock et al. (1997) determined that this ratio of luminance differences accounted for the independent effects of element luminance change, average luminance, and background luminance on the probability of motion perception. Multiplicativity would be indicated if motion is perceived approximately equally often when BRLC values for the two elements have the same product (e.g., 0.2/1.2 and 0.4/0.6). Additivity would be indicated if motion is perceived approximately equally often when BRLC values for the two elements have the same sum (e.g., 0.2/1.0, 0.4/0.8, and 0.6/0.6).

2.1. Method

Stimuli were presented with a Power Macintosh 7300/180 computer. Two simultaneously visible elements (small squares) were centered within a darker rectangular box (3.5° wide × 2.0° high; luminance, $L_b = 6.85$ cd/m^2), which in turn was centered in the screen of a Viewsonic 15GA monitor (screen luminance <0.001 cd/m^2). Two 6 × 12 min fixation lines were presented in the middle of the rectangle, one at the top, the other at the bottom. The elements each subtended a visual angle of 12 × 12 min and were 72 min apart (center-to-center) when viewed from a distance of 35.8 cm. (Viewing distance was maintained by a head restraint.)

Luminances were selected for both elements to give seven BRLC values: 0.2, 0.4, 0.6, 0.8, 1.0, 1.2, and 1.4 (Table 1). All 49 combinations of the seven BRLC values were tested. There were seven trials with equal BRLC values and 42 trials with unequal BRLC values at the two locations. When unequal, the smaller BRLC value was assigned to the left and right elements equally often. For half the trials, luminance values decreased for the left and increased for the right element (potentially resulting in rightward motion). The reverse was the case for the other half (potentially resulting in leftward motion).

The orthogonal combination of two motion directions and 49 pairings of BRLC values resulted in 98 distinctive trials, each repeated three times within blocks of 294 trials (order was randomized in sub-blocks of 98 trials). There were two blocks of trials during each of four testing sessions. Participants were instructed to fixate midway between the two squares with the aid of the fixation lines. After each trial, they indicated whether or not they perceived motion through the space between the squares anytime during the trial, and whether the motion was rightward or leftward. They pressed the spacebar if unsure of their response. The participants were an author (LG) and two undergraduate students at Florida Atlantic University. The latter were naïve with respect to the purpose of the experiment.

Table 1
Experiments 1 and 2: the BRLC values and their corresponding lower (L1) and upper (L2) luminance values; each pair of luminance values has a mean luminance of 55.0 cd/m^2

BRLC Value	L1 (cd/m^2)	L2 (cd/m^2)
0.2	50.25	59.75
0.3	47.75	62.25
0.4	45.25	64.75
0.5	43.00	67.00
0.6	40.50	69.50
0.7	38.25	71.75
0.8	35.75	74.25
1.0	31.00	79.00
1.2	26.00	84.00
1.4	21.25	88.75

The background luminance was 6.85 cd/m^2.

2.2. Results

An examination of the data indicated that when motion was perceived, it always was in the direction predicted by counter-changing luminance (from the element whose luminance changed toward the background to the element whose luminance changed way from the background), and further, that there were no systematic effects of leftward vs. rightward motion, or whether the smaller of the two BRLC values was assigned to the left or right element of the apparent motion stimulus. Consequently, the proportion of trials motion was perceived was collapsed into 28 points, 7 for stimuli with the same BRLC value and 21 for stimuli with different BRLC values for the two elements. It can be seen for each participant that the product of BRLC values (Fig. 3a) was a better predictor of motion perception than their sum (Fig. 3b) or squared-sum (Fig. 3c). This was quantitatively verified with best fitting Naka–Rushton functions (Naka & Rushton, 1966) obtained by varying the function's slope and semi-saturation value (i.e., the product, sum, or squared-sum of BRLC values for which motion is perceived for half the trials) until the residual variance was minimized. For each participant, the residual variance following the least squares fit was much greater for the additive and additive-squared than the multiplicative case (on average, 5.4 times greater). The results were thus consistent with nonlinearity in the perception of apparent motion resulting from the multiplication rather than post-addition squaring of the luminance changes occurring at each element location.

3. Experiment 2

Experiment 1 included BRLC values large enough for motion perception to be at ceiling for a large number of

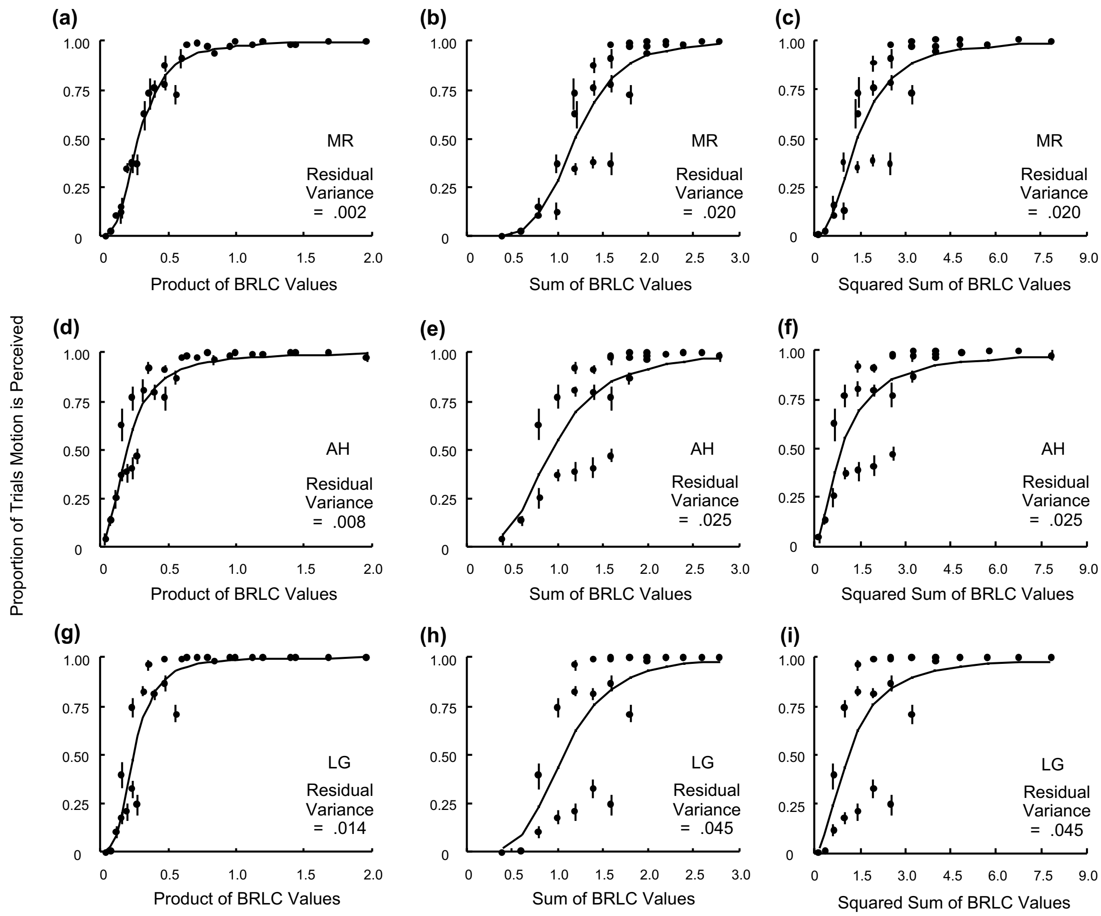

Fig. 3. Experiment 1: proportion of trials motion is perceived as a function of the product (a, d, g), sum (b, e, h), and squared-sum (c, f, i) of BRLC values at the two element locations. Error bars indicate one standard error above and below the mean proportion.

stimuli. The purpose of this experiment was to replicate the results of Experiment 1, but with ceiling effects minimized by reducing the range of BRLC values: 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, and 0.8 (luminance values in Table 1). With all other aspects as in Experiment 1 (including the participants), the product of BRLC values (Fig. 4a) again was a better predictor of whether motion would be perceived than the sum (Fig. 4b) or squared-sum (Fig. 4c) of BRLC values. The residual variance left unaccounted for was, on average, 3.2 times greater for the additive and additive-squared than the multiplicative prediction.

4. Discussion

The results indicate that motion perception for noncontiguous apparent motion stimuli is better accounted for by a detector which combines the responses to counter-changing luminance at two element locations by multiplication rather than addition (whether or not a post-addition squaring operation is included). Because the additive predictions were based on Adelson and Bergen's (1985) motion energy detector, we also examined the extent to which motion perception in the current experiments was predicted by the motion energy of the apparent motion stimuli. As in Hock et al. (2002), this was based on a measure of oriented energy derived from the space/time Fourier transformation of the 2-frame apparent motion stimulus. The measure, which is very similar to Dosher, Landy, and Sperling (1989) "directional power", entails the integration of motion energy over equal areas, starting at the origin of the upper-left and upper-right quadrants of the Fourier transform (as indicated in Fig. 2b). The integrations reflect the presence of rightward (R) and leftward (L) energy, and the difference between them (R–L) constitutes the directional energy (DE).

The integration range for calculating DE was between spatial frequencies of 0 and 0.2 cycles/deg (or 0 and −0.2 cycles/deg), and between temporal frequencies of 0 and 0.2 Hz. This range was selected to eliminate the contribution of the replications in the motion energy diagram that distinguish discontinuously from continuously displaced stimuli (Burr, Ross, & Morrone, 1986). Significantly for the current study, the sum of BRLC

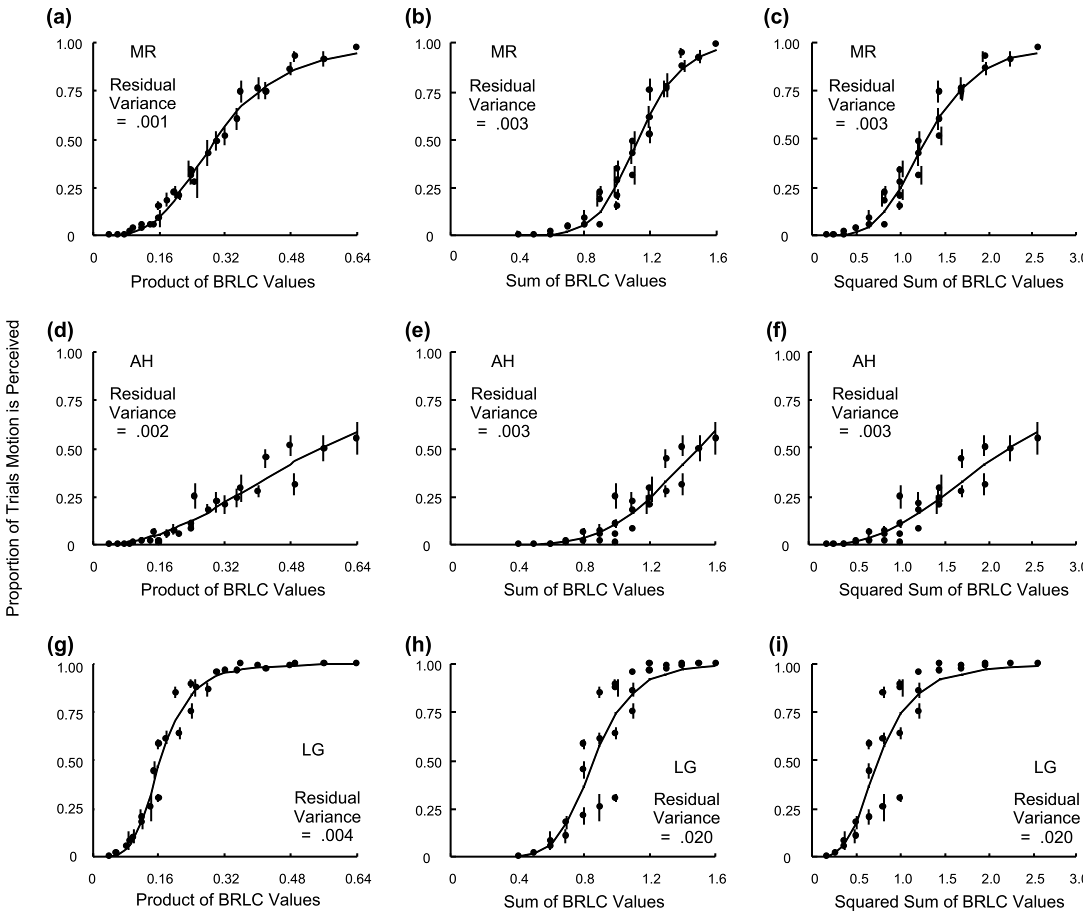

Fig. 4. Experiment 2: proportion of trials motion is perceived as a function of the product (a, d, g), sum (b, e, h), and the squared-sum (c, f, i) of BRLC values at the two element locations. Error bars indicate one standard error above and below the mean proportion.

values at the two element locations is linearly related to measured values of DE (this was the case regardless of the size of the integration range) and is also linearly related to the response of Adelson and Bergen's (1985) motion energy detector to the stimuli (as calculated through the direct implementation of their model). [2, 3] Hence, the predictability of motion perception based on motion energy is equivalent to that indicated for the sum of BRLC values (Figs. 3b and 4b).

To summarize, the multiplicative combination of background-relative luminance changes at the two element locations was a better predictor of motion perception than the sum or squared-sum of luminance changes, the motion energy in the stimulus, or the response calculated with Adelson and Bergen's (1985) motion detector model. The results thus confirm Hock et al.'s (2002) conclusion that the perception of apparent motion is not based on the detection of motion energy, and provide evidence for multiplicative nonlinearity in the perception of apparent motion. Although the latter was consistent with Reichardt-style motion detection, motion in the current study was specified by *simultaneous* changes in luminance toward and away from the background luminance. As discussed earlier, motion specification by simultaneous luminance change is inconsistent with the asymmetrical temporal delay inherent in the standard Reichardt model (and equivalently, the delay filter introduced in the elaborated Reichardt model). The temporal delay allows for the multiplicative combination of responses to spatially separated luminance changes occurring *at different times*, and in addition, establishes the directional selectivity of the motion detector; i.e., motion starts at the subunit with the delay and ends at the "undelayed" subunit. Alternatively, Hock et al. (2002) have proposed a version of the Reichardt model that is responsive to counter-changing luminance. That is, it is based on the principle that motion-specifying information for noncontiguous apparent motion stimuli is

[2] The sum of BRLC values at the two element locations also is linearly related to Clifford and Vaina's (1999) measure of directional energy: (R – L)/(R+L).

[3] We thank David Nichols for implementing Adelson and Bergen's (1985) motion energy detector.

carried by luminance changes occurring at different spatial locations, but *at the same time*. This simultaneity eliminates the need for temporal delays before the responses of pairs of detecting subunits to spatially separated events are combined. Moreover, directional selectivity is determined in Hock et al.'s model, not by which of the pair of subunits "carries" the delay, but by which of the pair of subunits responds to luminance changes toward the background luminance (the start of the motion path) and which responds to luminance changes away from the background luminance (the end of the motion path). That is, motion direction depends on asymmetrical stimulus information rather than asymmetrical delay.

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