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The Line Motion Illusion: The Detection of Counterchanging Edge and Surface Contrast

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A version of the line motion illusion (LMI) occurs when one of two adjacent surfaces changes in luminance; a new surface is perceived sliding in front of the initially presented surface. Previous research has implicated high-level mechanisms that can create or modulate LMI motion via feedback to lower-level motion detectors. It is shown here that there also is a non-motion-energy, feedforward basis for LMI motion entailing the detection of counterchange, a spatial pattern of motion-specifying stimulus information that combines changes in edge contrast with oppositely signed changes in background-relative surface contrast. It was concluded that (1) in addition to LMI motion, edge/surface counterchange could be the basis for perceiving continuous object motion, (2) counterchange detection is the likely basis for third-order motion perception (Lu & Sperling, 1995a), and (3) motion energy and counterchange mechanisms could be composed of different arrangements of the same spatial and temporal filters, the former detecting motion at a single location, the latter detecting the motion path between pairs of locations.

Keywords: motion, line motion illusion, counterchange, edges and surfaces, morphing

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The standard version of the line motion illusion (LMI) occurs when a square is presented; sometime later, a bar is presented adjacent to it (Figure 1a). Although the entire bar is presented simultaneously, motion is perceived away from the square, across the space occupied by the bar. It appears as if a surface is continuously sliding in front of the background when the bar is presented, and as if a surface is continuously "pulling back" to reveal the background when the bar is removed (Figure 1c).

Most accounts of LMI motion perception have proposed that is determined by such high-level mechanisms as attention, impletion/morphing, and grouping/parsing. For Hikosaka, Miyauchi, and Shimojo (1993a, 1993b, 1993b), LMI motion is induced by a gradient of attention-speeded processing that spatially spreads from the attention focused on the initially presented square. Because attention decreases with increasing distance from the square, changes in bar luminance near the square are detected before they are detected further from the square. Motion would begin where the luminance change is first detected and end where it is detected soon afterward. Attentionally tracking a feature (Cavanagh, 1992), say an edge, from the initially presented square to the far end of the subsequently presented bar, also could result in the perception of LMI motion. It also is thought that LMI motion can result from impletion/morphing processes that create perceptual continuity by "filling in" detected discontinuities in location or shape with continuous motion (Downing & Treisman, 1997; Holcombe, 2003; Tse, Cavanagh, & Nakayama, 1998), and further, that the direction of the motion is determined by prior operations that group the bar with one adjacent surface and parses it from others (Tse et al., 1998). All of the above could create or modulate LMI motion by providing feedback to lower-level motion detectors.

The experiments reported in this article determined whether there also is a feedforward basis for LMI motion that does not require the mediation of these higher-level mechanisms. It was anticipated that the to-be-detected, motion-specifying stimulus information would entail changes in the fundamental properties of objects, their surfaces and boundaries, rather than "objectless" first- and second-order motion energy (Sperling & Lu, 1998).[1] The detection of LMI motion therefore would be consistent with their third-order system for the perception of object motion; i.e., motion based on attentionally modifiable changes in salience/activation at different spatial locations (Lu & Sperling, 1995b; Ho, 1998; Blaser, Sperling, & Lu, 1999; Lu & Sperling, 2001).

It will be shown that changes in edge contrast (the difference in luminance at the boundary separating two surfaces), and simultaneous changes in surface/background contrast (i.e., the difference in luminance between a surface and its background) are the stimulus events that specify LMI motion. The proviso is that the changes in contrast must be opposite in sign. That is, edge or

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[1] In Lu and Sperling's (1995a) three-systems theory, first-order motion entails changes in the spatial distribution of luminance, and second-order motion entails changes in the spatial distribution of luminance contrast, both irrespective of the shape of the objects that vary in luminance or contrast.

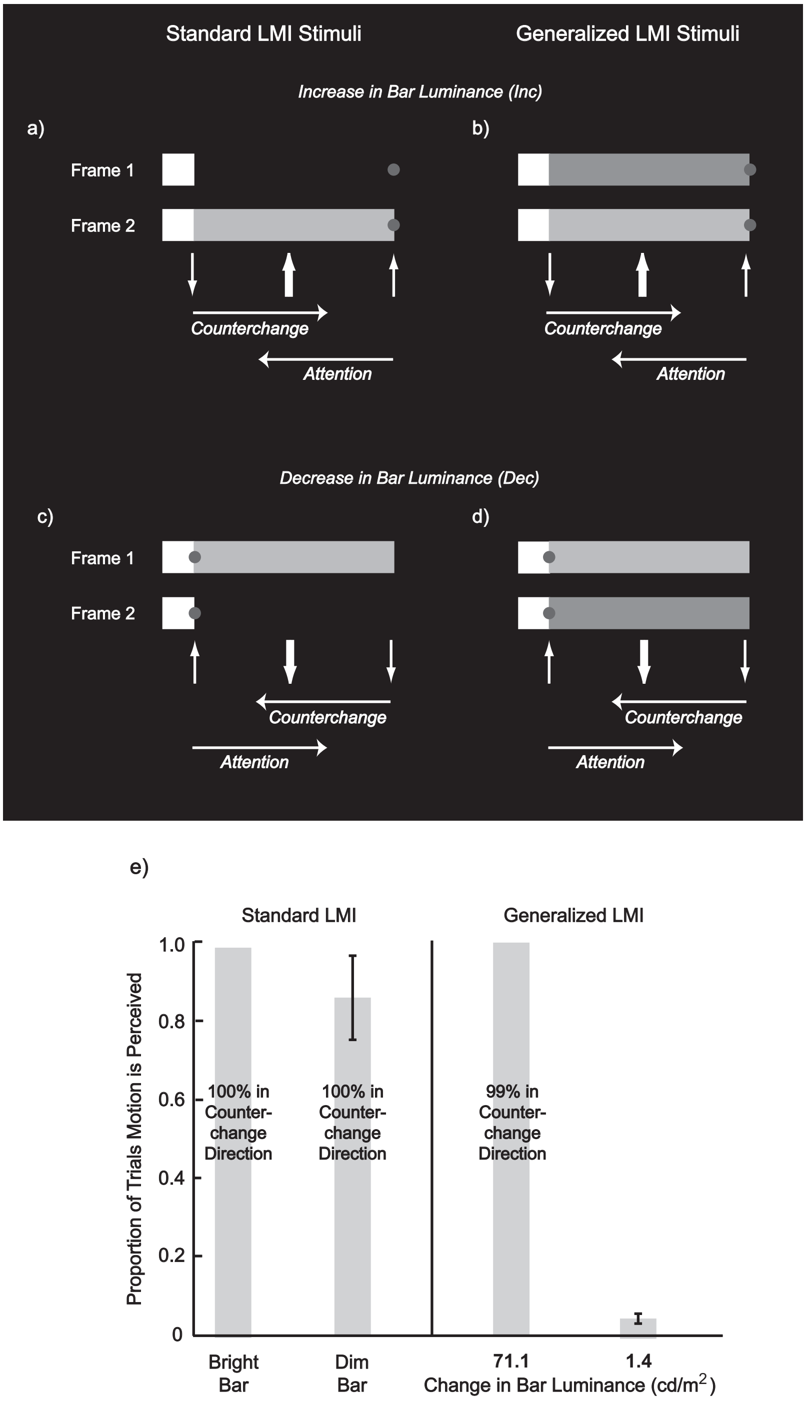

Figure 1. Experiment 1: (a–d) Standard and generalized stimuli for the line motion illusion (LMI). Although small fixation dots were presented equally often on the left edge, right edge, and in the center of the bar for every stimulus, they are shown here only in the locations for which attention-determined LMI motion (because of gradients of attention-speeded processing or attentive tracking) would be in the direction opposite to the direction of counterchange-determined motion. Both directions are indicated by horizontal arrows. The direction of the counterchange-specified motion is determined by oppositely signed changes in edge contrast and surface-to-background luminance contrast (or alternatively, oppositely signed changes in edge contrast). Changes in the bar's contrast with the background are indicated by thick vertical arrows. Changes in contrast at the bar's edges are indicated by thin vertical arrows. (e) The proportion of trials during which LMI motion was perceived, averaged over the three participants; the results for luminance increments and decrements are combined (the gray bars). The error bars indicate ±1 *SEM*. Superimposed on the gray bars is the percentage of the motion-perceived trials for which motion was in the counterchange-specified direction.

surface/background contrast must decrease at one location, specifying the start of the motion, and surface/background or edge contrast must increase at a second location, specifying the end of the motion. In addition, it will be argued that the detection of these changes in contrast are likely to constitute the informational basis for the perception of continuous object motion. This would be consistent with Gibson's (1968) assertion that motion is specified by a spatial pattern of change rather than by sequential changes in retinal location.

Evidence that motion can be specified by patterns of change has been reported for the perception of apparent motion by Hock, Gilroy, and Harnett (2002). They showed that apparent motion is perceived when there are oppositely signed changes in luminance contrast for two nonadjacent surfaces. Motion begins at the surface where there is a decrease in luminance relative to that of the background and ends at the surface where there is an increase in background-relative luminance contrast. This evidence for the detection of counterchanging luminance contrast was obtained with *generalized* apparent motion stimuli (Hock, Kogan, & Espinoza, 1997; Johansson, 1950), stimuli for which motion is perceived between pairs of nonadjacent surfaces that remain simultaneously visible while they change in luminance. (Standard apparent motion is a special case in which one of the alternating luminance values for each surface is equal to the luminance of the background. As a result, a surface disappears at one location and reappears at another.) Hock et al. (2002) showed that neither the detection of motion energy (Adelson & Bergen, 1985) nor the tracking of a stimulus feature over time by shifting attention from one location of the feature to another (Cavanagh, 1992) are necessary for the perception of generalized apparent motion.[2]

These results for a pair of nonadjacent surfaces suggest that counterchange detection is a viable mechanism for the perception of LMI motion for a pair of adjacent surfaces. Motion can be perceived between pairs of simultaneously visible, nonadjacent surfaces when oppositely signed changes in luminance contrast occur at the same time. Neither changes in the location occupied by a surface nor sequential changes in luminance are necessary for the perception of motion. This is apt for LMI stimuli. When an unchanging surface is continuously present, and an adjacent surface appears, disappears, or changes in luminance, neither of the surfaces changes their location, and whatever the stimulus information that is responsible for LMI motion perception, it need not be sequential. The experiments reported in this article therefore determined whether the counterchange principle, first observed for nonadjacent surfaces, also applies to the LMI motion perceived for adjacent surfaces.

Investigating the line motion illusion is challenging because there are many potential contributions to the perception of motion. In addition to identifying the stimulus information whose detection provides a feedforward basis for the perception of LMI motion, the experiments that follow also determine whether the perception of LMI motion requires gradients of attention-speeded processing (Hikosaka et al., 1993a, 1993b), attentive tracking (Cavanagh, 1992), exogenously oriented attention (Posner, 1980), impletion/morphing "filling in" processes that create continuity when there are discontinuous changes in luminance and/or shape (Downing & Treisman, 1985; Holcombe, 2003; Tse et al., 1998), or the detection of motion energy (Adelson & Bergen, 1985). How parsing/grouping (Tse et al., 1998) affects LMI motion perception is the subject of a forthcoming article (Hock & Nichols, in preparation).

Generalized Line Motion Stimuli

In the standard version of the LMI stimulus, the square appears to continuously change its global shape by expanding into new spatial locations upon the presentation of the bar (Figure 1a) and contracting back to its initial locations upon the removal of the bar (Figure 1c). This "morphing" of global shape (Holcombe, 2003; Tse et al., 1998), though perhaps sufficient for LMI motion when a surface suddenly appears or disappears, is not necessary for its perception. This is because LMI motion is perceived for generalized LMI stimuli even though changes in global shape do not occur; the bar always is visible and only its luminance changes, as in Figures 1b and 1d. (Analogous to apparent motion stimuli, the standard LMI stimulus is a special case of the generalized LMI stimulus for which one of the luminance values of the bar equals the background luminance.) The motion perceived for the generalized LMI stimulus is phenomenologically similar to the motion perceived for standard LMI stimuli. It appears as if a new surface is moving in front of and covering the initially presented surface when the bar's luminance increases, and as if the initially presented surface is "pulling back" to reveal the surface behind it when the bar's luminance decreases. (See supplemental Figures 1b and 1d in the online supplemental materials.)

The perception of motion for generalized LMI stimuli also dispels the argument that LMI motion is indistinguishable from classical apparent motion (Downing & Treisman, 1997). There are no changes in location for these stimuli, and any inference of motion from a rapid sequence of events can easily be eliminated by simultaneously presenting the square and the bar for an indefinitely long period of time before there is a change in bar luminance. LMI motion is perceived regardless of this duration.

Experiment 1

In addition to providing initial evidence that LMI motion can result from the detection of counterchange, this experiment determined whether high-level morphing can produce LMI motion that continuously "fills in" discontinuous changes in shape (Holcombe, 2003; Tse et al., 1998). It also showed that exogenously oriented attention is not necessary for the perception of LMI motion and

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[2] The possibility that apparent motion between two simultaneously visible, nonadjacent surfaces depends on the detection of motion energy was ruled out with stimuli for which luminance increased unequally for the two surfaces such that there was a change in the location of the surface with the higher luminance (i.e., there was a small increase in luminance for what initially was the lighter of the two surfaces, and a much larger increase in luminance for what initially was the darker of the two surfaces). There is motion energy for such stimuli, but motion is not perceived because there is no counterchange. The possibility that the motion perceived between two simultaneously visible surfaces depends on attentive tracking (Cavanagh, 1992) was ruled out with stimuli for which the lighter of two nonadjacent surfaces always remained at the same location, so there were no trackable features. Motion nonetheless is perceived because of the presence of counterchange when luminance decreases for the darker surface and increases for the lighter surface, or vice versa.

confirmed earlier reports that attentional gradients and attentive tracking also are not necessary for the perception of LMI motion.

Counterchange

As illustrated in Figures 1a through 1d, changes in the bar's luminance create changes in edge contrast and changes in surface-to-background luminance contrast for both the standard and generalized versions of the LMI stimulus. When the bar's luminance increases, edge contrast decreases at the square/bar boundary, the bar's contrast with the background increases, and edge contrast increases at the far end of the bar. Counterchange-determined motion would be from the decrease to the increase in contrast; it is rightward in Figures 1a and 1b. When the bar's luminance decreases, edge contrast increases at the square/bar boundary, the bar's contrast with the background decreases, and edge contrast decreases at the far end of the bar. Counterchange-determined motion therefore is leftward in Figure 1c and 1d.

Morphing

As indicated previously, the fact that motion can be perceived for generalized LMI stimuli indicates that morphing, the "filling in" of detected changes in the shape of LMI stimuli with a moving surface (Holcombe, 2003; Tse et al., 1998), is not necessary for the perception of LMI motion. This is because motion can be perceived for generalized LMI stimuli, stimuli for which there are no changes in shape to detect. Although morphing is not necessary, it is possible that it is sufficient for LMI motion perception. To test this, we included standard LMI stimuli in this experiment for which the bar was very dim. Changes in edge and surface-to-background contrast were minimal for this stimulus, so if LMI motion were perceived, it would be attributable to morphing rather than the detection of counterchange.

Attention

Hikosaka et al. (1993a, 1993b) have proposed that LMI motion is the result of a gradient of attention-speeded processing that emanates from the perceiver's locus of attention. For standard LMI stimuli, the gradient would spread from the initially presented square such that parts of the bar that are closer to the square receive more attention, and therefore are processed faster than parts of the bar that are further from the square. Motion would be perceived because the more quickly processed parts of the bar reach threshold before the more slowly processed parts. Another possibility is that motion is perceived as a result of the perceiver shifting attention during the course of tracking a feature from one location to another (Cavanagh, 1992). Such could be the case for the standard version of the LMI stimulus, for which a feature, like an edge, can be attentionally tracked from the boundary of the initially presented square to the far boundary of the subsequently presented bar.

The dependence of LMI motion on either a gradient of attention-speeded processing or attentive tracking has been challenged by the observation that motion is perceived toward the square when the bar is removed, as in Figure 1c. If attention were focused on the square, attention-determined motion would be in the opposite direction, away from the locus of attention (Downing & Treisman, 1997; Tse & Cavanagh, 1995). The location of the perceiver's locus of fixation/attention was varied in this experiment in order to further assess whether attentional gradients or attentive tracking are necessary for the perception of LMI motion. Attention-determined LMI motion would be indicated if motion were perceived away from the fixation dots in Figure 1. For these fixation locations, the attention-determined motion direction would be opposite to the motion direction determined by counterchange.

Finally, Shimojo, Miyauchi, and Hikosaka (1997) have shown that exogenously oriented attention (attention attracted to a location by a transient change in stimulation) is sufficient to create the perception of LMI motion. That is, when attention is attracted to where one end of a bar is about to be presented, LMI motion is perceived away from that end when the bar is presented. In this experiment we show that exogenously oriented attention is not necessary for LMI motion perception. To do so, we eliminated the possibility that the appearance of the fixation dot would serve as an exogenous orienting cue. This was done by keeping the fixation dot continuously present in the same location in the center of the screen, whether an LMI stimulus was present or not (the stimulus was shifted relative to the unchanging fixation dot in order for the fixation dot to be aligned with different stimulus locations). Participants were instructed to fixate and maintain attention on the fixation dot. They presumably did so, but it also is possible that their attention was oriented elsewhere while they maintained fixation (Posner, 1980). That is, an exogenous orienting cue, say the appearance of the square, might have attracted their attention when the first frame of the LMI stimulus was presented. If so, perceived motion would be away from the location of the square, regardless of whether there was an increase or decrease in bar luminance.

Method

In this and the remaining experiments, stimuli centered on the screen of an NEC MultiSync FP955 monitor were viewed from a distance of 30 cm, which was maintained with a head restraint. Each trial was composed of a 2,000-ms first frame and a 400-ms second frame. The stimuli varied with respect to whether: (1) they were standard or generalized, (2) the square was to the left or right of the bar, (3) the bar's luminance increased or decreased (for the standard version, the lower luminance value corresponded to the background luminance), (4) the luminance changes of the bar were large or small, and (5) the fixation dot was on the left edge, center, or right edge of the bar. The orthogonal combination of these variables created 48 distinct trials, each of which was repeated three times to form blocks of 144 order-randomized trials.

The square ($1 \times 1°$; luminance $= 89.3$ cd/m^2) and bar ($1 \times 4°$; variable luminance) were lighter than the dark background (0 cd/m^2). The bar's luminance changed between 0 and 75.4 cd/m^2 or between 0 and 4.3 cd/m^2 for the standard LMI stimuli, and between 4.3 and 75.4 cd/m^2 or between 4.3 and 5.7 cd/m^2 for the generalized LMI stimuli. For both versions, the luminance of the bar always was discriminable from the luminance of the square. The location of the stimulus was shifted from trial to trial in order to maintain the constant central location of the fixation dot.

Participants. Eleven students at Florida Atlantic University participated in up to three of the five experiments (three in Experiments 1, 2, 3, and 5; four in Experiment 4). All had normal or corrected-to-normal vision, and all were naïve with respect to the purposes of the experiments.

Procedure. The 3 participants in this first experiment were tested on three blocks of trials. They were instructed to maintain their attention at the fixation dot during the entire block of 144 trials. After each trial, they first indicated whether or not they perceived motion and, if they did, whether the direction of the motion was rightward or leftward.

Results

Differences in the frequency of LMI motion perception between trials with increased and decreased bar luminance were not statistically significant in this experiment or the experiments that follow. The results for increases and decreases in bar luminance are therefore combined within each experiment.

With one exception, motion perception in Experiment 1 was at ceiling or floor, regardless of fixation location, the one exception occurring for 1 participant, who perceived motion for 65% of the standard LMI trials with the dim bar. There was little effect of fixation location for these trials, so the data were combined for the three fixation locations, and for trials in which the square was to the left or right of the bar. The combined data, averaged over the 3 participants, is presented in Figure 1e (for each participant there were 108 trials for each of the four conditions). The interaction between stimulus type (standard vs. generalized) and the magnitude of the stimulus change (large vs. small) was statistically significant, $F(1, 2) = 62.51$, $p < .02$, indicating that the size of the luminance change had a greater effect for generalized compared with standard LMI motion.

Counterchange. Motion always was perceived for the standard LMI stimuli when the bar was relatively bright, and it almost always was perceived for the generalized LMI stimuli when there was a large change in bar luminance. For all these stimuli, LMI motion almost always was in the direction consistent with counterchange, although it could not be determined in this experiment whether the motion was due to the detection of counterchanging edge and surface-to-background contrast or the detection of counterchanging edge contrast on the opposite ends of the bar.

Morphing. Motion was not perceived for the generalized LMI stimuli when the change in bar luminance was barely detectable, likely because the changes in edge and surface-to-background contrast were too small to activate motion detectors responsive to counterchange. However, changes in edge and surface-to-background contrast also were very small for the standard LMI stimuli with very dim bars, yet LMI motion almost always was perceived. Indeed, motion was perceived for the standard LMI stimuli no matter how dim we made the bar, so long as it was detectable. It could be concluded that in the absence of counterchange detection, morphing motion that continuously "fills in" detected discontinuities in shape can be sufficient for the perception of LMI motion (Holcombe, 2003; Tse et al., 1998).

Attention. Motion almost always was perceived toward the locus of fixation/attention for the stimuli illustrated in Figure 1. It would have been perceived away from these fixation locations if it were the result of either attentive tracking or a gradient of attention-speeded processing that spreads from the locus of fixation/attention. Indeed, regardless of where the perceiver was attending, attention-determined motion would have been in the same direction, away from the locus of attention, regardless of whether the bar was presented or removed, or whether its luminance was increased or decreased. The same would be the case if attention were exogenously attracted to a stimulus feature other than the fixation dot; LMI motion always would be away from the location of this feature. The evidence that the perceived LMI motion was in counterchange-determined directions (opposite directions for increases and decreases in bar luminance) rather than attention-determined directions (the same direction for increases and decreases in bar luminance) confirmed that neither gradients of attention, attentive tracking, nor exogenous orientation of attention are necessary for the perception of LMI motion.

Experiment 2

We have proposed that there is a feedforward basis for LMI motion perception that entails the detection of motion-specifying stimulus events and, therefore, does not require the mediation of higher-level mechanisms. However, Downing and Treisman (1997) have claimed the opposite. They argue that the perception of LMI motion does not involve motion detection, and is instead the result of a high-level impletion process that modifies discontinuous stimulus changes ". . . in terms of the most likely real world state of affairs" (p. 768). From this point of view, when a discontinuous change in surface luminance is detected for generalized LMI stimuli, an impletion process would smooth the discontinuity by creating the perception of continuous LMI motion. Little if any motion was perceived for the generalized LMI stimulus in Experiment 1 when there was a small change in bar luminance, but this result was not sufficient to argue for or against impletion because the luminance change was barely detectable. In this experiment, a range of luminance changes was introduced, all of which were clearly detectable (confirmed by multiple observers). If LMI motion were based on impletion, it would have been perceived for all of these changes in bar luminance.

Method

Using generalized LMI stimuli, the magnitude of the change in bar luminance was varied while the bar's average luminance was kept approximately constant. The luminance of the square was 96.4 cd/m^2, and the bar luminance varied between 28.2 and 31.4, 24.3 and 36.1, 21.4 and 39.4, or 18.7 and 44.2 cd/m^2. The orthogonal combination of: (1) the size of the change in bar luminance, (2) whether the square was to the left or right of the bar, (3) whether the bar's luminance increased or decreased, and (4) whether the fixation dot was on the left edge, center, or right edge of the bar, created 48 distinct trials, each of which was repeated three times to form blocks of 144 order-randomized trials. Three participants were tested on three blocks of these 144 trials (for each participant there were 108 trials in each of the four luminance-change conditions).

Results

The proportion of trials for which LMI motion was perceived, averaged over the 3 participants, increased with the size of the change in bar luminance (Figure 2). This effect was statistically significant, $F(3, 6) = 26.96$, $p < .001$. The motion was in the

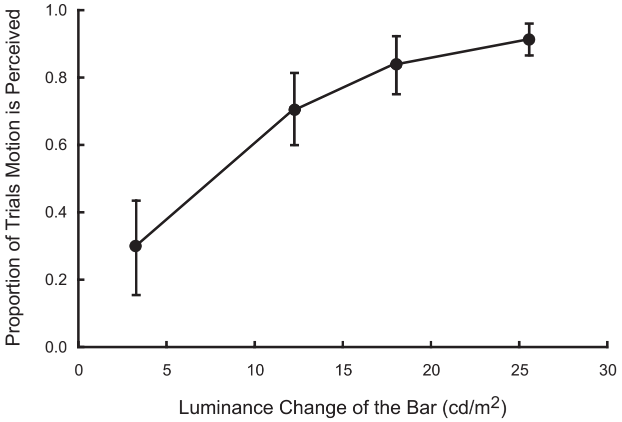

Figure 2. Experiment 2: The proportion of trials during which LMI motion was perceived as a function of the size of the luminance change for the bar (the results for luminance increments and decrements are combined). The results are averaged over the three participants. Error bars indicate ±1 *SEM*.

counterchange-specified direction for an average of 89% of the motion-perceived trials (the magnitude of the luminance change did not significantly affect the frequency of with which LMI motion was perceived in the counterchange direction, $F < 1.0$).

If impletion were necessary for the perception of LMI motion, the frequency with which it was perceived would not have depended on the magnitude of the luminance change. Impletion-determined LMI motion would have been perceived equally often for all the magnitudes of luminance change in this experiment because they all were detectable, and therefore sufficient for the initiation of a "filling in" impletion process that would create the perception of LMI motion. Instead, the results were consistent with LMI motion perception being based on counterchange detection mechanisms whose activation depends on the magnitude of motion-specifying changes in edge and surface contrast.

Experiment 3

The results of Experiments 1 and 2 were consistent with the perception of LMI motion being based on the detection of counterchange. One possibility is that the counterchange entails a change in edge contrast combined with an oppositely signed change in surface-to-background contrast for the bar. Another is that it entails oppositely signed changes in edge contrast on the two sides of the bar. Although the latter remains a possibility, it is precluded as the basis for LMI motion in this experiment and the experiment that follows because edge contrast always changed in the same direction on both sides of the bar. LMI motion is nonetheless perceived, so if the motion were determined by the detection of counterchange, it would have to be counterchange based on changes in edge and surface/background contrast.

The stimuli were generalized versions of a stimulus from Faubert and von Grünau (1995). They were composed of two squares with equal luminance and a connecting bar between them, all presented against a background that either was black or white (Figure 3). The bar was visible for the entire trial, and its luminance always was discriminable from the luminance of the flanking squares (both squares were lighter or both were darker than the bar). The bar's luminance either increased or decreased during the second frame of each trial, so depending on whether the background was black or white, the luminance change for the bar either increased or decreased its contrast with the background.

When the background was black and the squares were lighter than the bar, the changes in contrast at the square/bar boundaries and the change in the bar's contrast with the background were oppositely signed. This counterchange was expected to result in the perception of converging LMI motion when the bar's luminance increased (Figure 3a). That is, edge contrast was reduced at the bar's boundaries with the squares (the two locations where motion begins), and the contrast of the bar with the background increased (the common ending location for the two converging motions). Conversely, counterchange detection was expected to result in the perception of diverging LMI motion when the luminance of the bar decreased (Figure 3b). That is, the contrast of the bar with the background decreased (the common starting location for the two motions) and edge contrast increased at both of the bar's boundaries with the squares (the two end locations of the diverging motion). However, changes in edge contrast and bar/background contrast were same-signed when the squares were darker than the bar (Figures 3c and 3d), so little motion perception was anticipated. (See supplemental Figures 3a and 3d in the online supplemental materials.)

The reverse was expected when the background was white. Now when the squares were darker than the bar, changes in edge contrast and bar/background contrast were oppositely signed. This counterchange was expected to result in the perception of diverging motion when the bar's luminance increased (Figure 3g) and converging motion when the bar's luminance decreased (Figure 3h). However, changes in edge contrast and bar/background contrast were same-signed when the squares were lighter than the bar and the background was white (Figures 3e and 3f). For these stimuli, relatively little perception of LMI motion was anticipated.

Method

A square was presented on both sides of the bar (same spatial dimensions as in Experiment 1). For the black background (0 cd/m^2), the luminance of both squares was 6.3 or 89.3 cd/m^2 and the bar's luminance changed from 19.1 to 60.9 cd/m^2 (or vice versa). For the white background (89.3 cd/m^2), the luminance of both squares was 0 or 57.3 cd/m^2 and the bars luminance changed from 8.3 to 41.3 cd/m^2 (or vice versa). The fixation dot always was aligned with the center of the bar.

There were 96 order-randomized trials per block formed by the orthogonal combination of the two luminance values of the squares, whether the bar's luminance increased or decreased, and 24 repetitions. Three participants were tested on two blocks of 96 trials with the black background, then two blocks of 96 trials with the white background. After each trial, they indicated whether or not they perceived motion and, if so, whether the motion was convergent or divergent. For each participant, there were 96 trials in each of the four conditions.

Results

The results, averaged over the 3 participants, are presented in Figure 3i. Whether or not LMI motion was perceived depended on

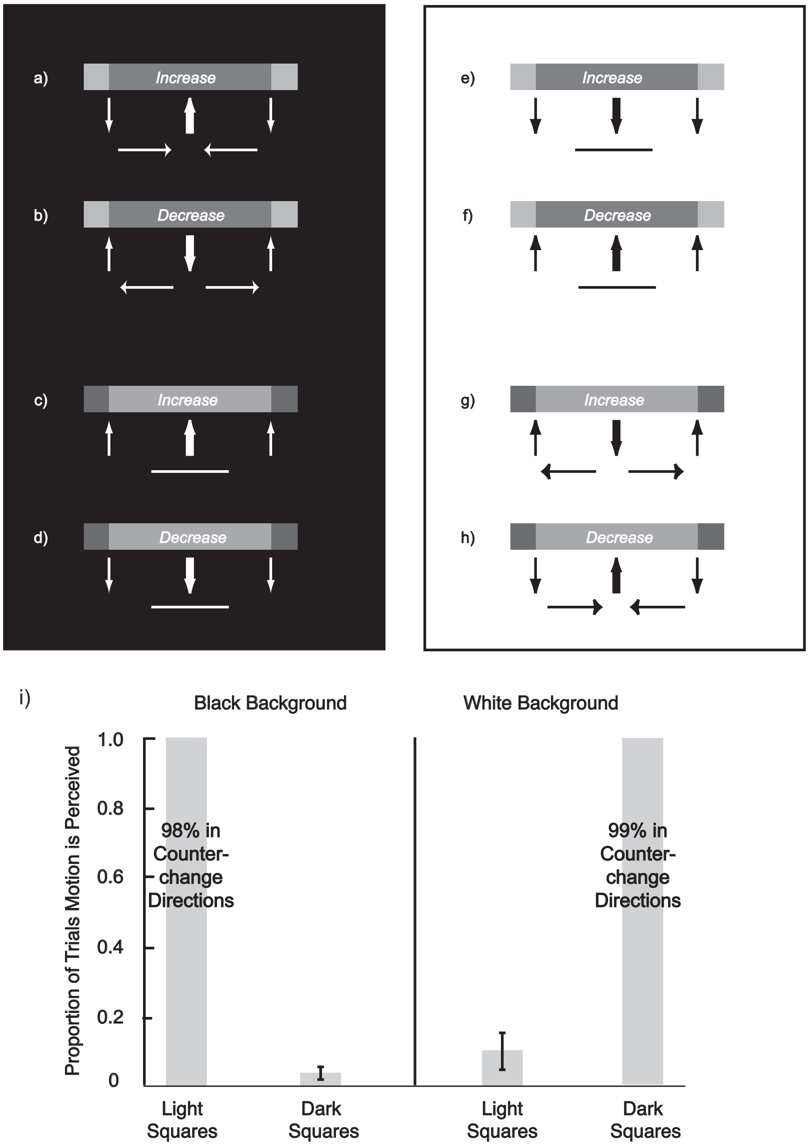

Figure 3. Experiment 3: Generalized versions of Faubert and von Grünau's (1995) LMI stimuli presented against a black background (a–d) and against a white background (e–h). The luminance for the two flanking squares always was the same for each trial, but varied from trial-to-trial depending on the condition. The thick vertical arrows indicate whether the background-relative contrast of the bar increases or decreases, and the thin vertical arrows indicate whether the luminance contrast at the edges of the bar increases or decreases. The horizontal arrows indicate the directions of the motion predicted on the basis of edge/surface counterchange. (i) The proportion of trials during which LMI motion was perceived, averaged over 3 participants; the results for luminance increments and decrements are combined (gray bars). The error bars indicate ±1 *SEM*. Superimposed on the gray bars is the percentage of the motion-perceived trials for which motion was in counterchange-determined directions.

the combination of the background luminance (black or white) and the luminance of the flanking squares (lighter or darker than the connecting bar). The interaction between these variables was statistically significant, $F(1, 2) = 1033.81$, $p < .001$ (Figure 3i). When the background was black and the squares were lighter than the bar, increases in bar luminance resulted in the perception of converging motion and decreases in bar luminance resulted in the perception of diverging motion, both consistent with the detection of counterchanging edge and surface/background contrast (changes in edge and surface/background contrast were oppositely signed). The minimal perception of LMI motion when the squares were darker than the bar was consistent with the absence of counterchange for these stimuli (changes in edge and surface-background contrast were same-signed).

When the background was white, the results were the reverse of those obtained with the black background, but again consistent with LMI motion being counterchange determined. That is, when the squares were darker than the bar, diverging motion was perceived for increasing bar luminance and converging motion for decreasing bar luminance, and when the squares were lighter than the bar, little motion was perceived, consistent with the absence of counterchange for these stimuli (changes in edge contrast and surface/background contrast were same-signed). As indicated earlier, the perceived LMI motion in this experiment could not have been based on the counterchange of edge contrast on the left and right sides of the bar; both always changed in the same direction in this experiment, regardless of the luminance of the background.

Additional results. Although there is little if any motion perception for the generalized Faubert and von Grünau (1995) stimulus in the absence of counterchange, this is not the case for the standard version of these stimuli (when the connecting bar appears during only one frame). Converging LMI motion is perceived when the bar is presented and diverging LMI motion is perceived when its is removed. This was consistent with the results for the dim bar in Experiment 1 in indicating that morphing is sufficient for the perception of LMI motion when there is a change in the shape of the stimulus.

Experiment 4

It has been shown thus far that a number of high-level alternatives to the detection of counterchange are not necessary for the perception of LMI motion. These include morphing, impletion, gradients of attention-speeded processing, attentive tracking, and exogenously oriented attention. It remains possible, however, that LMI motion perception results from the detection of shifts in the centroid of the luminance profile at the square/bar boundaries (Zanker, 1994). That is, LMI motion perception requires the detection of motion energy (Adelson & Bergen, 1985). For the stimuli in the preceding experiment with light flankers (Figures 3a and 3b), the directions specified by motion energy were consistent with the converging motion perceived when the bar's luminance increased, and the diverging motion perceived when the bar's luminance decreased. However, if LMI motion were based on the detection of motion energy, the same motion directions would have been perceived for the stimuli with dark flankers in Figures 3c and 3d, *unless* motion energy was much weaker for the stimuli with dark flankers. For this reason, luminance values were selected in Experiment 4 in order to match stimuli with respect to their first-order motion energy content (i.e., motion energy based on spatiotemporal changes in "raw" luminance). This matching was done by implementing Adelson and Bergen's (1985) motion energy model, as detailed in the Appendix. If LMI motion required the detection of motion energy, it would be perceived in the directions specified by motion energy when the flankers were lighter than the bar (and counterchange was present) as often as when they were darker than the bar (and counterchange was absent).

Method

Stimuli. The generalized LMI stimuli had the same spatial dimensions as in Experiment 3. When both flanking squares were darker than the bar (Figures 4c and 4d), their luminance was 28.4 cd/m^2, the luminance of the background was 0 cd/m^2, and the luminance of the bar changed from 58.9 to 97.0 cd/m^2 (Weber fraction = 0.65), or vice versa. When both squares were lighter than the bar (Figures 4a and 4b), their luminance was 58.9 cd/m^2 and the luminance of the background was 16.3 cd/m^2. Luminance values for the bar were selected to match the light-flanker to the dark-flanker stimuli with respect to the first-order motion energy calculated on the basis of Adelson and Bergen's (1985) model. This was done with spatial filters (receptive fields) that had either balanced or unbalanced excitatory and inhibitory zones.

Balanced spatial filters. For half of the trials with the light flanking squares, the bar's luminance changed between 28.4 and 54.0 cd/m^2 (Weber fraction = 0.90). For these luminance values, the calculated motion energy was matched to that of the stimuli with dark flanking squares. It should be noted, however, that the stimulus conditions differed with respect to the Weber fraction for the change in bar luminance; it was 0.65 for the stimuli with dark flankers.

Unbalanced spatial filters. For the other half of the trials with the light flanking squares, the bar's luminance changed from 28.4 to 48.5 cd/m^2 (Weber fraction = 0.71), and vice versa. For these luminance values, the calculated motion energy was matched to that of the stimuli with dark flanking squares, and in addition, the two conditions were similar with respect to the Weber fraction for the change in bar luminance.

Design/procedure. There were 96 order-randomized trials per block determined by the orthogonal combination of the luminance of the flanking squares, whether the bar's luminance increased or decreased, and 24 repetitions. The 4 participants were test on two blocks of 96 trials, one for the light and the other for the dark flanking squares. The fixation dot always was aligned with the center of the bar. After each trial, participants indicated whether or not they perceived motion and, if so, whether the motion was convergent or divergent. For each participant there were 96 trials in each of the four conditions.

Results

LMI motion almost always was perceived for both stimulus sets in the light-flanker condition (one stimulus set matched motion energy for the light- and dark-flanker conditions with balanced spatial filters, the other matched them with unbalanced spatial filters), so the combined results for the two stimulus sets, averaged over the four participants, are presented in Figure 4e. The major finding was that when LMI motion was perceived, it was in the direction specified by motion energy much less often when the flanking squares were darker than the bar (6% of the trials) compared with when they were lighter than the bar (98% of the trials), $t(3) = 87.95$, $p < .001$. If LMI motion depended on motion energy extraction, the frequency of its perception in directions specified by motion energy would have been similar for the stimuli with light and dark flankers.

Although it was possible to quantitatively match stimuli with respect to first-order motion energy, uncertainty regarding an appropriate quantitative measure of contrast precluded doing the same for second-order motion energy. However, when the bar changed in luminance, its contrast changed with respect to the background (the contrast of the flanking squares with the background was unchanged), so second-order motion energy specified motion in the same directions as first-order motion energy. Nonetheless, motion was rarely perceived in those directions for the stimuli in Figures 4c and 4d.

LMI motion was perceived for 99% of the trials in the light-flanker condition, for which counterchanging edge/surface contrast was present. The motion almost always was in the counterchange-specified direction. However, LMI motion was perceived for only 37% of the trials in the dark-flanker condition, for which edge/surface counterchange was not present. Because of large variability among the participants (and few degrees of freedom), this difference fell short of significance, $t(3) = 2.64$, $p = .08$. The residual motion perceived in the absence of counterchange (mostly in the non-motion-energy direction) may entail changes in the luminance similarity of the bar with the flanking squares. This possibility will be addressed in future research.

Baloch and Grossberg (1997). In their account of the line motion illusion, Baloch and Grossberg (1997) proposed that LMI motion is perceived by virtue of the sequential activation of arrays of "bipole cells" that lie along the horizontal boundaries of the bar. These hypothetical cells are composed of two lobes with the same orientation preference (horizontal in this example), one on each side of a connecting cell body. Because the stimulation of both lobes is necessary for bipole cells to reach their threshold, those cells that already are stimulated in one lobe by the horizontal boundaries of the square would reach threshold more quickly when the bar is presented (or its luminance increased) in its other lobe compared with bipole cells that are further from the square. LMI motion would result from the wave of boundary completion as successive bipole cells reach threshold.

The results obtained in this experiment for stimuli with dark flanking squares were inconsistent with Baloch and Grossberg's (1997) account. If the sequential activation of bipole cells were the basis for the perception of LMI motion, the motion that was perceived would have been convergent when the bar's luminance increased and divergent when the bar's luminance decreased (these would have been the same as the directions specified by motion energy in Figures 4c and 4d). However, the perceived motions were consistently in the opposite directions.

Experiment 5

This experiment provided evidence that the detection of edge/surface counterchange is sufficient for the perception of LMI motion under conditions in which there is detectable first-order

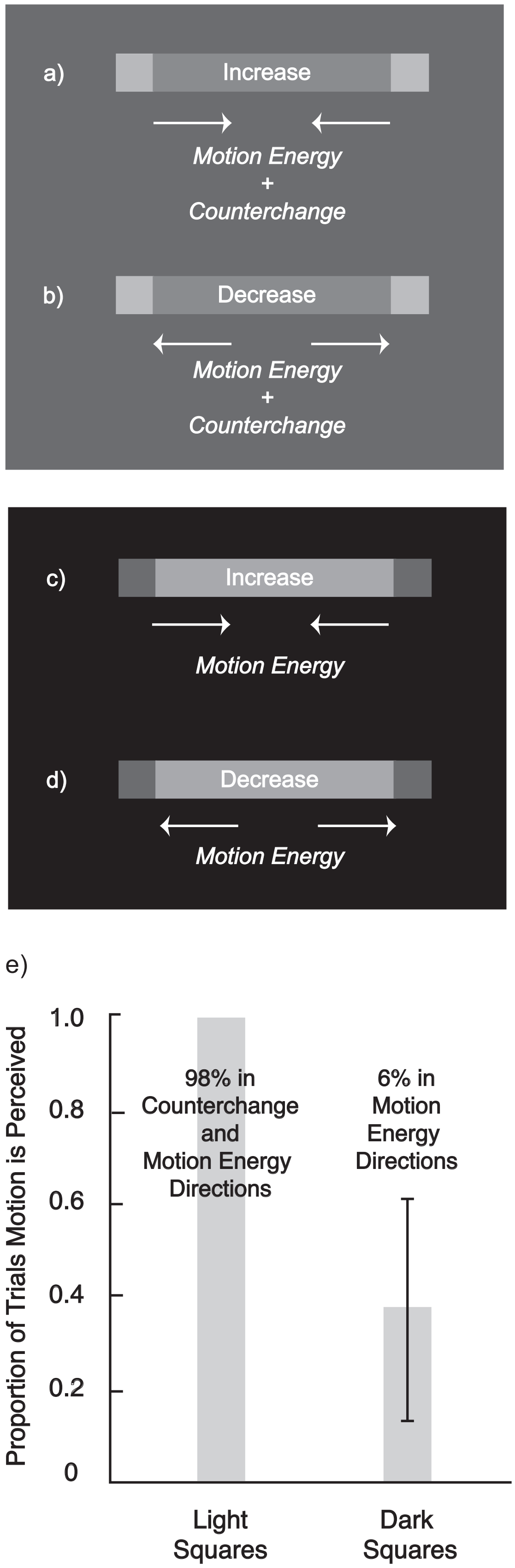

Figure 4. Experiment 4: Generalized versions of Faubert and von Grünau's (1995) LMI stimuli presented against a dark gray background or against a black background, Luminance values were selected such that the stimuli with light squares (a,b) and the stimuli with dark squares (c,d) were matched in motion energy, as computed with a detection model based on Adelson and Bergen (1985). Background-relative edge/surface counterchange was present only for the stimuli with light squares (a,b). The horizontal arrows indicate the directions of the motion predicted by edge/surface counterchange and by motion energy. (c) The proportion of trials during which LMI motion was perceived, averaged over 4 participants; the results for luminance increments and decrements are combined (gray bars). The error bars indicate ±1 *SEM*. Superimposed on the gray bars is the percentage of the motion-perceived trials for which motion was in directions specified by counterchange and/or motion energy.

motion energy in the opposite direction. Two-frame generalized LMI stimuli were created for which there was a gradient of luminance values for the bar during one frame, and uniform luminance for the bar during the second frame. The luminance value for the uniform bar was equal to the lowest luminance value of the gradient bar. As a result, the centroid of the luminance profile shifted toward the light end of the gradient bar when it replaced a bar that was uniform in luminance, producing first-order motion energy toward the light end (in the leftward direction for the stimuli illustrated in Figures 5a and 5c, and in the rightward direction for the stimuli illustrated in Figures 5b and 5d). Conversely, when the gradient bar was replaced by a bar with uniform luminance, the centroid of the luminance profile shifted toward what was the dark end of the gradient bar, producing first-order motion energy in that direction. The above motion energy directions were confirmed by the implementation of Adelson and Bergen's (1985) motion energy model described in the Appendix.

As can be seen in Figure 5a, edge/surface counterchange specifies motion when the gradient bar replaces the uniform bar, and the light side of the gradient bar is adjacent to the light flanking square. That is, edge contrast decreases at the square/bar boundary, and except for the far end of the bar, the luminance contrast of the bar with the background increases. However, there is no edge/surface counterchange when the dark side of the gradient bar appears next to the flanking square; decreases in edge contrast at the square/bar boundary are minimal because there is little change in the gradient bar's luminance alongside the square (Figure 5b). There is, as well, no edge/surface counterchange when the square is not present (Figures 5c and 5d).

When edge/surface counterchange was not present, it was anticipated that motion would be in the direction specified by first-order motion energy (e.g., the stimuli illustrated in Figures 5b, 5c, and 5d). When edge/surface counterchange was present, it specified motion in the direction opposite to the motion energy direction (Figure 5a). The perception of motion in the counterchange-specified direction for this stimulus would indicate that motion energy extraction is not necessary for the perception of LMI motion.

Method

The square and bar, which had the same spatial dimensions as in Experiments 1 and 2, were presented against a dark gray background (luminance = 11.4 cd/m^2). The bar was either uniform in luminance (16.8 cd/m^2), or it was composed of a gradient of luminance values that increased linearly from 16.8 cd/m^2 at one end to 45.4 cd/m^2 at the other end of the bar (the slope of the gradient was 7.2 cd/m^2 per degree of visual angle). The light side of the gradient was either on the left or right side of the bar. The flanking square (uniform luminance of 60.2 cd/m^2) was adjacent to the left edge of the bar for half the trials, and was not present during the other half of the trials. There were 96 order-randomized trials per block determined by the orthogonal combination of whether the square was present or not, whether the uniform bar was presented before or after the gradient bar, whether the light side of the gradient was on right or the left end of the bar, and 12 repetitions. The fixation dot always was aligned with the center of the bar. Three participants were tested on three blocks of 96 trials, so there were 72 trials for each participant in each condition.

Results

The results, averaged over the three participants, are presented in Figure 5e. Whether the flanking square was present or not, $F(1, 2) = 10.32$, $p = .09$, and whether the gradient was positive or negative, $F < 1.0$, did not significantly affect the frequency with which LMI motion was perceived. As in the preceding experiment, the most important data concerned the frequency with which LMI motion, when perceived, was in the direction specified by motion energy. When edge/surface counterchange was absent, perceived motion was most often in the direction specified by motion energy (Figure 5e), indicating that the extraction of first-order motion energy is sufficient for the perception of motion for surfaces with luminance gradients. However, even with luminance gradients, motion energy extraction is not necessary for the perception of LMI motion. When edge/surface counterchange was present, and it specified motion in the direction opposite to that specified by motion energy (as in Figure 5a), perceived motion was overwhelmingly in the direction specified by counterchange rather than motion energy. That is, when there was a light flanking square, LMI motion was in the direction specified by motion energy significantly less often when counterchange was present than when it was absent, $t(2) = 32.60$, $p < 001$. This difference between the negative and positive gradients was significantly greater when there was a flanking square compared with when there was not a flanking square; i.e., the interaction between gradient direction and whether the square was present or absent was significant, $F(1, 2) = 41.85$, $p < .05$.

A series of experimental conditions similar to those of the current experiment previously was reported by von Grünau, Saikali, and Faubert (1995). When they presented a gradient bar on a blank field, they found by a relatively small margin that the direction of perceived motion was toward the dark end of the gradient.[3] It was argued that this was because the light end was processed more rapidly than the dark end, consistent with the gradient of attention-speeded processing proposed by Hikosaka et al. (1993a, 1993b). In the current study, however, motion was perceived in the opposite direction, toward the light end of the gradient bar when it replaced the uniform bar, perhaps because motion energy is more readily extracted when the gradient bar is exchanged with a uniform bar compared with presenting it on a blank field. When a square was presented, and an adjacent gradient bar appeared afterward, von Grünau et al.'s (1995) results were very similar to ours. That is, they found that strong LMI motion was perceived when the square was adjacent to the light side of a gradient bar, but not when it was adjacent to its dark side. They argued that a more global process affected the differential processing of the light and dark ends of the bar, whereas we have argued for the detection of edge/surface counterchange. The relative merit of the counterchange explanation follows from its ability to ac-

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[3] In a more recent study, Hsieh, Caplovitz, and Tse (2006) did the opposite; i.e., they removed a previously presented gradient bar, leaving only the blank field. Their results differed from von Grünau et al. (1995) in two respects: (1) subjects were much more consistent in reporting the direction of the perceived motion, and (2) the perceived motion direction depended on the luminance polarity of the background. Hsieh et al. (2006) attributed their results to differences in decay rates within the afterimage of the gradient bar.

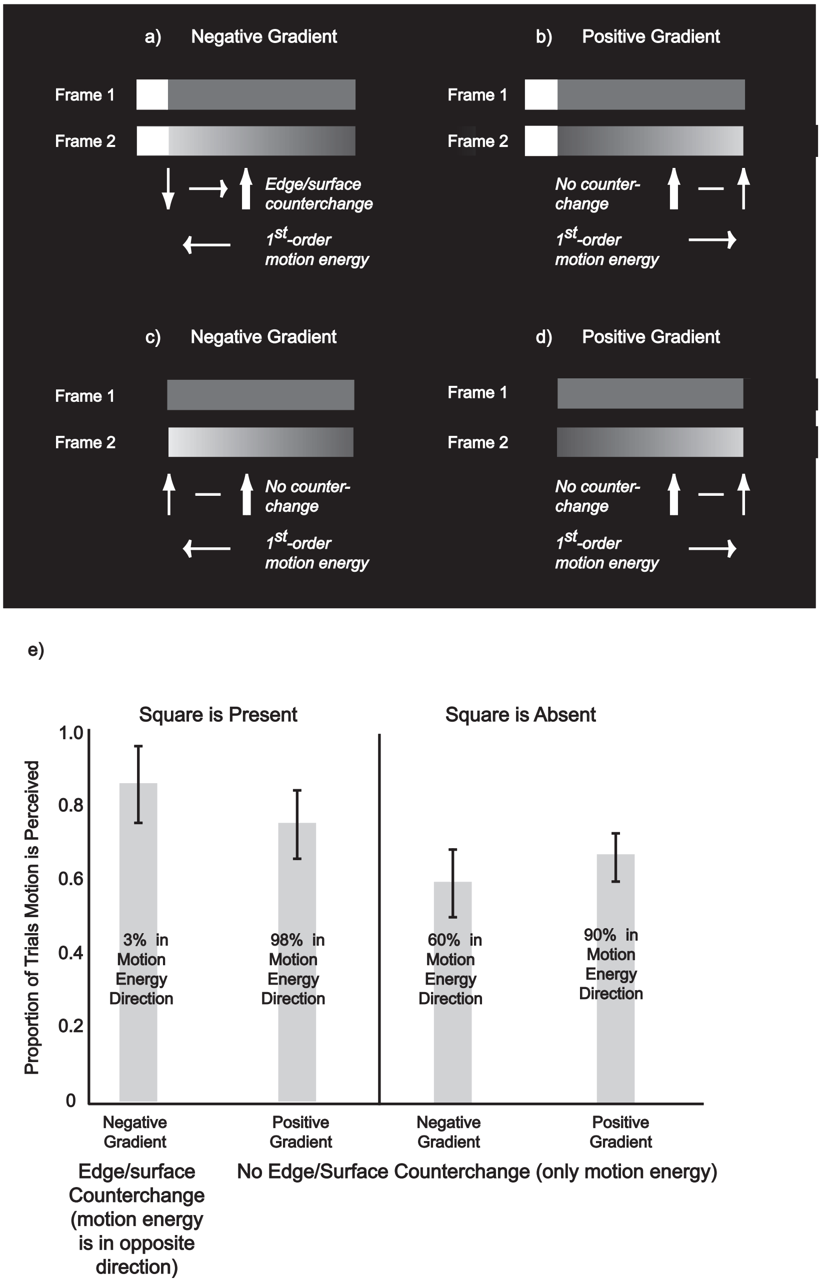

Figure 5. Experiment 5: (a,b) Generalized LMI stimuli for which the bar is presented adjacent to a lighter square. The bar either is uniform in luminance or is composed of a gradient of luminance values, the lowest of which corresponds to the luminance of the uniform bar. (c,d) Same stimuli as above, except that the square is not present. The thick vertical arrows indicate whether the luminance of the bar increases or decreases in its contrast with the background, and the thin vertical arrows indicate whether the luminance contrast at the edges of the bar increases or decreases. The horizontal arrows indicate the directions of motion predicted on the basis of edge/surface counterchange (when it is present), as well as the direction of motion predicted by the motion energy in the stimulus. (e) The proportion of trials during which LMI motion was perceived, averaged over 3 participants; the results for changes from the uniform to the gradient bar, and vice versa, are combined (gray bars). The error bars indicate ±1 *SEM*. Superimposed on the gray bars is the percentage of the motion-perceived trials for which the motion was in the motion energy direction.

count, not just for observations with the gradient bars, but also for results obtained for bars with uniform luminance.

General Discussion

The primary objective of this study was to determine whether there is motion-specifying stimulus information whose detection is sufficient for the perception of LMI motion for pairs of adjacent surfaces. If so, it would provide a feedforward basis for LMI motion that does not require the mediation of higher-level mechanisms, and as indicated in the introduction, a mechanism that potentially could account for the perception of continuous object motion.

Edge/Surface Counterchange

The results of the reported experiments indicate that motion for generalized LMI stimuli is specified by a nonsequential pattern of oppositely signed changes in edge contrast and surface-to-background contrast. (Either the detection of edge/surface counterchange or morphing could result in motion perception for standard LMI stimuli.) Counterchange-specified motion begins where edge contrast decreases and ends where background-relative surface contrast increases, or it begins where background-relative surface contrast decreases and ends where edge contrast increases.

Although edge/surface counterchange is sufficient for LMI motion, motion can nonetheless be perceived for stimuli without edge/surface counterchange. For example, Hsieh, Caplovitz, and Tse (2005) showed that LMI motion, once established, can be maintained as a series of LMI motions that reverse in direction while the bar alternates between different hues (and luminance levels). There was no edge/surface counterchange stimulating these motion reversals. In addition, LMI motion can be perceived in the absence of edge/surface counterchange when attention is drawn to one of the boundaries of a to-be-presented surface by an auditory or tactile orienting cue (Shimojo et al., 1997). In the current study, there was evidence that in the absence of counterchange, morphing (Experiment 1; additional results for Experiment 3) and changes in similarity for a pair of adjacent surfaces (Experiment 4) were sufficient for the perception of LMI motion. All reflect changes in perceptual organization being perceptually realized as LMI motion (Hock & Nichols, in preparation).

Attention

Studies of attention allocation often distinguish between endogenously and exogenously oriented attention (Posner, 1980; Nakayama & Mackeben, 1989). The former entails the intentional orientation of attention to a location, and the latter the non-intentional attraction of attention to a location by a transient change in stimulation. The endogenous orientation of attention appears to be neither necessary nor sufficient for the perception of LMI motion. Shimojo et al.'s (1997) experiments with transient orienting cues have shown that endogenously oriented attention is not necessary, and Christie and Klein (2005) have shown that it is not sufficient for the perception of LMI motion (see also Chica, Charras, & Lupianez, 2008).

The above-mentioned study by Shimojo et al. (1997) indicated that exogenously oriented attention is sufficient to create the perception of LMI motion. It is, however, not necessary for its occurrence. In all the experiments in the current article, the possibility that the fixation dot would exogenously attract attention was eliminated by continuously presenting it at the same location, regardless of whether the LMI stimulus was present or not. If, despite our instructions to maintain attention on the fixation dot, attention were exogenously drawn to a feature of the LMI stimulus (e.g., the square presented during the first frame), motion would

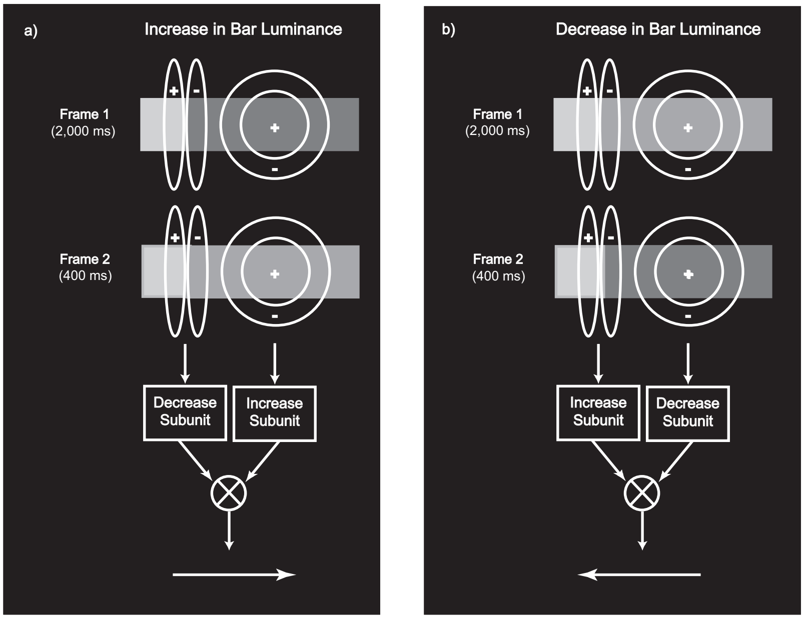

Figure 6. Schematic of counterchange model as applied to the perception of: LMI motion. (a) For increases in bar luminance. (b) For decreases in bar luminance.

always have been in the same direction, away from the location of the attention-attracting feature, regardless of whether the luminance of the bar increased or decreased. This, however, was never observed. Different motion directions always are perceived for increases vs. decreases in bar luminance, verifying the conclusions of Downing and Treisman (1997) and Tse and Cavanagh (1995) that neither gradients of attention-speeded processing nor attentive tracking are necessary for the perception of LMI motion.

Third-Order Motion and The Detection of Counterchange

Lu and Sperling (1995a, 2001) have presented substantial evidence for a three-systems theory of motion perception. Whereas the first- and second-order motion systems entail the extraction of motion energy, the third-order system is based on attentionally modulated changes in salience/activation created by stimulus attributes changing at different spatial locations. For example, Blaser et al. (1999) tested motion perception with a directionally ambiguous stimulus in which a red/green sine grating was presented during the odd-numbered frames (phase shifted by 180° with successive presentations), and a contrast-modulated noise grating was presented during the intervening even-numbered frames (phase shifted by 90° in relation to the preceding red/green grating). They found that attention to either red or green resulted in motion being perceived in the direction specified by that color. Attention was exogenously cued in their study. It was drawn to successive locations of the attended color as it reappeared during successive frames, amplifying the input to detectors signaling motion in that direction.

Evidence that the perception of LMI motion for two adjacent surfaces can be determined by exogenously oriented attention (Shimojo et al., 1993), that it is unaffected when the square and adjacent bar are presented separately to the two eyes (Faubert & von Grünau, 1995; Hikosaka et al., 1993b), and that it does not require the extraction of motion energy (Experiments 4 and 5 of this study) all point to its perception by Lu and Sperling's (1995a) third-order motion system. Parallel evidence that the perception of apparent motion between a pair of nonadjacent surfaces can be influenced by exogenously attracted attention (Hock et al., 2002; Stelmach, Herdman, & McNeill, 1994), that it can be perceived when the two surfaces are presented separately to the two eyes (e.g., Braddick, 1980), and that it does not require the extraction of motion energy (Hock et al., 2002) likewise points to its perception by the third-order motion system. Finally, evidence that the counterchange principle applies to the perception of both LMI motion and apparent motion suggests that oppositely signed stimulus changes at pairs of spatial locations provide feedforward input to the third-order system and, further, that counterchange detection might constitute an attentionally modulated, feature-invariant motion signaling mechanism for the third-order system.

A computational model for the detection of counterchanging activation has recently been developed by Hock, Schöner, and Gilroy (2009). The model is composed of a pair of subunits that respond biphasically to changes in input activation.[4] One subunit responds with excitation to decreases in input activation at one spatial location and the other responds with excitation to increases in input activation at another spatial location. Motion is signaled by the multiplicative combination of the transient outputs of these

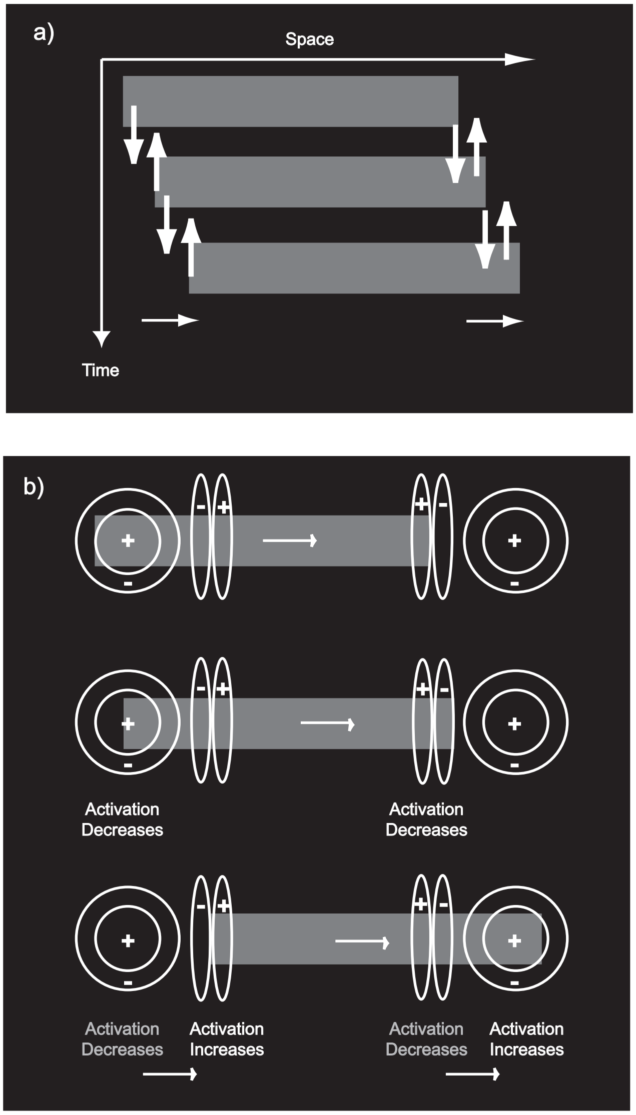

Figure 7. (a) Temporal discontinuities at each spatial location traversed by the leading and trailing boundaries of the moving object create a cascade of counterchanging edge/surface contrast. Rightward motion is specified at the leading boundary by the combination of decreased edge contrast (downward arrows) and increased surface/background contrast (upward arrows). Rightward motion is specified at the trailing boundary by the combination of decreased surface/background contrast (downward arrows) and increased edge contrast (upward arrows). (b) Schematic of counterchange model as applied to the perception of continuous object motion.

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[4] Biphasic detectors create transient responses to changes in input activation by giving positive weight to recent inputs and negative weight to older inputs. For the "Decrease" subunit, a recent decrease in input activation receives positive weight (excitation) and the preceding input activation receives negative weight (inhibition). For the "Increase" subunit, a recent increase in input activation receives positive weight (excitation) and the preceding input activation receives negative weight (inhibition).

"Decrease" and "Increase" subunits to changes in input activation; both subunits must be excited at the same time in order for motion to be perceived.

The evidence in the current article for edge/surface counterchange as the basis for LMI motion is consistent with edge filters (elongated receptive fields with one excitatory and one inhibitory lobe) providing the input to a biphasic "Decrease" or "Increase" subunit and center/surround filters (with excitatory centers and inhibitory surrounds, or vice versa, depending on the luminance polarity of the background) providing the input to a biphasic "Increase" or "Decrease" subunit. A schematic of the model shows how these spatial filters would account for the direction of the LMI motion perceived when one of two adjacent surfaces increases (Figure 6a) or decreases in luminance (Figure 6b).

Counterchange and Continuous Object Motion

When an object moves continuously across a darker background, luminance discontinuously increases at the leading edge of the object and discontinuously decreases at its trailing edge (Figure 7a). These temporal discontinuities create a cascade of simultaneous edge/surface counterchanges that specify motion in the same direction at both the leading and trailing edges of the object. At the first moment in time depicted in Figure 7a, there is edge contrast at the boundary separating the leading edge of the object from the background, and there is no surface luminance just in front of the object. As the object moves rightward, the edge contrast at the previous boundary location decreases to zero (the downward arrow in Figure 7a) and the previously vacant space in front of the object now is occupied by the object, increasing the surface/background contrast luminance at that location (the upward arrow in Figure 7a). Counterchange-determined motion is similarly specified at the trailing edge of the object.

Counterchanging edge and surface contrast could therefore constitute the stimulus information that specifies continuous object motion, and counterchange detection could be the basis for its perception. As illustrated in Figure 7b, the increase in activation for the edge filter when the leading boundary of the moving object enters the edge filter's excitatory lobe is followed a moment later by a decrease in its activation when it enters the edge filter's inhibitory lobe. Soon afterward (depending on the object's speed), the activation of the center/surround filter is increased when the moving object enters its excitatory center. Counterchange-specified rightward motion is signaled at the leading boundary of the moving object by this combination of decreased activation for the edge filter and increased activation for the center/surround filter. Counterchange-specified rightward motion is similarly signaled at the trailing boundary of the moving object by the combination of decreased center/surround activation and increased edge filter activation.

The stimulus depicted in Figure 8a demonstrates that the detection of a spatial pattern of oppositely signed changes in edge and

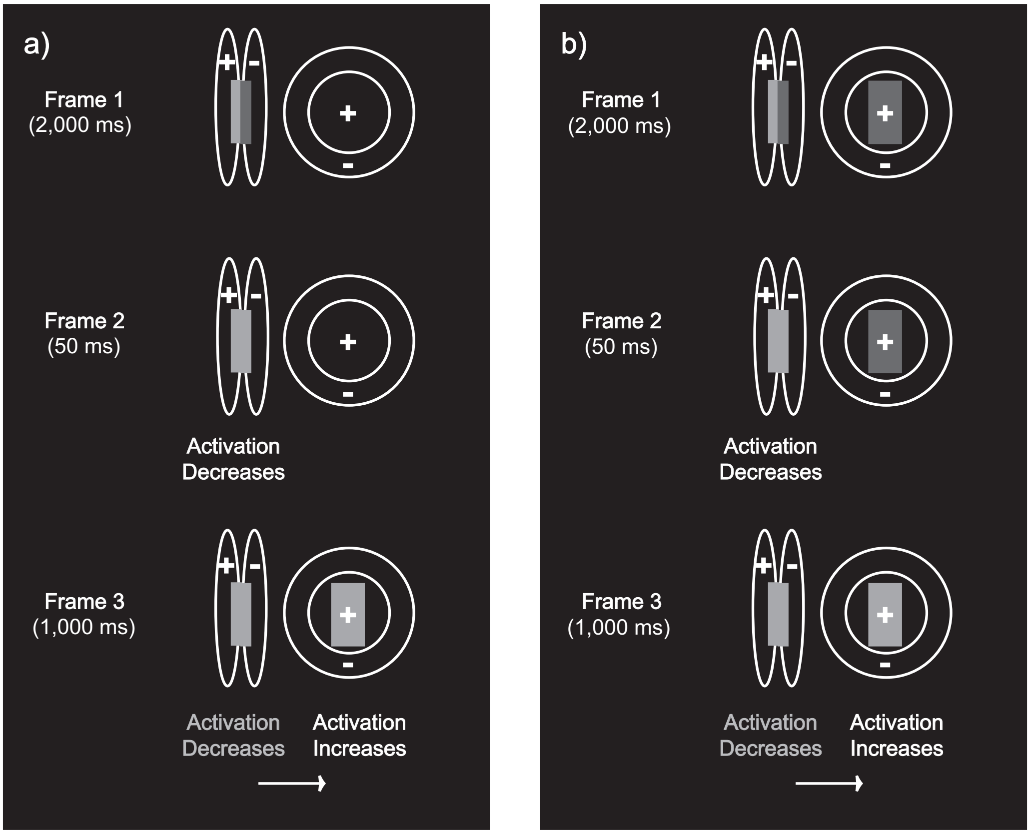

Figure 8. Stimuli demonstrating how the detection of edge/surface counterchange could result in the perception of motion for the leading boundary of a continuously moving object.

surface-to-background contrast is a likely basis for the perception of continuous object motion. There are only increases in luminance for this three-frame stimulus, which simulates the motion perception at the leading boundary of a continuously moving object. Frame 1 (2,000 ms) begins with the activation of an edge filter by the thin light and dark bars that presumably fall in its excitatory and inhibitory lobes. During Frame 2 (50 ms), luminance increases for the thin dark bar on the right, decreasing the activation of the edge detector, and during the Frame 3 (1,000 ms), the rectangular surface appears to the right of the thin bars, activating a center/surround filter at that location. Rightward motion is perceived across the gap between the thin bars and the rectangular surface to its right, consistent with how edge/surface counterchange would signal motion for the leading edge of a continuously moving object. (See supplemental Figure 8a in the online supplemental materials.) Rightward motion likewise is perceived across the gap when the rectangular surface on the right appears during Frame 1 and increases in luminance during Frame 3, as in Figure 8b, showing that changes in location are not required for perceiving this analog of continuous object motion. (See supplemental Figure 8b.)

Counterchange and Motion Energy Detection

The counterchange model proposed for the perception of LMI motion and continuous object motion has essentially the same component filters as Adelson and Bergen's (1985) motion energy model, but in a different arrangement. Both have "odd" spatial filters (edge detectors for the counterchange model) and "even" spatial filters (center/surround detectors for the counterchange model), and both have biphasic (bandpass) temporal filters that respond to changes in luminance. For motion energy detection, the "odd" and "even" spatial filters are aligned at the *same* spatial location and the bandpass temporal filters for each respond to same-signed changes in input activation. The motion energy detector thereby determines whether there is motion at a single point in space. For counterchange detection, the "odd" and "even" spatial filters are at *different* spatial locations, and the bandpass temporal filters for each respond to oppositely signed changes in input activation. The counterchange detector therefore determines whether there is motion between two points in space; that is, from the location with the decrease in activation to the location with an increase in input activation.

These different filter configurations could serve parallel perceptual functions. For example, the point-by-point computation of motion direction, as determined by motion energy analysis, could provide a suitable basis for the spatial integration that is necessary for the detection of global optic flow, while the motion path of an object that has been parsed from the background could be determined by counterchange. This distinction between two qualitatively different kinds of motion information is consistent with Sperling and Lu's (1998) description of first- and second-order motion energy systems as "objectless," and the third-order system as the basis for the perception of object motion.

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Appendix

Motion Energy Detection Model

Computations were done in Matlab 7.4.0, on a Macbook running OS X, 10.4.11. Space and time were sampled discretely with increments of .02° and 10 ms, respectively. The spatial and luminance values were as in the experiments. Temporal values were modified in order to isolate the luminance-change portion of the trials; 4-s intervals were successively assigned to an initial blank field, the first frame of the two-frame trials, the second frame of the two-frame trials, and a final blank field.

The spatial and temporal filters, as well as the algorithm to calculate motion energy, were as in Adelson and Bergen (1985). In executing the model, the time course of the stimulus was convolved with all four combinations of "even" and an "odd" spatial filters (Equations 1 and 2), and two temporal filters with a slight temporal offset between them (Equations 3 and 4). The spatial scaling factor for the filters, σ_s, was chosen to be 0.5, which gives a strong response in the correct direction for a basic LMI stimulus with the same spatial dimensions as in the experiments; narrower filters produce a weak response and broader filters respond most strongly to motion in the wrong direction. The parameters for the temporal filters were $k_1 = 0.014$ and $k_2 = 0.017$, which give a maximal response to sine wave stimuli moving at 10 Hz.

$$s_{even} = \frac{-x^2 + \sigma_s^2}{\sigma_s^5 \sqrt{2\pi}} e^{\frac{-x^2}{2\sigma_s^2}} \tag{1}$$

$$s_{odd} = \frac{-x^3 + 3x\sigma_s^2}{\sigma_s^7 \sqrt{2\pi}} e^{\frac{-x^2}{2\sigma_s^2}} \tag{2}$$

$$t_1 = k_1 t e^{-k_1 t}\left(\frac{1}{6} + \frac{(k_1 t)^2}{120}\right) \tag{3}$$

$$t_2 = k_2 t e^{-k_2 t}\left(\frac{1}{120} + \frac{(k_2 t)^2}{5040}\right) \tag{4}$$

Following this linear spatial and temporal filtering of the stimulus, the outputs of the four combinations of spatial and temporal filters were squared to give a directional output at each point in space and time. The magnitude and direction of the motion response at the square/bar boundaries was the maximum response within 0.5° of the edge of the square/bar boundary and within 3,000 ms of the change from the first to the second frame of each trial.

Also created was a modified version of Adelson and Bergen's (1985) motion energy detector. In the original version, the positive and negative portions of the spatial receptive field are balanced, i.e. they sum to zero for a uniform field. In the modified version they are imbalanced such that the inhibitory portion has 75% of the magnitude of the excitatory portion. As a result of the imbalance, the response to a change in the luminance level of a uniform field depends on its initial luminance level, as per Weber's law (Equations 5 and 6). The model is the same in all other respects.

$$s_{even}^{imb} = \frac{1}{\sigma_s \sqrt{2\pi}} e^{\frac{-x^2}{2\sigma_s^2}} - \frac{0.75}{2\sigma_s \sqrt{2\pi}} e^{\frac{-x^2}{2(2\sigma_s)^2}} \tag{5}$$

$$s_{odd}^{imb} = \frac{x}{\sigma_s^3 \sqrt{2\pi}} e^{\frac{-x^2}{2\sigma_s^2}} - \frac{0.75x}{(2\sigma_s)^3 \sqrt{2\pi}} e^{\frac{-x^2}{2(2\sigma_s)^2}} \tag{6}$$

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